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Inventory

A new inventory for fishes of headwater streams from the rio das Cinzas and rio Itararé basins, rio Paranapanema system, Paraná, Brazil

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Abstract: The rio das Cinzas and rio Itararé basins are important tributaries of the rio Paranapanema, a major left-bank tributary of the upper rio Paraná basin. The upper reaches of both drainages intersect the northern portion of the APA Escarpa Devoniana (Devonian Escarpment Environment Protection Area, EPA), an area considered crucial for the preservation of biodiversity. This study aimed to provide an ichthyofaunistic inventory for headwater streams of the rio das Cinzas and rio Itararé basins, both within and off of the borders of the EPA, increasing the knowledge about the species already known from streams in the rio Paranapanema system. We found 32 fish species, representing five orders and 12 families. Siluriformes was the richest order followed by Characiformes. Ten species presented high abundance of sampled individuals, contributing with 85.0% of all specimens. Most species were classified as occasional (captured in less than 25% of the samples) and only two species were classified as constant (captured in more than 50% of samples), which may reflect the altitudinal gradient. We did not record any introduced species in the sampled streams, reinforcing the need of, at least, maintaining the original area of the EPA. We expanded the geographic distribution of *Astyanax bifasciatus* to the upper rio Paraná system, confirming the cases of faunal exchange among several drainage systems in the limits of the Ponta Grossa Arch. Finally, we identified three putatively undescribed species that show a large biodiversity knowledge shortfall for the region studied.
Keywords: *Altitudinal gradient, Devonian Escarpment, faunal exchange, upper rio Paraná.*

Um novo inventário para peixes de riachos de cabeceira das bacias dos rio das Cinzas e rio Itararé, sistema do rio Paranapanema, Paraná, Brasil

Resumo: As bacias do rio das Cinzas e do rio Itararé são afluentes importantes do rio Paranapanema, um dos principais afluentes da margem esquerda do alto rio Paraná. Os trechos superiores de ambas as drenagens interceptam a porção norte da Área de Proteção Ambiental (APA) da Escarpa Devoniana, uma área considerada crucial para a preservação da biodiversidade. Este trabalho teve como objetivo fornecer um inventário ictiofaunístico para riachos de cabeceira das bacias do rio das Cinzas e do rio Itararé, dentro e fora das fronteiras da APA, aumentando o conhecimento sobre as espécies já conhecidas dos riachos do rio Paranapanema. Encontramos 32 espécies de peixes, representando cinco ordens e 12 famílias. Siluriformes foi a ordem mais rica seguida por Characiformes. Dez espécies apresentaram alta abundância de indivíduos amostrados, contribuindo com 85,0% de todos os espécimes. A maioria das espécies foi classificada como ocasional (capturada em menos de 25% das amostras) e apenas duas espécies foram classificadas como constantes (capturadas em mais de 50% das amostras), o que pode refletir o gradiente altitudinal. Não registramos nenhuma espécie introduzida nos riachos amostrados, reforçando a necessidade de, pelo menos, manter a área original do APA. Expandimos a distribuição geográfica de *Astyanax bifasciatus* para o sistema do alto rio Paraná, confirmando os casos de intercâmbio faunístico entre vários sistemas de drenagem nos limites do Arco de Ponta Grossa. Finalmente, identificamos três espécies supostamente não descritas que mostram um grande déficit de conhecimento da biodiversidade para a região estudada.
Palavras-chave: *Alto rio Paraná, Escarpa Devoniana, gradiente altitudinal, intercâmbio faunístico.*

Introduction

Freshwater environments provide numerous ecosystem goods and services that will be lost due to the rapid degradation of aquatic bodies by human activity (Azevedo-Santos et al. 2019a). Local biodiversity inventories are essential in environmental management projects, and provide support for studies involving ecological or biogeographic aspects (Oliveira et al. 2014; Frota et al. 2019). Given that many species in the Neotropical region remain undescribed (Ota et al. 2015) or poorly known, species inventories are essential for widening the known geographic range of the species, and also favor the discovery of new species (Carvalho 2009; Whittaker et al. 2005). In this way, the conservationist practice can only be realized knowing the biodiversity that is intended to be conserved, and inventories are crucial for this finality (Carvalho 2009).

The Neotropical region, the most ichthyologically rich biogeographical domain in the world, comprises about 9,000 fish species (Birindelli & Sidlauskas 2018). Of these, many are small and inhabit mostly low-order watercourses (Castro 1999; Winemiller et al. 2008), which are estimated to harbor about 50% of the freshwater fish richness in the tropics (Lowe-McConnell 1999; Winemiller et al. 2008). Even the highly impacted upper rio Paraná system has an estimated 310 species (236 natives), a number outdated by twelve years (Langeani et al. 2007).

Most of the sampling effort that yielded specimens from the rio Paraná basin is due to projects sponsored by the electrical sector, as a consequence of the intense damming to which the basin is subject (Baumgartner et al. 2012). However, these projects focused mostly on larger rivers and, until recently, low-order streams (especially in the Paraná State) still lacked samplings. This scenario changed in recent years as researchers started to focus ecological and biogeographical aspects of several sub-basins of the alto rio Paraná system, increasing our knowledge about the fish species resident in its streams (*e.g.,* Castro et al. 2003; Cetra et al. 2012; Cionek et al. 2012; Pagotto et al. 2012; Costa et al. 2013; Hoffmann et al. 2015; Cetra et al. 2016; Frota et al. 2016a,b; Larentis et al. 2016; Cavalli et al. 2018; Delariva et al. 2018; Claro-García et al. 2018; Frota et al. 2019).

The rio Paranapanema covers about 900 km (most of which defining the border between Paraná and São Paulo states) from its headwaters in the Serra de Paranapiacaba (São Paulo State) to its mouth in the rio Paraná, being one of its major left-bank tributaries (Ziesler & Ardizzone 1979). Ichthyofaunistic inventories are available for some of the main sub-basins of the rio Paranapanema system within the Paraná State (Shibatta et al. 2002; Castro et al. 2003; Cetra et al. 2012; Cionek et al. 2012; Pagotto et al. 2012; Costa et al. 2013; Hoffmann et al. 2015; Cetra et al. 2016; Claro-García et al. 2018), but the fishes from the rio das Cinzas and rio Itararé basins remain unknown to the scientific literature, except for one tributary of the former (Costa et al. 2013) and a few streams draining into the latter (Cetra et al. 2016). Thus, this study aimed to provide a new, more inclusive fish inventory for headwater streams of the rio das Cinzas and rio Itararé basins in the Paraná State.

Material and Methods

1. Study area

The rio das Cinzas basin is the main watercourse of the Norte Pioneiro mesoregion of the Paraná State. Its headwaters are located in the Serra de Furnas, in the municipality of Piraí do Sul, west of the Devonian Escarpment. With a 9,613 km^2 watershed encompassing about 5% of the area and 3% of the population of Paraná State (Paraná 2010) and a 240 km course, it forms the border between the municipalities of Santa Mariana and Itambaracá and is one of the main tributaries of the Capivara dam, situated in the rio Paranapanema main channel. The ribeirão Grande, ribeirão Jaboticabal, ribeirão Vermelho, and the rio Laranjinha are the main tributaries of the rio das Cinzas.

The rio Itararé basin is located in the Paraná and São Paulo states. It is born on the border between the municipalities of Bom Sucesso de Itararé (São Paulo State), and Sengés (Paraná State), and runs through much of Northeast of Paraná State until it empties into the rio Paranapanema between the municipalities of Ribeirão Claro (Paraná State) and Timburi (São Paulo State). This watershed has a total area of approximately 4,845 km^2, encompassing about 3% of the area and 1% of the population of the Paraná State. Its main tributaries situated in the Paraná State are the rio Jaguariaíva and rio Jaguaricatu, which flow into its left bank (Paraná 2010).

Within the rio das Cinzas and rio Itararé basins some protected areas are guaranteed by the National System of Conservation Units of Nature in Brazil, despite of imminent political attacks that are underway (see Alves et al. 2019). Between the municipalities of Cornélio Procópio and Santa Mariana is the Mata São Francisco State Park with 833 ha of Seasonal Forest, in addition to the Mina Velha State Park, in the municipality of Ibaiti, which has remnants of Araucaria forest (Paraná 2010). The Southern portion of the basin, in the municipalities of Piraí do Sul and Jaguariaíva, composes the Environment Protection Area (EPA) of Devonian Escarpment, whose Northern portion includes the rio Itararé, between the municipalities of Jaguariaíva and Sengés. This EPA is a crucial area for biodiversity preservation because it comprises within its limits important State and National Parks, Private Reserve of Natural Heritage, and integrates important Brazilian river basins such as the rio Paranapanema system (Alves et al. 2019).

2. Data collection

In all, 24 streams of low orders (less than three) were sampled (Table 1; Figure 1) on two collection trips: June 2017, and July 2018. Of these, seven streams are located in the rio das Cinzas basin, and 17 in the rio Itararé basin (Table 1; Figure 1). A 100-m stretch (the wadeable stream stretches have at least one sequence of riffle-run-pool meso-habitats) was defined at each site, which were georeferenced (Table 1) and sampled by electrofishing. This technique employs two electrified dip nets, producing an electric discharge between 200 and 400 V and current of 2 A, that stun the fish temporarily (Lobón-Cervia 1991). The specimens were anesthetized in benzocaine hydrochloride and fixed in 10% formalin in the field. After a few days, the fishes were transferred to 70% ethanol in the laboratory, identified in species-level, and deposited in the Coleção Ictiológica do Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (NUP).

Fish species were classified based on Van der Laan et al. (2019), species validity was based on Fricke et al. (2019), and species determinations were accomplished by comparison of the specimens with original descriptions or with specimens reported from the streams of rio Paranapanema system in Paraná State (Castro et al. 2003; Cetra et al. 2012; Cionek et al. 2012; Pagotto et al. 2012; Costa et al. 2013; Hoffmann et al. 2015; Cetra et al. 2016; Claro-García et al. 2018) and

Table 1. Information on the headwater streams sampled in the rio das Cinzas and rio Itararé basins, Paraná State, Brazil. Numbers in parentheses after each species name indicates abundance.

Sampled site	Remarks	Altitude (meters)	Coordinates	Municipality	Species caught
1	Rio do Tigre, affluent of rio das Cinzas, rio das Cinzas basin	~783	24°10'24.1"S, 49°53'54.6"W	Arapoti	*Phalloceros harpagos* (3) and *Rhamdia quelen* (2)
2	Unnamed river, affluent of rio Perdizes, rio das Cinzas basin	~926	24°13'47.2"S, 49°53'53.6"W	Arapoti	*Astyanax* aff. *paranae* (145), *Geophagus* aff. *brasiliensis* (3) and *Gymnotus inaequilabiatus* (2)
3	Unnamed river, affluente of rio do Tigre, rio das Cinzas basin	~820	24°11'4.9"S, 49°52'14"W	Arapoti	*Astyanax* aff. *paranae* (4), *Geophagus* aff. *brasiliensis* (2) and *Rhamdia quelen* (3)
4	Córrego Água Fria, affluent of rio Pinhalão, rio das Cinzas basin	~600	23°48'44.1"S, 50°7'55.14"W	Japira	*Bryconamericus* aff. *iheringii* (7), *Cambeva diabola* (5), *Hypostomus ancistroides* (7), *Imparfinis mirini* (19), *Phalloceros harpagos* (104) and *Rhamdia quelen* (3)
5	Córrego do Café, affluent of rio Pinhalão, rio das Cinzas basin	~606	23°56'9.25"S, 50°2'16.1"W	Pinhalão	*Astyanax bockmanni* (6), *Astyanax* aff. *paranae* (28), *Bryconamericus* aff. *iheringii* (11), *Cambeva davisi* (14), *Hypostomus ancistroides* (5), *Neoplecostomus selenae* (4) and *Rhamdia quelen* (26)
6	Unnamed river, affluent of rio das Pedras, rio das Cinzas basin	~626	23°57'28.05"S, 50°14'5.9"W	Ibaiti	*Astyanax* aff. *paranae* (3), *Cambeva diabola* (13), *Geophagus* aff. *brasiliensis* (11), *Hypostomus ancistroides* (6), *Imparfinis mirini* (1) and *Neoplecostomus selenae* (3)
7	Rio das Pedras, affluent of rio das Cinzas, rio das Cinzas basin	~624	23°56'4.6"S, 50°14'41.4"W	Ibaiti	*Astyanax bockmanni* (51), *Astyanax* aff. *paranae* (8), *Bryconamericus* aff. *iheringii* (78), *Cambeva davisi* (6), *Geophagus* aff. *brasiliensis* (42), *Gymnotus inaequilabiatus* (1), *Hoplias* aff. *malabaricus* (3), *Hypostomus ancistroides* (19), *Neoplecostomus selenae* (17), *Phalloceros harpagos* (11) and *Rhamdia quelen* (2)
8	Rio Lajeadinho, affluent of rio Barra Mansa, rio Itararé basin	~725	24°5'24.5"S, 49°47'14.9"W	Arapoti	*Astyanax* cf. *bifasciatus* (1), *Geophagus* aff. *brasiliensis* (22), *Hoplias* aff. *malabaricus* (1), *Hypostomus ancistroides* (1) and *Rhamdia quelen* (1)
9	Unnamed river, affluent of rio das Mortes, rio Itararé basin	~811	24°12'20.2"S, 49°38'8.7"W	Jaguariaíva	*Cambeva davisi* (10) and *Characidium schubarti* (4)
10	Unnamed river, affluent of rio do Bugre, rio Itararé basin	~770	24°7'5.1"S, 49°32'50.5"W	Sengés	*Astyanax* aff. *paranae* (51) and *Cambeva iheringi* (13)
11	Unnamed river, rio Itararé basin	~949	24°27'43.8"S, 49°31'27.8"W	Jaguariaíva	*Astyanax* aff. *paranae* (7), *Cambeva davisi* (4), *Characidium schubarti* (3), *Neoplecostomus selenae* (8), *Phalloceros harpagos* (3) and *Rhamdia quelen* (4)
12	Rio Preto, affluent of rio Jaguariaíva, rio Itararé basin	~567	24°4'25.8"S, 49°38'53.8"W	Jaguariaíva	*Apareiodon ibitiensis* (15), *Bryconamericus turiuba* (4), *Bryconamericus* aff. *iheringii* (9), *Cambeva davisi* (2), *Characidium* aff. *zebra* (1), *Imparfinis mirini* (2), *Neoplecostomus selenae* (16) and *Rhamdia quelen* (2)
13	Rio da Serrinha, affluent of rio Jaguariaíva, rio Itararé basin	~789	24°12'49.5"S, 49°41'9.1"W	Jaguariaíva	*Apareiodon ibitiensis* (5), *Cambeva davisi* (1), *Geophagus* aff. *brasiliensis* (2), *Neoplecostomus selenae* (11) and *Phalloceros harpagos* (20)
14	Rio das Samambaias, affluent of rio Jaguariaíva, rio Itararé basin	~813	24°10'43.7"S, 49°36'55.85"W	Jaguariaíva	*Cambeva davisi* (18), *Characidium schubarti* (1), *Neoplecostomus selenae* (8) and *Phalloceros harpagos* (11)

Continuation Table 1.

Sampled site	Remarks	Altitude (meters)	Coordinates	Municipality	Species caught
15	Rio Funil, affluent of rio Itararé, rio Itararé basin	~620	24°7'15.9"S, 49°23'28.8"W	Sengés	*Astyanax bockmanni* (4), *Geophagus* aff. *brasiliensis* (5), *Hoplias* aff. *malabaricus* (3) and *Neoplecostomus selenae* (50)
16	Rio Pelame, affluent of rio Itararé, rio Itararé basin	~609	24°7'6.9"S, 49°24'40.4"W	Sengés	*Apareiodon ibitiensis* (33), *Astyanax bockmanni* (2), *Astyanax* aff. *paranae* (1), *Bryconamericus turiuba* (20), *Cambeva diabola* (10), *Cambeva iheringi* (2), *Cetopsorhamdia iheringi* (2), *Characidium* sp. (3), *Eigenmannia* sp. (3), *Geophagus* aff. *brasiliensis* (5), *Hypostomus hermanni* (3), *Hypostomus tietensis* (5), *Imparfinis borodini* (5), *Neoplecostomus selenae* (15), *Otothyropsis biamnicus* (8), *Phenacorhamdia tenebrosa* (5) and *Piabarchus stramineus* (2)
17	Rio Jaguaricatu, affluent of rio Itararé, rio Itararé basin	~630	24°8'17.5"S, 49°29'48.1"W	Sengés	*Astyanax* aff. *paranae* (5), *Cambeva davisi* (20), *Geophagus* aff. *brasiliensis* (1) and *Neoplecostomus selenae* (52)
18	Riacho do Bugre, affluent of rio Jaguaricatu, rio Itararé basin	~585	24°7'55.2"S, 49°29'7.7"W	Sengés	*Apareiodon ibitiensis* (6), *Astyanax lacustris* (1), *Astyanax* aff. *paranae* (1), *Bryconamericus turiuba* (8), *Cetopsorhamdia iheringi* (7), *Hypostomus ancistroides* (4), *Hypostomus iheringii* (6), *Hypostomus strigaticeps* (3), *Imparfinis mirini* (1) and *Neoplecostomus selenae* (2)
19	Rio Lajeado Grande, affluent of rio Jaguariaíva, rio Itararé basin	~1092	24°20'25.8"S, 49°43'37.9"W	Jaguariaíva	*Astyanax* aff. *paranae* (1), *Characidium schubarti* (1) and *Phalloceros harpagos* (124)
20	Unnamed river, affluent of rio Espigão Alto, rio Itararé basin	~910	24°25'34.3"S, 49°40'42.4"W	Jaguariaíva	*Astyanax* aff. *paranae* (32), *Cambeva davisi* (18), *Cambeva iheringi* (3), *Characidium schubarti* (10), *Characidium* sp. (4), *Phalloceros harpagos* (8) and *Rhamdia quelen* (1)
21	Rio Espigão Alto, affluent of rio Jaguariaíva, rio Itararé basin	~899	24°24'19.4"S, 49°38'53.9"W	Jaguariaíva	*Astyanax* aff. *paranae* (80), *Cambeva davisi* (3), *Cambeva iheringi* (5), *Characidium* sp. (7), *Corydoras ehrhardti* (1), *Phalloceros harpagos* (2) and *Rhamdia quelen* (3)
22	Rio das Lanças, affluent of rio Jaguariaíva, rio Itararé basin	~889	24°24'40.7"S, 49°37'24.7"W	Jaguariaíva	*Astyanax* aff. *paranae* (5), *Cambeva iheringi* (2), *Characidium schubarti* (45), *Corydoras ehrhardti* (26), *Geophagus* aff. *brasiliensis* (22), *Hoplias* aff. *malabaricus* (4), *Hypostomus tietensis* (1), *Neoplecostomus selenae* (15), *Phalloceros harpagos* (5) and *Rhamdia quelen* (7)
23	Unnamed river, affluent of rio Jaguaricatu, rio Itararé basin	~942	24°28'18.8"S, 49°29'28.4"W	Jaguariaíva	*Astyanax* aff. *paranae* (55), *Bryconamericus* aff. *iheringii* (1), *Cambeva davisi* (6), *Cetopsorhamdia iheringi* (1), *Characidium schubarti* (3), *Characidium* sp. (6), *Neoplecostomus selenae* (3) and *Phalloceros harpagos* (19)
24	Riacho do Tombo, affluent of rio Jaguaricatu, rio Itararé basin	~956	24°29'33.9"S, 49°29'53.5"W	Jaguariaíva	*Astyanax* aff. *paranae* (15), *Cambeva davisi* (10), *Cetopsorhamdia iheringi* (6), *Characidium* sp. (6), *Neoplecostomus selenae* (4) and *Phalloceros harpagos* (11)

from the rio Paraná floodplain (Ota et al. 2018). Whenever possible, the determinations of the species were checked by specialists of each taxonomic group. The species were categorized by their frequency of occurrence (hereafter, constancy), which was calculated for all sampled streams according to Dajoz (1983). Species with a constancy up to 25% were classified as occasional, between 25 and 50% as accessory, and higher than 50% as constant. In addition, the species were categorized by origin to distinguish native and introduced species to the upper rio Paraná system, following Langeani et al. (2007), Frota et al. (2016a), Cavalli et al. (2018) and Ota et al. (2018).

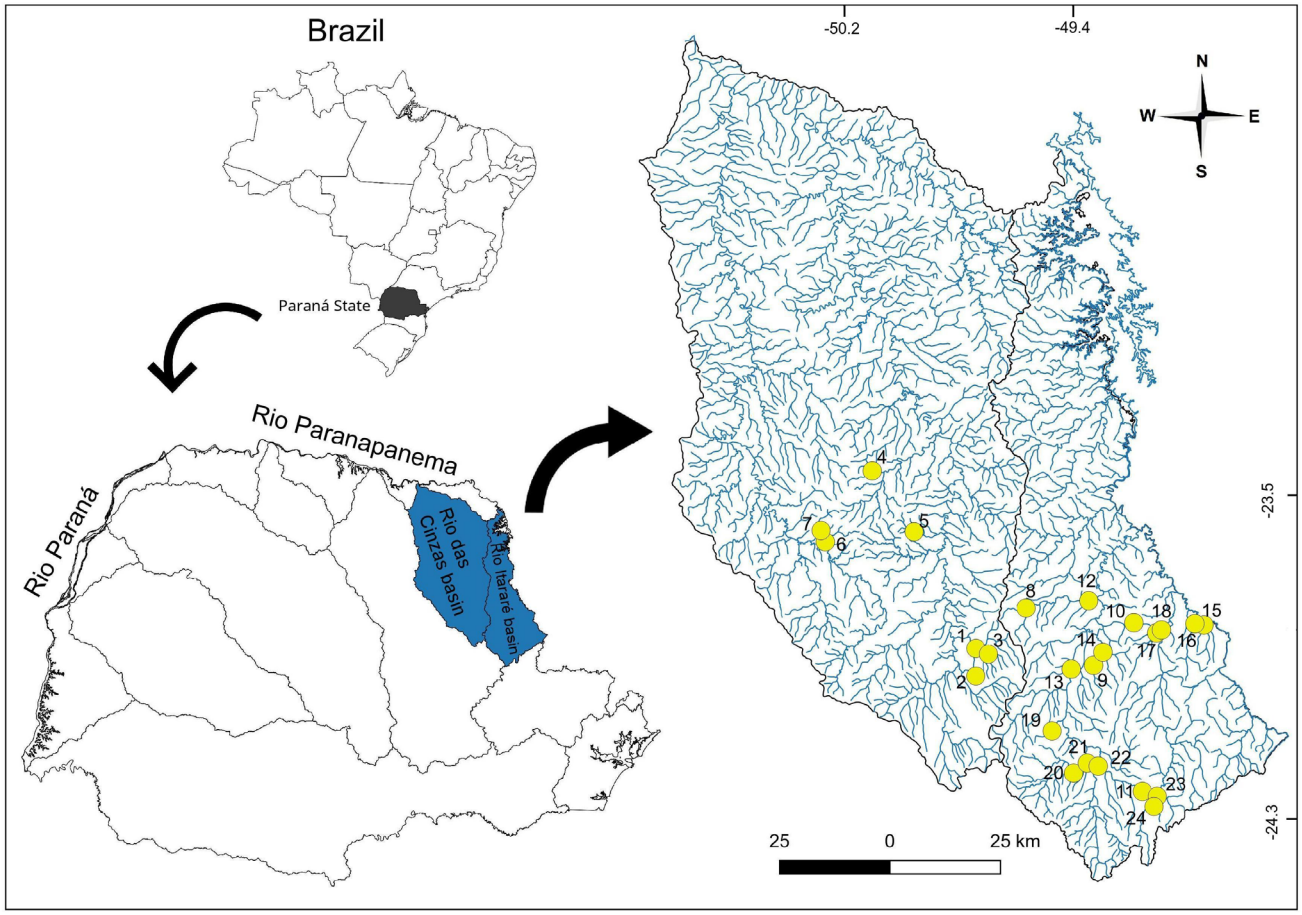


Figure 1. Map of the study area showing the location of the rio das Cinzas and rio Itararé basins within Paraná State and the 24 sampled sites (yellow circles), with its numbers corresponding to Table 1.

Results

A total of 1,823 individuals were collected, distributed in five orders, 12 families, and 32 species (Tables 1 and 2; Figures 2 and 3). Siluriformes (Figure 2) was the most representative order with 16 species (50.0% of all collected species) and four families, followed by Characiformes (Figure 3) with 12 species and four families. Among the families, Characidae and Loricariidae (both with seven species) presented higher richness contributing together with approximately 43.8% of all collected species, followed by Heptapteridae (five species) with approximately 15.6% of all collected species, Crenuchidae and Trichomycteridae (three species each) with approximately 8.8% of all collected species, and the other families (Table 2) that were represented by only one species.

Regarding the abundance of the sampled individuals (Figure 4), *Astyanax* aff. *paranae* Eigenmann, 1914 (447 individuals), *Phalloceros harpagos* Lucinda, 2008 (321 individuals), *Neoplecostomus selenae* Zawadzki, Pavanelli & Langeani, 2008 (208 individuals), *Geophagus* aff. *brasiliensis* (Quoy & Gaimard, 1824) (115 individuals), *Cambeva davisi* (Haseman, 1911) (112 individuals), *Bryconamericus* aff. *iheringii* (Boulenger, 1887) (106 individuals), *Characidium schubarti* Travassos, 1955 (67 individuals), *Astyanax bockmanni* Vari & Castro, 2007 (63 individuals), *Apareiodon ibitiensis* Amaral Campos, 1944 (59 individuals), and *Rhamdia quelen* (Quoy & Gaimard, 1824) (54 individuals) were the most abundant species, contributing with approximately 85.0% of all collected individuals. On the other hand, the other 22 species counted less than 50 individuals, representing approximately 15.0% of all collected individuals (Figure 4).

As for constancy (Table 2) most of the species were categorized as occasional (25 species). Five species (*C. schubarti*, *R. quelen*, *C. davisi*, *G.* aff. *brasiliensis*, and *P. harpagos*) were categorized as accessory, and only two species (*A.* aff. *paranae* and *N. selenae*) were categorized as constant. Regarding the origin of species (Table 2) none was considered as introduced to the rio Paranapanema system. It is noteworthy that the capture of *Astyanax bifasciatus* Garavello & Sampaio, 2010 represents the first record of this species from the upper rio Paraná system. Lastly, three putatively undescribed species (approximately 9.4% of all collected species) were also collected: *A.* aff. *paranae* (*sensu* Ota et al. 2018), *Characidium* sp., and *Eigenmannia* sp.

Discussion

With the predominance of Siluriformes and Characiformes, the taxonomic composition of the 24 sampled streams follows the pattern described for the Neotropical freshwater fish fauna (Castro 1999; Lowe-McConnell 1999; Albert et al. 2011). The number of species

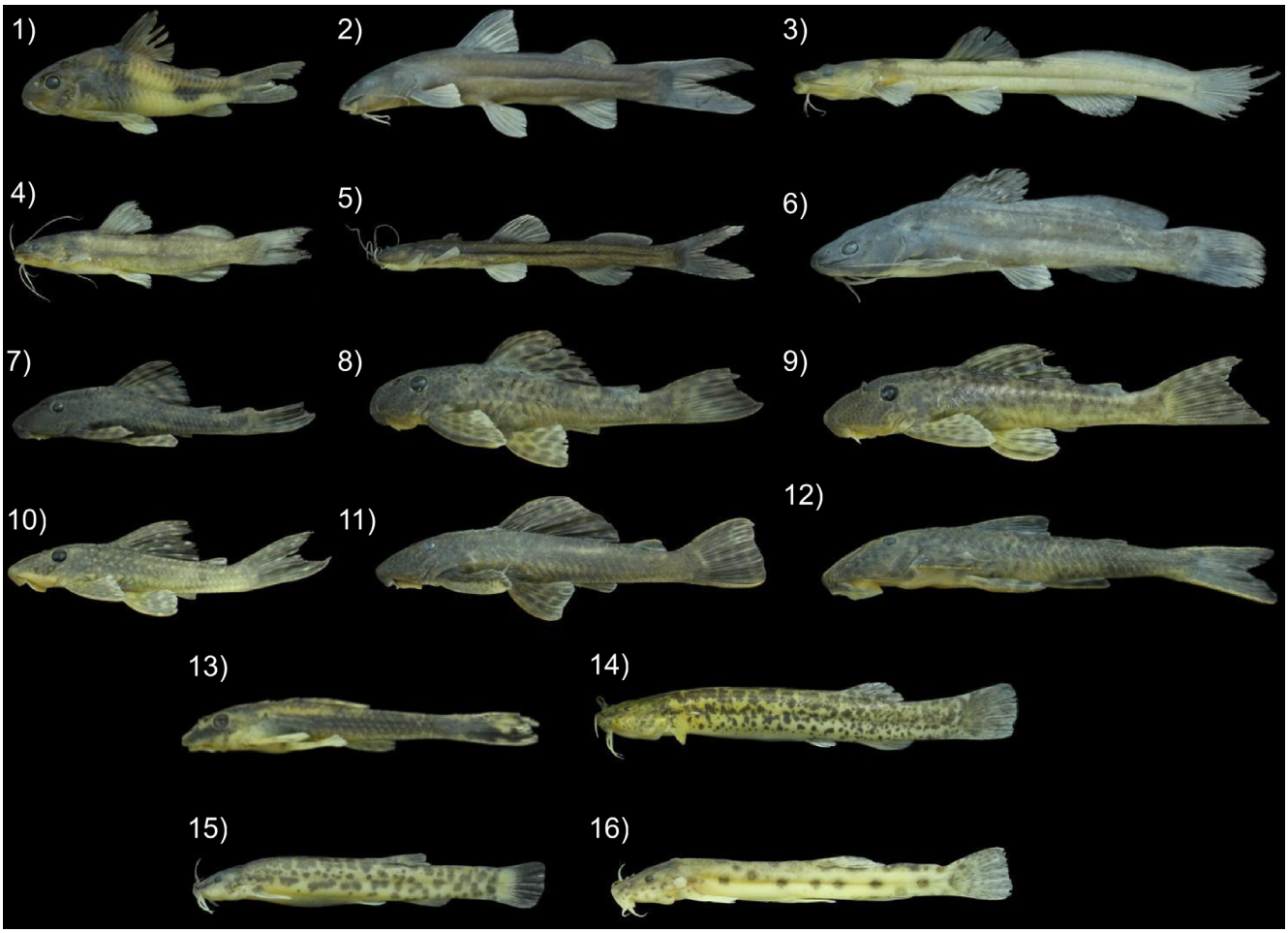


Figure 2. Representative individuals of the Siluriformes collected to the headwater streams from the rio das Cinzas and rio Itararé basins, rio Paranapanema system, Paraná State, Brazil. Their catalogue numbers in the Coleção Ictiológica do Nupélia (NUP) and standard lengths are presented after the names of species. 1) *Corydoras ehrhardti*, NUP 20473, 43.9 mm; 2) *Cetopsorhamdia iheringi*, NUP 20490, 70.9 mm; 3) *Imparfinis borodini*, NUP 20434, 105.2 mm; 4) *Imparfinis mirini*, NUP 20393, 68.0 mm; 5) *Phenacorhamdia tenebrosa*, NUP 20437, 59.9 mm; 6) *Rhamdia quelen*, NUP 20479, 94.8 mm; 7) *Hypostomus ancistroides*, NUP 20516, 63.8 mm; 8) *Hypostomus hermanni*, NUP 20432, 99.5 mm; 9) *Hypostomus iheringii*, NUP 20449, 98.6 mm; 10) *Hypostomus strigaticeps*, NUP 20450, 106.8 mm; 11) *Hypostomus tietensis*, NUP 20476, 125.4 mm; 12) *Neoplecostomus* selenae, NUP 20477, 67.3 mm; 13) *Otothyropsis biamnicus*, NUP 20436, 27.5 mm; 14) *Cambeva davisi*, NUP 20462, 74.5 mm; 15) *Cambeva diabola*, NUP 20510, 55.7 mm; 16) *Cambeva iheringi*, NUP 20470, 71.7 mm.

recorded in Characidae, Loricariidae, and Heptapteridae also follows the pattern of the most species-rich families in the upper rio Paraná system (Langeani et al. 2007). Similarly, several studies have indicated the prevalence of these families in other streams of this drainage system (*e.g.,* Hoffmann et al. 2015; Bifi et al. 2017; Batista-Silva et al. 2018; Claro-García et al. 2018; Azevedo-Santos et al. 2019b), especially for streams of the rio Paranapanema system, such as the rio das Cinzas (Costa et al. 2013) and the rio Itararé (Cetra et al. 2016) basins.

Our results showed that occasional species dominated the sampled streams. This may be related to the influence of the altitudinal gradient on the species distribution since the species richness tends to decrease with the altitude increase (Fu et al. 2004; Jaramillo-Villa et al. 2010; Askeyev et al. 2017; Frota et al. 2019). As verified in other studies relating fish species richness with the altitudinal gradient (*e.g.,* Askeyev et al. 2017), above 650 m of altitude few species were repeated in the streams sampled (Table 1). These species were classified as constant or accessory, in addition to being among the most abundant species such as *A.* aff. *paranae*, *N. selenae*, *C. davisi*, *R. quelen*, and *C. schubarti*. In fact, members of Heptapteridae, Loricariidae, and Trichomycteridae have morphological structures adapted to fixation in underwater structures, such as fortified pectoral fin rays, subterminal sucker mouths and/or spines in the operculum. These adaptations can guarantee the conquest of higher lands, such as headwater streams (Oyakawa et al. 2006). The great abundance and constancy of *A.* aff. *paranae* may be related to a short-distance migratory character (<100 km) already evidenced for some species of this genus (Agostinho et al. 2004).

Costa et al. (2013) found a few introduced species already inhabiting the waters of the rio das Cinzas basin, such as *Cyprinus carpio* Linnaeus, 1768, *Oreochromis niloticus* (Linnaeus, 1758), and *Poecilia reticulata* Peters, 1859. In contrast, the absence of such species from the headwater streams sampled herein suggests a greater integrity of that fish community, since biological invasions are among the main threats to freshwater environments (Daga et al. 2015; Ruaro et al. 2018), and especially detrimental for the fish fauna of Neotropical

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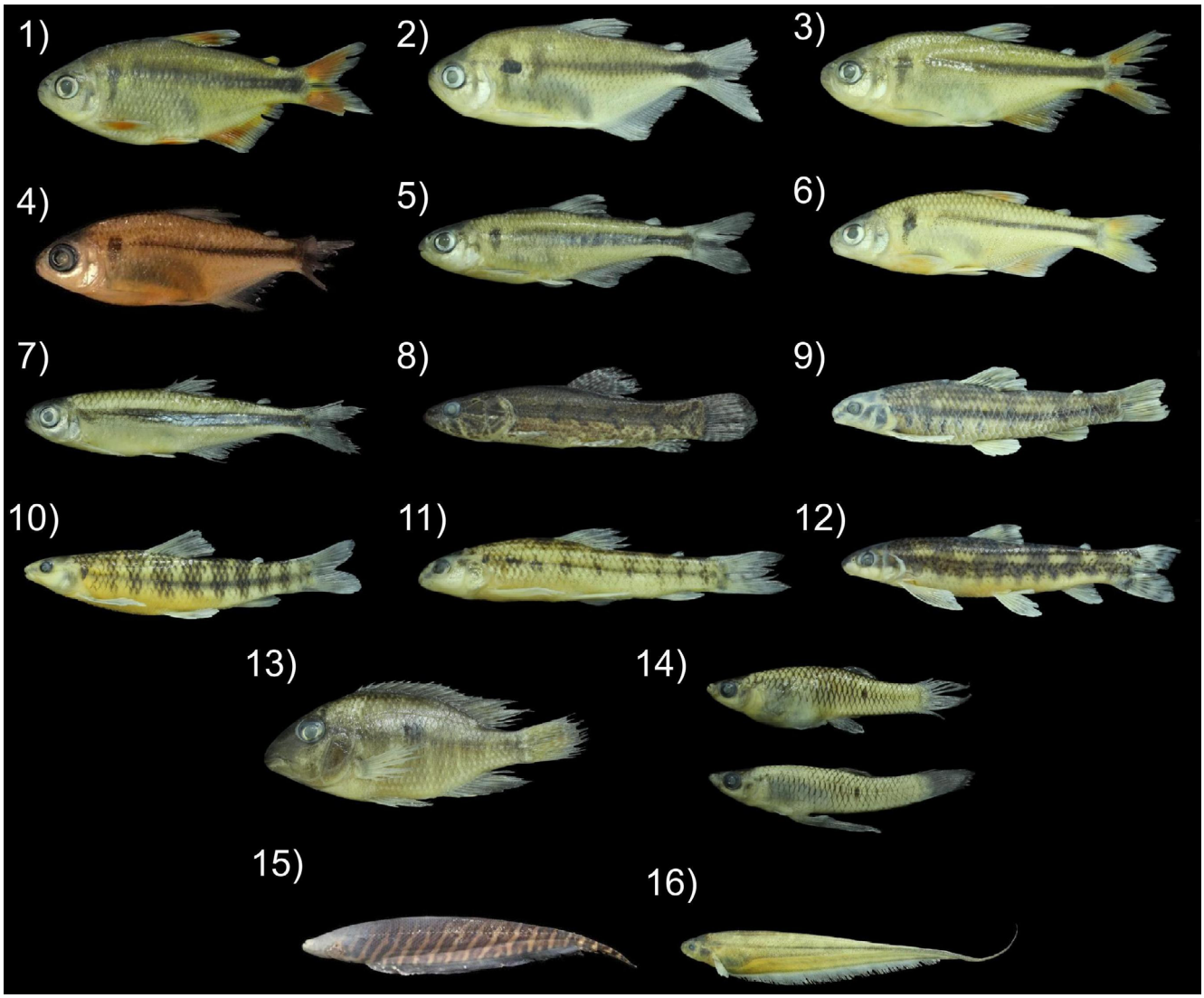


Figure 3. Representative individuals of the Characiformes, Cichliformes, Cyprinodontiformes, and Gymnotiformes collected to the headwater streams from the rio das Cinzas and rio Itararé basins, rio Paranapanema system, Paraná State, Brazil. Their catalogue numbers in the Coleção Ictiológica do Nupélia (NUP) and standard lengths (total lengths for Gymnotiformes) are presented after the names of species. 1) *Astyanax bockmanni*, NUP 20511, 66.3 mm; 2) *Astyanax lacustris*, NUP 20446, 58.2 mm; 3) *Astyanax* aff. *paranae*, NUP 20464, 59.8 mm; 4) *Astyanax* cf. *bifasciatus*, NUP 20405, 38.0 mm; 5) *Bryconamericus turiuba*, NUP 20426, 45.0 mm; 6) *Bryconamericus* aff. *iheringii*, NUP 20513, 45.0 mm; 7) *Piabarchus stramineus*, NUP 20438, 67.5 mm; 8) *Hoplias* aff. *malabaricus*, NUP 20475, 77.1 mm; 9) *Characidium schubarti*, NUP 20472, 68.4 mm; 10) *Characidium* aff. *zebra*, NUP 20409, 70.8 mm; 11) *Characidium* sp., NUP 20491, 48.3 mm; 12) *Apareiodon ibitiensis*, NUP 20414, 89.6 mm; 13) *Geophagus* aff. *brasiliensis*, NUP 20421, 77.5 mm; 14) *Phalloceros harpagos*, NUP 20487, 29.6 mm (above; female), 22.9 mm (below; male); 15) *Gymnotus inaequilabiatus*, NUP 21109, 108.5 mm; 16) *Eigenmannia* sp., NUP 20429, 149.0 mm.

streams (Winemiller et al. 2008; Ruaro et al. 2018). The Devonian Escarpment EPA is directly linked to the maintenance of this integrity, especially in the case of the rio Itararé basin, and conservation efforts are increasingly necessary to at least maintain the original area of this natural reserve (Alves et al. 2019).

Astyanax bifasciatus was thought to be endemic to the rio Iguaçu basin (Garavello & Sampaio 2010; Baumgartner et al. 2012), a drainage system of the lower rio Paraná that encompasses a large area of southern Paraná State and northern Santa Catarina State. In a recent inventory (Frota et al. 2019), this species had its geographical distribution extended to the rio Ribeira de Iguape basin, a coastal drainage bordered to the south by the rio Iguaçu basin and to the north by the rio Itararé basin. Another example of the interesting biogeographic (Ribeiro 2006; Frota et al. 2016a) and phylogeographic (Morais-Silva et al. 2018) patterns at the boundaries of the Ponta Grossa Arch. In fact, this arch is the most prominent geological structure in the headwater regions of the Paranapanema, Iguaçu and Ribeira de Iguape river basins (Ribeiro 2006).

Mainly due to their recent tectonic activities (Franco-Magalhães et al. 2010), the Ponta Grossa Arch is thought to be responsible for a particularly accelerated river dynamism between these adjacent drainage systems, enabling the faunal exchange between them (Ribeiro 2006). This same scenario can be found for other fish species. For example, adjacent tributaries of the Iguaçu, Paranapanema and Ribeira de Iguape river basins share the presence of *C. davisi* (see Ingenito et al. 2004; Ribeiro 2006; Morais-Silva et al. 2018), *Hyphessobrycon griemi*

Table 2. Fish species collected in headwater streams from the rio das Cinzas and rio Itararé basins, upper rio Paranapanema system, Paraná State, Brazil.

Ordem	Family	Species	Origin/Constancy	Voucher
Characiformes	Crenuchidae	*Characidium schubarti* Travassos, 1955	Native/Accessory	NUP 19250, NUP 19265, NUP 20455, NUP 20459, NUP 20472, NUP 20484, NUP 21055
		Characidium aff. *zebra* Eigenmann, 1909	Native/Occasional	NUP 20409
		Characidium sp.	Native/Occasional	NUP 20428, NUP 20458, NUP 20465, NUP 20485, NUP 20491
	Erythrinidae	*Hoplias* aff. *malabaricus* (Bloch, 1794)	Native/Occasional	NUP 20422, NUP 20475, NUP 20515, NUP 21008
	Parodontidae	*Apareiodon ibitiensis* Amaral Campos, 1944	Native/Occasional	NUP 20407, NUP 20414, NUP 20425, NUP 20445, NUP 21013, NUP 21017
	Characidae	*Astyanax bockmanni* Vari & Castro, 2007	Native/Occasional	NUP 20423, NUP 20431, NUP 20511, NUP 21111
		Astyanax lacustris (Lütken, 1875)	Native/Occasional	NUP 20446
		Astyanax aff. *paranae* Eigenmann, 1914	Native/Constant	NUP 19256, NUP 19258, NUP 19260, NUP 19262, NUP 20398, NUP 20441, NUP 20454, NUP 20457, NUP 20464, NUP 20471, NUP 20481, NUP 20489, NUP 21046, NUP 21054
		Astyanax cf. *bifasciatus* Garavello & Sampaio, 2010	Native/Occasional	NUP 20405
		Bryconamericus turiuba Langeani, Lucena, Pedrini & Tarelho-Pereira, 2005	Native/Occasional	NUP 20426, NUP 20447, NUP 21015, NUP 21041
		Bryconamericus aff. *iheringii* (Boulenger, 1887)	Native/Occasional	NUP 20392, NUP 20399, NUP 20408, NUP 20482, NUP 20513, NUP 21080
		Piabarchus stramineus (Eigenmann, 1908)	Native/Occasional	NUP 20438
Gymnotiformes	Gymnotidae	*Gymnotus inaequilabiatus* Valenciennes, 1839	Native/Occasional	NUP 19254, NUP 21109
	Sternopygidae	*Eigenmannia* sp.	Native/Occasional	NUP 20429, NUP 21044
Siluriformes	Heptapteridae	*Cetopsorhamdia iheringi* Schubart & Gomes, 1959	Native/Occasional	NUP 20427, NUP 20448, NUP 20483, NUP 20490, NUP 21029, NUP 21087
		Imparfinis borodini Mees & Cala, 1989	Native/Occasional	NUP 20434, NUP 21033
		Imparfinis mirini Haseman, 1911	Native/Occasional	NUP 20393, NUP 20410, NUP 20452, NUP 21012
		Phenacorhamdia tenebrosa (Schubart, 1964)	Native/Occasional	NUP 20437, NUP 21034
		Rhamdia quelen (Quoy & Gaimard, 1824)	Native/Accessory	NUP 19253, NUP 19259, NUP 19264, NUP 20396, NUP 20402, NUP 20406, NUP 20412, NUP 20461, NUP 20468, NUP 20479
	Trichomycteridae	*Cambeva davisi* (Haseman, 1911)	Native/Accessory	NUP 19251, NUP 19267, NUP 20403, NUP 20413, NUP 20420, NUP 20444, NUP 20462, NUP 20469, NUP 20488, NUP 20494, NUP 21003
		Cambeva diabola (Bockmann, Casatti & de Pinna, 2004)	Native/Occasional	NUP 20397, NUP 20439, NUP 20510, NUP 20999, NUP 21043
		Cambeva iheringi (Eigenmann, 1917)	Native/Occasional	NUP 19261, NUP 20440, NUP 20463, NUP 20470, NUP 20480, NUP 21042, NUP 21059

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Continuation Table 2.

Ordem	Family	Species	Origin/Constancy	Voucher
	Callichthyidae	*Corydoras ehrhardti* Steindachner, 1910	Native/Occasional	NUP 20466, NUP 20473, NUP 21075
	Loricariidae	*Hypostomus ancistroides* (Ihering, 1911)	Native/Occasional	NUP 20394, NUP 20400, NUP 20451, NUP 20509, NUP 20516
		Hypostomus hermanni (Ihering, 1905)	Native/Occasional	NUP 20432, NUP 21032
		Hypostomus iheringii (Regan, 1908)	Native/Occasional	NUP 20449
		Hypostomus strigaticeps (Regan, 1908)	Native/Occasional	NUP 20450, NUP 21050
		Hypostomus tietensis (Ihering, 1905)	Native/Occasional	NUP 20433, NUP 20476
		Neoplecostomus selenae Zawadzki, Pavanelli & Langeani, 2008.	Native/Constant	NUP 19266, NUP 20401, NUP 20411, NUP 20416, NUP 20418, NUP 20424, NUP 20435, NUP 20443, NUP 20453, NUP 20477, NUP 20486, NUP 20492, NUP 20517, NUP 21035, NUP 21115
		Otothyropsis biamnicus Calegari, Lehmann & Reis, 2013	Native/Occasional	NUP 20436, NUP 21040
Cichliformes	Cichlidae	*Geophagus* aff. *brasiliensis* (Quoy & Gaimard, 1824)	Native/Accessory	NUP 19255, NUP 19257, NUP 20404, NUP 20415, NUP 20421, NUP 20430, NUP 20442, NUP 20474
Cyprinodontiformes	Poeciliidae	*Phalloceros harpagos* Lucinda, 2008	Native/Accessory	NUP 19252, NUP 19263, NUP 20395, NUP 20417, NUP 20419, NUP 20456, NUP 20460, NUP 20467, NUP 20478, NUP 20487, NUP 20493

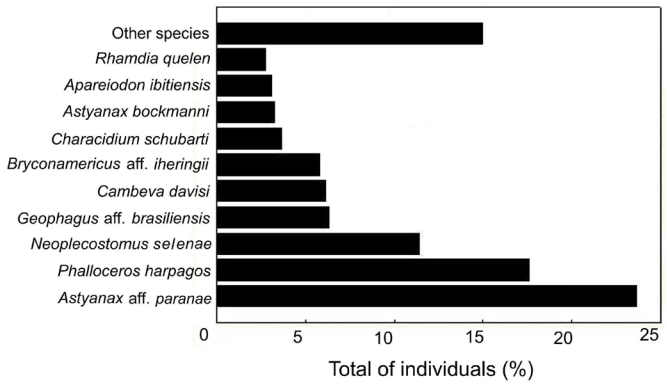


Figure 4. Percentages of number of individuals of each species with more than 50 individuals collected in the headwater streams from rio das Cinzas and rio Itararé basins, rio Paranapanema system, Paraná State, Brazil.

Hoedeman, 1957, *H. bifasciatus* Ellis, 1911, *H. reticulatus* Ellis, 1911 (see Ingenito et al. 2004; Ribeiro 2006), *Mimagoniates microlepis* (Steindachner, 1877) (see Ingenito et al. 2004; Ribeiro 2006; Menezes et al. 2008; Hoffmann et al. 2015), and *Rhamdiopsis moreirai* Haseman, 1911 (see Ferraris 2007; Hoffmann et al. 2015). The slopes of the upper rio Paraná system and the rio Ribeira de Iguape basin share the presence of *Hypostomus ancistroides* (Ihering, 1911) (Oyakawa et al. 2005). The Iguaçu and Ribeira de Iguape river basins share the presence of *Characidium travassosi* Melo, Buckup & Oyakawa, 2016 (Frota et al. 2016b; Melo et al. 2016). Now, the geographic distribution of *A. bifasciatus* is added to the mentioned examples since this species also occurs in all drainage systems mentioned.

Nine of the 32 fish species records presented herein are new for the Itararé and Cinzas river basins. Those are *Bryconamericus turiuba* Langeani, Lucena, Pedrini & Tarelho-Pereira, 2005, *Corydoras ehrhardti* Steindachner, 1910, *Hypostomus iheringii* (Regan, 1908), *Hypostomus tietensis* (Ihering, 1905), *Cambeva iheringi* (Eigenmann, 1917), *Gymnotus inaequilabiatus* Valenciennes, 1839, and the three putatively new species *A.* aff. *paranae* (*sensu* Ota et al. 2018), *Characidium* sp., and *Eigenmannia* sp. (compare with Costa et al. 2013; Cetra et al. 2016). Except for the latter two species, which are being reported for the first time herein, all of these species have a wide distribution range within the upper rio Paraná drainage. On the other hand, Costa et al. (2013) reported 11 species not collected by us (introduced species excluded): *Piabina argentea* Reinhardt, 1867, *Apareiodon affinis* (Steindachner, 1879), *Gymnotus sylvius* Albert & Fernandes-Matioli, 1999, *Gymnotus* sp., *Imparfinis schubarti* (Gomes, 1956), *Hypostomus albopunctatus* (Regan, 1908), *H. nigromaculatus* (Schubart, 1964), *H. paulinus* (Ihering, 1905), *Rineloricaria pentamaculata* Langeani & Araujo, 1994, *Crenicichla jaguarensis* Haseman, 1911, and *Synbranchus marmoratus* Bloch, 1795. Cetra *et al.* (2016) recorded 19 (introduced species excluded): *Astyanax biotae* Castro & Vari, 2004, *A. scabripinnis* (Jenyns, 1842), *Hyphessobrycon anisitsi* (Eigenmann, 1907), *Oligosarcus paranensis* Menezes &

Géry, 1983, *Piabina argentea*, *Characidium gomesi* Travassos, 1956, *Parodon nasus* Kner, 1859, *Gymnotus sylvius*, *Eigenmannia virescens* (Valenciennes, 1836), *Pimelodella avanhandavae* Eigenmann, 1917, *Hypostomus nigromaculatus*, *Hypostomus* sp. 1, *Hypostomus* sp. 2, *Otothyropsis* sp., *Rineloricaria pentamaculata*, *Trichomycterus* sp. 1, *Trichomycterus* sp. 2, *Phalloceros reisi* Lucinda, 2008, and *Synbranchus marmoratus*.

The identification of *A. biotae, H. anisitsi, P. argentea, O. paranensis, C. gomesi, A. affinis, H. albopunctatus, H. nigromaculatus, R. pentamaculata, P. avanhandavae, P. reisi, C. jaguarensis, and S. marmoratus* is pretty straightforward, meaning that at least 13 species, other than those presented by us, could be added to a complete list of the native stream fish fauna from the upper rio Paranapanema system. However, a careful analysis of the remaining species is necessary in order to verify whether they are in fact distinct from the species listed herein. *Gymnotus* species are hardly distinguishable from one another, especially at small sizes. *Imparfinis schubarti* has been considered a junior synonym of *I. mirini* Haseman, 1911, which suggests that the usual diagnostic characters may not be sufficient to distinguish those species, in the case that they are in fact two species. *Hypostomus paulinus* represents a species complex and is easily confused with *H. tietensis* (Zawadzki, personal communication).

Some species considered to be new by other authors (Costa et al. 2013; Cetra et al. 2016) may be variants of other, described species, which cannot be verified presently without the examination of the specimens. For example, regarding the two supposedly new species of *Trichomycterus* (= *Cambeva*), we found among our specimens a wide color-pattern variation, which nonetheless fall within the range of variation observed by Nascimento et al. (2017) for *C. davisi* and by da Silva et al. (2010) for *C. iheringi*. Thus, we cautiously hypothesize *Trichomycterus* sp. 1 and *Trichomycterus* sp. 2 of Cetra et al. (2016) to represent variants of these species.

In any case, in addition to the results of Cetra et al. (2016), our results point to the gap between existing evolutionary knowledge and current biological knowledge, which characterizes a large biodiversity shortfall (Hortal et al. 2015), especially for the stream fish fauna from the rio Paranapanema system. Future taxonomic studies with morphological and molecular methodologies can be conclusive on these issues. Here we have improved knowledge of the fish fauna of the rio das Cinzas and rio Itararé basins, upper rio Paranapanema system. However, we recognize that this inventory likely represents a small fraction of what remains to be sampled within these basins. Once again, sampling at headwater regions of high altitudes revealed possible unknown species to science, interesting biogeographic patterns and alarming biodiversity shortfalls, as well as inherent concerns about anthropogenic actions in Brazilian freshwater environments.

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Author Contributions

Augusto Frota: contributed to data acquisition, analysis and interpretation of data, drafting of the manuscript and wrote the paper.

Renata Rúbia Ota: contributed to analysis and interpretation of data, and critical revision for adding substantive intellectual content.

Gabriel de Carvalho Deprá: contributed to analysis and interpretation of data, and critical revision for adding substantive intellectual content.

Maria Julia Mileo Ganassin: contributed to analysis and interpretation of data, and critical revision for adding substantive intellectual content.

Weferson Júnio da Graça: contributed to data acquisition, analysis and interpretation of data, and critical revision for adding substantive intellectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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Article

Neriidae (Diptera: Schizophora) of the Northeastern Brazil: new records and an identification key

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Abstract: Here, we provide a list of seven species collected in the Brazilian states of Ceará, Maranhão and Piauí, housed in the Coleção Zoológica do Maranhão (CZMA), *Cerantichir peruana* (Hennig, 1937), *Glyphidops durus* (Cresson, 1926), *Glyphidops filosus* (Fabricius, 1805), *Glyphidops flavifrons* (Bigot, 1886), *Glyphidops vittatus* (Cresson, 1912), *Nerius pilifer* Fabricius, 1805 and *Nerius plurivittatus* Bigot, 1886. Representatives of Neriidae are recorded and mapped for the first time in the states of Ceará, Maranhão and Piauí, while the species *C. peruana*, *G. durus*, *G. flavifrons* and *G. vittatus* represent new records for the Northeast Region of Brazil. A key for the identification and diagnoses of Northeastern Brazilian neriids are provided.
Keywords: *Ceará, faunistic survey, Maranhão, Nerioidea, Piauí.*

Neriidae (Diptera: Schizophora) do Nordeste do Brasil: novos registros e uma chave de identificação

Resumo: Uma lista de sete espécies coletadas nos estados brasileiros do Ceará, Maranhão e Piauí é disponibilizada, baseada em material depositado na Coleção Zoológica do Maranhão (CZMA), *Cerantichir peruana* (Hennig, 1937), *Glyphidops durus* (Cresson, 1926), *Glyphidops filosus* (Fabricius, 1805), *Glyphidops flavifrons* (Bigot, 1886), *Glyphidops vittatus* (Cresson, 1912), *Nerius pilifer* Fabricius, 1805 e *Nerius plurivittatus* Bigot, 1886. Representantes de Neriidae são registrados e mapeados pela primeira vez nos estados do Ceará, Maranhão e Piauí, enquanto *C. peruana*, *G. durus*, *G. flavifrons* e *G. vittatus* representam novos registros para a Região Nordeste do Brasil. São apresentados uma chave para a identificação e diagnoses dos neríideos da Região Nordeste brasileira.
Palavras-chave: *Ceará, levantamento faunístico, Maranhão, Nerioidea, Piauí.*

Introduction

Neriidae is a cosmopolitan family of acalyptrate flies composed of 104 valid species classified in 16 genera (Pape et al. 2011, Sepúlveda et al. 2013a, Sepúlveda & de Carvalho 2019, Sepúlveda & Souza 2019, Sepúlveda et al. 2019). The first catalog of Neotropical Neriidae was published by Steyskal (1968), who listed 37 species from the region, of which 13 species were recorded for Brazil. In recent years, a number of studies on the taxonomy of Neriidae have been published, expanding the known distribution of several species (e.g., Carvalho-Filho & Esposito 2008, Sepúlveda et al. 2013a, b, 2014, Braga et al. 2017). Currently, 17 species of Neriidae are recorded for Brazil (Sepúlveda 2019). Brazil is the largest country in the Neotropical Region and comprises a great diversity of biomes, including 14 biogeographical provinces, of which five occur in the Northeast Region: Pará, Caatinga, Cerrado, Atlantic Forest and Paraná Forest (Morrone 2015).

Three studies focused on Neriidae from a particular region in Brazil have been published in the last years: North: Carvalho-Filho & Espósito (2008); Center-west: Calhau et al. (2017); and Northeast: Braga et al. (2017). The study of Braga et al. (2017) in Paraíba, Pernambuco and Bahia is complemented with information from this contribution, obtained after analysis of the material deposited in the Coleção Zoológica do Maranhão (CZMA) in the state of Maranhão, Brazil. The material in the CZMA collection was obtained in fieldwork at the states of Maranhão, Ceará and Piauí, between 2010 and 2017. Here, we provide a list of localities for seven species housed in the CZMA, representing the first records of Neriidae in Maranhão, Ceará and Piauí and the first records for Northeastern Brazil of *Cerantichir peruana* (Hennig, 1937), *Glyphidops durus* (Cresson, 1926), *Glyphidops flavifrons* (Bigot, 1886), *Glyphidops vittatus* (Cresson, 1912), raising to nine the number of species known to occur in Northeastern Brazil.

Materials and Methods

The material belongs to Coleção Zoológica do Maranhão (CZMA), Brazil. The genera were identified using Buck (2010). For specific identifications, we used keys published in revisions of each genus (Sepúlveda *et al*., 2013b, 2014) and for the species of *Nerius* (lacking taxonomical revision), we used the key by Aczél (1961). Photographs were taken with an Auto-Montage Imaging System® Leica DFC 500 in the Taxonline (UFPR). Information on the distribution of the species listed in Table 1 was obtained from Aczél (1961), Steyskal (1968), Carvalho-Filho & Espósito (2008), Sepúlveda et al. (2013b), Sepúlveda et al. (2014) and Braga et al. (2017). Distribution maps are based on records of Neriidae mostly from the Taxonomic Catalog of the Brazilian Fauna, TCBF and Braga et al. (2017); they were prepared in QGIS 3.6.0-'Noosa' software (https://www.qgis.org/en/site/) using the freely available DIVA-GIS country borders data (http://www.diva-gis.org/).

Results

Recently, Braga et al. (2017), presented the first list of species for the Brazilian Northeast, with four species. This list was mostly based on a few previous records and material collected in the states of Paraíba, Pernambuco and Bahia. Herein, new records of seven species and three genera of Neriidae in three Brazilian states are presented: *Glyphidops filosus* (Fabricius, 1805) for Ceará, Maranhão and Piauí; *Nerius pilifer* Fabricius, 1805 for Maranhão and Piauí; and *Cerantichir peruana* (Hennig, 1937), *Glyphidops durus* (Cresson, 1926), *Glyphidops flavifrons* (Bigot, 1886), *Glyphidops vittatus* (Cresson, 1912) and *Nerius plurivittatus* Bigot, 1886 for Maranhão, raising to nine the number of species recorded for the Brazilian Northeast (Figures 1 and 2). Also, the distributional maps of the Neriids species from the Brazilian Northeast are presented (Figure 3), including the seven species found in our survey and the other two species previously known to Brazilian Northeast (*Eoneria blanchardi* Aczél, 1951 and *Glyphidops carrerai* Aczél, 1961, Figures 3B and 3C respectively).

Key for the species of Neriidae from the Northeast Region of Brazil

1. Six dorsocentral setae. Syntergite 1+2 with one long lateral seta and a few conspicuous marginal setae not inserted in a protuberance. Antennal base pale brown and opaque …..... *E. blanchardi*
1'. One dorsocentral seta. Syntergite 1+2 without lateral seta and thick marginal setae gathered in a protuberance. Antennal base shiny, if opaque, black .....…. 2
2. Presutural scutum and antepronotal ridge, distinctly anterior to postpronotal carina. Pedicel elongate, length at least twice the width. Occiput length is at least its height …..... *C. peruana*
2'. Presutural scutum and antepronotal ridge at same level as postpronotal carina. Pedicel not elongate, length is at most 1.5 times width. Occiput length is shorter than height …..... 3
3. Prosternum wide, reaching the proepisternum laterally. Inner process of pedicel wide-triangular .....…. 4 [*Nerius* Fabricius]
3'. Prosternum linear, separated from proepisternum by wide membranous area. Inner process of pedicel narrow triangular to finger-like .....…. 5 [*Glyphidops* Enderlein]
4. (3) Thorax with wide greyish stripe dorsally on presutural and postsutural scutum, divided by median narrow brown stripe. Inner vertical seta inconspicuous and outer vertical seta absent. Occiput inflated, mostly shiny .....…. *N. pilifer*

Table 1. List of species of Neriidae with distribution in the Brazilian Northeast Region. *=new records.

Species	Northeastern Distribution	Other Brazilian records	Other countries distribution
Cerantichir peruana	Maranhão*	Acre, Pará, Rondônia, Mato Grosso	Costa Rica, Colombia, Peru, Bolivia
Eoneria blanchardi	Bahia, Paraíba, Pernambuco	Mato Grosso do Sul	Venezuela, Paraguay, Argentina
Glyphidops carrerai	Paraíba, Bahia	Amazonas, Pará, São Paulo, Rio de Janeiro	Colombia, Guyana
Glyphidops durus	Maranhão*	Amazonas, Amapá, Pará, São Paulo, Paraná	Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, Bolivia, Argentina
Glyphidops filosus	Paraíba, Bahia, Ceará*, Maranhão*, Piauí*	Acre, Alagoas, Amazonas, Bahia, Espírito Santo, Mato Grosso, Minas Gerais, Pará, Rio de Janeiro, Roraima, Santa Catarina, São Paulo	Guatemala, Costa Rica, Honduras, Panama, Trinidad, Colombia, Ecuador, Guyana, Montserrat, Venezuela, Suriname, Bolivia
Glyphidops flavifrons	Maranhão*	Amazonas, Pará, Acre, Espírito Santo	USA (Arizona, Florida), Mexico, Honduras, Nicaragua, Costa Rica, Panama, Trinidad and Tobago, Guyana, Colombia, Ecuador, Bolivia
Glyphidops vittatus	Maranhão*	Amazonas	Guyana, Peru, Bolivia
Nerius pilifer	Maranhão*, Piauí*, Paraíba, Bahia	Acre, Amazonas, Goiás, Mato Grosso do Sul, Mato Grosso, Minas Gerais, Pará, Rio de Janeiro, Rondônia, São Paulo and Tocantins	Mexico, Costa Rica, Haiti, Nicaragua, Panama, Colombia, Ecuador, Venezuela, Guyana, Suriname, Paraguay, Peru, Bolivia, Argentina
Nerius plurivittatus	Maranhão*	Pará, Acre, Amazonas	Mexico, El Salvador, Panama, Dominican Republic, Trinidad, Guyana, Venezuela, Colombia, Peru, Bolivia

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4'. Thorax with two grey stripes dorsally on presutural scutum, separated by median wide brown stripe narrowing toward scutoscutellar suture, and one dorsocentral brown stripe on postsutural scutum. Inner and outer vertical setae well-developed. Occiput velvet pruinose ..... *N. plurivittatus*

5. Arista white entirely, or at least basal third, with dense white pubescence 6

5'. Arista brown and bare or with brown micropubescence .. 8

6. Pleuron yellowish-brown and partly yellow with katatergite yellow. Occiput with reduced ventral brown stripe. Abdomen dorsally with median yellow stripe from tergite 1 to tergite 6 or shorter ..... *G. flavifrons*

6'. Pleuron brown with bluish reflections, even katatergite. Occiput with wide ventral brown stripe. Abdomen dorsally without median yellow stripe 7

7. Anterior notopleural seta hair-like and slender. Hind femur dorsally with two distomedian setae. Tibia yellow without brown ring ..... *G. carrerai*

7'. Anterior notopleural seta absent. Hind femur dorsally without seta. Tibia yellow with distomedian pale brown ring, darker on mid and hind tibiae ..... *G. durus*

8. Supra-alar seta present. Frontal vitta with two narrow black stripes in lateral margins anteriorly. Antennal base rounded and inflated; margins rounded in dorsal view ..... *G. vittatus*

8'. Supra-alar seta absent. Frontal vitta with ovate black spot on posterior third, covering the ocellar triangle. Antennal base not inflated and at most slightly rounded ..... *G. filosus*

***Cerantichir peruana* (Hennig, 1937)**

Figures 1A, 1B and 3A

Diagnosis. Arista densely white pubescent; pedicel and scape elongate, being length at least twice the width; antennal base with inner margins close together; fronto-orbital plate shiny wide; ocellar triangle protrude; outer vertical setae absent; occiput shiny elongate and as long as high; vibrissa absent; thorax elongate, with mesoscutum and antepronotal ridge distinctly anterior to postpronotal carina; scapular seta present; posterior notopleural seta and apical scutellar seta inserted in a tubercle (adapted from Sepúlveda et. al. 2013b).

New records: BRAZIL – **Maranhão**: 1 ♀, C.[=Centro] N.[Novo] Maranhão, Reserva Biológica Gurupi (REBIO), 03°14′01″S, 46°40′52″W, 01-06.iii.2011, F. Limeira-de-Oliveira, E. A. S. Barbosa & F. Limeira-de-Oliveira; same locality: 1 ♀, 02-11.ix.2010, F. Limeira-de-Oliveira, E. A. S. Barbosa & M. M. Abreu; 1 ♀, 05-15.vi.2010, F. Limeira-de-Oliveira & J. C. Silva; 1 ♂ and 3 ♀♀, 05-15.vi.2010, F. Limeira-de-Oliveira, J. C. Silva & D. W. A. Marques.

***Glyphidops durus* (Cresson, 1926)**

Figures 1C, 1D and 3D

Diagnosis. Fronto-orbital setae increasing in size posteriorly, two anterior pairs closer than posterior pair; first flagellomere oblong with arista apical; posterior notopleural seta inserted on a small tubercle; scutum dorsally with two white pruinose stripes, separated by wide median brown stripe that widens and fades after transverse suture; katatergite brown; tibia yellow with median pale brown ring; halter yellow. (Sepúlveda et al. 2014).

New records: BRAZIL – **Maranhão**: 34 ♂♂ and 57 ♀♀, Bom Jardim, Reserva Biológica Gurupi (REBIO) [-3.557624, -45.613928], 17-27.i.2010, F. Limeira-de-Oliveira, J. T. Câmara & M. B. Aguiar Neto; same locality: 9 ♂♂ and 24 ♀♀, 05-15.vi.2010, F. Limeira-de-Oliveira, J. C. Silva & D. W. Marques; 1 ♂, 05-15.vi.2010, F. Limeira-de-Oliveira & J. C. Silva; 9 ♂♂ and 17 ♀♀, 12.ix-30.x.2010, F. Limeira-de-Oliveira & E. A. S. Barbosa; 3 ♂♂ and 11 ♀♀, 02-11.ix.2010, F. Limeira-de-Oliveira, E. A. S. Barbosa & M. M. Abreu; 3 ♀♀, 01-06.ix.2010, F. Limeira-de-Oliveira & E. A. S. Barbosa; 1 ♂, 07-15.i.2011, F. Limeira-de-Oliveira & D. W. A. Marques; 1 ♀, C.[=Centro] N.[Novo] Maranhão, Reserva Biológica Gurupi (REBIO), 03°14′05″S, 46°41′83″W, 07-15.xi.2011, F. Limeira-de-Oliveira & E. A. S. Barbosa; same locality: 2 ♂♂ and 1 ♀, 01-06.iii.2011, E. A. S. Barbosa & F. Limeira-de-Oliveira; 2 ♀♀, 03-07.v.2011, E. A. S. Barbosa & F. Limeira-de-Oliveira.

***Glyphidops filosus* (Fabricius, 1805)**

Figures 1E, 1F and 3E

Diagnosis. Frontal vitta yellow with ovate black spot well delimited by color on posterior third and covering the ocellar triangle. First flagellomere lanceolate with arista apical; scutum with two white pruinose stripes dorsally, separated by one wide median brown stripe that narrows after transverse suture; supra-alar seta absent (Sepúlveda et al. 2014).

New records: BRAZIL – **Ceará:** 10 ♂♂ and 15 ♀♀, Ubajara, Parque Nac.[=Nacional] de Ubajara, Cachoeira do Cafundó, 03°50′13″S, 40°54′35″W, 21-24.iv.2012, J. A. Rafael & F. Limeira-de-Oliveira; same locality: 2 ♂ and 2 ♀, 22-24.iv.2012, O. H. H. Milke & M. M. Casagrande. **Maranhão:** 2 ♀♀, Bom Jardim, Reserva Biológica Gurupi (REBIO) [-3.557624, -45.613928], 01-06.xi.2010, M. M. Abreu, E. A. S. Barbosa & J. A. Silva; same locality: 1 ♂ and 23 ♀♀, 01-06.xi.2010, F. Limeira-de-Oliveira & E. A. S. Barbosa; 1 ♂ and 5 ♀♀, 01-06.xi.2010, M. M. Abreu, E. A. S. Barbosa & J. A. Silva; 26 ♂♂ and 41 ♀♀, 17-27.i.2010, F. Limeira-de-Oliveira, J. T. Câmara & M. B. Aguiar Neto; 3 ♂♂ and 3 ♀♀, 05-15.vi.2010, F. Limeira-de-Oliveira, J. C. Silva & D. W. A. Marques; 1 ♂, 05-15.vi.2010, F. Limeira-de-Oliveira & J. C. Silva; 1 ♂, 05-16.i.2010, F. Limeira-de-Oliveira, J. C. Silva & D. W. A. Marques; 1 ♀, 02-11.xi.2010, F. Limeira-de-Oliveira, E. A. S. Barbosa & M. M. Abreu; 1 ♂, 02-11.xi.2010, F. Limeira-de-Oliveira, J. C. Silva & D. W. A. Marques; 1 ♀, 12.ix-31.x.2010, F. Limeira-de-Oliveira & E. A. S. Barbosa; 1 ♀, 05-15.vi.2010, J. C. Silva, J. A. Silva, A. A. Santos & T. T. A. Silva; 1 ♂, 03°14′01″S, 46°40′52″W, 01-05.vii.2011, F. Limeira-de-Oliveira & R. M. P. Campos; 1 ♂, 07-15.i.2011, F. Limeira-de-Oliveira & D. W. A. Marques; 1 ♀, 07-15.i.2011, F. Limeira-de-Oliveira & M. M. Abreu; 13 ♂♂ and 14 ♀♀, C.[=Centro] N.[Novo] Maranhão, Reserva Biológica Gurupi (REBIO), 03°14′05″S, 46°41′83″W, 03-07.v.2011, E. A. S. Barbosa & F. Limeira-de-Oliveira; same locality: 7 ♂ and 6 ♀, 01-06.iii.2011, E. A. S. Barbosa & F. Limeira-de-Oliveira; 2 ♀, 07-15.xi.2010, F. Limeira-de-Oliveira & E. A. S. Barbosa; 1 ♂ and 4 ♀♀, 03°14′01″S, 46°40′52″W, 03-07.v.2011, E. A. S. Barbosa & F. Limeira-de-Oliveira; 1 ♂, 01-06.iii.2011, E. A. S. Barbosa & F. Limeira-de-Oliveira; 1 ♀, Carolina, Parq.[=Parque] Nac.[=Nacional] Chapada das Mesas, Riacho Cancela, 225m, 20-30.ix.2013, J. A. Rafael & F. Limeira-de-Oliveira. **Piauí:** 1 ♀, Piracuruca, P.[=Parque] N.[=Nacional] de Sete Cidades, Posto ICMBio, 17-19.vii.2012, 04°05′57″S, 41°42′34″W, J. S. Pinto Júnior & J. A. Rafael.

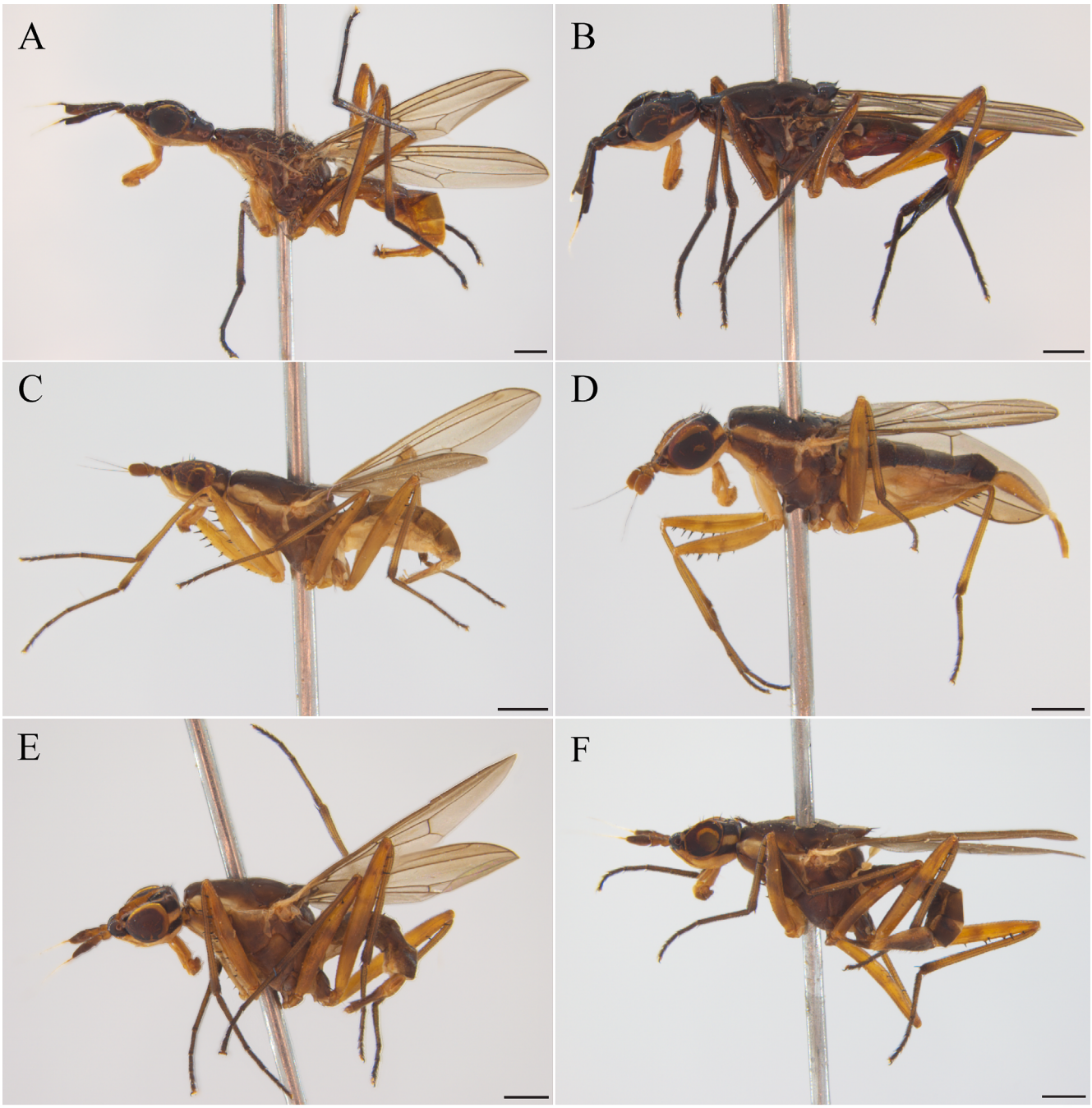


Figure 1. Habitus in lateral view. *Cerantichir peruana* (Hennig, 1937), male (A) and female (B). *Glyphidops durus* (Cresson, 1926), male (C) and female (D). *Glyphidops filosus* (Fabricius, 1805), male (E) and female (F). Scale bars = 1 mm.

***Glyphidops flavifrons* (Bigot, 1886)**

Figures 2A, 2B and 3F

Diagnosis. Frontal vitta yellow; first flagellomere oblong with arista apical; ocellar triangle blackish-brown, contrasting by color with the yellow frontal vitta; scutum dorsally with two white pruinose stripes, separated by one wide median brown stripe that narrows after transverse suture; pleuron variable in color, from pale brown to entirely yellow; katatergite yellow (Sepúlveda et al. 2014).

New records: BRAZIL – **Maranhão:** 7 ♂♂ and 15 ♀♀, Bom Jardim, Reserva Biológica Gurupi (REBIO) [-3.557624, -45.613928], 05-15.vi.2010, F. Limeira-de-Oliveira, J. C. Silva & D. W. A. Marques; same locality: 5♂♂ and 12 ♀♀, 17-27.i.2010, F. Limeira-de-Oliveira, J. T. Câmara & M. B. Aguiar Neto; 1♂ and 1♀, 12.ix-31.x.2010, F. Limeira-de-Oliveira & E. A. S. Barbosa; 1♀, 05-06.xi.2010, F. Limeira-de-Oliveira & E. A. S. Barbosa; 3 ♂♂ and 7 ♀♀, 02-11.xi.2010, F. Limeira-de-Oliveira, E. A. S. Barbosa & M. M. Abreu; 1 ♂, C.[=Centro]

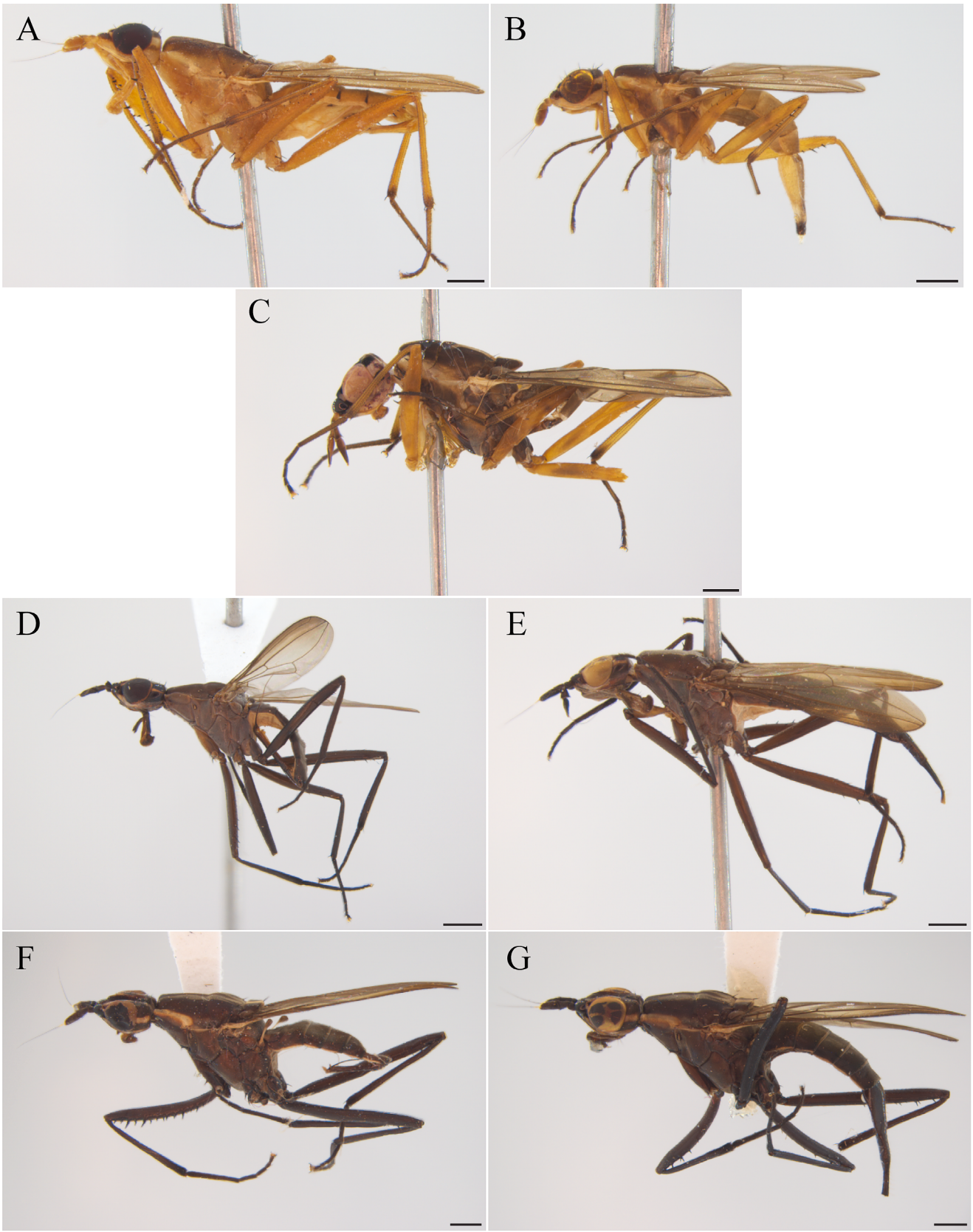


Figure 2. Habitus in lateral view. *Glyphidops flavifrons* (Bigot, 1886), male (A) and female (B). *Glyphidops vittatus* (Cresson, 1912), male (C). *Nerius pilifer* Fabricius, 1805, male (D) and female (E). *Nerius plurivittatus* Bigot, 1886, male (F) and female (G). Scale bars = 1 mm.

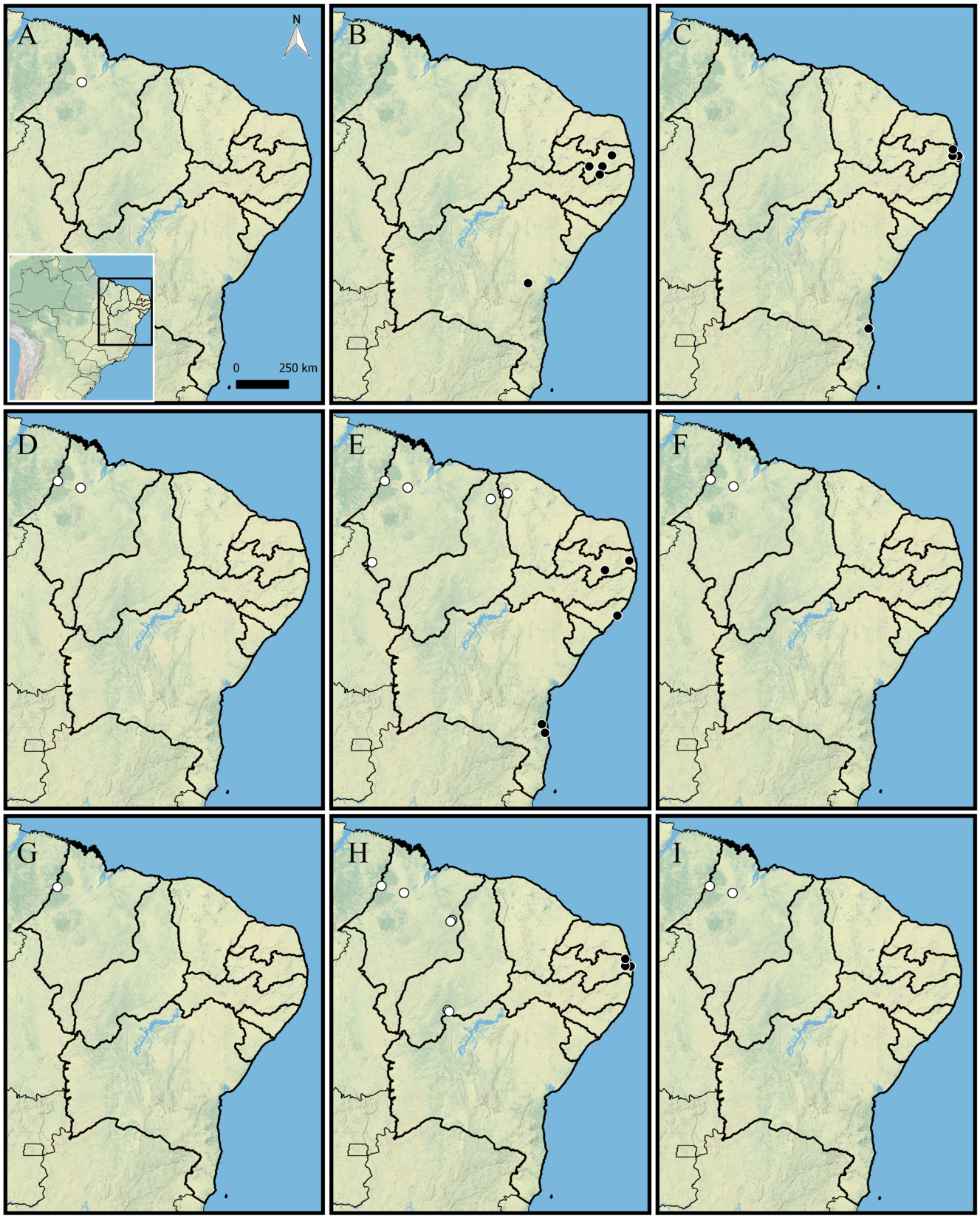


Figure 3. Distribution records of Neriidae in the Brazilian Northeast Region. *Cerantichir peruana* (Hennig, 1937) (A); *Eoneria blanchardi* Aczél, 1951 (B); *Glyphidops carrerai* Aczél, 1961 (C); *Glyphidops durus* (Cresson, 1926) (D); *Glyphidops filosus* (Fabricius, 1805) (E); *Glyphidops flavifrons* (Bigot, 1886) (F); *Glyphidops vittatus* (Cresson, 1912) (G); *Nerius pilifer* Fabricius, 1805 (H); *Nerius plurivittatus* Bigot, 1886 (I). White circle (new records); black circle (records from literature).

N.[=Novo] Maranhão, Reserva Biológica Gurupi (REBIO), 03°14′05″S, 46°41′83″W, 01-06.iii.2011, E. A. S. Barbosa & F. Limeira-de-Oliveira.

***Glyphidops vittatus* (Cresson, 1912)**

Figure 2C and 3G

Diagnosis. Head not elongate in lateral view; first flagellomere lanceolate with arista apical; frontal vitta yellow with two narrow black spots laterally near anterior margin and one triangular blackish-brown spot posteriorly, in front of the ocellar triangle; fronto-orbital plate shiny black; antennal base inflated, with lateral and distal margins rounded in dorsal view; scutum dorsally with two white pruinose stripes, separated by one narrow median brown stripe that narrows and fades after transverse suture; supra-alar seta present (Sepúlveda et al. 2014).

New records: BRAZIL – **Maranhão:** 3 ♂♂, C.[=Centro] N.[=Novo] Maranhão, Reserva Biológica Gurupi (REBIO), 03°14′01″S, 46°40′52″W, 01-06.iii.2011, E. A. S. Barbosa & F. Limeira-de-Oliveira.

***Nerius pilifer* Fabricius, 1805**

Figures 2D, 2E and 3H

Diagnosis. Scape and pedicel brown, antennal base shiny and dark brown; frontal vitta red-ferruginous, with one central brown band from the middle to posterior region; occiput shiny; thorax brown with pale pruinescence; thorax in dorsal view with one wide grayish stripe, separated by a median brown stripe very thin; anterior notopleural seta reduced; basicosta with one small seta; one dorsocentral seta; legs dark brown; fore femur with outstanding anteroventral row of spines (Aczél 1951).

New records: BRAZIL – **Maranhão:** 5 ♀♀, Bom Jardim, Reserva Biológica Gurupi (REBIO) [-3.557624, -45.613928], 05-15.vi.2010, F. Limeira-de-Oliveira, J. C. Silva & D. W. A. Marques; same locality: 1 ♀, 13-27.i.2010, F. Limeira-de-Oliveira, J. T. Câmara & M. B. Aguiar Neto; 1 ♀, 12.ix-31.x.2010, F. Limeira-de-Oliveira & E. A. S. Barbosa; 1 ♂ and 1 ♀, 17-27.i.2010, F. Limeira-de-Oliveira & M. B. Aguilar Neto; 2 ♀♀, 02-11.ix.2010, F. Limeira-de-Oliveira, E. A. S. Barbosa & M. M. Abreu; 5 ♂♂ and 29 ♀♀, C.[=Centro] N.[=Novo] Maranhão, Reserva Biológica Gurupi (REBIO), 03°14′05″S, 46°41′83″W, 03-07.v.2011, E. A. S. Barbosa & F. Limeira-de-Oliveira; same locality: 1 ♂ and 2 ♀♀, 01-06.iii.2011, E. A. S. Barbosa & F. Limeira-de-Oliveira; 1 ♂, 03°14′01″S, 46°40′52″W, 03-07.v.2011, E. A. S. Barbosa & F. Limeira-de-Oliveira; 5 ♂♂ and 6 ♀♀, Caxias, 04°52′43″S, 43°19′31″W, 01-15.viii.2017, F. Limeira-de-Oliveira & D. Limeira; same locality: 6 ♂♂ and 15 ♀♀, 23-31.vii.2017, F. Limeira-de-Oliveira & D. Limeira; 1 ♀, Caxias, 04°51′19″S, 43°20′33″W, 01-15.viii.2017, D. Limeira & D. P. Silva; 1 ♀, Caxias, 04°52′11″S, 43°20′48″W, 15-31.vii.2017; 2 ♀♀, Caxias, 04°54′43″S, 43°25′30″W, Caxias, Reserva Inhamum, 01.viii.2011, J. T. Câmara, T. M. S. Coutinho. **Piauí:** 1 ♀, Caracol, Parq.[=Parque] Nac.[=Nacional] Serra das Confusões, 09°13′11.9″S, 43°29′26.2″W, 575m, 15-31.vii.2013, J. A. Rafael, F. Limeira-de-Oliveira & T. T. A. Silva; same locality: 1 ♂ and 3 ♀♀, 20-31.iii.2014, J. A. Rafael, F. Limeira-de-Oliveira, T. L. Rocha & G. A. Reis; 2 ♂♂, Guaribas, Parque Nacional Serra das Confusões, 09°08′27.8″S, 43°33′42.1″W, 515m, 10-20.ix.2014, J. A. Rafael, T. L. Rocha & G. A. Reis; 1 ♂, Caracol, Parq.[=Parque] Nac.[=Nacional] Serra das Confusões, 09°12′48.9″S, 43°27′59.9″W, 705m, 01-10.ix.2014, J. A. Rafael, F. Limeira-de-Oliveira, T. L. Rocha & G. A. Reis.

***Nerius plurivittatus* Bigot, 1886**

Figures 2F, 2G and 3I

Diagnosis. Antennal base shiny; distal margin slightly concave in dorsal view; occiput opaque with one median yellow stripe; thorax in dorsal view with one wide grayish medially divided by one median brown stripe and by intra-alar stripe in postsutural scutum; fronto-orbital plate slightly pruinose, with anterior half yellow and posterior half brown.

New records: BRAZIL – **Maranhão:** 1 ♂, C.[Centro] N.[Novo] Maranhão, Reserva Biológica Gurupi (REBIO), 03°14′05″S, 46°41′83″W, 01-06.iii.2011, E. A. S. Barbosa & F. Limeira-de-Oliveira; 1 ♂, Bom Jardim, Reserva Biológica Gurupi (REBIO) [-3.527534, -46.680510], 12.ix-31.x.2010, F. Limeira-de-Oliveira & E. A. S. Barbosa; same locality: 1 ♂, 02-11.ix.2010, F. Limeira-de-Oliveira, E. A. S. Barbosa & M. M. Abreu; 1 ♀, 02-11.ix.2010, F. Limeira-de-Oliveira & J. C. Silva.

Discussion

In the revision of the *Glyphidops*, Sepúlveda et al. (2014) revalidated *G. vittatus* from synonymy with *G. filosus*, based on a variety of characters present in *G. vittatus* and absent in *G. filosus*. These characters include the antennal base inflated with rounded margins, head not elongate in lateral view and supra-alar seta present. We have found that *G. filosus* also bears a very well-defined ovate black spot surrounding the ocellar triangle, which is absent in *G. vittatus*, making both species easily distinguishable. Braga et al. (2017) followed the classification of *Glyphidops* as used by Koch et al. (2015), which considers *G. vittatus* as a junior synonym of *G. filosus*. However, Braga et al. (2017) noticed the presence of an ovate black spot covering the ocellar triangle and the lack of supra-alar seta in the material they determined as *G. filosus*. Here, as we follow the classification proposed by Sepúlveda et al. (2014), the characters cited by Braga et al. (2017) for *G. filosus*, allowed us to confirm that the specimens studied by the authors are not *G. vittatus*. Thus, although Braga et al. (2017) cited new records for *G. filosus* considering it as senior synonym of *G. vittatus*, we can say with confidence that the localities recorded by these authors correspond to *G. filosus sensu* Sepúlveda et al. (2014).

Carvalho-Filho & Esposito (2008) presented a key for the identification of Neriidae from the Brazilian Amazon with 10 species recorded for this area, one of which, *G. flavipes* (Wiedemann), is considered a *species inquirendum* (Steyskal, 1968) and one other species, *N. dispar* Cresson, has been proposed as a junior synonym of *G. durus* (Sepúlveda et al. 2014). In a subsequent publication, Sepúlveda et al. (2014), recorded *G. vittatus* and *G. steyskali* Sepúlveda, Wolff & de Carvalho for the Brazilian Amazon, restoring the number of species of Neriidae known from the Brazilian Amazon to 10. Of these species recorded for the Brazilian Amazon, we did not find *G. steyskali* nor *G. limbatus*, but all the other species in this region are also present in the Northeast and presented in Table 1, revealing a mostly homogenous distribution of species of Neriidae within the northern part of the country.

This survey updated the distributional knowledge of the Neriidae from the Brazilian Northeast (Figure 3). It adds a substantial number of records to the area, totalizing 10 new records to the states of Ceará (1 new record), Maranhão (7 new records) and Piauí (2 new records).

Also, the records of *G. filosus* in Ceará and Piauí, and *N. pilifer* in Piauí are the first records of these species in the Brazilian Semiarid. Before our survey, *E. blanchardi* was the only record of Neriidae in the semiarid area, in the Bahia, Paraíba and Pernambuco states (Braga et al. 2017). Our faunistic survey enables a range of possibilities for further studies, mainly in ecology and biogeography of the Brazilian Northeast and its biomes.

Author Contributions

Tatiana A. Sepúlveda, prepared the manuscript and participated in data collection;

Lucas R. P. Gomes, made a substantial contribution to the concept and design of the study and participated in data collection;

Francisco Limeira-de-Oliveira, made a substantial contribution to the concept and design of the study and participated in data collection;

All authors contributed with data analysis and interpretation, made critical revision and added intellectual content.

Conflict of interest

The authors declare that they have no conflicts of interest related to the publication of this manuscript.

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Article

Rediscovering a forgotten scientific collection in the Rio Grande do Norte State, Brazil: The herpetological collection of the zoologist José Santiago Lima-Verde

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Abstract: The zoologist Dr. José Santiago Lima-Verde (1945-2019) made a number of major contributions to the field of animal biology in the northeastern Brazil, in particular through his research with snakes. While employed as a professor at Escola Superior de Agricultura de Mossoró, currently the Universidade Federal Rural do Semi-Árido, Prof. Lima-Verde established a herpetological collection which remained forgotten for a number of decades. In the present study, we describe the revitalization of this collection, which included the updating of the identification of the species and the compilation of the metadata on the collection, which is now named the Coleção Herpetológica Lima-Verde. We catalogued 80 specimens representing 30 species, including 23 species of snakes, five lizards, and two amphisbaenians. One third (30%) of the specimens had information on dates and sites, with the majority of these specimens being collected in the Brazilian State of Rio Grande do Norte during the 1970's. We also catalogued 315 eggs of seven snake species, from 22 clutches laid in captivity. The collection presents unpublished data and will constitute a reference for future herpetological research on the species found in western region of State of Rio Grande do Norte. Our findings reinforce the importance of zoological collections for the understanding of patterns of biodiversity, and we would recommend the creation of more regional scientific collections and the broader recognition of their value as a basic source of biological data.
Keywords: *Biodiversity, Caatinga, Northeastern Brazil, Scientific Collections, Semiarid.*

Redescobrindo uma coleção científica esquecida no Estado do Rio Grande do Norte, Brasil: A coleção herpetológica do zoólogo José Santiago Lima-Verde

Resumo: O zoólogo Dr. José Santiago Lima-Verde (1945-2019) fez uma série de importantes contribuições para o campo da biologia animal no nordeste do Brasil, em particular através de sua pesquisa com serpentes. Enquanto professor da Escola Superior de Agricultura de Mossoró, atualmente Universidade Federal Rural do Semi-Árido, o Prof. Lima-Verde estabeleceu uma coleção herpetológica que permaneceu esquecida por várias décadas. No presente estudo, descrevemos a revitalização dessa coleção, que incluiu a atualização da identificação das espécies e a compilação dos metadados da coleção, que agora é denominada Coleção Herpetológica Lima-Verde. Nós catalogamos 80 espécimes representando 30 espécies, incluindo 23 espécies de serpentes, cinco lagartos e duas anfisbenas. Um terço (30%) dos exemplares possuíam informações sobre datas e locais de coleta, sendo a maioria desses espécimes coletados no Estado do Rio Grande do Norte durante a década de 1970. Também catalogamos 315 ovos de sete espécies de serpentes, provenientes de 22 ninhadas obtidas em cativeiro. A coleção apresenta dados inéditos e constituirá uma referência para futuras pesquisas herpetológicas sobre as espécies encontradas na região oeste do Estado do Rio Grande do Norte. Nossos achados reforçam a importância das coleções zoológicas para a compreensão dos padrões de biodiversidade, e nós recomendamos a criação de mais coleções científicas regionais e o reconhecimento mais amplo de seu valor como fonte básica de dados biológicos.
Palavras-chave: *Biodiversidade, Caatinga, Nordeste do Brasil, Coleções Científicas, Semiárido.*

Introduction

Zoological collections provide a wealth of information on wild animals, ranging from specimens (complete or partial) to samples of tissues, photographs, and recordings of vocalizations (Franco 2002, Vivo et al. 2014). These collections support the continuous and systematic accumulation of biological data, which provide important insights into the present and past configuration of a region's fauna (Marinoni & Peixoto 2010, Zaher & Young 2003). Given their historical context and wealth of information, zoological collections constitute one of the principal sources of data for a range of research fields, including taxonomy, ecology, and biogeography.

The zoologist Dr. José Santiago Lima-Verde (1945-2019) was one of the principal scientists responsible for the late advances in herpetological research in the Northeast region of Brazil in the second half of the 20th Century (Fernandes-Ferreira et al. 2014). His legacy includes the first records of a number of Amazonian reptiles in the semi-arid Caatinga domain, such as the *Imantodes cenchoa* (Linnaeus, 1758) and *Mastigodryas boddaerti* (Sentzen, 1796) (Nascimento & Lima-Verde, 1989), as well as descriptions of new species, including the lizard, *Colobosauroides cearensis* Cunha, Lima-Verde & Lima, 1991, and the caecilian, *Chthonerpeton arii* Cascon & Lima-Verde, 1994. Some of Dr. Lima-Verde's most important contributions on the reptilian fauna of the Caatinga of Rio Grande do Norte were the study "Fisioecologia e etologia de algumas serpentes da Chapada do Apodi" (Lima-Verde 1976), in which he described the ecology and behavior of 20 species, and the description of the snake *Erythrolamprus mossoroensis* (Hoge & Lima-Verde, 1972), whose type-locality is the municipality of Mossoró (Hoge & Lima-Verde 1972).

As a professor at Escola Superior de Agricultura de Mossoró (ESAM), currently the Universidade Federal Rural do Semi-Árido (UFERSA), Dr. Lima-Verde collected a number of reptile specimens during his research activities, creating a personal herpetological collection. Years later, after being transferred to the Universidade Federal do Ceará (UFC), Dr. Lima-Verde founded this institution's herpetological collection using specimens from his personal collection (Fernandes-Ferreira et al. 2014). However, part of this personal collection remained at the ESAM, where it was, forgotten, for a number of decades. Given the importance of zoological collections for the understanding of patterns of biodiversity, and the scientific legacy of Dr. Lima-Verde, in the present study, we *i.* revitalized the remaining material of his particular collection; *ii.* updated the identification of the specimens, and *iii*. made the collection available for future herpetological research.

Material and Methods

1. Revitalization of the collection

We retrieved the specimens collected by Dr. Lima-Verde, which had been left in the annex of the Laboratório Didático de Zoologia from the UFERSA, and transferred them to the Laboratório de Ecologia e Comportamento Animal (LECA). The material was poorly preserved, with many containers being damaged or inadequately sealed. Some specimens were exposed (not immersed properly), while others were in alcohol at concentrations of below 70%. We replaced the containers of the specimens that could be recuperated, and renewed the preserving fluid. We discarded the specimens that had decomposed due to inadequate storage conditions, and obtained a photographic record of all the revitalized specimens.

2. Taxonomic update

We identified all the specimens recovered from the Laboratório Didático de Zoologia to the lowest possible taxonomic level, using sources on the target taxa (Peters & Orejas-Miranda 1970, Campbell & Lamar 2004, Passos & Fernandes 2008, Pyron et al. 2013, Bernarde 2014). We made an individually-numbered plastic label for each of the specimens recuperated, but we also took care to maintain the original, handwritten labels still attached to the specimens. We deposited all the material that had information on the collecting locality and date in the scientific collection Coleção Herpetológica do Semiárido (CHSA).

Results

We recuperated 80 specimens and 315 eggs (Figure 1). This set of biological specimens now constitutes the Coleção Herpetológica Lima-Verde - CHLV. The specimens we recuperated belong to 30 species, including 23 snakes (N = 56 specimens), five lizards (N = 21), and two amphisbaenians (N = 3). *Erythrolamprus poecilogyrus* (N = 11 specimens), *Ameivula ocellifera* (N = 9), and *Amphisbaena vermicularis* (N = 2) were the most abundant species of snakes, lizards, and amphisbaenians, respectively (Table 1).

Overall, 19 (24%) of the 80 specimens we recuperated were labeled with information on the locality and 24 (30%) with the collection date. These specimens were collected between 1970 and 1994 (Figure 2), although the majority (58%; N = 14) were obtained in the 1970's. The vast majority (74%; N = 14) of the specimens from known localities were collected in the municipality of Mossoró (Figure 3). With the exception of the four *Bothrops* species (17% of the total), all the taxa occur in the Caatinga biome.

The 315 snake eggs we recuperated during the study were derived from clutches obtained in captivity between June and November, 1971 (Figure 1a). Based on the labels, 275 of these eggs were produced by seven different snake species (Table 2), although 40 eggs from six clutches were unlabeled. While *Lygophis dilepis* had the largest number of eggs (N = 150), *Philodryas nattereri* was represented by the largest number of clutches (N = 7).

Discussion

The specimens deposited in the Coleção Herpetológica Lima-Verde were collected predominantly in the Rio Grande do Norte. This is related to the fact that Dr. José Santiago Lima-Verde conducted extensive research in the region of the Apodi Plateau, which lies on the border between the states of Ceará and Rio Grande do Norte (Lima-Verde 1976, Fernandes-Ferreira et al. 2014). Most of the species in the collection present wide geographic distribution, and are found in more than one South American morphoclimatic domain, including the Caatinga (Cavalcanti et al. 2014, Caldas et al. 2016). The exceptions are *Epicrates assisi*, *Epictia borapeliotes*, and *Erythrolamprus mossoroensis* which are endemic to the Caatinga (Hoge & Lima-Verde 1972, Guedes et al. 2014), and the four pitvipers (*Bothrops brazili*, *B. jararacussu*, *B. fonsecai*, and *B. neuwiedi*), which may have been acquired by Dr.

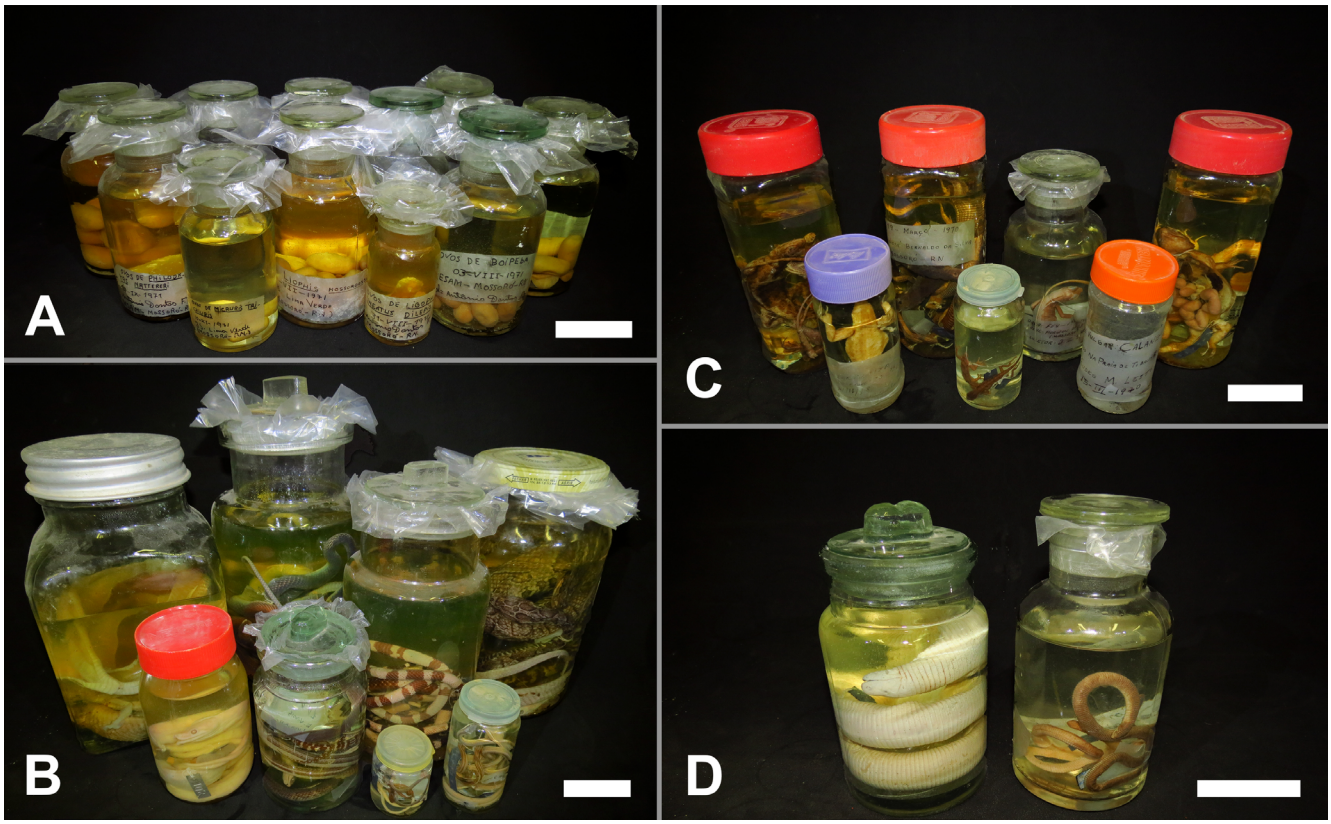


Figure 1. Sample of eggs (A), snakes (B), lizards (C), and amphisbaenians (D) of the Coleção Herpetológica Lima-Verde (CHLV). Scale bars = 5 cm.

Lima-Verde through scientific partnerships with the Instituto Butantan in São Paulo (e.g. Hoge & Lima-Verde 1972) and the Museu Paraense Emílio Goeldi in Belém (e.g. Cunha et al. 1991).

Most (70%) of the specimens deposited in the Coleção Herpetológica Lima-Verde are snakes, reflecting the research interests of Dr. Lima-Verde (Hoge & Lima-Verde 1972, Lima-Verde 1976, Nascimento & Lima-Verde 1989). The most numerous species in the collection (*Erythrolamprus poecilogyrus* and *Ameivula ocellifera*) are known to be common in the Depressão Sertaneja Setentrional ecoregion (Mesquita et al. 2013, Passos et al. 2016). Three specimens (two snakes and one lizard) could not be identified due to their advanced decomposition, and a further three snake specimens could only be identified to genus. Despite this lack of identification, we can speculate on the taxonomic status of these last three specimens. The *Thamnodynastes* specimen was identified by Lima-Verde (1976) as *Thamnodynastes nattereri*, although, in fact, it seems likely be the recently described *Thamnodynastes phoenix* Franco, Trevine, Montingelli & Zaher, 2017, whose name refers to the fact that the type series was rescued from the fire that destroyed the herpetological collection of the Instituto Butantan in 2010 (Franco et al. 2017). The *Micrurus* specimen may represent a species from the Caatinga domain that has yet to be described formally, but is normally identified as *Micrurus ibiboboca* (Merrem, 1820) (Argôlo 2004, Guedes et al. 2014). The *Xenodon* specimen, which was dissected and is badly damaged, appears to be *Xenodon merremii* (Wagler *in* Spix, 1824), the only species of this genus found in the northern portion of the Caatinga domain (Costa & Bérnils 2018).

During the time he spent in Mossoró, Dr. Lima-Verde conducted a number of behavioral studies of captive snakes. These snakes were cared for by the ESAM's laboratory assistant, Mr. Antônio Dantas Feitoza, who stored the clutches produced by the snakes in separate containers labeled with information on the species, origin, and date of oviposition. This systematic record contributed to the recuperation of the 315 snake eggs listed here (Table 2), which constituted probably part of the reproductive data presented by Lima-Verde (1976) in his study on the snakes of the Apodi Plateau. Despite this, no data have ever been published on the size of the eggs or clutches in these species. In this context, the data on *Lygophis dilepis* and *Philodryas nattereri* are especially interesting, given that the reproductive parameters of these species are known only from a few Caatinga populations (Vitt 1980, 1983, Mesquita et al. 2011, Passos et al., 2014). The two clutches recorded here for *Erythrolamprus mossoroensis* are also extremely important, given that the biology of this Caatinga endemic species is still virtually unknown. We have now made these data available for future research on the snake species of the Caatinga region.

The rediscovery of the Coleção Herpetológica Lima-Verde has not only permitted the recuperation of one of Dr. Lima-Verde's most important contributions to the zoology of northeastern Brazil, but also represents a valuable scientific legacy, which provides important insights into research conducted almost half a century ago. The revitalization of this collection has also expanded our historical knowledge on the herpetofauna of the semi-arid region of Rio Grande do Norte, given that the collection provides novel data on the biology of a number of

Table 1. Number of specimens recuperated of each reptile species deposited in the Coleção Herpetológica Lima-Verde (CHLV). The species are ranked by the number of specimens, in decreasing order. The specimens for which information on the collecting locality and date is available were deposited in the Coleção Herpetológica do Semiárido (CHSA), with the respective catalogue number being shown within parentheses.

TAXON	NUMBER OF SPECIMENS	CATALOG NUMBER CHLV (CHSAR)
Snakes		
Erythrolamprus poecilogyrus (Wied, 1824)	11	CHLV 12 (CHSAR 387), CHLV 13 (CHSAR 388), CHLV 16 (CHSAR 391), CHLV 34, CHLV 35, CHLV 36, CHLV 37, CHLV 38, CHLV 39, CHLV 56, CHLV 57
Pseudoboa nigra (Duméril, Bibron and Duméril, 1854)	7	CHLV 14 (CHSAR 389), CHLV 22, CHLV 27, CHLV 45, CHLV 46, CHLV 54, CHLV 74
Lygophis dilepis (Cope, 1862)	5	CHLV 11 (CHSAR 386), CHLV 28, CHLV 29, CHLV 30, CHLV 31
Erythrolamprus viridis (Günther, 1862)	4	CHLV 18 (CHSAR 393), CHLV 47, CHLV 50, CHLV 24
Oxyrhopus trigeminus Duméril, Bibron and Duméril, 1854	3	CHLV 25, CHLV 26, CHLV 61
Erythrolamprus mossoroensis (Hoge and Lima-Verde, 1973)	2	CHLV 49, CHLV 55
Epictia borapeliotes (Vanzolini, 1996)	2	CHLV 51, CHLV 52
Micrurus ibiboboca (Merrem, 1820)	2	CHLV 41, CHLV 42
Philodryas olfersii (Lichtenstein, 1823)	2	CHLV 43, CHLV 44
Psomophis joberti (Sauvage, 1884)	2	CHLV 58, CHLV 59
Xenodon merremii (Wagler in Spix, 1824)	2	CHLV 40, CHLV 60
Apostolepis cearensis Gomes, 1915	1	CHLV 53
Boa constrictor Linnaeus, 1758	1	CHLV 62
Bothrops brazili Hoge, 1954	1	CHLV 33
Bothrops fonsecai Hoge and Belluomini, 1959	1	CHLV 77
Bothrops jararacussu Lacerda, 1884	1	CHLV 32
Bothrops neuwiedi Wagler in Spix, 1824	1	CHLV 78
Crotalus durissus Wagler in Spix, 1824	1	CHLV 80
Epicrates assisi Machado, 1945	1	CHLV 24 (CHSAR 426)
Micrurus sp.	1	CHLV 48
Oxybelis aeneus (Wagler in Spix, 1824)	1	CHLV 15 (CHSAR 390)
Thamnodynastes sp.	1	CHLV 17 (CHSAR 392)
Xenodon sp.	1	CHLV 79
Not identified	2	CHLV 75, CHLV 76
Lizards		
Ameivula ocellifera (Spix, 1825)	9	CHLV 2 (CHSAR 377), CHLV 3 (CHSAR 378), CHLV 4 (CHSAR 379), CHLV 5 (CHSAR 380), CHLV 6 (CHSAR 381), CHLV 7 (CHSAR 382), CHLV 8 (CHSAR 383), CHLV 20, CHLV 21, CHLV 68
Tropidurus hispidus (Spix, 1825)	8	CHLV 9 (CHSAR 384), CHLV 10 (CHSAR 385), CHLV 19, CHLV 63, CHLV 64, CHLV 65, CHLV 66, CHLV 67
Hemidactylus mabouia (Moreau de Jonnès, 1818)	1	CHLV 69
Iguana iguana (Linnaeus, 1758)	1	CHLV 1 (CHSAR 375)
Polychrus marmoratus (Linnaeus, 1758)	1	CHLV 70
Not identified	1	CHLV 71
Amphisbaenians		
Amphisbaena vermicularis Wagler in Spix, 1824	2	CHLV 23, CHLV 72
Amphisbaena alba Linnaeus, 1758	1	CHLV 73

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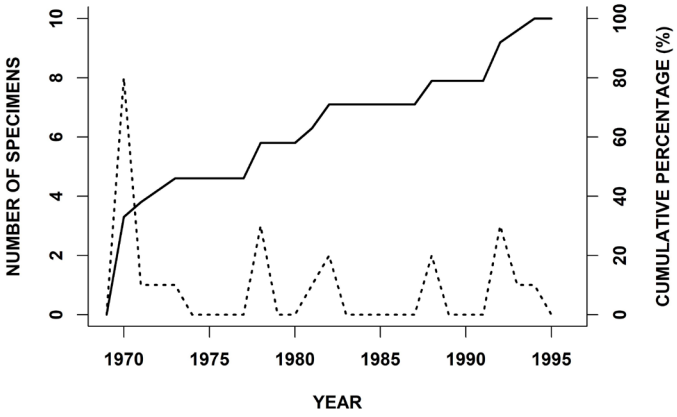


Figure 2. Number of the dated specimens (N = 24) collected per year (dotted line) and the cumulative percentage of dated specimens in the Coleção Herpetológica Lima-Verde between 1970 and 1994.

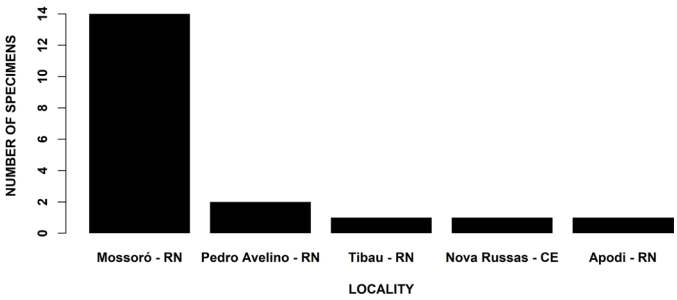


Figure 3. Collecting localities (municipality - state; CE = Ceará, RN = Rio Grande do Norte) of the 19 labeled specimens in the Coleção Herpetológica Lima-Verde, collected between 1970 and 1994.

Table 2. The number of eggs and clutches per snake species recuperated during the present study, now part of the Coleção Herpetológica Lima-Verde (CHLV). The material was collected between June and November, 1971. The species are ranked by the number of eggs, in decreasing order.

Species	Clutches	Eggs
Lygophis dilepis (Cope, 1862)	6	150
Philodryas nattereri Steindachner, 1870	7	56
Erythrolamprus mossoroensis (Hoge & Lima-Verde, 1973)	2	33
Erythrolamprus viridis (Günther, 1862)	4	15
Xenodon merremii (Wagler in Spix, 1824)	1	12
Micrurus sp.	1	5
Pseudoboa nigra (Duméril, Bibron & Duméril, 1854)	1	4
Not identified	6	40

very poorly-known species. Our findings also highlight the importance of regional scientific collections, which may provide valuable insights into the diversity of local faunas, as well as helping to offset the loss of material caused by recent incidents in major collections. The recent losses of collections in the fires at the Instituto Butantan in 2010, and at the Museu Nacional in 2018, were both the result of reduced investment in infrastructure and maintenance. In this context, we would emphasize the need for official incentives for the curatorship and maintenance of scientific collections throughout Brazil, but especially in poorly-studied regions, like the Caatinga, which are highly underrepresented. Long-term support for these collections will be essential to guarantee the understanding of the country's biodiversity by future generations.

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Author Contributions

Alcéster Diego Coelho-Lima: Contribution to data collection, contribution to data analysis and interpretation, contribution to manuscript preparation, contribution to critical revision, adding intelectual content.

Marcelo Almeida de Sousa Jucá: Contribution to data collection, contribution to data analysis and interpretation.

Ellen Beatriz Fontes da Fonseca: Contribution to data collection, contribution to data analysis and interpretation.

Leticia Cely Vieira de Medeiros: Contribution to data collection.

Pamella Barbara Coutinho Soares: Contribution to data collection, contribution to data analysis and interpretation.

Paulo Victor Araujo Cunha: Contribution to data collection.

Daniel Cunha Passos: Substantial contribution in the concept and design of the study, contribution to data collection, contribution to data analysis and interpretation, contribution to manuscript preparation, contribution to critical revision, adding intelectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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The genus *Tryblionella* W. Smith (Bacillariaceae, Bacillariophyta) in southern Brazil salt marshes

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Abstract: *Tryblionella* is a large epipelic genus, widespread from fresh to marine waters. Most of the studies including the genus are based only in light microscopy. Few recent studies are exclusively dedicated to *Tryblionella* and the ultrastructure of some species is still little known. In this paper we present eleven species of *Tryblionella* found in epiphyton and microphytobenthos in Patos Lagoon salt marshes. All the species are described, illustrated in light and scanning electron microscopy and comments about their taxonomy, distribution and ecology are provided. Two taxa are reported for the first time in the State of Rio Grande do Sul and one in Southern Brazil. The number of species registered in this study comprises nearly a half of the number of species registered in the country. The high richness observed may be related to the dynamics of the salt marshes, which provides both the mixing of fresh and marine waters communities and the diversity of microhabitats. The great variability among the species analyzed allowed to extend the general concept of *Tryblionella*, adding features which were not considered in the previous characterizations of the genus.
Keywords: *diatoms, Patos Lagoon, periphyton, taxonomy, ultrastructure.*

O gênero *Tryblionella* W. Smith (Bacillariaceae, Bacillariophyta) em marismas do Sul do Brasil

Resumo: *Tryblionella* é um gênero de diatomáceas epipélicas, distribuído de águas doces a marinhas. A maioria dos estudos que incluem o gênero baseia-se apenas em microscopia óptica. Poucos estudos recentes são exclusivamente dedicados à *Tryblionella* e a ultraestrutura de algumas espécies ainda é pouco conhecida. No presente artigo, apresentamos onze espécies de *Tryblionella* encontradas no epifíton e no microfitobentos nas marismas da Lagoa dos Patos. Todas as espécies foram descritas, ilustradas em microscopia óptica e eletrônica de varredura e comentários sobre a taxonomia, distribuição e ecologia foram fornecidos. Dois táxons foram registrados pela primeira vez para o estado do Rio Grande do Sul e um para a região Sul do Brasil. O número de espécies registradas neste estudo compreende cerca de metade das espécies registradas para o país. A grande riqueza observada pode estar relacionada à dinâmica das marismas, que proporciona tanto a mistura de comunidades de águas doces e marinhas quanto diversidade de microhabitats. A grande variabilidade entre as espécies analisadas permitiu que o conceito geral de *Tryblionella* fosse ampliado, incluindo características que não haviam sido consideradas nas caracterizações anteriores do gênero.
Palavras-chave: *diatomáceas, Lagoa dos Patos, perifíton, taxonomia, ultraestrutura.*

Introduction

Since the genus *Tryblionella* W. Smith was erected, it has undergone some changes both in its circumscription and in its taxonomic position. Smith (1853) described the genus comparing it to *Campylodiscus* Ehrenberg ex Kützing and *Surirella* Turpin. In the following years, many authors pointed out the resemblance between the genus *Tryblionella* and some species of *Nitzschia* Hassall (Grunow 1862, Rabenhorst 1864, Kitton 1873) and, thus, the genus was transferred to a section of *Nitzschia*, due to the absence of sufficiently distinct features to support the generic entity (Grunow 1879, 1880, Cleve & Grunow 1880). The proposition of the section *Tryblionella* did not conclude the discussion about the taxonomic position of these organisms. During more than one century, a few researchers refused to accept the new status and many suggested changes in the sections of *Nitzschia* (joining or splitting them) in order to better classify the specimens formerly included in the genus *Tryblionella* (Mann 1978).

Round et al. (1990) grouped four sections of *Nitzschia* to raise *Tryblionella* back to the generic status, expecting that the upcoming studies would follow this classification, but it was not applied by several researchers (e.g. Witkowski et al. 2000, 2004, Metzeltin et al. 2005). Recently, molecular studies have shown that *Nitzschia sensu lato* is not monophyletic (Lundholm et al. 2002a, b) and that some groups should be considered separated from it, such as *Psammodyction* and *Tryblionella* (Rimet et al. 2011). Phylogenetic studies with larger data sets, including specimens from various sections of *Nitzschia*, which could finally set a course to the end of this discussion, are still unavailable.

It is estimated that *Tryblionella* comprises 134 specific and infraspecific taxa, of which only 75 are taxonomically accepted (Guiry & Guiry 2019). Twenty-three species have been recorded in Brazil, the majority in the southern region (Cavalcante et al. 2013, Eskinazi-Leça et al. 2015, Bertolli et al. 2019). In the State of Rio Grande do Sul there is a higher concentration of studies in the Central Depression freshwaters and a few species have been registered in the Coastal Plain (Torgan et al. 1999, Bes & Torgan 2008). Although the genus is not considered frequent in brackish and marine waters (Round et al. 1990), it has been found among the genera with greater contribution to the surface sediment diatom assemblages of Patos Lagoon salt marshes (Silva et al. 2010) and, recently, two new species were described at the same salt marsh, undergoing salinity variations (Bertolli et al. 2019).

This study aimed to describe the specific taxonomic composition of the genus *Tryblionella* found in epiphyton and microphytobenthos from Patos Lagoon salt marshes. It also aimed to contribute to a better understanding of their taxonomy, ecology and distribution.

Materials and methods

The study was carried out at the salt marshes adjacent to Patos Lagoon estuary, State of Rio Grande do Sul, Brazil (31º50'-32º09'S 52º00'-52º15'W). Three sites with progressive distances from the Atlantic Ocean were established on the estuary outfall: São José do Norte (32º 06' 49.984'' 52º 04' 22.980'', 9 km from the outfall), Ilha da Pólvora (32º 01' 14.424'' 52º 05' 59.095'', 18 km from the outfall) and Saco do Silveira (31º 52' 48.821'' 52º 14' 38.762'', 36 km from the outfall) as shown in Figure 1.

Four species of herbaceous plants represented the prevailing vegetation of the salt marshes: *Sporobolus montevidensis* (Arechavaleta) Peterson & Saarela (= *Spartina densiflora* Brongniart), *Sporobolus alterniflorus* (Loisel.) Peterson & Saarela (= *Spartina alterniflora* Loiseleur-Deslongchamps), *Bolboschoenus maritimus* (L.) Palla (= *Scirpus maritimus* Linnaeus), and *Juncus kraussii* Hochstetter (1845: 342). Stems of these plants and the surface sediment close to them were gathered in winter (September 2010) and summer (February 2011). Abiotic data of the interstitial water were obtained during the sampling: pH (with PHTEK® pH meter), salinity (with YSI® 30 salinometer) and temperature (with Incoterm® thermometer). The surface sediment was collected with a core with 10 cm of diameter and 2 cm of depth. Live and motile cells were removed from the samples in the laboratory, following the 'Trapping method' (Eaton & Moss 1966 adapted by Laudares-Silva & Cimardi 1989). In addition, in the laboratory, the epiphyton was scrapped of the vegetal stems using a metal blade and deonized water.

Samples were oxidized with nitric acid over heat (15 minutes) and distilled water was rinsed until reaching neutral pH. Epiphytic and microphytobenthic cleaned samples were mounted in glass slides using Naphrax® (RI=1.74) for observation under Light Microscope (LM) Zeiss Axioplan. Images were captured with Axiocam ERc 5s both in bright field and in phase contrast. Aliquots of the cleaned samples were dried in aluminum stubs and covered with gold/palladium (16 nm) for observation under Scanning Electron Microscopes (SEM) Jeol JSM-5200 (20 mm working distance, 25 kV) and Jeol 6060 (10 mm working distance, 25 kV). The slides were housed at Herbarium Alarich Schultz, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil.

Taxa identification followed classic and modern literature such as Bailey (1850), Smith (1853), Grunow (1862, 1880), Cleve & Grunow (1880), Van Heurck (1880-1881, 1986), Kützing (1844), Pritchard (1861), Hustedt (1930), Frenguelli (1942), Cholnoky (1961), Peragallo & Peragallo (1897-1908), Krammer & Lange-Bertalot (1988), Hartley (1996), Witkowski et al. (2000), Metzeltin et al. (2005), Cavalcante et al. (2013) and Bertolli et al. (2019). Morphological terminology for the descriptions followed Hendey (1964), Anonymous (1975), Barber & Haworth (1981) and Round et al. (1990). All images were assembled using Corel Designer X6®.

Results

1. Taxonomic composition

A total of eleven species were found. Their descriptions under light and scanning electron microscopy and illustrations are presented as follows.

***Tryblionella acuminata* W. Smith (1853: 36, plate 10, Figure 77)**
Figures 2 A-D; 5 A-C

Light microscopy: Valves linear-lanceolate, slightly constricted in the middle, 42.8-49.5 µm long and 7.8-10.8 µm wide. Apices cuneate to subrostrate slightly produced. Transapical ribs parallel in the middle of the valve to radiate in the extremities, 13-16 in 10 µm, interrupted by a very noticeable longitudinal fold, the axial area may extend for almost one-third of the valvar face. Fibulae weakly distinguishable, regularly distributed and coinciding with the transapical ribs.

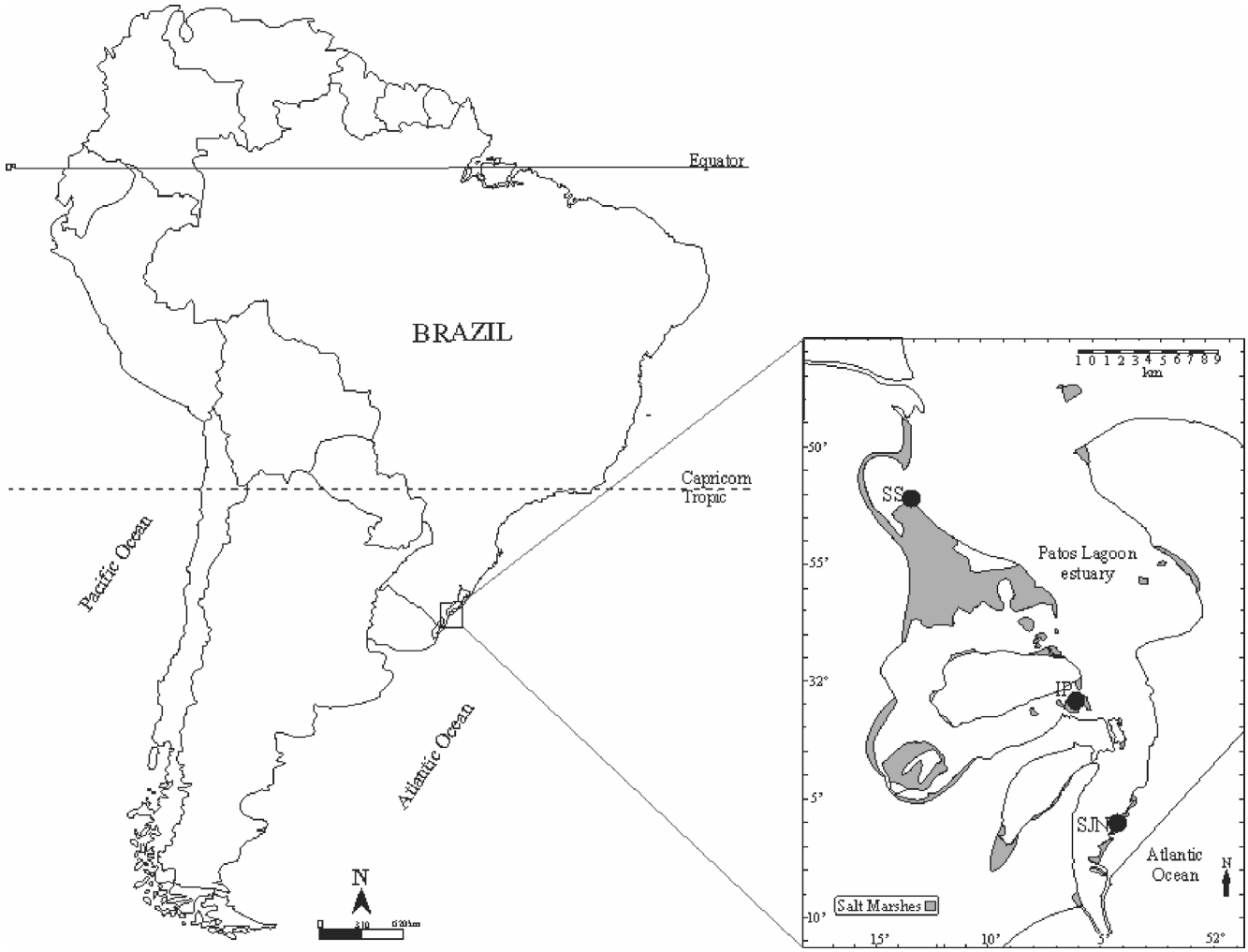


Figure 1. Location of sampling sites: Saco do Silveira (SS), Ilha da Pólvora (IP) and São José do Norte (SJN) in Patos Lagoon estuary, southern Brazil. Modified from Costa (1998).

Scanning electron microscopy: Longitudinal fold not clearly evident, but a slight depression can be noticed in the axial area region (Figure 5 A). Striae unevenly lengthened near the axial area and formed by a single row of poroids, 50-60 in 10 µm (Figures 5 B, C). Mantle striate, 30 striae in 10 µm (Figure 5 B).

***Tryblionella calida* (Grunow) Mann in Round et al. (1990: 678)**
Figures 2 E-H; 5 D-G

Light microscopy: Valves linear-lanceolate, with a very slight constriction in the middle, more noticeable in the fibulate margin, 29.7-46.2 µm long and 8.0-10.3 µm wide. Apices cuneate and produced to slightly rostrate in some specimens. Axial area absent. Transapical ribs parallel in the whole valve extension, 15-17 in 10 µm. Longitudinal fold scarcely visible. Fibulae regularly distributed, 8-9 in 10 µm, the two medians further apart.

Scanning electron microscopy: Longitudinal fold discernible in the middle of the valve, both in external and internal view (Figures 5 D, E). Striae formed by one or two rows of rounded poroids, 50-60 in 10 µm (Figures 5 F, G). A small helictoglossa is visible in each apex of the valve in internal view (Figure 5 E). Mantle striate, 40 striae in 10 µm (Figures 5 D-G). Girdle bands lacking perforations (Figure 5 G).

***Tryblionella circumsuta* (Bailey) Ralfs in Pritchard (1861: 792)**
Figures 2 I - J; 6 A - D

Light microscopy: Valves elliptic-lanceolate to obovate with cuneate-rounded apices, 131.1-242.8 µm long and 52.9-68.2 µm wide. Axial area absent. The valvar surface exhibits a rough appearance (Figure 3 A); however, it is not possible to discern striae and areolae in LM. Longitudinal fold conspicuous in the middle of the valve, fibulae equidistant 4-6 in 10 µm.

Scanning electron microscopy: Longitudinal fold very clear in the external face, bearing a narrow ridge of silica (Figure 6 A). Striae (32-40 in 10 µm) formed by a single row of poroids (36-50 in 10 µm), whose openings are rounded to transapically elongate in external view and rounded in internal view (Figure 6 B, C). The pattern of ornamentation of the valve face is different near the raphid margin, presenting narrow stripes of silica, which were defined by Sims & Padock (1982) as a gill-like arrangement of transapical laminae. The valve margin is thickened, and grooves can be observed running parallel with the raphe fissure. Central nodule is diverted in a V-shaped structure. Mantle striate, 32-36 in 10 µm (Figure 6 C). Internally, the poroids openings are rounded (Figure 6 C) and a small helictoglossa is visible at each apex of the valve (Figure 6 C).

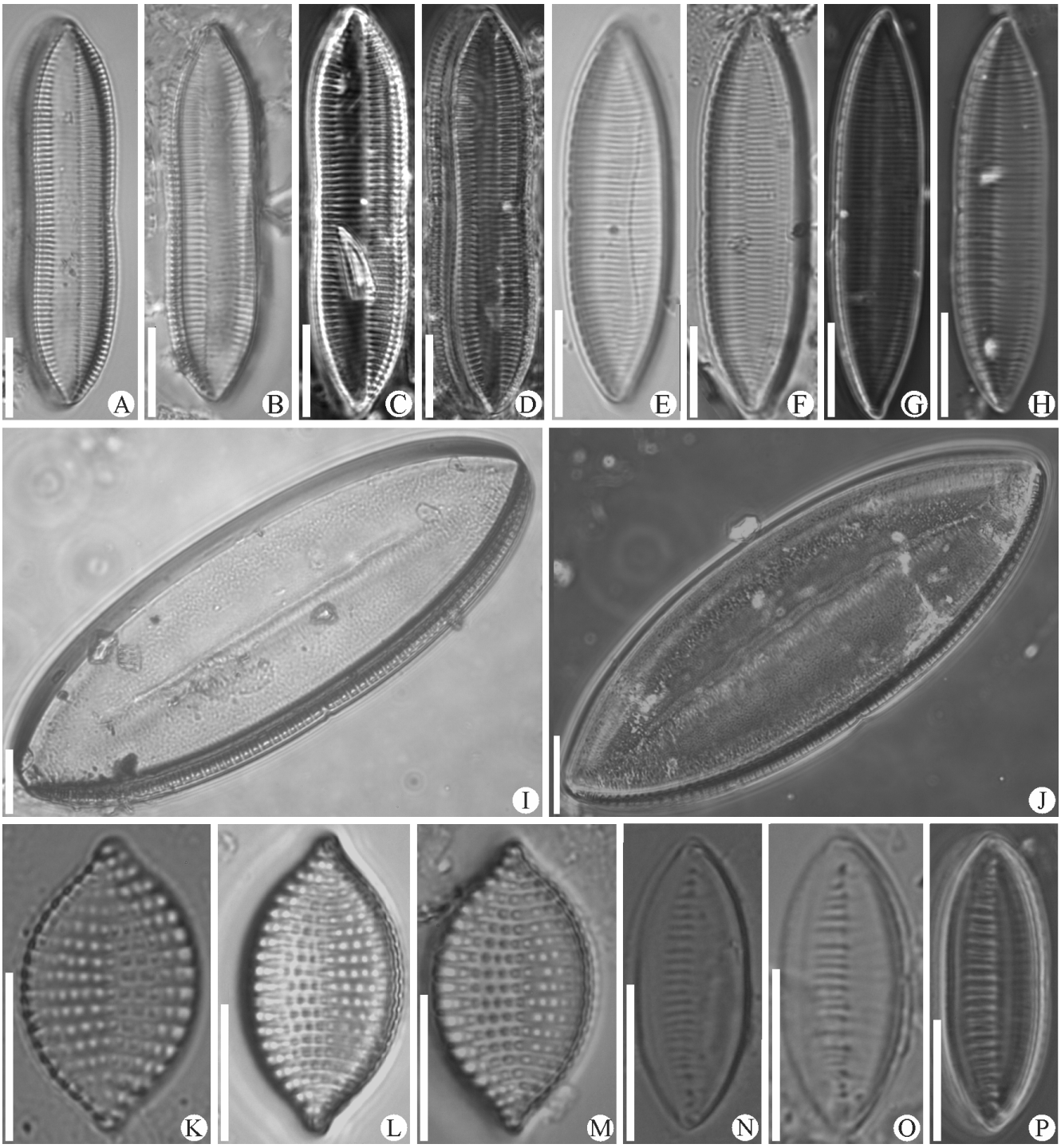


Figure 2. *Tryblionella* species in LM. A-D *T. acuminata*. E-H *T. calida*. I-J *T. circumsuta*. K-M *T. compressa*. N-P* *T. confusa*. Scale bars = 10 µm. *images adapted from Bertolli et al. (2019).

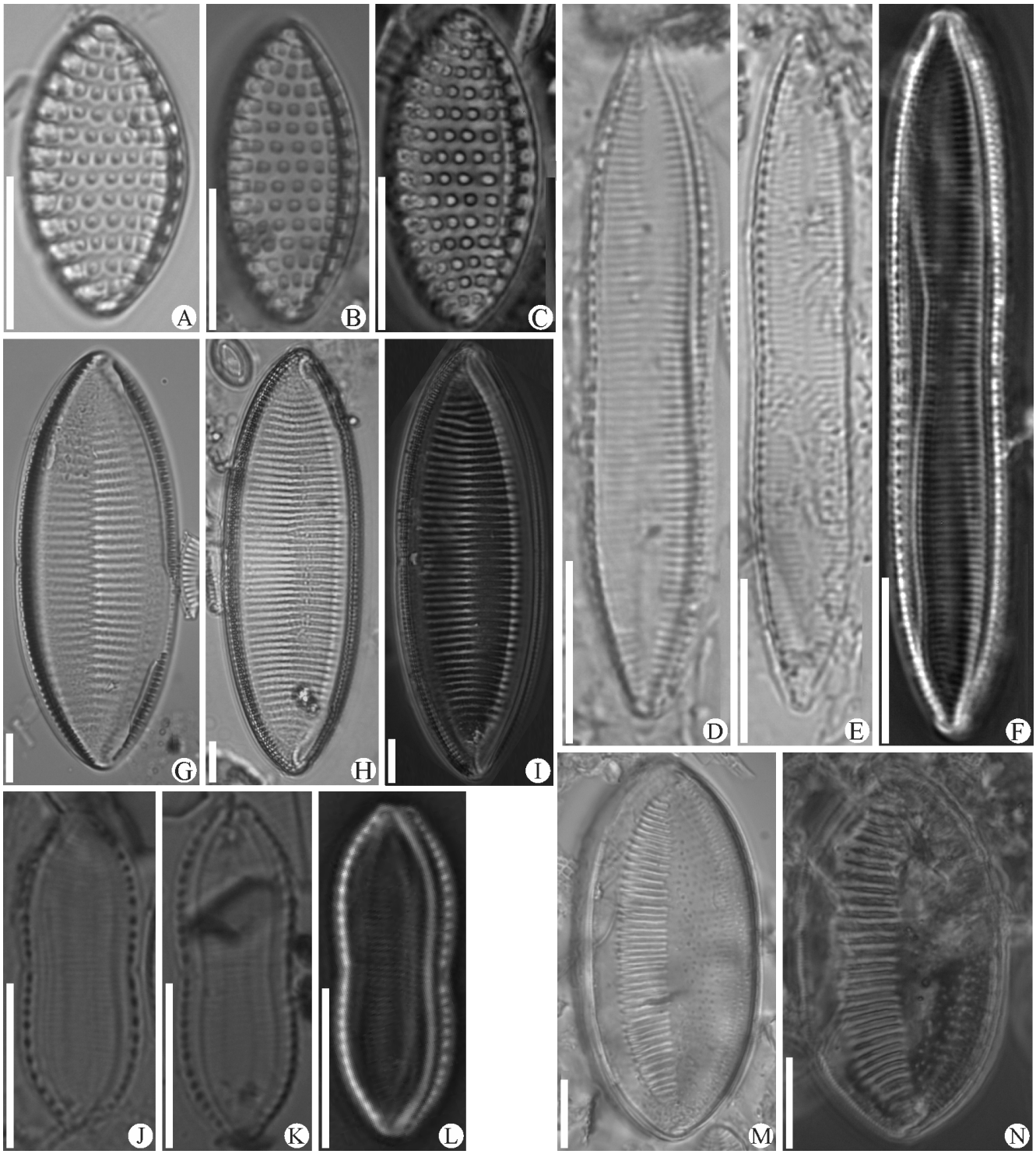


Figure 3. *Tryblionella* species in LM. A-C *T. granulata*. D-F *T. hungarica*. G-I* *T. ornata*. J-L *T. persuadens*. M-N *T. perversa*. Scale bars = 10 µm. *images adapted from Bertolli et al. (2019).

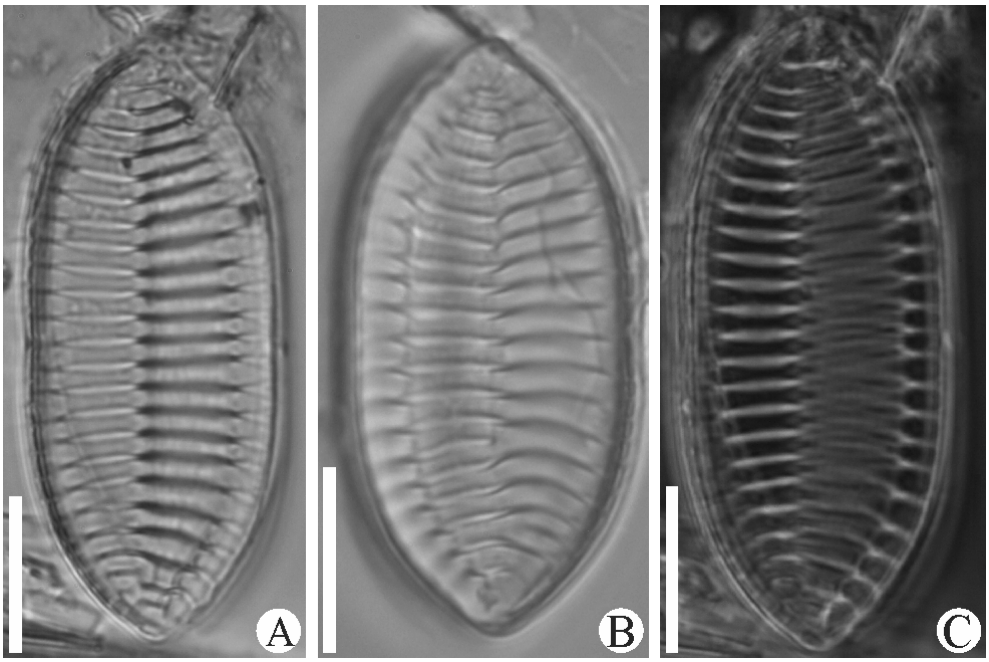


Figure 4. *Tryblionella* species in LM. A-C *T. victoriae*. Scale bars = 10 µm.

***Tryblionella compressa* (J. W. Bailey) M. Poulin in Poulin et al. (1990: 96, Figure 98)**

Figures 2 K-M; 6 E-G

Light microscopy: Valves broadly lanceolate with produced rostrate or somewhat apiculate apices, 17.3-25.9 µm long and 8.9-12.7 µm wide. Longitudinal fold not distinguishable. Axial area absent. Fibulae weakly distinguishable (9-11 in 10 µm). Striae uniseriate, equidistant and parallel across the entire valve (9-11 in 10 µm), formed by large rounded poroids, 12-14 in 10 µm.

Scanning electron microscopy: Valve face remarkably undulated (Figures 6 E,F). A line of warts can be observed disposed on the external transapical costae at one margin (Figure 6 E). Poroids occluded by a delicate vola (Figure 6 G). Girdle bands lacking perforations (Figure 6 E).

***Tryblionella confusa* Bertolli & Torgan in Bertolli et al. (2019: 175, Figures 2-21)**

Figures 2 N-P; 7 A-C

Light microscopy: Valves elliptic-lanceolate, slightly constricted in the middle, with slightly cuneate to rounded apices, 16.3-27.6 µm long and 7.2-10.0 µm wide. Axial area absent. Fibulae weakly distinguishable (7-10 in 10 µm). Unequally spaced transapical ribs (13-16 in 10 µm) occupying only one side of the valvar face.

Scanning electron microscopy: Asymmetric transapical ribs, with spatulate ends towards the valve center (Figures 7 A, B). Striae parallel, 40-42 in 10 µm, formed by a single line of rounded poroids, 80 in 10 µm (Figures 7 B, C). Valve margin thickened in the raphe side (Figure 7 A). A flattened silica projection is deflected towards the valve face, as well as distal raphe endings (Figure 7 B). Cingulum composed by several non-perforated bands (Figures 7 A, B). The mantle is striated, 40-42 in 10 µm, (Figures 7 A-C).

***Tryblionella granulata* (Grunow) Mann in Round et al. (1990: 678)**

Figures 3 A-C; 7 D-F

Light microscopy: Valves elliptic-lanceolate with apices rounded to slightly cuneate, 17.1-26.8 µm long, 8.7-13.9 µm wide. Axial area absent. Fibulae equidistant (6-8 in 10 µm). Striae equidistant (6-8 in 10 µm), uniseriate to biseriate towards the fibulate margin, parallel in the middle of the valve and slightly radiate at the apices. Large rounded or elliptical poroids (8-12 in 10 µm).

Scanning electron microscopy: Longitudinal fold slightly apparent in external view, as a light depression (Figure 7 D). Striae formed by a single row of large poroids occluded by vola in the valve face (Figures 7 E, F) and by a double row of smaller poroids towards the valve mantle (Figure 7 D). Valvocopula presenting a row of large perforations (Figure 7 D).

***Tryblionella hungarica* (Grunow) Frenguelli (1942: 178, plate 8, Figure 12)**

Figures 3 D-F; 8 A-F

Light microscopy: Valves linear-lanceolate, slightly constricted in the middle, 41.6-63.0 µm long and 6.0-10.0 µm wide. Apices subrostrate, somewhat produced. Transapical ribs very remarkable, 17-20 in 10 µm, interrupted by an axial area not always clearly distinguishable. Fibulae irregularly distributed, 8-10 in 10 µm.

Scanning electron microscopy: Longitudinal fold slightly perceptible, by the depression in the axial area region (Figures 8 A,B). Axial area ornamented with small granules (Figures 8 C, E). Both striae and transapical ribs are unevenly lengthened (Figures 8 D, F). Striae formed by a double row of poroids (80 in 10 µm), that may become single closer to the axial area (Figures 8 D, F). Distal raphe endings deflected (Figure 8 D). Mantle striate, 30 striae in 10 µm (Figures 8 C, E). Girdle bands lacking perforations and presenting rows of small granules (Figure 8 C).

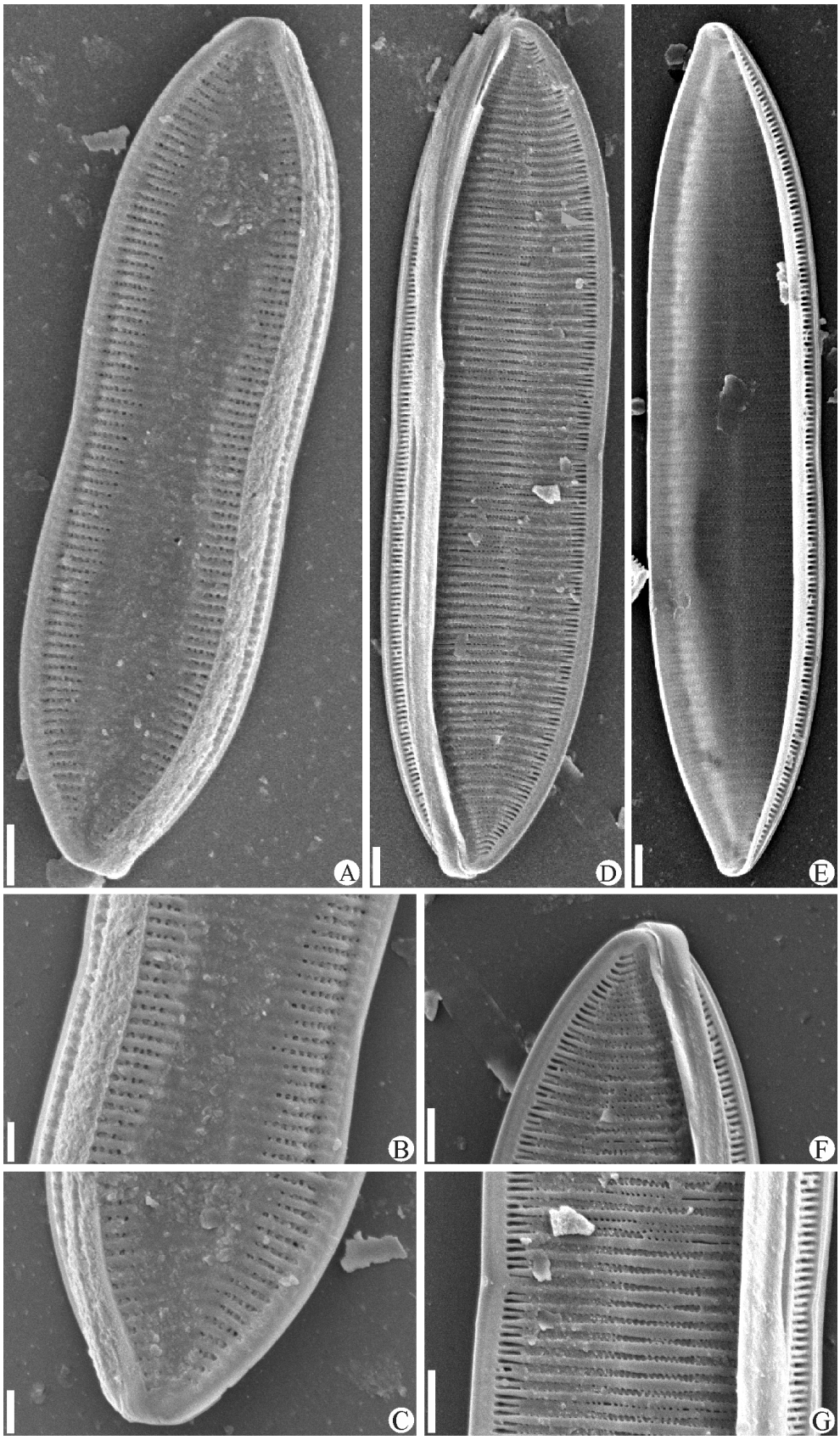


Figure 5. *Tryblionella* species in SEM. A-C *T. acuminata*. D-G *T. calida*. Scale bars = 1 µm (A), 2 µm (B-G).

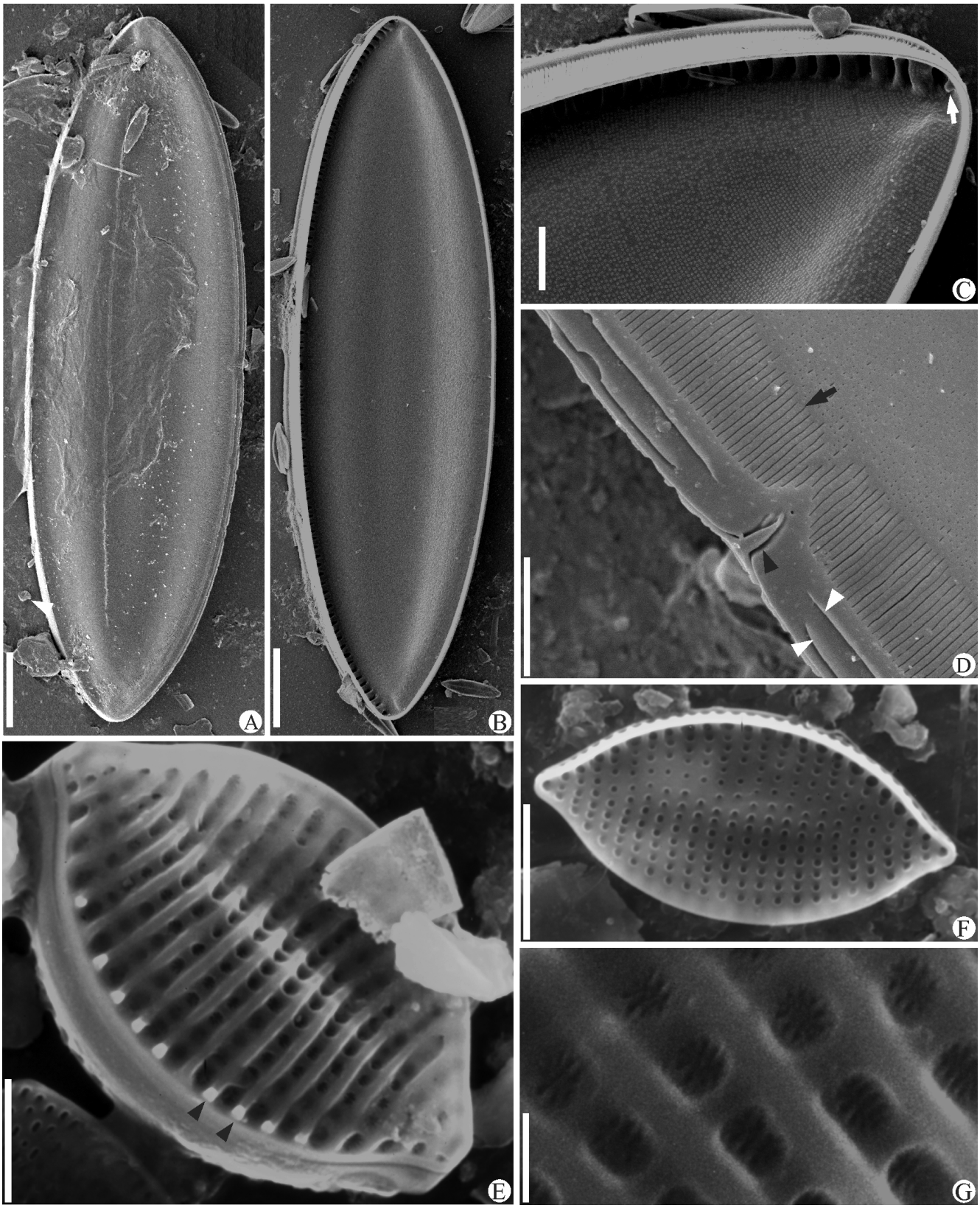


Figure 6. *Tryblionella* species in SEM. A-D *T. circumsuta*. Note the small helictoglossa (white arrow in Fig. 6 C) and the "gill-like" arrangement of transapical laminae (black arrow), the grooves parallel to the raphe fissure (white arrow heads) and central nodule (black arrow head) in figure 6 D. E-G *T. compressa*. Note the warts on the transapical costae (black arrow heads in Fig. 6 E). Scale bars = 20 µm (A, B), 10 µm (F), 5 µm (C-E), 1 µm (G).

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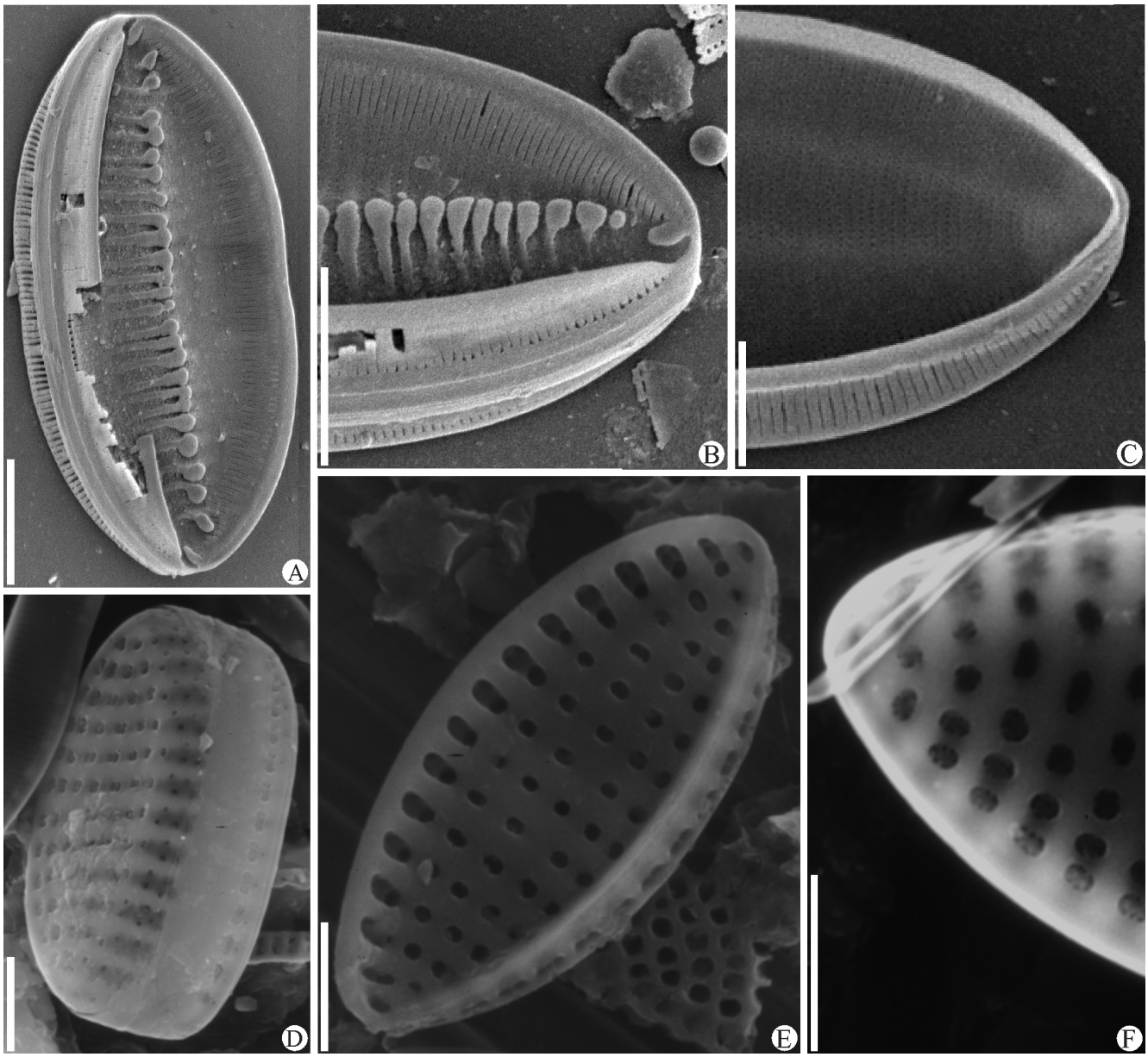


Figure 7. *Tryblionella* species in SEM. A-C *T. confusa*. D-F *T. granulata*. Scale bars = 5 µm (A, B, D-F), 1 µm (C*). *image adapted from Bertolli et al. (2019).

***Tryblionella ornata* Bertolli, Talgatti & Torgan in Bertolli et al. (2019: 178, figs. 22-40)**

Figures 3 G-I; 9 A-C

Light microscopy: Valves broadly lanceolate with cuneate apices, 85.7-108.3 µm long and 31.4-35.0 µm wide. Remarkable transapical ribs, 5-7 in 10 µm, sometimes presenting branches. Axial area absent. Fibulae equidistant, 6-8 in 10 µm.

Scanning electron microscopy: the space between two consequent transapical ribs is ornamented by a pattern that reminds a lace texture (Figure 9 B). Striae (36 in 10 µm) formed by single rows of poroids (40 in 10 µm). Proximal raphe endings deflected towards the valve face, forming a small obtuse central nodule (Figure 9 A). Valve margins thicker than the valve face with irregular grooves throughout its extension (Figures 9 A, B). Mantle striate, 10 striae in 10 µm (Figures 9 A, B). A very small helictoglossa is visible at each valve end (Figure 9 C).

***Tryblionella persuadens* (Cholnoky) Cavalcante, Tremarin & Ludwig in Cavalcante et al. (2013: 1420)**

Figures 3 J-L; 10 A, B

Light microscopy: Valves slightly panduriform with cuneate to subrostrate apices, 17.6-25.3 µm long and 5.8-6.5 µm wide. Striae parallel in almost all the valve extension, becoming slightly radiate on the apices, 24-28 in 10 µm. Axial area absent. Fibulae irregularly distributed, the two medians further apart, 14-16 in 10 µm.

Scanning electron microscopy: Longitudinal fold noticeable by the presence of a depression in the middle of the valve (Figures 10 A, B). Striae formed by a single row of poroids rounded to more rectangular nearer the non fibulate margin, 35 in 10 µm (Figure 10 A). Mantle striate 40 striae in 10 µm (Figure 10 A). A small helictoglossa is observed at each valve end internally (Figure 10 B).

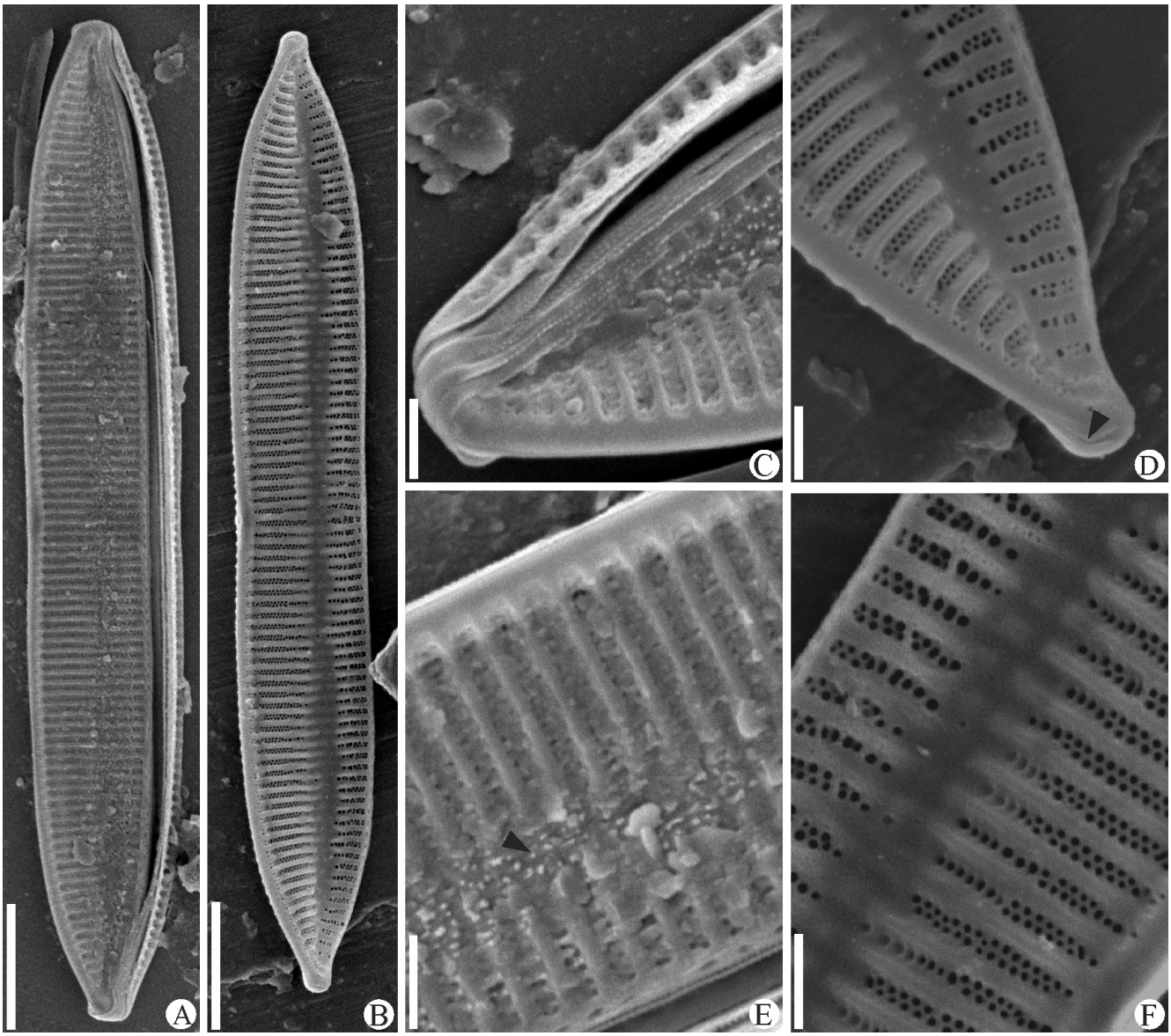


Figure 8. *Tryblionella* species in SEM. A-F *T. hungarica*. Note the distal raphe ends deflected (black arrow head in Fig. 8 D) and the small granules in the axial area (black arrow head in Fig. 8 E). Scale bars = 5 µm (A, B), 1 µm (C-F).

***Tryblionella perversa* (Grunow) Mann in Round et al. (1990: 679)**
Figures 3 M, N; 10 C

Light microscopy: Valves broadly elliptic-lanceolate, with a slight constriction in the middle and cuneate to slightly obtuse apices, 39.6-51.2 µm long and 19.4-20.8 µm wide. The valvar face presents two different patterns of ornamentation. One side presents radiate transapical ribs (9-12 in 10 µm) and the other side lacks these structures and presents irregularly distributed granules. Axial area absent. Fibulae are weakly distinguishable at the granulate side margin.

Scanning electron microscopy: Valve margins presenting longitudinal stripes, similar to the gill-like structures observed in *T. circumsuta* (Figure 10 C). The granulate area may advance towards the apices of the transapical ribs side (Figure 10 C). The internal aspects of the valve were not observed.

***Tryblionella victoriae* Grunow (1862: 553, plate 28, Figure 34)**
Figures 4 A-C; 11 A-D

Light microscopy: Valves linear-lanceolate, slightly constricted in the middle, with cuneate to sub-rostrate apices, 33.6-39.1 µm long and 15.2-16.9 µm wide. Large equidistant transapical ribs (6-7 in 10 µm) distributed alternately on both sides of the remarkable longitudinal fold, producing a zigzag pattern appearance. Axial area absent. Fibulae eccentric, equidistant, the two medians further apart (6-10 in 10 µm).

Scanning electron microscopy: Striae are delicate (50-60 in 10 µm) formed by a row of small poroids, 6-7 in 10 µm (Figures 11 A-D). Thin apical silica projections rise from the transapical ribs and extend to the areolate areas, sometimes connecting two consequent ribs (Figures 11 A, B, D). The transapical ribs may cross all the valve face or be interrupted in the longitudinal fold region (Figure 11 D). Internally, a

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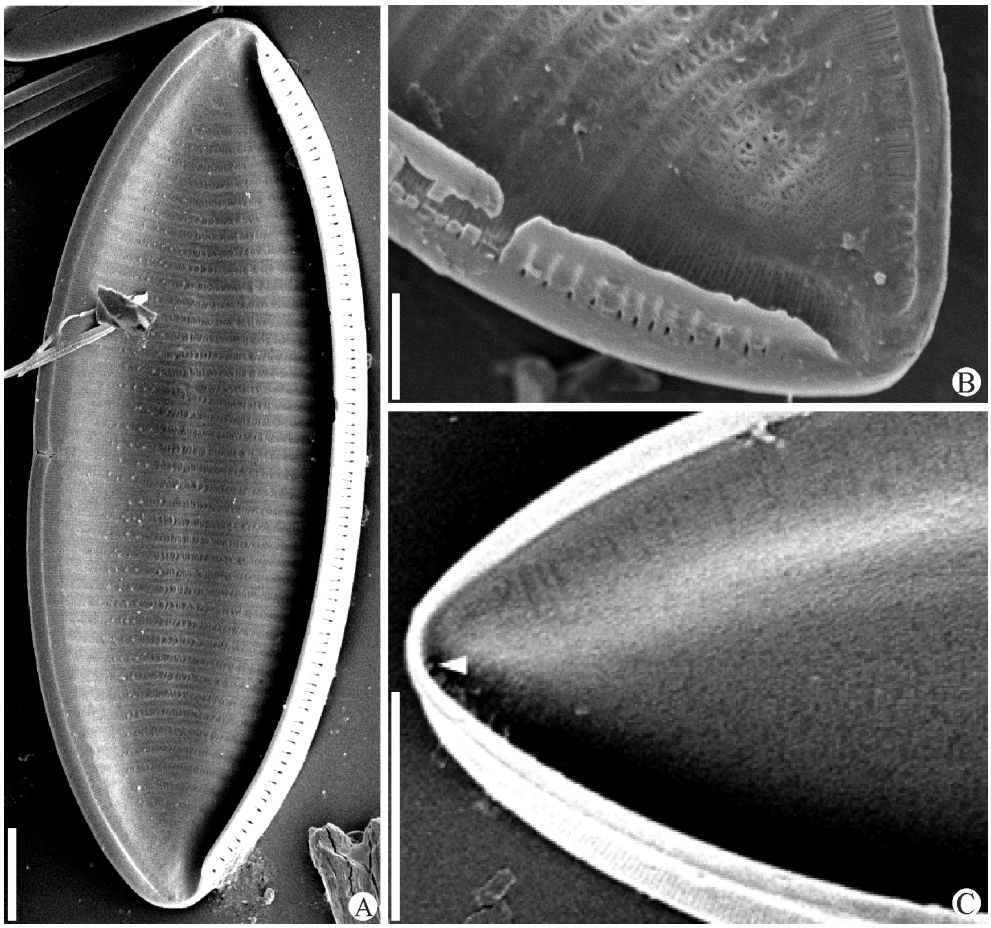


Figure 9. *Tryblionella* species in SEM. A-C *T. ornata*. Note the small helictoglossa (white arrow head) in Fig. 9 C. Scale bars = 10 µm (A*, C*), 5 µm (B). *images adapted from Bertolli et al. (2019).

small helictoglossa is visible at each valve end (Figure 11 C), and the striation pattern continues throughout the fibulae (Figure 11 C). The girdle bands lack perforations and present small granules (Figures 11 B, D).

2. *Species distribution and environmental data*

The distribution of the species in the sites, seasons and substrates is summarized in Table 1. All the taxa showed wide distribution in the study area, and no species was restricted to a certain substrate, site or season. However, the distribution of the taxa showed some differences among the sites. On Ilha da Pólvora site, *T. circumsuta* was not registered in summer, all the other species were registered, at least in one substrate. In Saco do Silveira site, *T. acuminata* was observed only in summer microphytobenthic samples. *Tryblionella ornata* and *T. persuadens* occurred only in winter microphytobenthic samples and *T. perversa* occurred only in epiphytic samples. In São José do Norte site, *T. persuadens* occurred only in winter microphytobenthic samples.

The environmental data of the sampling sites are shown in Table 2. Salinity ranged from 1.5 to 3.4 and 4.2 to 14.0 on Ilha da Pólvora, from 0.1 to 0.3 and 15.0 to 16.0 in Saco do Silveira and from 0.7 to 1.9 and 10.0 to 30.0 (winter and summer, respectively). The values of pH varied from slight acid to slight alkaline, with few registers of more intense acidity (Ilha da Pólvora and São José do Norte during summer).

3. *Extending the interpretation of Tryblionella*

Round et al. (1990) defined some diagnostic features to identify *Tryblionella*, such as elliptical, linear or panduriform valves, with bluntly rounded or apiculate poles, striae formed by small round poroids, occluded by hymenes and girdle narrow, containing plain or sparsely porous, open bands. The treatment used by Lowe (2013) does not add new features to the genus characterization, but points out the undulation along the apical axis as a diacritical feature among *Tryblionella* and *Nitzschia*. The examination of the specimens found in Patos Lagoon salt marsh revealed several features which are not included in the former descriptions. It shows that the concept used previously does not reach the entire diversity of the genus. Our findings were assembled to Round et al. (1990) characterization, providing a broader interpretation of the genus.

Tryblionella specimens are characterized by solitary cells, usually lying in valve view. Frustules diagonally symmetrical about the median valvar plane. Two plastids, one at each end of the cell. Valves robust, broad and symmetric both by apical and transapical axis, presenting an undulation along the apical axis and frequently constricted in the middle portion. Valve outlines vary from linear to elliptic, may be panduriform, lanceolate, elliptic or obovate. Apices rounded, rostrate, cuneate or apiculate, produced or not. Valve face undulate, ornamented by warts, granules, ridges or transapical ribs, which may be parallel radiate or convergent, symmetric or asymmetric by the transapical plane, disposed

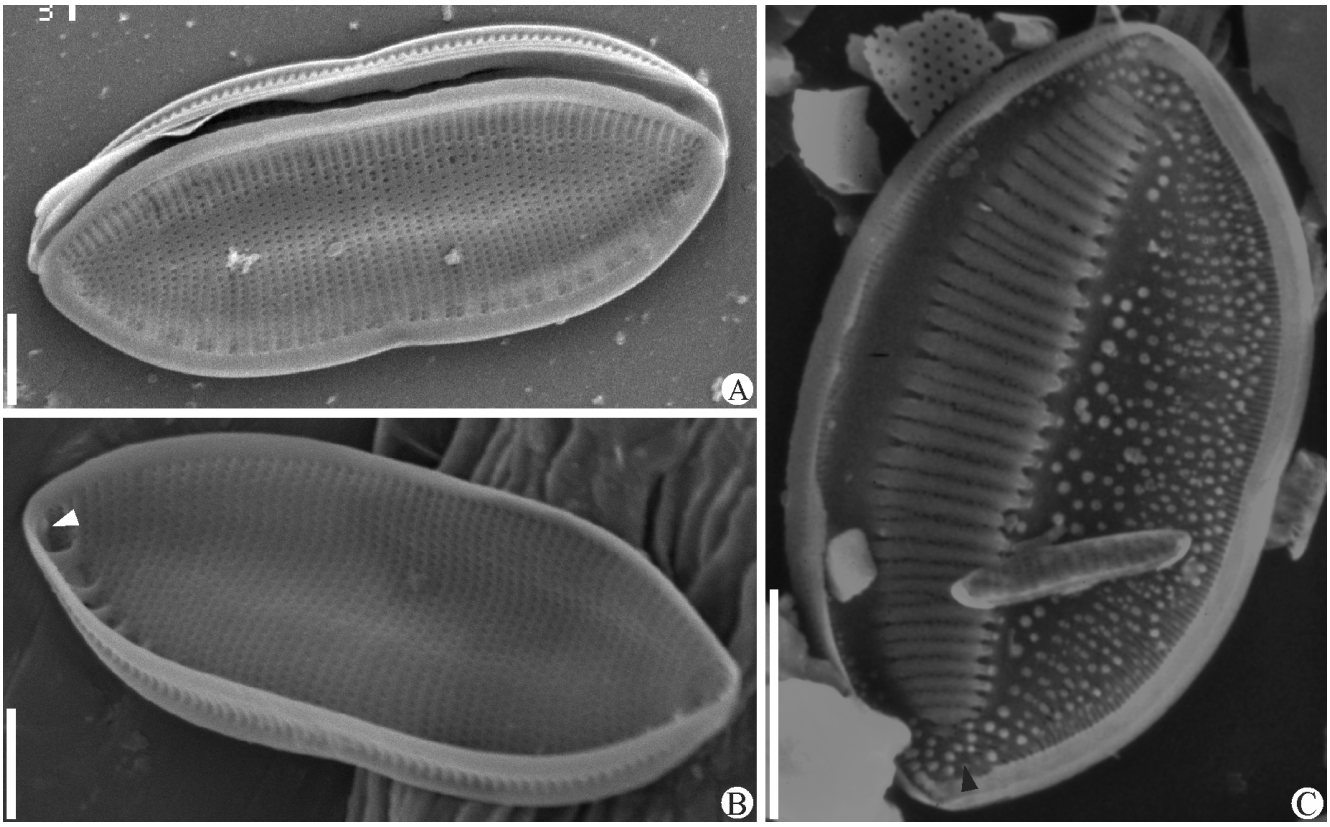


Figure 10. *Tryblionella* species in SEM. A-B *T. persuadens*. Note the small helictoglossa (white arrow head) in Fig. 10 B. C *T. perversa*. Scale bars = 2 µm (A-B), 10 µm (C). Note the granules advancing towards the transapical ribs side (black arrow head) in Fig. 10 C.

in one or both sides of the valve face, sometimes disposed alternately forming a 'zig-zag' pattern. The pattern of ornamentation may vary along the valve face, silica projections rising from the transapical ribs may be present. Striae uniseriate to multiseriate, containing small rounded, rectangular or elongate poroids, occluded by hymenes or volae; rarely alveolate. Striae may be interrupted by broad or narrow axial area (one or more), sometimes ornamented with small granules. Valve face bounded on one side by the keeled raphe system, sometimes presenting narrow stripes of silica (gill-like arrangement) at this margin; on the other side often bearing a marginal ridge. Valve margins may be thickened and present groves. Mantle shallow, plain or presenting elongate striae. Raphe system strongly eccentric, keeled, fibulate. Proximal external raphe endings close together slightly expanded or deflected; occasionally absent. Terminal fissures short, deflected, internally ending in a double helictoglossa. Fibulae squat, often as broad or broader apically than transapically, equidistant or irregularly distributed, the two medians further apart; striate like the valve or hollow. Narrow girdle, formed by opens bands, plain or containing sparse porous, open bands, sometimes presenting small granules. A benthonic genus, occurring more frequently in epipelon, but also in periphyton, widespread in marine and brackish waters but also present in high conductivity fresh waters.

Discussion

Tryblionella's characterization, especially under LM, is complex, since many metric and meristic characters are overlapping and some species may present, for example, a broad variation of valve or apices outlines. The analysis under SEM provided a more detailed characterization of the taxa, leading to better understand their morphology. Due to the morphological overlapping and, sometimes, to nomenclatural issues, many species can be misinterpreted and misidentified. Our attempt to better understand *Tryblionella's* morphological variability, by adding new features to its characterization, seems far from ending the genus' taxonomic issues. The great variability in the features observed may indicate a great phenotypic plasticity, which may occur not only among the species, but also among specimens of the same species in response to environmental variation. However, we can't ignore the possibility of being grouping different lineages of diatoms under the same genus over the centuries, since phylogenetic studies are scarce. Not only *Tryblionella*, but the whole Bacillariaceae family should be the focus of an extensive revision, including phylogenetics and large data sets, and then, we will be closer to more trustworthy interpretations and circumscriptions of the taxa.

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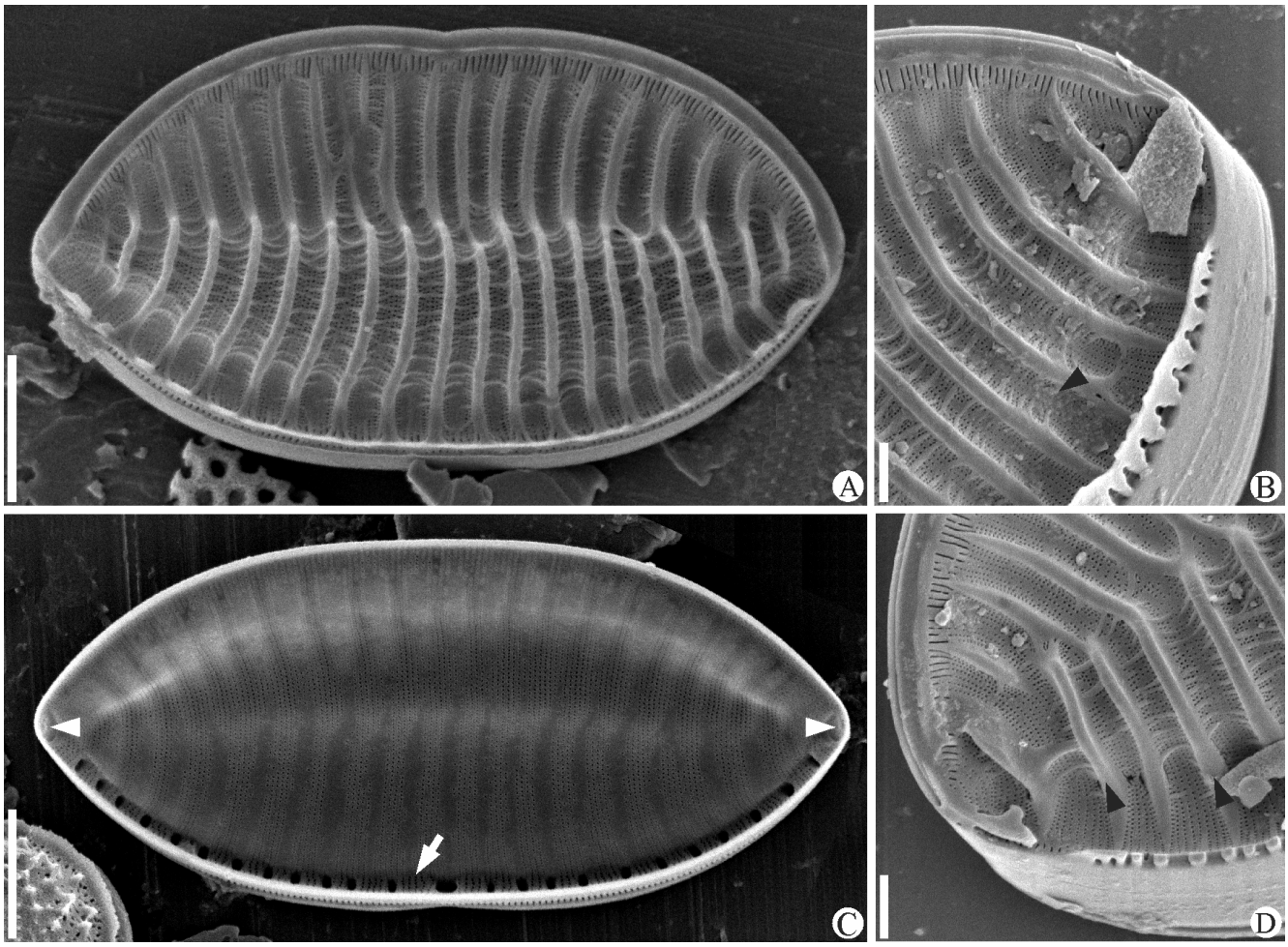


Figure 11. *Tryblionella* species in SEM. A-D *T. victoriae*. Scale bars = 5 µm (A, C), 2 µm (B, D). Note the silica projections between two transapical ribs (black arrow head in Fig. 11 B), the small helictoglossa (White arrow heads) and the striation continuing throughout the fibulae (white arrow) in Fig. 11 C, and the transapical rib interrupted in the longitudinal fold region (black arrow head in Fig. 11 D).

Table 1. Distribution of the *Tryblionella* species in the sites along the Patos Lagoon Estuary in the winter of 2010 and the summer of 2011. Abbreviations: (EPP) epiphyton, (MPB) microphytobenthos.

	Ilha da Pólvora				**Saco do Silveira**				**São José do Norte**			
	Winter		**Summer**		**Winter**		**Summer**		**Winter**		**Summer**	
	EPP	**MPB**	**EPP**	**MPB**	**EPP**	**MPB**	**EPP**	**MPB**	**EPP**	**MPB**	**EPP**	**MPB**
T. acuminata	-	X	X	X	-	-	-	X	X	X	X	-
T. calida	X	X	X	X	X	X	X	X	X	X	X	X
T. circumsuta	X	X	-	-	X	X	X	X	X	X	X	X
T. compressa	X	X	X	X	X	X	X	X	X	X	X	X
T. confusa	X	X	X	X	X	X	X	X	X	X	X	X
T. granulata	X	X	X	X	X	X	X	X	X	X	X	X
T. hungarica	X	X	X	X	X	X	X	X	X	X	X	X
T. ornata	X	X	X	X	-	X	-	-	X	X	-	X
T. persuadens	X	X	X	-	-	X	-	-	-	X	-	-
T. perversa	X	X	X	X	X	-	X	-	X	-	X	X
T. victoriae	X	X	X	-	-	X	X	X	X	X	X	X

Table 2. Samples code, type of vegetal substrate, sediment main component, epiphyton (EPP) and microphytobenthos (MPB) slide numbers at Herbarium Alarich Schultz, Temperature (T, ºC), salinity. (Sal., ‰) and pH ranges of the interstitial water registered in the three sampling sites in Winter (September 2010) and Summer (February 2011). IP: Ilha da Pólvora, SS: Saco do Silveira, SJN: São José do Norte.

Sample	Vegetal substrate	Sediment main component	Sal.	T	pH	EPP slide number	MPB slide number
Winter							
IPA	*Bolboschenus maritimus*	Sand	1.6	16.7	7.3	6520	6242
IPB	*Sporobolus montevidensis*	Sand	1.6	15.4	7.2	6523	6244
IPC	*B. maritimus*	Sand	1.5	15.9	6.8	6526	6246
IPE	*B. maritimus*	-	2.8	16.0	7.5	6532	-
IPG	*S. montevidensis*	-	3.4	16.2	6.0	6538	-
IPH	*S. montevidensis*	-	3.4	19.5	7.2	6540	-
SSA	*Juncus kraussii*	Sand	0.1	20.6	8.8	6548	6263
SSB	*J. kraussii*	Sand	0.3	21.2	7.8	6553	6249
SSC	*S. montevidensis*	Sand	0.3	20.4	7.1	6554	6251
SSE	*Sporobolus alterniflorus*	-	0.1	21.0	7.5	6561	-
SSF	*J. kraussii*	-	0.2	19.6	6.9	6565	-
SSJ	*S. alterniflorus*	-	0.3	19.9	6.5	6577	-
SJNA	*S. alterniflorus*	Silt	1.2	17.0	7.2	6579	6254
SJNC	*J. kraussii*	-	0.7	17.0	7.3	6584	-
SJNE	*J. kraussii*	-	1.2	20.4	7.3	6590	-
SJNF	*S. alterniflorus*	-	1.3	20.6	7.7	6593	-
SJNG	*S. montevidensis*	Silt	1.9	21.5	7.7	6596	6260
SJNI	*S. alterniflorus*	Sand	1.9	19.1	7.7	6602	6256
Summer							
IPA	*S. alterniflorus*	Sand	14.0	28.0	8.6	6610	6497
IPB	*B. maritimus*	-	7.2	27.0	6.8	6611	-
IPC	*B. maritimus*	Sand	8.0	29.0	6.6	6614	6499
IPF	*S. alterniflorus*	-	10.0	29.0	8.8	6624	-
IPG	*S. alterniflorus*	Sand	4.2	29.0	7.2	6626	6503
IPI	*B. maritimus*	-	8.2	30.0	5.2	6632	-
SSA	*J. kraussii*	Sand	15.0	27.0	7.9	6639	6505
SSC	*S. montevidensis*	-	15.0	26.0	7.9	6644	-
SSD	*J. kraussii*	Sand	16.0	25.0	7.5	6647	6507
SSE	*J. kraussii*	-	15.0	26.0	8.0	6652	-
SSF	*S. montevidensis*	Sand	15.0	26.0	6.8	6653	6509
SSH	*S. montevidensis*	-	15.0	29.0	7.8	6660	-
SJNC	*J. kraussii*	-	13.0	31.0	7.0	6676	-
SJND	*J. kraussii*	Silt	16.0	27.0	7.3	6678	6511
SJNE	*J. kraussii*	-	15.0	27.0	7.4	6680	-
SJNG	*S. alterniflorus*	Silt	30.0	27.0	4.0	6686	6514
SJNI	*S. alterniflorus*	Silt	15.0	28.0	7.4	6692	6516
SJNJ	*S. alterniflorus*	-	10.0	26.0	8.2	6696	-

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The *Tryblionella acuminata* specimens observed are smaller than the originally described to the taxon (63.5-106.7 of length, Smith 1853); however, the valve outline and striae density are conserved. The species occurs from fresh to marine waters (Smith 1853, Hartley 1996, Witkowski et al. 2004). In southern Brazil the species have been recorded in a wide range of salinity, occurring in lakes, rivers, lagoons and estuaries (Torgan et al. 1999, Procopiak et al. 2006). Silva et al. (2010) recorded *Tryblionella apiculata* Gregory in the Patos Lagoon salt marsh, however the individual illustrated presents characteristics, such as valve outline, apices and axial area width, that fits more with *T. acuminata* than with the referred taxon.

Tryblionella calida was originally recorded in thermal fountains in Hungary (Cleve & Grunow 1880), however, nowadays it is considered widespread in slightly brackish and in electrolyte rich inland waters (Witkowski et al. 2000). *Tryblionella calida* was registered in freshwater environments (unpublished data) in the State of Paraná, southern Brazil (Tremarin et al. 2009). This is the first record of the taxon in the State of Rio Grande do Sul.

Tryblionella circumsuta resembles some specimens of *T. littoralis* (Grunow) Mann. However, the latter species is characterized by smaller specimens (30-100 µm versus 130-300 µm) and a higher number of fibulae in 10 µm (3-5 versus 6-9) as noticed by Krammer & Lange-Bertalot (1988). The species is considered cosmopolitan, occurring in brackish and marine waters (Hartley 1996, Witkowski et al. 2000). In southern Brazil it has been recorded in coastal waters in the State of Paraná (Procopiak et al. 2006), in the State of Santa Catarina (Fernandes et al. 1990, Felício-Fernandes 1996, Souza-Mosimann & Roos-Oliveira 1998, Souza-Mosimann & Laudares-Silva 2005) and in the State of Rio Grande do Sul at Patos Lagoon, both in salt marsh surface sediment (Silva et al. 2010) and in core sediment samples (Abreu et al. 1987).

Tryblionella compressa is sometimes identified as *Tryblionella* (or *Nitzschia*) *punctata* W. Smith (Van Heurck 1896, Gandhi 1967). We chose to use the epithet '*compressa*' assuming that the species is a synonym of *Pyxidicula compressa* Bailey as also considered by Krammer & Lange-Bertalot (1988) and Lopez-Fuerte et al. (2010). *Pyxidicula compressa* has nomenclatural priority since it was formerly published (Bailey 1850 vs. Smith 1853). It is considered a marine to brackish-water species, widespread on marine coasts (Hartley 1996; Witkowski et al. 2000). There are many records of *T. compressa* in the coastal waters of the State of Santa Catarina (Souza-Mosimann 1982;1988; Fernandes et al. 1990, Felício-Fernandes 1996, Souza-Mosimann & Roos-Oliveira 1998). In the State of Paraná, the species has been mentioned as *T. punctata* (Procopiak et al. 2006). Rosa & Garcia (2013) registered *Nitzschia pararostrata* (Lange-Bertalot) Lange-Bertalot, in a stream nearby Patos Lagoon, the species is similar to *T. compressa*, but differs by the smaller dimensions and areolae density (Lange-Bertalot et al. 1996). This is the first record of the species in the State of Rio Grande do Sul.

Tryblionella confusa may resemble specimens of *T. perversa* (Grunow) Mann and *Tryblionella debilis* Arnot ex O'Meara in light microscopy, however, the analysis under scanning electron microscopy reveals several differences among the taxa, especially the pattern of ornamentation. *Tryblionella confusa* was recently proposed and its distribution is still limited to Patos Lagoon salt marshes (Bertolli et al. 2019).

Tryblionella granulata presents dimensions and coarse areolation similar to *T. compressa*, however, the species are distinguishable by the valve shape. *T. granulata* does not present elongated valves towards the ends, forming produced apices, as occurs in *T. compressa*. It is considered a cosmopolitan species, especially common in tidal flats (Witkowski et al. 2000). The species was registered in Patos Lagoon core sediment samples (Santos-Fischer et al. 2016) and in the coastline along the States of Paraná and Santa Catarina (Araújo et al. 1989; Fernandes et al. 1990, Felício-Fernandes 1996, Souza-Mosimann 1988, Souza-Mosimann & Roos-Oliveira 1998, Souza-Mosimann & Laudares-Silva 2005, Procopiak et al. 2006, Souza-Mosimann et al. 2011).

Tryblionella hungarica is very frequently recorded and considered a cosmopolitan species, inhabiting brackish and freshwater environments (Krammer & Lange-Bertalot 1988). The current concept of *T. hungarica* (see Witkowski et al. 2000, Metzeltin et al. 2005 and Hofmann et al. 2011, for example) is somewhat different from the original illustrated by Grunow (1862) and also by Frenguelli (1942). It is more likely that a complex of similar species has been misidentified as *T. hungarica* throughout the years, what may explain the wide range of dimensions, valve outlines and ends shapes observed in the literature. A detailed examination of the type material and the phylogenetic analysis of similar morphotypes would help to better circumscribe the species. The species is largely recorded in southern Brazil, occurring in continental and coastal environments (Torgan et al. 1999, Procopiak et al. 2006, Tremarin et al. 2009, Bes & Torgan 2008) and in core sediment samples in the State of Rio Grande do Sul (Hermany et al. 2013).

Tryblionella ornata may resemble specimens of *T. circumsuta* and *T. victoriae*, however the morphometric patterns and the features of the transapical ribs allow the differentiation. *Tryblionella ornata* was recently described, its distribution is still restricted to Patos Lagoon salt marshes (Bertolli et al. 2019).

Tryblionella persuadens is similar to *T. aerophila*; however, it presents a higher density of fibulae in 10 µm (12-16 versus 9-11) and lacks the longitudinal axial area formed by the interruption in the striae observed in the referred species (Cavalcante et al. 2013). The species was originally described for brackish waters (Cholnoky 1961) however, it has already been found in freshwaters in northeastern Brazil (Cavalcante et al. 2013). This is the first record of the species in southern Brazil.

Krammer & Lange-Bertalot (1988, p. 271, Figures 10 and 11) and Witkowski et al. (2000, p. 813, Figures 8-10) illustrated specimens that raise doubts about their determination as *T. perversa* or *T. debilis*. However, the valvar shape and the arrangement of the granules over the valvar face made us believe that the specimens are more similar to *T. perversa*. The species is considered estuarine (Cleve & Grunow 1880). It has been recorded to coastal environments in southern Brazil (Fernandes et al. 1990, Felício-Fernandes 1996, Procopiak et al. 2006), in Patos Lagoon salt marsh by Silva et al. (2010) and in core sediment samples from different geologic formations in the State of Rio Grande do Sul (Abreu et al. 1987, Santos-Fischer et al. 2016).

Tryblionella victoriae is similar to *T. levidensis* W. Smith and has already been considered one of its many varieties. The differentiation is based on the higher width/length ratio and the number of transapical ribs (seven or less in 10 µm) presented by *T. victoriae* (Witkoswki et al. 2000). The species has been originally found in freshwaters (Grunow 1862) but is also spread in marine and brackish waters (Hartley 1996,

Witkoswki et al. 2000). In southern Brazil it is widely recorded in continental and coastal waters (Souza-Mosimann 1982, Felício-Fernandes 1996, Souza-Mosimann & Roos-Oliveira 1998, Torgan et al. 1999, Souza-Mosimann & Laudares-Silva 2005, Procopiak et al. 2006, Tremarin et al. 2009, Bes & Torgan 2008, Bes et al. 2012), in Patos Lagoon salt marsh by Silva et al. (2010) and in in core sediment samples from different geologic formations in the State of Rio Grande do Sul (Hermany et al. 2013, Santos-Fischer et al. 2016).

A high number of *Tryblionella* species was observed in Patos Lagoon salt marsh, comprising nearly a half of the richness known to the country. The spatial heterogeneity of the salt marshes, which favors the formation of microhabitats, allied to the mixing of communities from fresh and marine waters, may be responsible for the high richness observed. The occurrence of species concomitantly in epiphyton and in microphytobenthos was already observed in other species in the same sites and is probably related to the environmental dynamics (Talgatti et al. 2014, Bertolli et al. 2016, 2019). The temperature variation among the seasons was expected. However, the fluctuations among sites and samples may be related to the depth of water column in each circumstance. The abiotic conditions were affected by the seasonal period and by the distance of the sites from the Atlantic Ocean, resulting in different marine water input. Nevertheless, such environmental variation did not seem to interfere in the presence of *Tryblionella* species, since they occured in a broad spectrum of pH, salinity and temperature. The occurrence of the species in the three sites, in both periods, in both substrates and in a wide range of environmental variables, evidences a community adjusted to the fluctuations observed in Patos Lagoon estuary.

Two species were firstly registered in the State of Rio Grande do Sul and one in southern Brazil. This study represents an important contribution to *Tryblionella*, since there are few studies dedicated to the genus, and little is known about some species' ultrastructure, such as *T. compressa* and *T. perversa*. Besides that, these results reinforce the importance of studying this kind of heterogenous environment to diatom biodiversity knowledge.

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Authors contributions

Lucielle Merlym Bertolli: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Dávia Marciana Talgatti: Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Thamires Mariah da Silveira Nascimento: Contribution to data collection; Contribution to data analysis and interpretation.

Lezilda Carvalho Torgan: Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intelectual content.

Conflict of interests

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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Article

Fish fauna from the Paranapanema River basin, Brazil

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Abstract: The Paranapanema River is an important, extensively explored tributary of the Upper Paraná River basin. The fish fauna of the Paranapanema River has been investigated since the 1990s; however, no study has characterized the richness of fish species throughout the basin, including the main channel of the river, marginal lagoons, its tributaries, and sub-tributaries. Thus, we performed a review with 90 independent studies conducted at the upper, middle, and lower sections of the basin. We recorded 225 species, of which 165 were native, and 60 were non-native. We found that 77% of the species within the basin are composed by Siluriformes and Characiformes. Cichliformes had a significant number of non-native species established in impoundment sections of the basin. Incidence-Based Estimators (Bootstrap and Chao 2) demonstrated that the richness of native species is still underestimated. Some native (*e.g.*, *Hypostomus ancistroides*) and non-native species (*e.g.*, *Plagioscion squamosissimus*) are widely distributed in the basin, while others had a more restricted distribution. Among the registered species, the family Bryconidae had the highest number of representatives with threatened conservation status. In addition, we observed that the Capivara Reservoir and its tributaries were the most sampled regions, with the majority of studies performed in the Lower Paranapanema basin. The species richness recorded in large tributaries, such as Tibagi, Cinzas, Congonhas, and Pirapó rivers is critical for maintaining the fish fauna in the Paranapanema River. Our contribution may be used to support management actions and conservation strategies, as well as to indicate regions in the basin that need to be better inventoried.
Keywords: *freshwater, Neotropical region, species inventory, Upper Paraná River.*

Fauna de peixes da bacia do rio Paranapanema, Brasil

Resumo: O rio Paranapanema é um importante tributário, amplamente explorado da bacia do Alto rio Paraná. A fauna de peixes do rio Paranapanema vem sendo investigada desde a década de 1990; no entanto, nenhum estudo caracterizou a riqueza de espécies de peixes em toda a bacia, incluindo o canal principal do rio, lagoas marginais, seus tributários e sub-tributários. Assim, realizamos uma revisão com 90 estudos independentes conduzidos nas regiões superior, média e inferior da bacia. Foram registradas 225 espécies, das quais 165 eram nativas e 60 eram não nativas. Verificamos que 77% das espécies dentro da bacia são compostas por Siluriformes e Characiformes. Cichliformes apresentou um número significativo de espécies não nativas estabelecidas em áreas de represamento da bacia. Estimadores de riqueza baseados em incidência (Bootstrap e Chao 2) demonstraram que a riqueza de espécies nativas ainda é subestimada. Algumas espécies nativas (*e.g.*, *Hypostomus ancistroides*) e não nativas (*e.g.*, *Plagioscion squamosissimus*) estão amplamente distribuídas na bacia, enquanto outras tem sua distribuição mais restrita. Entre as espécies registradas, a família Bryconidae obteve o maior número de representantes com status de conservação ameaçado. Além disso, observamos que o reservatório de Capivara e seus afluentes foram as regiões mais amostradas, sendo a maioria dos estudos realizados na bacia do baixo Paranapanema. A riqueza de espécies registrada em grandes afluentes, como os rios Tibagi, Cinzas, Congonhas e Pirapó, é fundamental para a manutenção da ictiofauna no rio Paranapanema. Nossa contribuição pode ser usada para apoiar ações de manejo e estratégias de conservação, bem como para indicar regiões na bacia que precisam ser melhor inventariadas.
Palavras-chave: *água doce, região Neotropical, inventário de espécies, Alto rio Paraná.*

Introduction

South America has the greatest diversity of freshwater fish fauna in the world, with a high taxonomic, phylogenetic, and functional variety (Barletta et al. 2010, Reis et al. 2016, Vitule et al. 2017). Such diversity is sheltered mainly in the Amazon (Santos & Ferreira 1999), and Paraná (Brea & Zucol 2011) river basins. The Upper Paraná River basin is one of most studied basins in terms of fish fauna (Agostinho et al. 2007a), being composed of between 270 to 310 species (Agostinho et al. 2007b, Langeani et al. 2007). The Upper Paraná River basin is the second largest basin in South America (Lowe-McConnell 1999) and is composed of sub-basins originating in the Brazilian states of Goiás, Minas Gerais, São Paulo, Mato Grosso do Sul, and Paraná. The basin is constituted from the confluence of major tributaries, such as the Paranaíba, Grande, Tietê, and Paranapanema rivers.

The Paranapanema River - one of the most important tributaries of the left margin of the Paraná River (Maack 2002, Duke Energy 2008) - hosts a significant part of this diversity, as evidenced by several fish inventories and ecological studies performed on its main course (Carvalho et al. 1998, Pelicice et al. 2005, Britto & Carvalho 2006, Orsi 2010, Orsi & Britton 2014, Pelicice et al. 2018), tributaries, and sub-tributaries (Castro et al. 2003, Cerqueira & Smith 2015, Vidotto-Magnoni et al. 2015, Rosa et al. 2016). Past works suggest that species compilations from the Paranapanema River alone vary from 155 (Duke Energy 2008) to 161 (Pelicice et al. 2018).

This novel study investigates the richness of fish species throughout the Paranapanema River basin, including its main channel, marginal lagoons, tributaries, and sub-tributaries. An accurate assessment of the species within this ecosystem is a necessary step towards the maintenance of its biodiversity (Cudmore-Vokey & Crossma 2000). To gain the most benefit from previous surveys, updates are needed to indicate changes over time. These changes can include the establishment of species (both native and introduced), introductions that are not established (Garcia et al. 2018), and species that become extirpated or extinct. Thus, an updated fish inventory on the Paranapanema River basin is fundamental to optimize its management in relation to low impact actions, resources conservation, and recovering degraded ecosystems (Melo 2008). Therefore, we aimed to complement the knowledge of the fish fauna diversity present in the Paranapanema basin through a compilation of all survey studies and species descriptions from all aquatic environments. Our study may help the understanding of the richness and distribution of species present along the basin.

Material and Methods

1. Study area

The Paranapanema River headwater is located within the state of São Paulo, municipality of Capão Bonito, is protected by the State Parks of Intervales and Carlos Botelho. The basin has an area of 106.500 km^2 and crosses 247 municipalities, 115 in the state of São Paulo, and 132 in the state of Paraná (ANA 2016). Its waters run for approximately 930 km inland to the west until draining into the left margin of the Paraná River. Starting the mouth of the river Itararé, the Paranapanema forms a border (330 km) between the states of São Paulo and Paraná. According to Sampaio (1944), its course is divided into three main sections: the Upper, Middle, and Lower Paranapanema. The Upper Paranapanema constitutes a 180 km extension from its headwater until the confluence with the Apiaí-Guaçu River, this, together with the Itapetininga River, are the main tributaries of this stretch. The Middle Paranapanema is a 328 km extension from the Apiaí-Guaçu mouth to the Salto Grande Dam. The Lower Paranapanema comprises of a 421 km stretch from the Salto Grande Dam, to its mouth in the Paraná River, also known as Pontal do Paranapanema (Figure 1).

In recent past, the drainage area of the Paranapanema River basin was predominantly covered by Atlantic Rainforest and Brazilian Savannah biomes (Sampaio 1944, Huek & Seibert 1972). However, following deforestation, the basin is now an agricultural region, with margins generally surrounded by narrow and degraded riparian forest (Castro et al. 2003). Throughout the entire basin, the only significant and continuous forests fragments along its margins are the Intervales, Carlos Botelho, and the Morro do Diabo State Parks (Inventário Florestal do Estado de São Paulo 1993).

2. Data Collection

A list of species was generated from an extensive search of available scientific literature about the Paranapanema River basin. This list included species descriptions, inventories, and ecological studies. We performed searches between April to September 2018 in online databases (Web of Science, Scopus, Scielo, and Google Scholar), private libraries, and cross-reference searches using the keyword 'Paranapanema', combined with the keywords 'fish', 'survey', 'ichthyofauna', 'fish fauna', and 'diversity'. All different types of aquatic environments were considered in our search, including reservoirs, rivers, streams, marginal lagoons, and fish ladders. The survey resulted in 90 studies, comprising 74 articles, nine book chapters, two books, and five Ph.D. theses published between 1995 to 2018. Subregions were hierarchically delimited according to the main tributaries of the Paranapanema River basin, as assessed by the studies inventoried herein. Some studies investigated more than one site, resulting in our samples covering 57 subregions (Table 1).

Taxonomic classification and species naming were determined following the studies from Eschmeyer & Fong (2018) and Eschmeyer et al. (2018). Updates on species identification, valid names, and new combinations were performed when necessary. A list of species that have had their taxonomic status modified over the past years has been provided in Table 3. Unprecise species identification recorded as 'sp.' or 'spp.' were not considered in the study. The species identification was not checked for all surveyed literature. The conservation status of the species was derived from works by Mikich & Bérnils (2004) for the state of Paraná, Bressan et al. (2009) and ALESP (2014) for the state of São Paulo; and ICMBio (2014, 2018) for Brazil. Threat categories were defined according to Gärdenfors et al. (2001).

The non-native species were classified according to the possible cause of occurrence in the Paranapanema River basin (the introduction vector). These were: (1) fish stocking via sport-angling, (2) bait, live-bait fishes used in sport angling; (3) fish farming, escapes from fish farms; (4) biological control, primarily mosquito control; (5) Itaipu Dam, invasion of non-native fish upstream following flooding of the natural biogeographic barrier of the Sete Quedas Falls between the Medium and Upper Paraná River regions; and (6) the aquarium trade. The identification of the introduction vector was based in CESP (1997), Orsi & Agostinho (1999), Bennemann et al. (2000), Graça &

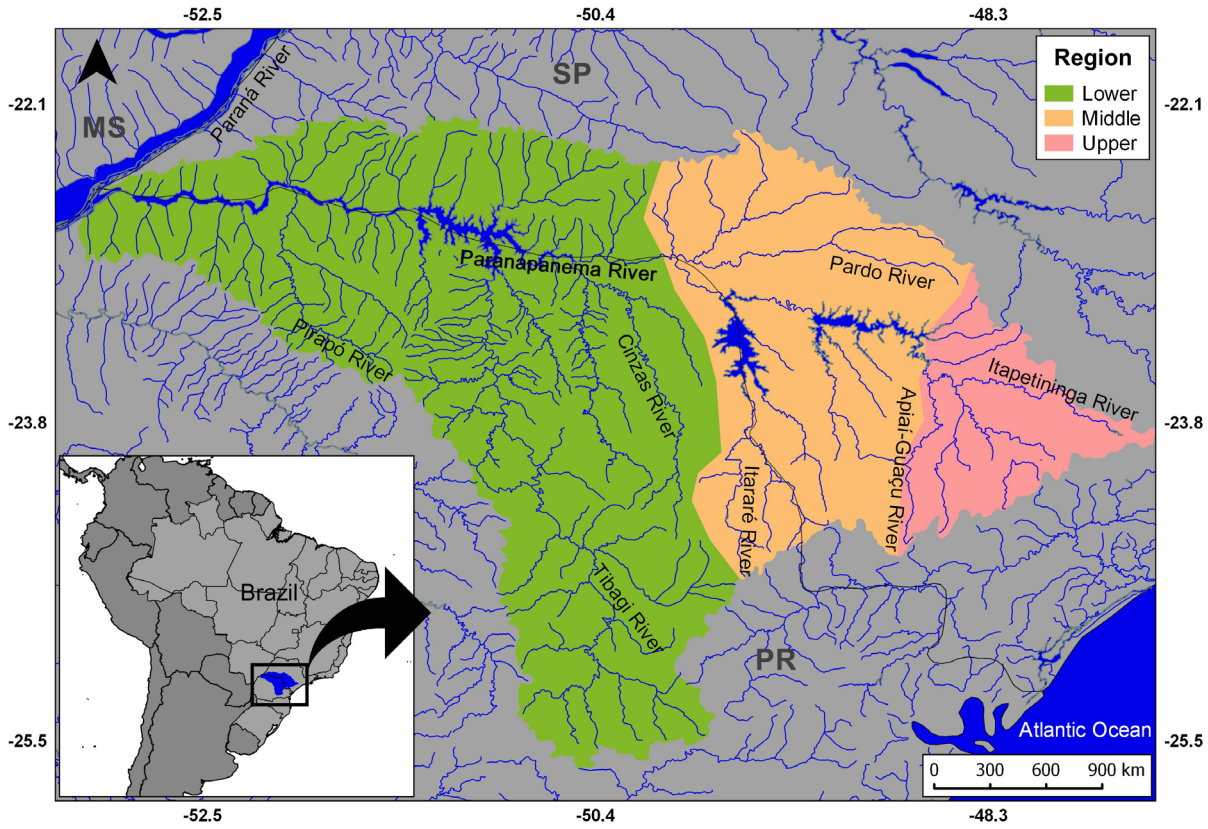


Figure 1. Inset: Location of the study area in Brazil. Main: the Paranapenema River basin divided in its three main regions according to Sampaio (1944). MS: state of Mato Grosso do Sul; SP: state of São Paulo; PR: state of Paraná.

Pavanelli (2007), Langeani et al. (2007), Júlio Júnior et al. (2009), Pelicice & Agostinho (2009), Britton and Orsi (2012), Ortega et al. (2015), Azevedo-Santos et al. (2016), and Ota et al. (2018).

3. *Data Analysis*

The total taxonomic richness was assessed using species accumulation curves. Non-parametric Incidence-Based Estimators: Bootstrap (Smith & van Belle 1984) and Chao 2 (Chao 1984), were used to obtain estimates of native species richness from Paranapanema River basin, considering the species presence/absence distribution in the subregions. For this analysis, we used the *EstimateS 9.1* software (Colwell 2006). For generating the map of Paranapanema River basin and their regions, the *Quantum GIS 2.18* software was employed (QGIS Development Team 2018).

Results

The compilation of 90 studies resulted in the identification of 10 orders, 40 families, 118 genera, and 225 species within the Paranapanema River basin. Of these, 165 species were identified as native, while 60 were non-native species introduced into the basin through several vectors (Table 2). Siluriformes (91 species) and Characiformes (83 species) represented the most species-rich orders, accounting together for 77% of all species from the basin. Cichliformes were the third species-rich order with 20 species found. The families with the highest number of species in the basin were Loricariidae (39 species), and Characidae (33 species), followed by Cichlidae (20 species), Anostomidae (16 species) and Pimelodidae (13 species).

Hypostomus was the richest genus with 16 identified species (four of which were non-native) distributed along the basin. Most species of this genus were present in the Tibagi River with 13 species, followed by Cinzas River (10 species), and finally Paranapanema River (Capivara Reservoir) and Pirapó River both with eight species. The next richest genera were *Astyanax* (eight species), *Leporinus,* and *Crenicichla* (both with six species each). Among the non-native species, the genus *Cichla* had five species, all introduced due to fish stocking for recreational fishing. There were no records of *Cichla* on the Upper Paranapanema River (Table 2).

The most common native species, widely distributed in the Paranapanema River basin, were *Astyanax lacustris* and *Hypostomus ancistroides* - present in 43 subregions - followed by *Rhamdia quelen* (34 subregions), *Hoplias* cf. *malabaricus* (33), *Geophagus brasiliensis* (30), *Astyanax* aff. *fasciatus* (29) and *Steindachnerina insculpta* (24). A comprehensive summarized list of species, with their current taxonomic status, are shown in Table 3.

In the Paranapema River basin, 22 species were classified as being threatened (Table 2), with the family Bryconidae having the highest number of threatened species in the basin. *Brycon nattereri* and *Brycon orbignyanus* are considered Critically Endangered in the state of São Paulo (Table 2). *Brycon nattereri* was found only

Table 1. Subregions sampled by 90 studies that investigated fish diversity in the Paranapanema River basin.

Subregion	Site	Source
	Lower Paranapanema	
1	Conceição Stream	Cionek et al. (2012)
2	Scherer Stream	Cionek et al. (2012)
3	Paranapanema (downstream of Rosana Reser-voir)	Barrella & Petrere Jr. (2003)
4	Paranapanema (Rosana Reservoir)	Barrella & Petrere Jr. (2003), Casatti et al. (2003), Abilhôa & Bastos (2005), Pelicice et al. (2005), Pelicice & Agostinho (2009), Garcia & Benedito (2010), Ferrareze & Nogueira (2011), Pelicice et al. (2014), Kipper et al. (2011), Almeida et al. (2017), Garcia et al. (2017)
5	Águas Claras Stream	Casatti (2004)
6	São Carlos Stream	Casatti (2004, 2005)
7	Diamante Stream	Garcia & Benedito (2010)
8	Pirapó River	Cunico et al. (2006, 2009), Garcia et al. (2012), Pagotto et al. (2012), Souza et al. (2014), Almeida et al. (2017)
9	Pirapozinho River	Almeida et al. (2017), Garcia et al. (in prep)
11	Santa Clara Stream	Castro et al. (2003)
12	Estação Stream	Castro et al. (2003)
13	Água Mole Stream	Castro et al. (2003)
14	Piau River	Castro et al. (2003)
15	Paranapanema (Taquaruçu Reservoir)	Carvalho et al. (2005b), Britto & Carvalho (2006), Almeida et al. (2017)
15	Anhumas River	Almeida et al. (2017), Garcia et al. (in prep)
16	Centenário Stream	Vidotto-Magnoni et al. (2015)
17	Tenente Stream	Vidotto-Magnoni et al. (2015)
18	Capim Stream	Vidotto-Magnoni et al. (2015)
19	Boa Esperança Stream	Castro et al. (2003)
20	Unnamed stream, municipality of Narandiba	Castro et al. (2003)
21	Paranapanema (Capivara Reservoir)	Barrella & Petrere Jr. (2003), Dias (2003), Carvalho et al. (2005b), Hoffmann et al. (2005), Bennemann et al. (2006, 2011), Orsi (2010), Orsi & Britton (2014)
22	Tibagi River	Bennemann et al. (1995, 2000, 2006, 2011), Dias (2003), Luiz et al. (2003), Shibatta & Cheida (2003), Hoffmann et al. (2005, 2015), Oliveira & Bennemann et al. (2005), Jerep et al. (2006), Sant'Anna et al. (2006), Shibatta et al. (2002, 2006a, b, 2007, 2008), Galves et al. (2007), Vieira & Shibatta (2007), Orsi (2010), Raio & Bennemann (2010), Garcia et al. (2012, 2014, 2015), Silva et al. (2015), Frantine-Silva et al. (2015), Almeida et al. (2017), Jerep & Shibatta (2017), Claro-Garcia et al. (2018)
23	Congonhas River	Frantine-Silva et al. (2015), Almeida et al. (2017), Garcia et al. (2019)
24	Cinzas River	Hoffmann et al. (2005), Vianna & Nogueira, (2008), Orsi (2010), Bennemann et al. (2011), Garcia et al. (2012), Costa et al. (2013), Galindo (2014), Frantine-Silva et al. (2015), Almeida et al. (2017)
25	Água Seca Stream	Castro et al. (2003)
26	Água do Macaco Stream	Castro et al. (2003)
27	Água da Laranjinha Stream	Castro et al. (2003)
28	Congonha Stream	Castro et al. (2003)
29	Canoas I Reservoir (Fish ladder)	Britto & Sirol (2005)
30	Paranapanema (Canoas I Reservoir)	Dias (2003), Orsi (2010), Almeida et al. (2013, 2017), Britto & Carvalho (2013), Frantine-Silva et al. (2015), Casimiro et al. (2017)
31	Canoas II Reservoir (Fish ladder)	Britto & Sirol (2005)

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Continuation Table 1.

Subregion	Site	Source
32	Paranapanema (Canoas II Reservoir)	Dias (2003), Souto et al. (2011), Almeida et al. (2013, 2017), Britto & Carvalho (2013), Frantine-Silva et al. (2015), Casimiro et al. (2017)
33	Pau D'alho Stream	Shibatta & Benine (2005)
	Middle Paranapanema	
34	Paranapanema (Salto Grande Reservoir)	Dias & Garavello, 1997, Dias (2003), Vianna (2008), Brandão et al. (2009), Deprá et al. (2018)
35	Pardo River	Roxo et al. (2012)
36	Novo River	Brandão et al. (2009)
37	Turvo River	Brandão et al. (2009)
38	Santana Stream	Castro et al. (2003)
39	Água das Antas Stream	Castro et al. (2003)
40	Ourinhos Fish ladder	Arcifa & Esguícero (2012).
41	Paranapanema (Chavantes Reservoir)	Vidotto-Magnoni (2009), Zanatta et al. (2010)
42	Verde River	Vidotto-Magnoni (2009)
43	Itararé River	Vidotto-Magnoni (2009)
44	Cruz Stream	Rosa et al. 2016
45	Taquaruçu Stream	Rosa et al. 2016
46	Taquaruçu II Stream	Barrella & Petrere Jr. (2003), Rosa et al. (2016)
47	Paranapanema (Jurumirim Reservoir)	Carvalho et al. (1998), Carvalho & Silva (1999), Barrella & Petrere Jr. (2003), Carvalho et al. (2003), Carvalho et al. (2005a, b), Novaes & Carvalho (2013) Kurchevski & Carvalho (2014), Sousa et al. (2016), Chuctaya et al. (2018), Nobile et al. (2018)
48	Veados Stream	Sousa et al. (2016)
49	Tamanduá River	Ochoa et al. (2017)
50	Taquari River	Nobile (2015), Sousa et al. (2016), Nobile et al. (2017), Nobile et al. (2018)
51	Unnamed stream, municipality of Paranapanema	Castro et al. (2003)
52	Virado Stream	Castro et al. (2003)
53	Unnamed stream, municipality of Pirajú	Castro et al. (2003)
54	Claro Stream	Castro et al. (2003)
	Upper Paranapanema	
55	Itapetininga River	Cerqueira & Smith (2015), Cerqueira et al. (2016)
56	Poço dos Patos Stream	Castro et al. (2003)
57	Alto Paranapanema Streams	Castro et al. (2004), Martins & Barrella (2008), Zawadzki et al. (2008), Cetra et al. (2012, 2016)

in the Tibagi and Cinzas rivers (Lower Paranapanema), and *Brycon orbignyanus* was also found only in two tributaries – the Cinzas, and Ribeirão dos Veados rivers of the Middle Paranapanema. *Salminus brasiliensis* is considered Vulnerable in Brazil and state of Paraná (only in the Lower Paranapanema). Members of Pimelodidae, such as the migratory catfishes *Steindachneridion scriptum* and *Zungaro jahu* are also Endangered in the state of São Paulo, and Vulnerable in the state of Paraná. Other species that are Critically Endangered in at least one of the lists are *Piaractus mesopotamicus* (Serrasalmidae) and *Crenicichla jupiaensis* (Cichlidae), which were found only in the Cinzas River (Table 1).

The most widely distributed non-native species were *Plagioscion squamosissimus*, present in 17 subregions, and *Oreochromis niloticus* which was registered in 16 subregions in the three primary areas of the basin. In the lower area, the Tibagi River was the subregion with the greatest diversity of non-native species (29 species), followed by the Rosana Reservoir (19 species), Cinzas River (17 species), and the Capivara Reservoir (16 species). In the middle area, the non-native species were concentrated in Salto Grande (15 species), and Jurumirim reservoirs (15 species). In the Upper Paranapanema River, only four non-native species were recorded: *Misgurnus anguillicaudatus*, *Cyprinus carpio*, *Satanoperca pappaterra* and *Poecilia vivipara*.

Table 2. Fish fauna from the Paranapanema River basin. Taxonomic classification followed Eschmeyer & Fong (2018). Vector introduction: (AT) Aquarium trade, (B) Bait, (BC) Biological control, (FF) Fish farming, (FS) Fish stocking, (ID) Itaipu Dam and (UK) Unknown. Conservation Status: (CR) Critically Endangered, (EN) Endangered, (VU) Vulnerable, (NT) Near Threatened. State of Paraná (PR) followed Mikich & Bérnils (2004). State of São Paulo (SP) followed Bressan et al. (2009) and ALESP (2014). Brazil (BR) followed ICMBio (2014, 2018). * = non-native species.

Class/Order/Species	Region			Vector	Conservation Status
	Lower	Middle	Upper		
Elasmobranchii					
Rajiformes					
Potamotrygonidae					
Potamotrygon motoro (Müller & Henle 1841)*	X			ID	
Actinopteri					
Cypriniformes					
Cobitidae					
Misgurnus anguillicaudatus (Cantor 1842)*		X	X	AT	
Cyprinidae					
Ctenopharyngodon idella (Valenciennes 1844)*	X			FF	
Cyprinus carpio Linnaeus 1758*	X	X	X	FS/FF	
Characiformes					
Crenuchidae					
Characidium fasciatum Reinhardt 1867		X			
Characidium gomesi Travassos 1956	X		X		
Characidium oiticicai Travassos 1967			X		VU (BR)
Characidium schubarti Travassos 1955	X		X		
Characidium aff. *zebra* Eigenmann 1909	X	X	X		
Erythrinidae					
Erythrinus erythrinus (Bloch & Schneider 1801)*	X			ID/B	
Hoplias cf. *malabaricus* (Bloch 1794)	X	X	X		
Hoplias intermedius (Günther 1864)*	X	X		UK	
Hoplias lacerdae Miranda Ribeiro 1908*	X	X		FS	VU (SP)
Parodontidae					
Apareiodon affinis (Steindachner 1879)	X	X			
Apareiodon ibitiensis Amaral Campos 1944	X		X		
Apareiodon piracicabae (Eigenmann 1907)	X	X			
Parodon nasus Kner 1859	X	X	X		
Cynodontidae					
Raphiodon vulpinus Spix & Agassiz 1829	X				
Serrasalmidae					
Metynnis lippincottianus (Cope 1870)*	X	X		ID	
Metynnis cf. *maculatus* (Kner 1858)*	X			ID	
Metynnis mola Eigenmann & Kennedy 1903		X			
Myloplus tiete (Eigenmann & Norris 1900)	X	X			EN (BR)
Piaractus mesopotamicus (Holmberg 1887)	X	X			CR (SP)
Serrasalmus maculatus Kner 1858	X	X	X		
Serrasalmus marginatus Valenciennes 1837*	X	X		ID	
Anostomidae					
Leporellus pictus (Kner, 1858)		X			
Leporellus vittatus (Valenciennes 1850)	X	X			
Leporinus amblyrhynchus Garavello & Britski 1987	X	X			

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Continuation Table 2.

Class/Order/Species	Region			Vector	Conservation Status
	Lower	Middle	Upper		
Leporinus friderici (Bloch 1794)	X	X	X		
Leporinus lacustris Amaral Campos 1945	X	X			
Leporinus octofasciatus Steindachner 1915	X	X	X		
Leporinus paranensis Garavello & Britski 1987	X	X	X		
Leporinus striatus Kner 1858	X	X	X		
Megaleporinus elongatus (Valenciennes 1850)	X	X			
Megaleporinus macrocephalus (Garavello & Britski 1988)*	X	X		FF/FS	
Megaleporinus obtusidens (Valenciennes 1837)	X	X			
Megaleporinus piavussu (Britski, Birindelli & Gara-vello 2012)		X			
Schizodon altoparanae Garavello & Britski 1990	X	X			
Schizodon borellii (Boulenger 1900)*	X	X		ID/FS	
Schizodon intermedius Garavello & Britski 1990	X	X			
Schizodon nasutus Kner 1858	X	X	X		
Curimatidae					
Cyphocharax modestus (Fernández-Yépez 1948)	X	X	X		
Cyphocharax naegelii (Steindachner 1881)	X	X			
Steindachnerina brevipinna (Eigenmann & Eigen-mann 1889)*	X			ID	
Steindachnerina insculpta (Fernández-Yépez 1948)	X	X	X		
Prochilodontidae					
Prochilodus lineatus (Valenciennes 1837)	X	X	X		
Lebiasinidae					
Pyrrhulina australis Eigenmann & Kennedy 1903	X	X			
Triportheidae					
Triportheus angulatus (Spix & Agassiz 1829)*	X	X		FS	
Triportheus nematurus (Kner 1858)*	X	X		ID/FS	
Bryconidae					
Brycon nattereri Günther 1864	X				CR (SP)/VU (BR)
Brycon orbignyanus (Valenciennes 1850)	X	X			CR (SP)/EN (BR) (PR)
Salminus brasiliensis (Cuvier 1816)	X				VU (BR) (PR)/NT (SP)
Salminus hilarii Valenciennes 1850	X	X	X		NT (BR) (SP)
Acestrorhynchidae					
Acestrorhynchus lacustris (Lütken 1875)	X	X			
Characidae					
Aphyocharax anisitsi Eigenmann & Kennedy 1903	X				
Aphyocharax dentatus Eigenmann & Kennedy 1903*	X			ID	
Astyanax biotae Castro & Vari 2004			X		
Astyanax bockmanni Vari & Castro 2007	X	X	X		
Astyanax aff. *fasciatus* (Cuvier 1819)	X	X	X		
Astyanax lacustris (Lütken 1875)	X	X	X		
Astyanax aff. *paranae* Eigenmann 1914	X	X	X		
Astyanax paranae Eigenmann 1914	X				
Astyanax aff. *scabripinnis* (Jenyns 1842)	X	X	X		

Continuation Table 2.

Class/Order/Species	Region			Vector	Conservation Status
	Lower	Middle	Upper		
Astyanax schubarti Britski 1964		X			
Bryconamericus aff. *iheringii* (Boulenger 1887)	X	X	X		
Bryconamericus coeruleus Jerep & Shibatta 2017	X				
Bryconamericus exodon Eigenmann 1907*	X			ID	
Cheirodon stenodon Eigenmann 1915	X	X			
Galeocharax gulo (Cope 1870)	X	X			
Hemigrammus marginatus Ellis 1911	X	X			
Hyphessobrycon anisitsi (Eigenmann 1907)	X	X	X		
Hyphessobrycon bifasciatus Ellis 1911		X			
Hyphessobrycon eques (Steindachner 1882)*	X	X		AT	
Hyphessobrycon reticulatus Ellis 1911	X				
Mimagoniates microlepis (Steindachner 1877)	X				
Moenkhausia intermedia Eigenmann 1908	X				
Moenkhausia sanctaefilomenae (Steindachner 1907)	X				
Odontostilbe avanhandava Chuctaya, Bührnheim & Malabarba 2018		X			
Oligosarcus paranensis Menezes & Géry 1983	X	X	X		
Oligosarcus pintoi Amaral Campos 1945	X	X			
Piabarchus stramineus (Eigenmann 1908)	X	X	X		
Piabina argentea Reinhardt 1867	X	X	X		
Planaltina britskii Menezes, Weitzman & Burns 2003		X			
Planaltina glandipedis Menezes, Weitzman & Burns 2003		X			
Roeboides descalvadensis Fowler 1932*	X			ID	
Serrapinnus heterodon (Eigenmann 1915)		X			
Serrapinnus notomelas (Eigenmann 1915)	X	X	X		
Gymnotiformes					
Gymnotidae					
Gymnotus carapo Linnaeus 1758	X	X	X		
Gymnotus inaequilabiatus (Valenciennes 1839)*	X	X		UK	
Gymnotus omarorum Richer-de-Forges, Crampton & Albert 2009	X				
Gymnotus pantanal Fernandes, Albert, Daniel-Silva, Lopes, Crampton & Almeida-Toledo 2005*	X			ID/B	
Gymnotus sylvius Albert & Fernandes-Matioli 1999	X	X	X		
Rhamphichthydae					
Rhamphichthys hahni (Meinken 1937)*	X			ID	
Rhamphichthys cf. *rostratus* (Linnaeus 1766)	X				
Hypopomidae					
Brachyhypopomus pinnicaudatus (Hopkins, Comfort, Bastian & Bass 1990)*		X		B	
Sternopygidae					
Eigenmannia trilineata López & Castello 1966	X	X			
Eigenmannia virescens (Valenciennes 1836)	X	X	X		
Sternopygus macrurus (Bloch & Schneider 1801)	X	X			

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Continuation Table 2.

Class/Order/Species	Region			Vector	Conservation Status
	Lower	Middle	Upper		
Apteronotidae					
Apteronotus albifrons (Linnaeus 1766)	X				
Apteronotus brasiliensis (Reinhardt 1852)	X				
Apteronotus caudimaculosus de Santana 2003*	X			ID	
Apteronotus ellisi (Alonso de Arámburu 1957)*	X	X		ID	
Sternarchorhynchus britskii Campos-da-Paz 2000	X				VU (SP)
Siluriformes					
Cetopsidae					
Cetopsis gobioides Kner 1858	X				
Aspredinidae					
Bunocephalus larai Ihering 1930	X				
Auchenipteridae					
Ageneiosus militaris Valenciennes 1835	X	X			
Auchenipterus osteomystax (Miranda Ribeiro 1918)*	X			ID	
Glanidium cesarpintoi Ihering 1928	X				
Tatia intermedia (Steindachner 1877)*	X			UK	
Tatia neivai (Ihering 1930)	X	X			
Trachelyopterus galeatus (Linnaeus 1766)*	X			ID	
Doradidae					
Ossancora eigenmanni (Boulenger 1895)*	X			ID	
Pterodoras granulosus (Valenciennes 1821)*	X			ID	
Rhinodoras dorbignyi (Kner 1855)	X	X			
Trachydoras paraguayensis (Eigenmann & Ward 1907)*	X			ID	
Heptapteridae					
Cetopsorhamdia iheringi Schubart & Gomes 1959	X	X	X		
Imparfinis borodini Mees & Cala 1989	X		X		
Imparfinis mirini Haseman 1911	X	X	X		
Phenacorhamdia hoehnei (Miranda Ribeiro 1914)	X				
Phenacorhamdia tenebrosa (Schubart 1964)	X	X	X		
Pimelodella avanhandavae Eigenmann 1917	X	X	X		
Pimelodella gracilis (Valenciennes 1835)	X	X			
Pimelodella meeki Eigenmann 1910	X	X			
Rhamdia quelen (Quoy & Gaimard 1824)	X	X	X		
Rhamdiopsis moreirai Haseman 1911	X				VU (PR)
Pimelodidae					
Hypophthalmus edentatus Spix & Agassiz 1829*	X			ID	
Iheringichthys labrosus (Lütken 1874)	X	X			
Megalonema platanum (Günther 1880)	X				
Pimelodus absconditus Azpelicueta 1995	X				
Pimelodus maculatus Lacepède 1803	X	X	X		
Pimelodus microstoma Steindachner 1877	X	X			
Pimelodus ornatus Kner 1858*	X			ID	
Pimelodus paranaensis Britski & Langeani 1988	X				VU (SP)
Pinirampus pirinampu (Spix & Agassiz 1829)	X				

Continuation Table 2.

Class/Order/Species	Region			Vector	Conservation Status
	Lower	Middle	Upper		
Pseudoplatystoma corruscans (Spix & Agassiz 1829)	X				VU (SP)/NT (PR)
Sorubim lima (Bloch & Schneider 1801)*	X			ID	
Steindachneridion scriptum (Miranda Ribeiro 1918)	X	X			EN (SP) (BR)/VU (PR)
Zungaro jahu (Ihering 1898)	X				EN (SP)/VU (PR)
Pseudopimelodidae					
Microglanis garavelloi Shibatta & Benine 2005	X				
Pseudopimelodus mangurus (Valenciennes 1835)	X				VU (SP) (PR)
Rhyacoglanis paranensis Shibatta & Vari 2017	X				
Clariidae					
Clarias gariepinus (Burchell 1822)*	X			ID	
Ictaluridae					
Ictalurus punctatus (Rafinesque 1818)*		X		ID	
Trichomycteridae					
Paravandellia oxyptera Miranda Ribeiro 1912	X				
Trichomycterus candidus (Miranda Ribeiro 1949)	X				
Trichomycterus castroi de Pinna 1992	X				
Trichomycterus davisi (Haseman 1911)	X		X		
Trichomycterus diabolus Bockmann, Casatti & de Pinna 2004	X	X	X		
Trichomycterus pascuali Ochoa, Silva, Costa e Silva, Oliveira & Datovo 2017		X			
Callichthyidae					
Callichthys callichthys (Linnaeus 1758)	X	X			
Corydoras aeneus (Gill 1858)	X	X			
Corydoras ehrhardti Steindachner 1910	X				
Corydoras longipinnis Knaack 2007	X				
Corydoras paleatus (Jenyns 1842)	X				
Hoplosternum littorale (Hancock 1828)	X	X	X		
Loricariidae					
Ancistrus cf. *cirrhosus* (Valenciennes 1836)	X				
Curculionichthys insperatus (Britski & Garavello 2003)	X				
Hisonotus depressinotus (Miranda Ribeiro 1918)	X				
Hisonotus francirochai (Ihering 1928)	X				
Hypostomus albopunctatus (Regan 1908)	X				
Hypostomus ancistroides (Ihering 1911)	X	X	X		
Hypostomus hermanni (Ihering 1905)	X	X			
Hypostomus iheringii (Regan 1908)	X	X			
Hypostomus margaritifer (Regan 1908)	X	X	X		
Hypostomus multidens Jerep, Shibatta & Zawadzki 2007		X			
Hypostomus myersi (Gosline 1947)*	X			UK	
Hypostomus nigromaculatus (Schubart 1964)	X	X	X		
Hypostomus paulinus (Ihering 1905)	X	X			
Hypostomus regani (Ihering 1905)	X	X			
Hypostomus cf. *roseopunctatus* Reis, Weber & Malabarba 1990*		X		UK	

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Continuation Table 2.

Class/Order/Species	Region			Vector	Conservation Status
	Lower	Middle	Upper		
Hypostomus strigaticeps (Regan 1908)	X	X			
Hypostomus ternetzi (Boulenger 1895)*		X		ID	
Hypostomus tietensis (Ihering 1905)	X	X			
Hypostomus topavae (Godoy 1969)	X	X			
Hypostomus variostictus (Miranda Ribeiro 1912)*	X			UK	
Isbrueckerichthys alipionis (Gosline 1947)			X		
Isbrueckerichthys calvus Jerep, Shibatta, Pereira & Oyakawa 2006	X				
Isbrueckerichthys duseni (Miranda Ribeiro 1907)			X		VU (SP)
Isbrueckerichthys saxicola Jerep, Shibatta, Pereira & Oyakawa 2006	X				CR (BR)
Loricaria simillima Regan 1904	X				
Loricariichthys labialis (Boulenger 1895)*	X			UK	
Loricariichthys platymetopon Isbrücker & Nijssen 1979*	X			ID	
Megalancistrus parananus (Peters 1881)	X	X			
Neoplecostomus botucatu Roxo, Oliveira & Zawadzki 2012		X			VU (BR)
Neoplecostomus paranensis Langeani 1990	X		X		VU (SP)/(EN) BR
Neoplecostomus selenae Zawadzki, Pavanelli & Langeani 2008	X		X		VU (SP)
Neoplecostomus yapo Zawadzki, Pavanelli & Lange-ani 2008	X		X		
Otothyropsis biamnicus Calegari, Lehmann A. & Reis 2013	X	X	X		
Paraloricaria vetula (Valenciennes 1835)	X				
Proloricaria prolixa (Isbrücker & Nijssen 1978)	X	X			
Pterygoplichthys ambrosettii (Holmberg 1893)*	X	X		ID/AT	
Rhinelepis strigosa Valenciennes 1840	X				
Rineloricaria latirostris (Boulenger 1900)	X	X			
Rineloricaria pentamaculata Langeani & de Araujo 1994	X	X	X		
Synbranchiformes					
Synbranchidae					
Synbranchus marmoratus Bloch 1795	X	X	X		
Pleuronectiformes					
Achiridae					
Catathyridium jenynsii (Günther 1862)*	X			ID	
Cichliformes					
Cichlidae					
Astronotus crassipinnis (Heckel 1840)*		X		ID/FS/FF/AT	
Astronotus ocellatus (Agassiz 1831)*	X	X		UK	
Australoheros facetus (Jenyns, 1842)	X		X		
Cichla kelberi Kullander & Ferreira 2006*	X	X		FS	
Cichla monoculus Spix & Agassiz 1831*	X	X		FS	
Cichla ocellaris Bloch & Schneider 1801*		X		FS	
Cichla piquiti Kullander & Ferreira 2006*		X		FS	
Cichla temensis Humboldt 1821*		X		FS	

Continuation Table 2.

Class/Order/Species	Region			Vector	Conservation Status
	Lower	Middle	Upper		
Cichlasoma paranaense Kullander 1983	X	X			
Coptodon rendalli (Boulenger 1897)*	X	X		FS	
Crenicichla britskii Kullander 1982	X	X			
Crenicichla haroldoi Luengo & Britski 1974	X	X			
Crenicichla jaguarensis Haseman 1911	X	X			
Crenicichla jupiaensis Britski & Luengo 1968	X				CR (SP)/EN (BR)
Crenicichla lepidota Heckel 1840	X				
Crenicichla niederleinii (Holmberg 1891)	X	X			
Geophagus brasiliensis (Quoy & Gaimard 1824)	X	X	X		
Laetacara araguaiae Ottoni & Costa 2009*	X			AT	
Oreochromis niloticus (Linnaeus 1758)*	X	X	X	FS/FF	
Satanoperca pappaterra (Heckel 1840)*	X			FF/AT	
Cyprinodontiformes					
Cynolebiidae					
Melanorivulus apiamici (Costa 1989)	X				
Poeciliidae					
Cnesterodon hypselurus Lucinda & Garavello 2001	X				EN (BR)
Phalloceros harpagos Lucinda 2008	X	X	X		
Phalloceros reisi Lucinda 2008			X		
Poecilia reticulata Peters 1859*	X	X		BC/AT	
Poecilia vivipara Bloch & Schneider 1801*			X	BC/AT	
Xiphophorus hellerii Heckel 1848*	X			AT	
Perciformes					
Centrarchidae					
Micropterus salmoides (Lacepède 1802)*	X			FS	
Sciaenidae					
Plagioscion squamosissimus (Heckel 1840)*	X	X		FS/FF	

When considering only the species native to the Paranapanema basin (165 species) which occurred in each of the 57 subregions, the accumulation curve tended to stabilize (Figure 2), but non-parametric estimators indicated that the total richness of native species to the basin is underestimated (Bootstrap = 182.29 ± 0.00, Chao-2 = 223.98 ± 25.43). Our compilation from the studies represents 74% (Chao-2) and 91% (Bootstrap) of the native species estimated for the basin.

The Lower Paranapanema was the region with the highest species richness (146 native and 51 non-native species) (Figure 3). Most of its richness was in the Tibagi River which presented 158 species, followed by Cinzas (114 species), Pirapó (76 species) and Congonhas (63 species) rivers respectively. Of these, 79 occurred only in the Lower Paranapanema as a medium to large sized native species including *Brycon nattereri*, *Salminus brasiliensis*, *Megalonema platanum*, *Pimelodus paranaenses*, *Pinirampus pirinampu*, *Pseudoplatystoma corruscans*, *Zungaro jahu,* and *Pseudopimelodus mangurus*.

The middle region presented 103 native and 27 non-native species, with 75 native species recorded to the Salto Grande Reservoir alone. Some of these were recorded only within the middle region, such as *Characidium fasciatum*, *Leporellus pictus,* and *Odontostilbe avanhandava*. In the Upper Paranapanema, 61 species (57 of which are native) were recorded (Figure 3), with the majority of them being small to medium size species, such as *Characidium oiticicai, Isbrueckerichthys duseni* and *Phalloceros reisi.* Most of the species in this region (45 species) were collected in headwater streams.

A majority of the investigated studies were performed within the lower region of the Paranapanema River (56 studies), comprising 61% of those reviewed. The Capivara Reservoir and its direct tributaries presented 32 studies, most of them concentrated in the Tibagi River (29 studies). The Rosana Reservoir and tributaries were the second most studied subregion (17 studies). In the Middle Paranapanema 20 studies were conducted, with the Jurumirim Reservoir and its tributaries (11 studies) being the most studied site. The Upper Paranapanema was the

Table 3. Current taxonomic status of the species names found the literature from the Paranapanema River basin, based on Eschmeyer et al. (2018).

Previous Identification	Current Identification
Ageneiosus valenciennesi Bleeker 1864	Synonym of *Ageneiosus militaris* Valenciennes 1835
Astyanax altiparanae Garutti & Britski 2000	Synonym of *Astyanax lacustris* (Lütken 1875)
Astyanax bimaculatus (Linnaeus 1758)	*Astyanax lacustris* (Lütken 1875)
Astyanax scabripinnis (Jenyns 1842)	*Astyanax paranae* Eigenmann 1914
Bryconamericus stramineus Eigenmann 1908	Valid as *Piabarchus stramineus* (Eigenmann 1908)
Cheirodon notomelas (Eigenmann 1915)	Valid as *Serrapinnus notomelas* (Eigenmann 1915)
Cichlasoma facetum (Jenyns 1842)	Valid as *Australoheros facetus* (Jenyns 1842)
Dysichthys larai (Ihering 1930)	Valid as *Bunocephalus larai* Ihering 1930
Galeocharax knerii (Steindachner 1879)	Synonym of *Galeocharax gulo* (Cope 1870)
Hisonotus insperatus Britski & Garavello 2003	Valid as *Curculionichthys insperatus* (Britski & Garavello 2003)
Imparfinis schubarti (Gomes 1956)	Synonym of *Imparfinis mirini* Haseman 1911.
Leporinus elongatus Valenciennes 1850	Valid as *Megaleporinus elongatus* (Valenciennes 1850)
Leporinus macrocephalus Garavello & Britski 1988	Valid as *Megaleporinus macrocephalus* (Garavello & Britski 1988)
Leporinus obtusidens Valenciennes 1836	Valid as *Megaleporinus obtusidens* (Valenciennes 1837)
Leporinus piavussu (Britski, Birindelli & Garavello 2012)	Valid as *Megaleporinus piavussu* (Britski, Birindelli & Garavello 2012)
Loricaria prolixa (Isbrücker & Nijssen 1978)	Valid as *Proloricaria prolixa* (Isbrücker & Nijssen 1978)
Loricaria vetula (Valenciennes 1835)	Valid as *Paraloricaria vetula* (Valenciennes 1835)
Megalancistrus aculeatus (Perugia 1891)	Synonym of *Megalancistrus parananus* (Peters 1881)
Microlepidogaster depressinotus Miranda Ribeiro 1918	Valid as *Hisonotus depressinotus* (Miranda Ribeiro 1918)
Myleus tiete (Eigenmann & Norris 1900)	Valid as *Myloplus tiete* (Eigenmann & Norris 1900).
Odontostilbe stenodon (Eigenmann 1915)	Valid as *Cheirodon stenodon* Eigenmann 1915
Otocinclus depressicauda Miranda Ribeiro 1918	Valid as *Hisonotus depressicauda* (Miranda Ribeiro 1918)
Parodon tortuosus Eigenmann & Norris 1900	Synonym of *Parodon nasus* Kner 1859
Pimelodus heraldoi Azpelicueta 2001	Synonym of *Pimelodus microstoma* Steindachner 1877
Porotergus ellisi Alonso de Arámburu 1957	Valid as *Apteronotus ellisi* (Alonso de Arámburu 1957)
Pseudocetopsis gobioides (Kner 1858)	Valid as *Cetopsis gobioides* Kner 1858
Pseudopimelodus roosevelti Borodin 1927	Synonym of *Pseudopimelodus mangurus* (Valenciennes 1835)
Pseudopimelodus zungaro (Humboldt 1833)	Valid as *Zungaro jahu* (Ihering 1898).
Rhamdia hilarii (Valenciennes, 1840)	Synonym of *Rhamdia quelen* (Quoy & Gaimard 1824)
Roeboides paranensis Pignalberi 1975	Synonym of *Roeboides descalvadensis* Fowler 1932
Steindachneridion scripta (Miranda Ribeiro 1918)	Valid as *Steindachneridion scriptum* (Miranda Ribeiro 1918)
Tilapia rendalli (Boulenger 1897)	Valid as *Coptodon rendalli* (Boulenger 1897)

least investigated region (seven studies), five of which were species inventories, and two were new species descriptions for *Astyanax biotae* in 2004 and *Neoplecostomus selenae* in 2008.

Discussion

The number of species identified by our study (225) is significantly higher than reports conducted exclusively in reservoirs, which recorded 155 (Duke Energy 2008) and 161 species (Pelicice et al. 2018) for the Paranapanema River, respectively. Here, we have used both basin-wide surveys (*i.e.,* from reservoirs and fish ladders and free-flowing stretches including tributaries, streams, and marginal lagoons), as well as species descriptions to more comprehensively evaluate the species diversity of the region. The accumulation curve indicated that a majority of the native species (165) were represented and we estimate that the total richness would be between 182 and 223 species of native fish in the basin, a higher value than predicted by Pelicice et al. (2018) (125 to 132).

The most species-rich genus in this study, *Hypostomus,* is widely distributed in the rivers of the Paraná-Paraguay system (Weber 2003). The armored catfish species of *Hypostomus* are known for living in clear running water on the rocky bottoms of mostly large South American rivers (Garavello & Garavello, 2004). Within the genus, the species *Hypostomus ancistroides* is a common and widely distributed species, occurring throughout the Upper Paraná River system from where it was initially described (Weber 2003). *Astyanax lacustris* is also widely

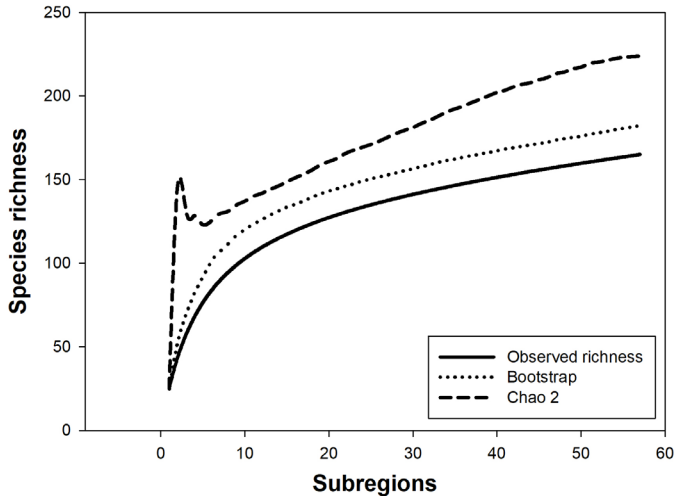


Figure 2. Native species accumulation curves controlled by presence/absence of native species in 57 subregions.

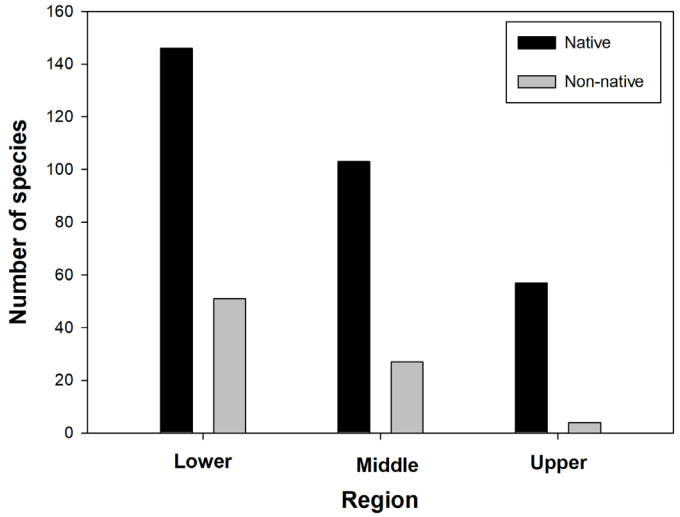


Figure 3. Species richness separated as native and non-native fishes in the Paranapanema River basin.

distributed, and along with its congeners, is the most diversified of the Characidae, comprising more than a hundred species widely distributed and abundant in the Brazilian watersheds. This extensive distribution indicates that the genus probably has significant ecological importance and adaptive plasticity (Orsi et al. 2004).

The highest richness was recorded for the orders Siluriformes and Characiformes, as usually found in the Neotropical region (Lowe-McConnell 1999). Cichliformes were the third most species-rich order in the basin, though mainly by the presence of non-native species. Among them, the genus *Cichla,* which was introduced to the basin in 1999 (Orsi & Agostinho 1999) to provide fish stocking for sport-angling, stands out with five introduced species. The species of this group benefit from lentic environments (Franco et al. 2018) provided by the reservoirs of the Paranapanema River. This scenario can be observed in other basins of the Upper Paraná River (Langeani et al. 2007). Many non-native species are more abundant in lentic environments, especially those of the family Cichlidae (Langeani et al. 2007, Franco et al. 2018). Regarding non-native fishes, there still appears to be no consensus on the exact number of species, with previous studies having reported 47 (Garcia et al. 2018), and 50 (Pelicice et al. 2018) non-native species in the basin.

In this study, 60 non-native fish species were registered in the Paranapanema River basin. In addition to the actual number of introduced species, the Paranapanema River basin can be considered the most invaded of the Upper Paraná River basin (Ortega et al. 2015, Garcia et al. 2018). Among the non-native species, 30 species occurred within the Paranapanema River (and Upper Paraná) after the flooding of the Sete Quedas Falls (Júlio Jr. et al. 2009), 16 species were introduced for restocking, nine species due to the aquarium trade, seven by escapes from fish farms, five by live-bait fish used in sport angling, and one for biological control. Among the most distributed non-native species in the basin, *P. squamosissimus* was introduced by stocking, while *O. niloticus* often escapes from fish farms (Ortega et al. 2015). The introduction of non-native species, compounded by other anthropic actions, threaten the richness of fish species present in this critical basin (Pelicice & Agostinho 2009, Garcia et al. 2018).

The occurrence of several species with some degree of threat and restricted distribution indicates that biodiversity conservation in the Paranapanema River is a highly relevant issue. Past studies have shown Bryconidae populations are in decline, with few occurrences in the basin (ICMBio 2018). Meanwhile, *Brycon nattereri* and *B. orgbignyanus* are critically endangered in the state of São Paulo but occur in the rivers Tibagi, Cinzas, and Ribeirão dos Veados (Mikich & Bérnils 2004, Bressan et al. 2009, ALESP 2014). Also, the occurrence of *Piaractus mesopotamicus* and *Crenicichla jupiaensis* in the Cinzas River highlights the importance of dam-free tributaries for the maintenance of native species in the basin (Nunes et al. 2015, Marques et al. 2018). *Salminus brasiliensis*, *Steindachneridion scriptum*, and *Zungaru jahu* – three long distances migratory species – have a low occurrence within this study. This decline in migratory species is demonstrated in several previous works (Okada et al. 2005, Godinho & Kynard 2008, Pelicice & Agostinho 2008; Pompeu et al. 2012, Orsi et al. 2016). The Cascade reservoir system along the Paranapanema River interrupts long-distance migration and creates unsuitable environments for migratory fish resulting from the presence of lentic areas and flow regulation (Agostinho et al. 2003, Agostinho et al. 2008, Pelicice et al. 2018). Among the species with restricted distribution, we found several small species that inhabit small streams of headwaters, namely *Characidium fasciatum* (Carvalho et al. 2005a), *Planaltina* spp. (Brandão et al. 2009, Deprá et al. 2018), *Characidium oiticicai* (Cetra et al. 2012), *Metynnis mola*, *Hyphessobrycon bifasciatus* (Arcifa & Esguícero 2012), *Isbrueckerichthys alipionis* (Martins & Barrella 2008), *Paraloricaria vetula* (Barrella & Petrere Jr. 2003), *Neoplecostomus botucatu* (Roxo et al. 2012), and *Cnesterodon hypselurus* (Silva et al. 2015). These species present a high degree of endemism and restricted geographic distribution, while having no commercial value and being highly dependent on riparian vegetation for food, reproduction, and shelter. They are more likely to have their conservation threatened because theses species tend to pass their entire life cycles in geographically restricted areas (Castro and Menezes, 1998, Castro et al. 2003).

The Tibagi River basin is the most studied region of the Paranapanema River. Together with the Cinzas River, the Tibagi assists in the maintenance of species of the Paranapanema River (Shibatta et al. 2002, Hoffmann et al. 2005, Shibatta et al. 2007). However, it is noteworthy that studies of universities near these sub-basins, such

as Universidade Estadual de Londrina, and Universidade Estadual de Maringá have likely contributed to the highest number of species survey data in these rivers. In the Middle Paranapanema, studies carried out by the Universidade Estadual Paulista within the Jurumirim and Chavantes reservoirs have been especially valuable. Conversely, the Upper Paranapanema region was investigated to a lesser extent. The region is characterized by numerous streams, which are underexplored and serve as shelters for smaller species (Langeani et al. 2007). The previous description of new species in the Upper Paranapanema River (Castro & Vari, 2004, Zawadzki et al. 2008), coupled with a general lack of studies for this region, suggests that there is still great potential for new descriptions in the headwaters of the tributaries (Buckup et al. 2007, Langeani et al. 2007). More importantly, there are also species that have a threatened conservation status, such as *Isbrueckerichthys duseni*, as well as the high percentage of species for which there is little to no scientific knowledge (Castro et al. 2003), reinforcing Castro & Menezes (1998) recommendation to prioritize scientific exploration of streams and headwaters in these regions.

Despite the significant richness of fish species known, the region of the Paranapanema River has the highest population density in Brazil (ANA 2016) as a result of electricity production, agribusiness, industry, and water supply (Novaes & Carvalho 2013) occurring in the area. Additionally, it is also used as a source of livelihood for riverside communities (Agostinho et al. 2007b, 2016). The conservation of fish fauna is one of the greatest challenges faced today (Cerqueira & Smith 2015). It must be emphasized that, despite the importance of developing the country through the exploitation basin's resources, maintenance of its biodiversity is just as crucial.

Tributaries where threatened fishes occur should remain un-dammed (*e.g.,* Tibagi, Cinzas, Pirapó, and Congonhas rivers) to protect such species. Many of these endangered species migrate from long distances and present population decline mainly due to the damming of the mainstem (Agostinho et al 2003). Furthermore, the number of non-native fish species in the Paranapanema River basin is alarming. Urgent actions should be taken to promote awareness and educate the population about the environmental, social, and economic risks caused by these invasive species.

Conservation actions must be carried out by all who depend on the resources of the Paranapanema River Basin, including the appropriate use of water, reduction of fertilizers, and agrochemicals, since the preservation of sources, headwaters, tributaries, and the riparian vegetation relied upon by various species of aquatic fauna. Our findings may be used to support management actions and conservation strategies, and to identify regions within the basin that require better inventories or conservation status updates of its species.

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Author Contributions

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Ana Paula Vidotto-Magnoni: Contribution to data collection; data analysis and interpretation; contribution to critical revision, adding intellectual content.

Armando Cesar Rodrigues Casimiro: Contribution to data collection; data analysis and interpretation; manuscript preparation.

Norberto Castro Vianna: Contribution in the concept of the study; contribution to critical revision, adding intellectual content.

Fernanda Simões de Almeida: Contribution in the concept of the study; contribution to critical revision, adding intellectual content.

Fernando Camargo Jerep: Contribution to data collection; data analysis and interpretation; manuscript preparation; contribution to critical revision, adding intellectual content.

Mario Luis Orsi: Contribution in the concept of the study; manuscript preparation; contribution to critical revision, adding intellectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

We declare that the procedures used in this study have no conflict with the Brazilian Laws regarding the use of vertebrates in scientific research.

Data availability

Our data was compiled from published literature, and appropriated cited along the manuscript.

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Short Communication

A new synonym for *Micropholis gardneriana* (Sapotaceae) with complete description, anatomy and distribution notes

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Abstract: In the present work, we synonymize *Micropholis compta* under *M. gardneriana* due to the overlap of morphoanatomical characters and the absence of distinctive attributes, verified during taxonomic and anatomical study of the genus *Micropholis* for Brazil. This study provides an updated description of *M. gardneriana*, including macro- and micro-morphological data, a distribution map, and comments on conservation status, ecological and taxonomy.

Keywords: *Chrysophylloideae, leaf anatomy, Neotropics, South America, taxonomy.*

Um novo sinônimo para *Micropholis gardneriana* (Sapotaceae) com descrição completa, anatomia e notas de distribuição

Resumo: No presente trabalho, sinonimizamos *Micropholis* compta sob *M. gardneriana* devido à sobreposição de caracteres morfoanatômicos e ausência de atributos distintivos, verificado durante estudo taxonômico e anatômico do gênero *Micropholis* para o Brasil. Este estudo fornece uma descrição atualizada de *M. gardneriana*, incluindo dados macro e micromorfológicos, um mapa de distribuição e comentários sobre status de conservação, ecologia e taxonomia.

Palavras-chave: *Chrysophylloideae, anatomia foliar, Neotrópicos, América do Sul, taxonomia.*

Introduction

Micropholis (Griseb.) Pierre, a Neotropical genus of Sapotaceae (Chrysophylloideae), currently comprises 38 species distributed across tropical and subtropical regions of Central and South America and the Caribbean islands, with the highest taxonomic diversity concentrated in humid tropical areas of Brazil (Pennington 1991; Swenson & Anderberg 2005). Twenty-nine species of *Micropholis* occur in Brazil, predominantly in the Amazon Forest, where 26 taxa have been documented, 22 of which are endemic (Pennington 2006; Brazilian Flora 2020 under construction). Some species, though, occur in the Atlantic Forest, the Caatinga and the Cerrado (Pennington 2006; Brazilian Flora 2020 under construction). *Micropholis* represents an important component of lowland humid forest of South America the genus is ecological valuable and certain species are used by the lumber industry (Cruz & Carvalho 2003; Reis et al. 2013; Raabe et al. 2017).

Representatives of *Micropholis* are characterized by their arboreal or shrubby habit, simple, alternate distichous or spiraled leaves, secondary and tertiary veins, often closely parallel, giving a striated appearance to the leaf lamina, unisexual and bisexual flowers, included or exserted stamens, lanceolate, subulate or petaloid staminodes, present or absent disc, (4-)5-locular ovary, bacoid fruits and laterally compressed seeds, with endosperm (Pennington 1990).

Pennington (1990) organized the genus into two sections. *Micropholis* sect. *Micropholis* comprised 29 species widely distributed throughout tropical America. The section is characterized by the presence of included stamens and corolla less than 10 mm long, with erect lobes. While *M.* sect. *Exsertistamen* comprises only nine species, distributed in the Guianas region that extends through the Brazilian Amazon to Peru; the species are characterized by exserted stamens and corolla over 10 mm long, with spaced or reflexed lobes.

The morphology of the corolla is important in delimiting the sections and species of *Micropholis.* However, the absence of flowers on many herbarium specimens possibly a consequence of the ephemeral nature of the flower of many Chrysophylloideae species (Terra-Araujo et al. 2012) impedes interspecific delimitation. Moreover, vegetatively, *Micropholis* can be easily confused with some species of the genera

Chrysophyllum L., *Diploon* Cronquist and *Pouteria* Aubl., owing to similarities in their morphological characters.

The taxonomic delimitation of some species of *Micropholis*, such as *M. compta* and *M. gardneriana*, is not consistent across the taxonomic and floristic treatments (Pierre 1904; Pennington 1990; Souza et al. 2017). Despite being treated as distinct taxa, the current circumscriptions of these species describe overlapping diagnostic morphological characters, the differences between them being predominantly quantitative.

Quantitative and qualitative morphological variations, often observed in leaves, can be influenced by the different environmental conditions to which the plants are subjected (Bunger et al. 2015). Therefore, taxonomic and biosystematic studies must necessarily include specimens from several regions to ensure that taxonomic delimitations are precise, especially for widely distributed species (Landrum 1986).

During the elaboration of the taxonomic synopsis of the Brazilian species of *Micropholis* for this, we analyzed the protologues, the most recent taxonomic review of the species (Pennington 1990), the *typus* collections of the *Micropholis* species, and the anatomical material we concluded that *M. compta* Pierre exhibits morphological and anatomical characters that support its inclusion as a synonym of *Micropholis gardneriana* (A. DC.) Pierre.

Materials and Methods

The present study was based on an analysis of specimens from collections of the herbariums ASE, ALCB, BHCB, CEN, CENARGEN, CEPEC, CVRD, EUA, F, G, HUA, INPA, NY, MO, MBML, NL, PEURF, RB, UEC and US [acronyms according to Thiers (2019)]. The types were examined through images available on the website JSTOR Global plants (https://plants.jstor.org) (Ithaka 2019), and the protologues were consulted for all names.

Morphological attributes were obtained through direct observation of all specimens using a stereo microscope. To analyze the morphological variation between *M. compta* and *M. gardneriana*, we created a matrix containing the following vegetative and reproductive measurements for each species: leaf length, leaf width, petiole length, petiole width, flower length, sepal length, sepal width, and corolla length. Four of the seven measured characters were chosen because they were used by Pennington (1990) to establish the analyzed species (Table. 1). The measurements were taken with the aid of a digital pachymeter and a millimeter ruler. We conducted a descriptive statistical analysis of the absolute values of each character to obtain the measures of central tendency (average and median) and measures of dispersion (standard deviation, coefficient of variation, and amplitude); for this analysis, we used the software Excel (Microsoft Corporation 2009). Table 2 shows the variation in the measurements of each species. The terminology used to describe the morphological characters follows Beentje (2016). Information about the coloration of the fruits and seeds is based on dry material. Data related to habit, habitat, distribution and phenology were obtained through consulting herbarium labels and field notes.

The anatomical study was based on leaves of the specimens listed in the Table 3. Herborized leaf samples were submitted to the process of herborization reversal (Smith & Smith 1942), dehydrated in ethyl series and stored in 70% ethanol. Cross and longitudinally sections of the leaf lamina (region middle) and the petiole, which were performed manually, were clarified in 50% sodium hypochlorite and stained with basic fuchsin and astra blue. The semi-permanent laminas were mounted in glycerinated gelatin and sealed with colorless nail polish (Kraus & Arduin 1997). Analysis and image capture were performed using a light microscope (model NO216T, New Optics, Ningbo, China) and an CMOS-0.5 Microscope Camera (Haryana, India). Images were captured using the software TCapture. The terminology used to describe the anatomical characters follows Howard (1979), Theobald et al. (1979) and Metcalfe & Chalk (1983). The conservation status of the species was defined according to the criterion "B" proposed by the IUCN Red List, Version 3.1 (IUCN 2001), considering the extent of occurrence (EOO) and area of occupation (AOO), both obtained based on the geographic coordinates of the species locations, plotted on the GeoCAT (http://geocat.kew.org/) (Bachman et al. 2011). We created the distribution map in QGIS 2.18.28 software (Quantum GIS Development Team 2012) considering only confirmed occurrences.

Results

1. Morphometric aspects

The descriptive statistical data on the quantitative morphological characters are summarized in Table 2. The character of flower length presented the highest coefficient of variation (CV) for the analyzed taxa (*M. gardneriana*: 0.27 and *M. compta*: 0.65), followed by the character of sepal length (0.41; 0.14). Among the vegetative characters, leaf length (0.32; 0.49) and petiole length (0.36; 0.47) presented the highest CV values for *M. gardneriana* and *M. compta*.

2. Taxonomic treatment

Micropholis gardneriana (A. DC.) Pierre, Not. Bot. 39. 1891. Type:—BRAZIL. Goiás, *G. Gardner 3310* (holotype: G-DC; isotypes: G G00139918 [image!], K K000641491 [image!], K K000641492 [image!]). Figure 1A. *Micropholis compta* Pierre *in* Pierre & Urban, Symb. Antill. 5: 125. 1904. Type: —BRAZIL. Rio de Janeiro: *Glaziou 17691* (holotype: P P00648164 [image!]; isotypes, F F0072093F [image!]; G G00237370 [image!]). Figure 1B. *syn. nov.*

Trees or shrubs of up to 27 m in height, pubescent branches with rusty, glabrescent trichomes, usually without lenticels. Leaves alternate distichous to spiraled, 4–26 × 2–7 cm, oblong, elliptic, oblanceolate or obovate, base cuneate, narrowly cuneate, obtuse or attenuated, rarely rounded, apex cuspid, acuminate, attenuate, emarginate, acute or obtuse, rarely mucronate, adaxial face glabrous, abaxial face glabrescent, trichomes rusty malpighiaceous along the main vein, whole, chartaceous to coriaceous, discolor; brochidodromous venation, main vein grooved on the adaxial face and protruding on the abaxial face, closely parallel secondary veins with striated aspect, indistinguishable from tertiary veins and superior orders on both faces, intramarginal vein present; petioles 0.3–1.12 cm long, canaliculate, pubescent to glabrous, rusty trichomes. Fascicles 2–8 flowers, axillary or ramiflorous. Flowers unisexual or bisexual, pedicel 1–6 mm long, pubescent, trichomes malpighiaceous, rusty. Sepals 5, 0.8–4 × 1–3 mm long, ovate to suborbicular, apex cuneate to rounded, outer face pubescent, inner face with bristled trichomes, margin non-ciliated. Petals 5, tube 1–3 mm long, lobes 0.4–1 mm long, ovate to suborbicular, apex cuneate to rounded,

Table 1. Diagnostic characters in the separation of *M. compta* and *M. gardneriana*, according to Pennington (1990), and our observations about the variations of these characters.

Character	*M. compta*	*M. gardneriana*	Observations based on the analysis of exsiccates
Leaf length	9–15.5 cm	3.5–9.5 cm	Vary according to locality and microhabitat. With exception of corolla length, these characters are highly variable, even in a single individual. Specimens of intermediate length were found in both fresh and herborized material. This variation was also observed in relation to leaf length
Leaf width	3.5–5.2 cm	1–4.2 cm	
Petiole length	0.9–1.5 cm	0.3–1.0 cm	
Corolla length	5.5 mm	2–4.5 mm	
Phyllotaxis	Alternate distichous	Usually spiraled	The protologue of both species did not describe the organization of the leaves. The analyzed examples had alternate distichous to gently spiraled leaves at the apex of the branches
Geographic distribution	Endemic to Atlantic Forest	Occurs in the Atlantic and Amazon Forests, Caatinga and Cerrado	The species is widely distributed. However, it colonizes environments highly disturbed by anthropic activity

Table 2. Average ± standard deviation, coefficients of variation and intervals (minimum–maximum) for the seven characters used in the morphometric analyses.

Plant parts/Characters		*Micropholis gardneriana*				*Micropholis compta*			
		M	Std	CV	Min-Max	M	Std	CV	Min-Max
Leaf	1. length	7	2.24	0.32	2.2-12.2	10.25	5	0.49	5.7-26
	2. width	3	0.89	0.29	1-11.3	3.5	1.2	0.35	2.2-7
Petiole	3. length	0.6	0.21	0.36	0.3-1.2	0.65	0.3	0.47	0.4-1.7
Flower	4. length	0.7	0.18	0.27	0.4-1.1	0.6	0.39	0.65	0-1
Sepal	5. length	0.22	0.09	0.41	0.1-0.8	0.25	0.03	0.14	0.1-0.3
	6. width	0.2	0.06	0.33	0.1-0.35	0.2	0.04	0.21	0.11-0.3
Corolla	7. length	0.2	0.06	0.34	0.1-0.4	0.25	0.05	0.2	0.2-0.3

Table 3. Specimens of *Micropholis* (Sapotaceae) analyzed in relation to the anatomy of the petiole and the leaf blade.

Species	*Voucher* (Herbarium and registration)	Habitat
M. gardneriana	BHCB 123798	Semideciduous Seasonal Forest
	BHCB 17738	Atlantic forest
	BHCB 43492	Atlantic forest
	INPA 91085	Cerrado
	INPA 136474	Transitional vegetation between gallery forest and Cerrado
	MBML 6923	Atlantic Forest situated on slopes
M. compta	ALCB 27284	Atlantic Forest
	MBML 9837	Atlantic Forest situated on slopes at altitude of 650-850 m
	UEC 170041	Submontane Dense Ombrophylous Forest 450 m
	UEC 174840	Atlantic Forest situated on slopes at altitude of 120 m
	PEUFR 42055	Ombrophilous Dense Lowland Forest

glabrous. Stamens 5, included, 0.2–0.5 mm long, anthers 0.7–0.8 mm long, glabrous; vestigial stamens on female flowers; staminodes 5, 1–1.2 mm long, lanceolate, subulate or petaloid, glabrous. Disc present or absent. Ovary 5-locular, 1.8–3 mm long, ovoid to triangular, densely pubescent, trichomes rusty, golden, forming an arch at the base of the ovary or covering up to 2/3 of the stylet; stylet 1–2 mm long, glabrous; simple stigma, slightly lobed to 5-lobed. Fruits 1–1.7 × 0.6–2 cm long, ovoid to ellipsoid, glabrescent; residual trichomes at apex and base, with apiculus, persistent calyx, brown to blackish. Seed 0.6–1.4 cm long, laterally compressed ellipsoid, with smooth, glossy and rigid tegument, chestnut to brown; linear ventral scar extending along the length of the seed 1.1 × 1.94 cm long, whitish to beige, matte.

Material examined: BRAZIL. Bahia: Entre Rios, RPPN Lontra Saudade, 31/V/1998, *M.R. Fonseca et al. 0537* (INPA). Espírito Santo: Santa Teresa, Estação Biológica de Santa Lúcia, margem direita do Rio Timbuí, 8/X/1990, *S.V. Pereira & S.R. Cardoso s/n* (MBML); Santa Teresa, Estação Biológica de Santa Lúcia, mata Atlântica de Encosta, 13/IV/1993, *L.D. Thomaz 919* (MBML); Santa Teresa, mata do Banestes, 16/VIII/2004, *L. Kollmann & W. Pizziolo 6941* (MBML); Linhares, Reserva Natural Vale, mata de Tabuleiro, 6/IV/1994, *D.A. Folli 2274* (CVRD); 20/I/1994, *D.A. Folli 2184* (CVDR). Goiás: Caldas Novas, mata de Galeria, 18/XI/1993, *G.P. da Silva et al. s/n* (CEN); Luziânia, fazenda corumbá, margem direita do Rio Corumbá, área de mata ciliar, 9/VI/2003, *G. Pereira-Silva et al. 77789* (CEN); Silvânia, mata



Figure 1. Type specimens (A) Holotype of *Micropholis compta* Pierre (P) e (B) Isotype of *M. gardneriana* (A. DC.) Pierre (P).

de Galeria, 2/VI/2003, *G. Pereira-Silva et al. 7722* (CEN); Luziânia, floresta Estacional Semidecidual em estágio secundário, 9/XII/2007, *C.H.G. Cezare et al. 428* (INPA). Goiás, 50 km S of Caiaponia, X/1838, *W.J. Burchell 8244* (K). Goiás, IX/1839, *G. Gardner 3310* (K). Maranhão: Estreito, Cerrado, 19/X/2005, *G. Pereira-Silva et al. 10208* (CEN); Transamazônica à 35 km da cidade de Carolina, vegetação transicional entre mata de Galeria e Cerrado, 15/IV/1983, *N.A. Rosa et al. 1101* (INPA). Minas Gerais: Caratinga, região de mata Atlântica, 20/I/1990, *L.V. Costa et al. 404* (BHCB); Catas Altas, Serra do Caraça, mata de galeria, 16/XII/2000, *R.C. Mota 1164* (BHCB); Barão de Cocais, floresta Estacional Semidecidual Montana 7/V/2008, *S.G. Rezende et al. 2689* (BHCB); Marliéria, Parque Estadual do Rio Doce 8/VII/2004, *G.S. França & F. Raggi 605* (BHCB); Itambé do Mato Dentro, Distrito de Santana do Rio, APA do Parque Nacional da Serra do Cipó, 16/III/2008, *M.F. Santos & H. Serafim 319* (BHCB). Pernambuco: Recife, mata de Dois Irmãos, 17/II/1990, *M.L. Guedes 2289*, (ALCB); Igarassu, mata da Usina São José, floresta Ombrófila Densa das Terras Baixas, *H.C.H. Silva 197* (PEUFR); *H.C.H. Silva et al. 168* (PEUFR). Rio de Janeiro: Rio das Ostras, Reserva Biológica União, região de Morro, 27/VIII/1998, *P.P. de Oliveira 4111* (BHCB); Rio de Janeiro, 13/V/1975, *A. Glaziou 8224* (K). Rondônia: Pimenta Bueno, estrada do rio Pimenta Bueno km 11, 8/XI/1979, *M.G.G. Vieira et al. 1029* (INPA); 10/XI/1979, *M.G.G. Vieira et al. 1061* (INPA); Vilhena, 85 km from Vilhena toward Guaporé on BR 364, 9/XI/1979, *B.W. Nelson et al. 394* (INPA). São Paulo: Ubatuba, Picinguaba, mata Atlântica de Encosta, 12/I/1997, *M. Sanchez & F. Pedroni 740* (UEC); Ubatuba, floresta Ombrófila Densa Submontana, VII/2006, *A.L.C. Rochelle 856* (UEC). Sergipe: Santa Luzia do Itanhi, Castro, cerca de 2 km na estrada de Castro para Santa Luzia do Itanhi, mata costeira, Restinga arbórea intercalada com coqueiral, várzea e campos úmidos, 5/X/1993, *A.M. de Carvalho et al. 4317* (ASE); Estância, povoado Fonte Nova, nascente um, 17/XII/2009, *C. Calazans et al. 333* (ASE); Povoado Aguada Carmópolis, capoeira de mata subperenifolia, 15/VI/1982, *E. Carneiro 383* (ASE); Itaporanga D 'Ajuda, fazenda trapsa, mata Atlântica, 21/VII/2009, *J.P. Souza-Alves s/n* (ASE); Itaporanga D 'Ajuda, 19/V/2014, *F.B. Gonçalves 160* (ASE). Tocantins: Paranã, fazenda Petrolina, mata de Galeria, 13/IX/2003, *A.C. Sevilha et al. 3549* (CEN); São Domingos, área de inundação da usina São Domingos, mata ciliar, 25/VI/2001, *A.C. Sevilha 2061* (CEN).

Additional material examined: BOLIVIA. Velasco: Serrania de Huanchaca, Santa Cruz, Parque Nacional Noel Kempff M. Unos 5-7 km al sur del Rio Itenez o Guaporé ~15 km al sureste del estancia Flor de Oro. Bosque enano sobre margen de la maseta, 13/VIII/1992, *M. Toledo 68* (F). COLOMBIA. Vichada: Puerto Carreño, 23/X/ 1938, *J. Cuatrecasas 3984* (F). VENEZUELA. Guarico: 6 km from Estacíon Biologica Calabozo, XII/1965, *L, Aristeguieta 5939* (US). GUIANA. U. Takatu-U. Essequibo: Acarai Mts; Sipu River 8-10 km from juncture with Essequibo River, 12/III/1994, *T.W. Henkel et al. 5123* (US). PERU. Las Piedras, Reserva Amazónica, Trocha G, 8/IV/2004, L. *Valenzuela et al. 3340* (MO).

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3. *Distribution and habitat*

Brazil (BA, DF, ES, GO, MA, MG, MT, PA, PE, RJ, RO and SE), Colombia and Venezuela (Figure 2). With the inclusion of *M. compta* in the circumscription of *M. gardneriana*, and based on recent collections and further study of the herbarium material, the geographic distribution of the species was widened in Brazil, with new records for the states of Amazonas, Mato Grosso do Sul and São Paulo. Additionally, the species was reported for the first time in Bolivia, Guyana, and Peru, expanding its distribution in South America (Figure 2). In Brazil, the species occurs in a wide variety of habitats, including dry areas with strongly seasonal climate, gallery forest, transitional vegetation between gallery forest and Cerrado (sensu lato), rocky environments, Caatinga (sensu stricto), evergreen forests in Amazon, Atlantic forest, in forests of restinga and tabuleiro, and occasionally in montane forest (Figure 2).

4. *Phenology*

Flowers from February to December and produces fruit in March–April and October–December.

5. *Conservation status*

M. gardneriana s.l presents a wide distribution, extending evenly through large expanses of South America (Fig. 2). In a case of formal assessment, the species would possibly be categorized as least concern (LC), owing to an EOO of 8,589,669,704 km^2, and as endangered, due to an AOO of 380,000 km^2 (IUCN 2001). This species occurs within some legally designated conservation units, throughout their entire area or in small fragments, encompassing a wide area of occurrence, as its AOO value reflects.

6. *Anatomic notes*

M. gardneriana and *M. compta* are closely related in their leaf anatomy (compare Figure 3A-C with Figure 3D-F). The petiole presents a concave-convex contour in the cross section (Figure 3A and 3D). The epidermis is covered by a thin cuticle, and malpighiaceous unicellular trichomes of the T type are visible (Figure 3A and 3D). The epidermal cells are isodiametric, quadrangular and have thickened walls. The external periclinal wall presents U-shaped secondary thickening. The cortex is formed by external angular collenchyma and by internal filling of parenchyma (Figure 3B and 3E). The vascular system has a concave-convex shape, formed by a collateral bundle of greater diameter. Two to four accessory collateral bundles are arranged adaxially on each side of the main vascular bundle (Figure 3A-B and 3D-E). Idioblasts containing prismatic monocrystals occur in cells of the collenchyma and of the cortical (Figure 4A) and medullary parenchyma (Figure 4B). Laticifers occur in association with the vascular tissue and the cortical and medullary parenchyma.

The leaves are bifacial. The epidermis is unistratified on the adaxial and abaxial surfaces, the cells are isodiametric, quadrangular and rectangular, with straight anticlinal walls covered with a smooth, thin cuticle, presenting U-shaped thickening on the abaxial surface of the principal vein, where the external periclinal wall is thickest (Figure 3A-F and Figure 4C). Subjacent to the adaxial epidermis sits a layer of

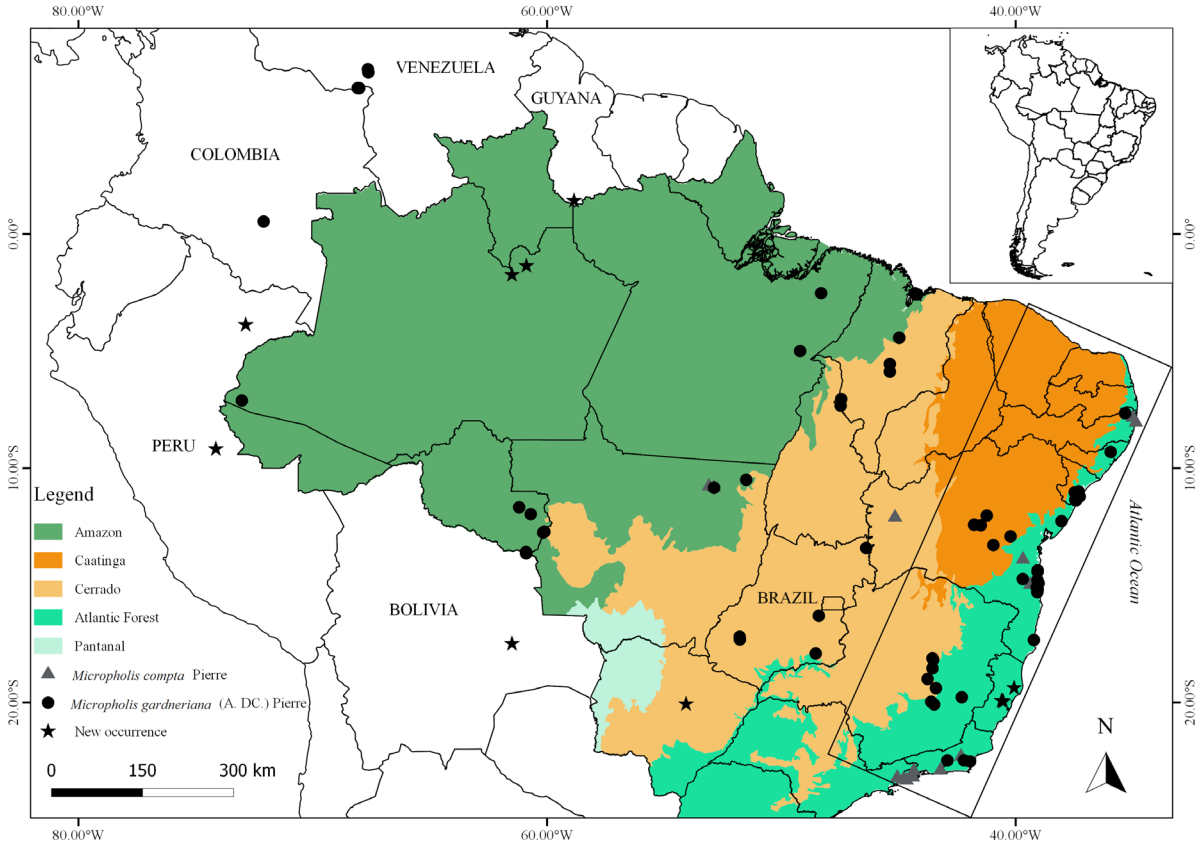


Figure 2. Map indicating the distribution of *Micropholis gardneriana s.l* in South America.

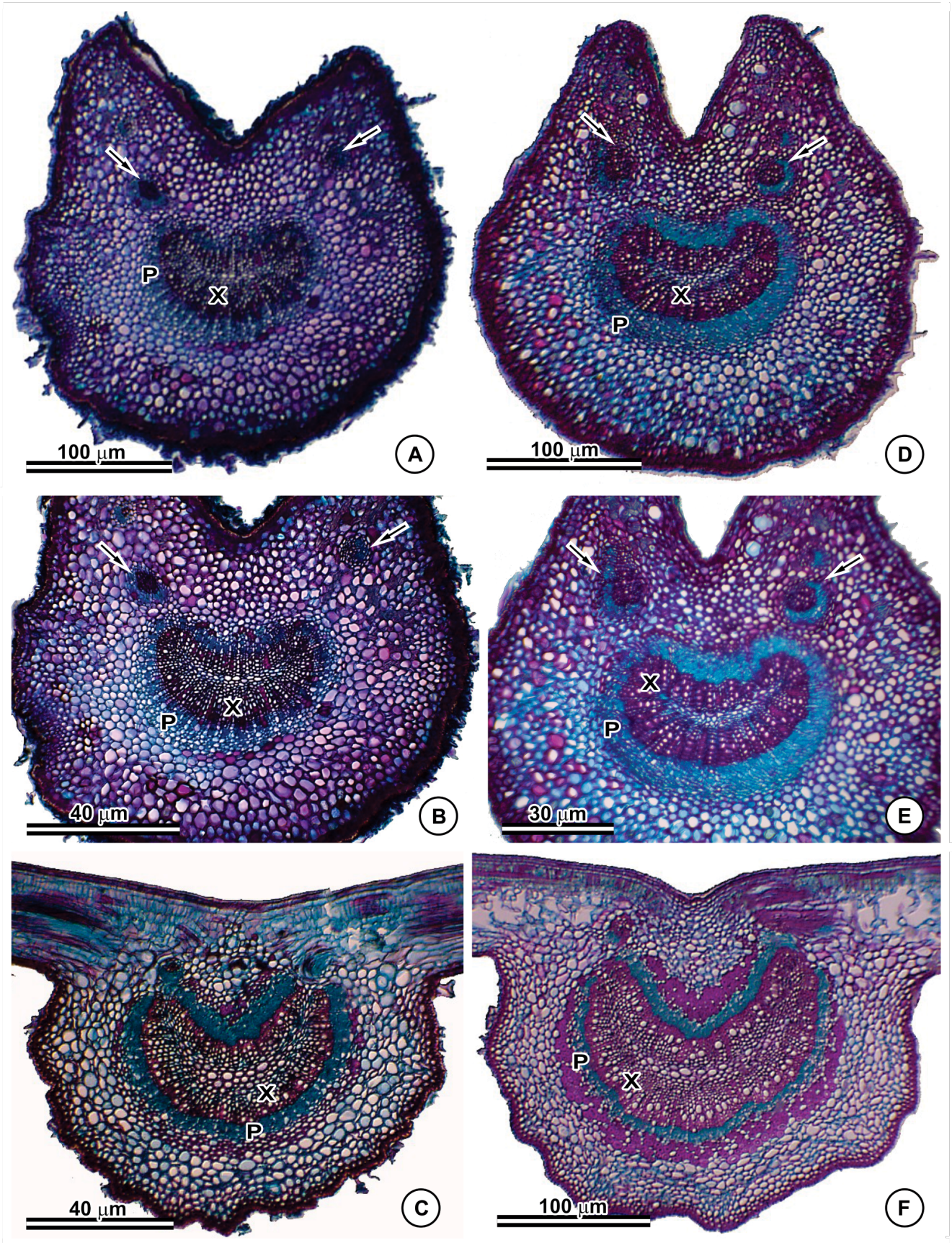


Figure 3. Leaf anatomy of *Micropholis gardneriana* (left column) and *Micropholis compta* (right column) in transversal sections. A-D. overview of the petiole with accessory bundles (arrows); E and F. overview of the midrib. *C*=idioblasts containing prismatic monocrystals, *P*=phloem, *X*=xylem.

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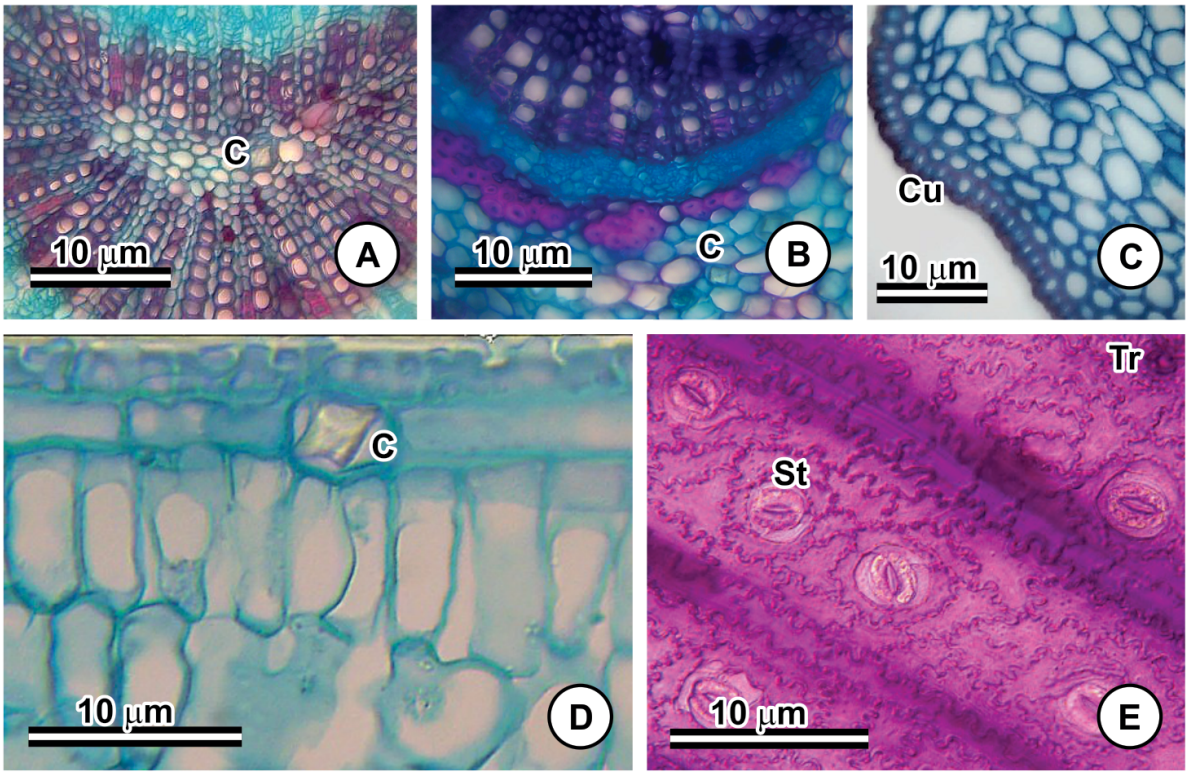


Figure 4. Leaf anatomy of *Micropholis gardneriana sl.* in transverse and paradermic sections. **A.** detail of the prismatic monocrystals in parenchyma medular of the petiole; **B.** detail of the prismatic monocrystals in parenchyma cortical of the midrib; **C.** detail of U-shaped cuticle that is thicker on the abaxial side of the midrib; **B.** detail of the mesophyll, palisade parenchyma, prismatic monocrystals and subepidermal layer; **C.** detail of the anisocytic stomas and scars left by trichomes; *C*=idioblasts containing prismatic monocrystals, *Cu*=cuticle, *St*=stomas, *Tr*=scars left by trichomes.

periclinally elongated achlorophyllous cells of unknown origin (Figure 4D). The leaf lamina is hypostomatic, with anisocytic stomas situated on the same level as the ordinary epidermal cells (Figure 4E).

The mesophyll is dorsiventral (Figure 3C and 3F). The palisade parenchyma is composed of two noncontinuous layers of elongated anticlinal cells, while the other layers of the mesophyll constitute the lacunar parenchyma (Figure 4D). Unicellular T-shaped malpighiaceous trichomes occur sparsely on the abaxial surface of the mesophyll, concentrated in the midrib (Figure 3C and 3F). Sclereids, laticifers and idioblasts containing prismatic monocrystals occur in the mesophyll (Figure 4D). In cross section, occurs angular collenchyma adaxially and abaxially in the midrib (Figure 3C and 3F). The contour of the midrib varies from flat to concave-convex (Figure 3C and 3F). The vascular system is concave-convex, formed by a single collateral bundle enveloped by a sclerenchymatous sheath (Figure 3C and 3F). Laticifers occur, preferentially, in the parenchyma intercalated in the vascular bundle. Idioblasts containing prismatic monocrystals occur in the cells of the cortical parenchyma (Figure 4B).

Discussion

Morphological and anatomical attributes of *M. compta* and *M. gardneriana* overlap in all of the examined samples (Figure 1 and 2). Variations in the length of the leaf, petiole and corolla were the quantitative attributes mentioned by Pennington (1990) in the distinction between the two species (Table 1). These characteristics were observed in the present study; however, the descriptive statistics suggest that the separation of the two species is not supported by these characters, indicating that these taxa form a morphological continuum (Table 2).

Mapping all the specimens showed that the geographic distributions of these species overlaps in the Atlantic and Amazon Forests and the Cerrado (Figure 2). Furthermore, the two analyzed taxa are characterized by their presentation of oblong, elliptical, oblanceolate or obovate leaves. This variation occurs within the same individual and may be related to the different environmental conditions of the habitats colonized by *M. gardneriana l.s*, since some of the species can occupy a wide ecological niche, exhibiting high phenotypic plasticity (Bunger et al. 2015; Ribeiro et al. 2018).

Leaf anatomical characters, including epidermal attributes (Metcalfe & Chalk 1979; Dickison 2000, Ospina 2016), may support taxonomic delimitation at different hierarchical levels (Solereder 1908; Metcalfe & Chalk 1950a, 1979b; Monteiro et al. 2007; Coutinho et al. 2016). In cross section, the leaves of all examined specimens have a distinguishable subepidermal layer on the adaxial surface (hypodermis), with periclinally elongated cells, and the epidermis of the abaxial surface presents U-shaped thickening in the region of the principal vein.

The number of strata of the palisade parenchyma may vary in response to environmental conditions (Eames & Mac Daniels 1945; Metcalfe & Chalk 1983). Independent of where they were collected, however, all examined specimens have two noncontinuous strata of

palisade parenchyma. This characteristic was considered relevant by Monteiro et al. (2007) for the delimitation of species belonging to *Pouteria* Aubl. of the Southeast region of Brazil.

In cross section, the contour of the principal vein can vary from flat to concave-convex, but the shape of the vascular system is always concave-convex, with a collateral vascular bundle enveloped by a sheath of sclerenchymatous cells. The petiole, in cross section, presents the contour and shape of the concave-convex vascular system. Two to three conspicuous accessory bundles are visible. The specimens attributed to *M. compta* exhibit the same pattern of anatomical characters, which supports the synonymization of the species.

In contrast, the salient characteristics of several genera of Sapotaceae, including *Pouteria* Aubl. Monteiro et al. (2007), *Manilkara* Adans. Almeida Jr. et al. (2012), and *Diploon* Cronquist Lima et al. (2019), are the occurrence of prismatic monocrystals; anisocytic stomas restricted to the abaxial surface of the leaf; the occurrence of malpighiaceous T-shaped trichomes, most dense in the region of the principal vein; articulated laticifers; and the dorsiventral organization of the mesophyll. These attributes were also observed in all of the examined specimens and must therefore be used with caution in the distinction between the taxa.

Our results showed that the anatomical and morphological attributes compared between all the analyzed specimens confirm that all the assessed characteristics, including those cited by Pennington (1990) as diagnostic for the separation of *M. compta* and *M. gardneriana*, overlap considerably, meaning that they are included within the same pattern of variation. Therefore, we propose *M. compta* as a new synonymy under *M. gardneriana*.

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Author Contributions

Angélica Cândida Ferreira: Substantial contribution in the concept and designer of the study; Contribution to data collection; Contribution to manuscript preparation; Contribution to critical revision adding intellectual content.

Carmen Silvia Zickel: Substantial contribution in the concept and designer of the study; Contribution to data collection; Contribution to manuscript preparation; Contribution to critical revision adding intellectual content.

Josiane Silva Araújo: Contribution to data collection; Contribution to manuscript preparation; Contribution to critical revision adding intellectual content.

Eduardo Bezerra de Almeida Jr: Contribution to manuscript preparation; Contribution to critical revision adding intellectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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Article

Insights for policy-based conservation strategies for the Rio de la Plata Grasslands through the IPBES framework

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Abstract: The Río de la Plata Grasslands (RPG) are one of the most modified biomes in the world. Changes in land use and cover affect the RPG's rich biodiversity. In particular, the expansion of crops, overgrazing, afforestation, and the introduction of exotic species pose a major threat to the conservation of biodiversity and ecosystem services (BES). In this study, we applied the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) conceptual framework as a new lens to approach biodiversity conservation enactments in the RPG. First, we systematically reviewed published scientific literature to identify direct and indirect drivers that affect the RPG's BES. Further, we conducted an extensive analysis of management policies affecting the BES directly in the region, at a national and international level. We conclude by offering recommendations for policy and praxis under the umbrella of the IPBES framework.
Keywords: *Land Use Change; Biodiversity; Ecosystem Services; Drivers, Nature's Contributions to People.*

Insights para estratégias de conservação baseadas em políticas para as pradarias do Rio da Prata através da estrutura do IPBES

Resumo: As pradarias do Rio da Prata são um dos biomas mais modificados no mundo. Alterações nos usos do solo afetam a rica biodiversidade deste ecossistema. A expansão da agricultura, sobrepastoreio, arborização e a introdução de espécies exóticas, principalmente, representam uma grande ameaça para a conservação da biodiversidade e dos serviços ecossistêmicos (BES). Neste estudo, aplicamos a estrutura conceptual da Plataforma Intergovernamental sobre Biodiversidade e Serviços Ecossistêmicos (IPBES) como uma nova forma de abordar as políticas de conservação da biodiversidade neste bioma. Primeiro, revisamos sistematicamente artigos científicos publicados de forma a identificar fatores diretos e indiretos que afetam os BES nas pradarias do Rio da Prata. Adicionalmente, realizamos uma extensa análise das políticas de gestão que afetam diretamente os BES na região, quer a nível nacional, quer internacional. Concluímos com propostas e recomendações de políticas e práticas sob a égide do quadro do IPBES.
Palavras-chave: *Alterações de Uso do Solo; Biodiversidade; Serviços Ecossistêmicos; Contribuições da Natureza para as Pessoas.*

Introduction

Obtaining natural resources for fulfilling human needs has been made at the expense of environmental degradation (Foley et al. 2005, MEA 2005, Zhang et al. 2019a). Based on the current trends in land use and land cover (LULC) changes worldwide, humans can obtain goods and services to improve their quality of life only by diminishing the capacity of global ecosystems to sustain the provision of such benefits (Foley et al. 2005, MEA 2005). Hence, contemporary societies face the challenge of developing regional land-use strategies that recognize short and long-term needs while reducing the negative environmental impacts and maintaining social and economic benefits (Foley et al. 2005, MEA 2005).

The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) is an international body that works to strengthen the science-policy interface for biodiversity and ecosystem services. IPBES aims to assess the state of biodiversity and ecosystem services (BES) incorporating different disciplines and types of knowledge (Díaz et al. 2015). Nature's contribution to people (NCP) is a concept promoted by IPBES that refers to all the positive and negative contributions of nature to the quality of life of people, which can be recognized and valued in a range of existing worldviews. This approach underlines the central and pervasive role that culture plays in defining all links between people and nature (Díaz et al. 2018). According to Pascual et al. (2017), a multiple value perspective should be encouraged in decision making, focusing on three types of values: intrinsic, relational, and instrumental. In order to achieve sustainable development, it is important to consider long-term human well-being, the drivers, and the consequences of land-use changes (Crossman et al. 2013, Nagendra et al. 2013, Ellis et al. 2019). Therefore, the link between drivers, valuations, and NCPs might serve as holistic guidance for policy formulation.

Grasslands are one of the most modified biomes of the world (Hannah et al. 1995, Paruelo et al. 2007, Baldi & Paruelo 2008), which cover over 50 million km^2, accounting for 37% of the earth's terrestrial surface (O'Mara 2012). Native grasslands have been replaced or degraded by intensively managed agricultural lands (Hannah et al. 1995, Vega et al. 2009, O'Mara 2012, Gang et al. 2014), representing 70% of the agricultural areas worldwide (Schlesinger & Andrews 2000, Ramesh et al. 2019). Thus, grasslands play a unique role in food security by providing agricultural products (O'Mara 2012).

In the Neotropics, the Río de la Plata Grasslands (RPG) are the most extensive grassland ecosystem, covering an extent of 750,000 km^2 (Soriano et al. 1991, Carbutt et al. 2011). The RPGs are shared by eastern Argentina, southern Brazil, and Uruguay, encompassing two main sub-regions, Pampas and Campos (Soriano et al. 1991) (Figure 1). The mean annual temperature of the region is 10 to 20ºC, and the mean annual rainfall is between 400 and 1,600 mm (Soriano et al. 1991).

After the European colonization, the native grasslands of the RPG have become one of the most essential regions of grain and beef production in the world (Bilenca & Miñarro 2004, Paruelo et al. 2005, Baldi et al. 2006). Until the 20th century, cattle ranching was the most common and important land use, but then, cropping became the most important one (Vervoorst 1967, Soriano et al. 1991, Viglizzo et al. 2001, Baldi et al. 2006). For example, between 2000 and 2010, the cultivation of genetically modified soybean generated an intensification and expansion of monocultures of this crop in the region (Aizen et al. 2009, Redo et al. 2012, Modernel et al. 2016). Although there was a predominance of soybean, other crops also increased, such as sunflower, maize, rice, wheat, pine, and eucalyptus (Baldi & Paruelo 2008, Cubbage et al. 2012). In the last decade, the cropping systems became less diverse raising concerns about the sustainability and environmental risks associated with crop production in a region which is relevant for the world grain and oil market (FAO 2014). As such, the RPG have represented one of the most rapidly expanding agricultural frontiers not only in Latin America but in the world (Baeza & Paruelo 2020). Currently, most of the area is represented by sown pastures, annual crops, overgrazed areas, and tree plantations, and only a small portion of semi-natural native grasslands remain (Modernel et al. 2016, Paruelo et al. 2005).

All aforementioned LULC changes have affected the ecosystem functioning, the provision of ecosystem services (ES), and the state of biodiversity in RPG (Paruelo et al. 2005, Modernel et al. 2016). This region represents a biodiversity-rich area encompassing more than 550 different species of grass, 450-500 birds, with some endemic species, and a hundred species of terrestrial mammals (Bilenca & Miñarro 2004; Di Giacomo & Parera 2008, Azpiroz et al. 2012, Andrade et al. 2018). However, these species are being threatened by LULC changes in the area (Di Giacomo & Krapovickas 2005, Codesido et al. 2013, Dotta et al. 2015). Based on these and the fact that the RPG are the least protected sub-region in South America (Henwood 2004, Michelson 2009, Baeza & Paruelo 2020), it highlights the importance of protecting this area in order to conserve and maintain its BES (Baldi & Paruelo 2008, Modernel et al. 2016, Oyarzabal et al. 2019).

Most of the land is private in the region, belonging to families and corporations, often international (Modernel et al. 2016). LULC transformation is also driven, in turn, by global economic issues (the increase in the prices of commodities) and the availability of new technologies (no-tillage cropping, genetically modified organisms, afforestation know-how, etc.) (Satorre 2005, Trigo 2005, Céspedes-Payret et al. 2009). Therefore, land-use policies play a fundamental role in determining LULC dynamics (Lambin et al. 2003, van Meijl et al. 2006, Brannstrom et al. 2008). These policies can promote or restrain particular crops or types of land management using taxes and regulations (Redo et al. 2012). Internal policies established within a given country are the primary underlying drivers of LULC changes (Geist & Lambin 2002). Furthermore, political boundaries and biophysical heterogeneity of RPG also influence these trends (Vega et al. 2009).

New strategies should be considered to allow the coexistence of agricultural activities with grassland biodiversity conservation in the RPG. In this study, we applied the IPBES framework (Díaz et al. 2015) as a new lens to approach biodiversity conservation enactments in the RPG. Specifically, we sought to 1) identify the main drivers (direct and indirect) that are affecting the BES in the RPG and link them with the different values and categories defined by IPBES, 2) identify national and international policies related to RPG that affect the drivers underlying the BES, 3) build a conceptual framework for the RPG using the IPBES framework, based on the drivers, values, and policies identified in the previous objectives; 4) and finally, propose policies that could help the co-management of grasslands in this region and halt the rapid loss of BES.

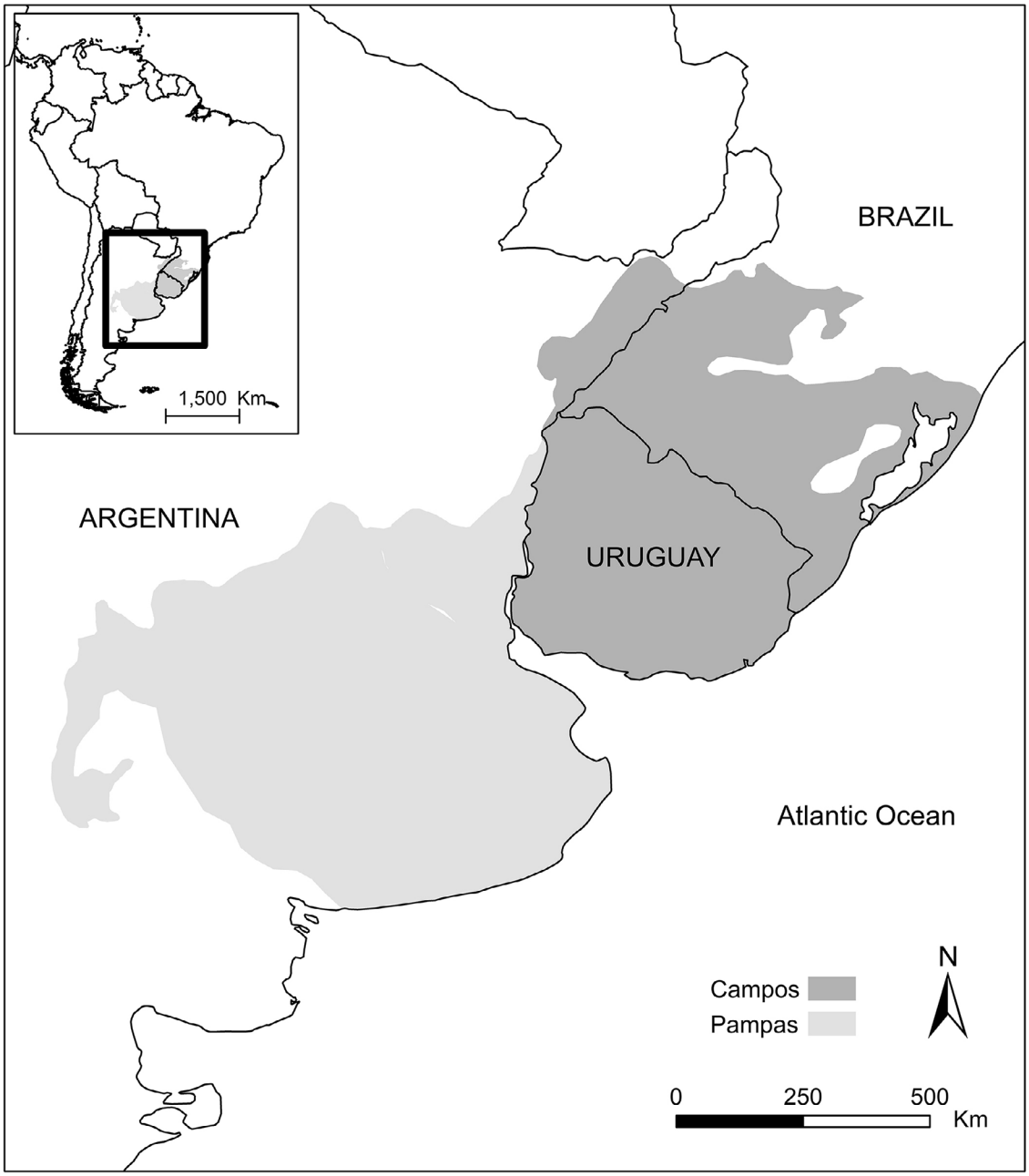


Figure 1. Location of the Río de la Plata Grasslands (RPG) and sub-regions, Pampas and Campos, in Southeastern South America (sensu Soriano et al. 1991).

Material and Methods

We engaged in a qualitative systematic review approach (Finfgeld-Connett & Johnson 2013) to centralize and consolidate pre-existing knowledge on LULC changes and BES in the RPG.

1. *Scientific literature review: Linking BES with IPBES in the RPG*

A literature search was conducted in two steps. First, we performed a Boolean search in Web of Science platform (July 22nd, 2019), using the following string of keywords: ("Río de la Plata grasslands" OR "Pampas grasslands" OR "Campos Grasslands") AND ("land use" OR "agriculture" OR "afforestation" OR "pasture" OR "grazing") AND ("ecosystem services" OR "biodiversity"). To add several papers that did not appear in the first search but were relevant for this study, we performed an ad hoc search using various resources, e.g., other database searches, such as Google Scholar, checked cited literature, etc. Following this procedure, we included different reviews and other articles relevant to the study area. From the selected papers, we chose the ones that were published between 2015 and 2019, because most of the papers before this period were included in the other reviews (e.g. Bilenca & Miñarro 2004; Modernel et al. 2016). From each one of the selected papers, we extracted the main ES mentioned in the study and the drivers of the loss of the BES (direct and/or indirect). We then organized the information following the 18 categories of the NCP and placed them into the types of contribution (regulating, material, and non-material) (Díaz et al. 2018).

2. *Review of current policy-based conservation in the RPG*

Current policies for RPG management were reviewed by conducting a systematic search of policies, regulations, and legislation available on official websites for each one of the countries. For our analysis, we identified and selected policies that are exclusively related to issues of BES conservation in RPG. We took into account historical national and regional legislation. Relevant information was extracted, in order to contrast to what extent these policies are addressing the drivers depicted in the scientific literature. We listed applicable laws or initiatives that promoted the LULC changes in RPG and represented the conservation situation within each country. Finally, we described the conservation efforts at an international and national level.

3. *An approach to IPBES conceptual framework*

Based on the key findings of these searches, we developed a conceptual model for the RPG using the IPBES framework (Díaz et al. 2018).

Results

1. *Scientific papers review: Linking BES with IPBES in RPG*

Based on our literature search, we found that most studies in the region focused on regulating contributions, highlighting material ones, while a few studies considered non-material contributions (Table 1).

Several papers focused on the ecological functions of RPG's biodiversity and the effect that agricultural activities have on them, highlighting and emphasizing nature's intrinsic value. In particular, these studies identify the importance of the RPG as habitat for pollinators (Sabatino et al. 2016, Marrero et al. 2017), and areas of high plant and animal diversity (Modernel et al. 2016). All the studies agree that biodiversity loss is associated with the transformation, homogenization, and perturbation of the habitat. Modernel et al. (2016) described other drivers of biodiversity loss, such as the invasion of exotic species, expansion of crops and implanted pastures, urbanization, and overgrazing. Illegal hunting and zoonotic diseases introduced by exotic species also threaten native species (Bilenca & Miñarro 2004).

Instrumental values were identified in several publications studying the benefits people can obtain from grasslands and associated biodiversity (Table 1). Goijman et al. (2015) stated that the agricultural intensification is detrimental to birds and their ecological functions, potentially causing a decrease in ES provided by them. For instance, insectivore birds play a role as pest controllers, a valuable ES in agricultural landscapes. Native grasslands provide regulation of water quality and availability, climate regulation, water provision, nutrient cycling, and erosion control (Modernel et al. 2016, Eguren et al. 2018, Villarino et al. 2019). All these benefits are affected by LULC changes, crop type and management, and climate change. Most of these papers reiterate the adverse consequences of climate change and LULC changes in the provision of agricultural products, which highlights the importance of sound and sustainable practices for the economy in the RPG.

Finally, we found that studies on both relational values and non-material contributions are scarce for the RPG (Table 1). Auer et al. (2017) identified agricultural activities that provided cultural benefits based on traditional activities in particular geographical areas. Furthermore, different aspects of the natural landscape sustained cultural values, giving local people a sense of place and cultural heritage. The authors also stated that although this study is from a small local area, the trends in agriculturalization processes follow a general pattern in the region, and based on socio-ecological similarities along the Pampas, this effect could be found in the entire sub-region (Auer et al. 2017).

Although we made a classification, it is recognized that the NCPs are perceived by people in different ways and each contribution can fit more than one category (Pascual et al. 2017, Díaz et al. 2018).

2. *Review of current policy-based conservation in the RPG*

2.1. *National laws and initiatives that promote the degradation of grasslands*

In Argentina, during the first half of the 20th century, there were cattle ranching and agriculture development under extensive or semi-intensive conditions, which consolidated the crop rotation model with annual pasture and forage (Viglizzo & Jobbágy 2010). By the 1970s and 1980s, increases in production were correlated to the expansion of cultivated areas over native grasslands and other types of environments (Carreño & Viglizzo 2007). In fact, between 1960 and 1990, the rate of grain production was six times higher than that of cattle ranching (Sturzenegger 2006). By the 1990s, intensive use of agricultural inputs and technology was prevalently escalating the LULC changes in the region (Viglizzo et al. 2001), while biotechnological innovations allowed an increase in yield per hectare. Technological advances were simultaneous to economic policy reforms that favoured Argentina's agriculture, such as export tax elimination; the reductions in tariff and non-tariff protection on fertilizers, agrochemicals, machinery and irrigation equipment; the deregulation of private economic activities, mainly commercial and financial, which allowed the reductions of agricultural financial marketing costs (Sturzenegger 2006). In 2002, the government announced the application of withholdings to exports primary products, and both agricultural and industrial manufactures (Colomé 2008). The tax retentions were by 2015, 23% for wheat, 20% for corn, and 35% for soy. In 2016, a new government adopted different measures such as the elimination of withholdings to exports wheat, corn, and meat and a 5% decrease for soybean retention (MA 2015).

From the mid-1990s, timber production has experienced significant growth driven by legislation that promoted forest plantations. In 1999, a law of Investments in Forestry in Planted Forests (Nº 25,080) was promulgated and later expanded in 2019 (Law Nº 27,487). The aim was to increase the stock from 1.3 to 2 million ha of cultivated forests by 2030, which contributed both to sustainable development goals and the climate change commitments assumed with the Paris Agreement (MAGyP 2018). This law established a regime that promotes investments made in new forestry ventures and the expansion of existing forests. It also favors the initiation of forest industry enterprises and the development of existing ones, as long as the timber supply is increased through the introduction of new forests. The benefits granted are tax stability for at least 30 years, tax benefits, and non-reimbursable economic support which will consist of an amount per hectare, variable by zone, species, and forestry activity. These ventures must comply with the zoning of forestry basins that must respect the territorial planning of native forests established by national law of minimum budgets for

Table 1. Summary of Nature´s Contribution to People (NCP) studied in the Río de La Plata Grasslands (RPG) based on the scientific paper review. The NCP is organized based on the generalizing perspective of the IPBES framework, and 18 reported categories are distinguished (Díaz et al. 2018*): 1. Habitat creation and maintenance; 2. Pollination and dispersal of seeds and other propagules; 3. Regulation of air quality; 4. Regulation of climate; 5. Regulation of ocean acidification; 6. Regulation of freshwater quantity, location, and timing; 7. Regulation of freshwater and coastal water quality; 8. Formation, protection, and decontamination of soils and sediments; 9. Regulation of hazards and extreme events; 10. Regulation of detrimental organisms and biological processes; 11. Energy; 12. Food and feed; 13. Materials, companionship, and labor; 14. Medicinal, biochemical and genetic resources; 15. Learning and inspiration; 16. Physical and psychological experiences; 17. Supporting identities and 18. Maintenance of options.* The NCP categories are divided into three broad groups depending on the type of contribution they provide to people into Material, Non-material, and Regulating (Díaz et al. 2018). The studied region of each paper is specified: Argentina (ARG), Uruguay (URU), Brazil (BR); the entire region (All).

Type of contribution	NCP Categories	ES	Specification	Drivers of the loss of the BES	Reference
Regulating	2, 14 and 18	Biodiversity and ecosystem functioning	Pollination	LULC change, agriculture intensification	Sabatino et al. 2016 (ARG), Marrero et al. 2017 (ARG)
Regulating	14 and 18		Species richness and diversity	Expansion of eucalyptus plantations, land-use type, loss of natural and semi-natural habitats and farming intensification	Phifer et al. 2016 (ARG), Hodara & Poggio 2016 (ARG), Winck et al. 2017 (BR)
Regulating	1, 14 and 18	Biodiversity and ecosystem functioning	Plant diversity	Low forage, high stocking rates, invasion of exotic species, expansion of crops and implanted pastures, overgrazing	Modernel et al. 2016 (All)
Regulating	14 and 18	Biodiversity and ecosystem functioning	Animal diversity (endemic species, migratory species)	Landscape perturbation and homogeneity, agricultural expansion (high proportions of cereal crops and forest), habitat loss and fragmentation, hunting pressure and zoonotic diseases introduced by exotic	Modernel et al. 2016 (All). Pedrana et al. 2015, 2018 (ARG), Bilenca & Miñarro 2004 (ARG)
Regulating	10	Biological control of insects and weeds by grassland species	ES provided by bird species	Agricultural intensification and monoculture, hunting pressure	Goijman et al. 2015 (ARG), Gorosábel et al. 2019 (ARG)
Regulating	10			Expansion of eucalyptus plantations	Phifer et al. 2016 (ARG)
Regulating	2	Seed dispersal by bird species		Expansion of eucalyptus plantations	Phifer et al. 2016 (ARG)
Regulating	6 and 7	Water quality and availability	Groundwater contamination control	LULC change, type and management of the crop	Rositano et al. 2018 (ARG), Modernel et al. 2016 (All), Eguren et al. 2018 (URU)
Regulating	6		Regional hydrology	LULC change (from native grasslands to crop)	Modernel et al. 2016 (All), Garcia et al. 2019 (ARG)
Regulating	6		Groundwater levels	Afforestation, agricultural expansion	Cerri et al.2015 (All), Modernel et al. 2016 (All)
Regulating	6 and 9	Flooding mitigation (water regulation)	Flood regulation	Agricultural expansion	Cerri et al 2015 (All), Barral et al. 2019 (ARG), Garcia et al. 2019 (ARG)
Regulating	4	Climate regulation and/or mitigation	Soil organic carbon stock	LULC change (from native grasslands to crops)	Modernel et al.2016 (All), Villarino et al. 2019 (ARG)
Regulating	4		N2O emission control	Type and management of the crop	Rositano et al. 2018 (ARG)
Regulating	4		Carbon footprint	Beef production	Modernel et al. 2016 (All)

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Regulating	8	Soil conservation	Soil C and N balance	Type and management of the crop	Rositano et al. 2018 (ARG), Ferraro & Gagliostro 2017 (ARG), Lara et al. 2018 (ARG), Villarino et al. 2019 (ARG)
Regulating	8		Aboveground net primary productivity	Precipitation and water balance, climate change, energy and biomass flows.	Durante et al. 2016 (ARG), Modernel et al. 2016 (All), Baeza et al. 2018 (All)
Regulating	8		Carbon and nitrogen cycling	Agricultural intensification	Bedano & Dominguez 2016 (ARG), D'Acunto et al. 2018 (ARG)
Regulating	8		Soil erosion	Land use transformation (grassland to crops)	Cerri et al. 2015 (All), Modernel et al 2016 (All), Villarino et al. 2019 (ARG)
Material	12	Food and feed provision	Low input, cattle grazing beef production	LULC change Indirect: Soil productivity, transportation cost, economic gains	Piquer-Rodríguez et al. 2018 (ARG), Modernel et al. 2018 (All)
Non-material	15, 16 and 17	Cultural identity		Industrial agriculture and economic values	Modernel et al. 2016 (All), Auer et al. 2017 (ARG)

environmental protection of native forests (Law Nº 26,331). This zoning aims to conserve native forests, but not other native ecosystems.

In Brazil, several policies that favor the expansion of different types of land-use activities have existed for decades. Within these activities are agriculture, mainly corn, soy and wheat crops, afforestation, and cattle ranching. Additionally, policies have been directed to manage productivity in beef cattle in pastures, through the establishment of minimum stocking rates (number of a particular type of animal per unit area). As a result of these policies, in 1970, there were 14,078 million hectares of natural pastures, but by 1996, only 10,524 million hectares remained. An example of cattle management was the project S3CR11 (1969/1970), which involved a forage improvement phase of the native grasslands of Rio Grande do Sul (Pillar et al. 2009).

Recently, the National Strengthening Program for Family Farming (PRONAF in Portuguese) was enforced. Although this program contributed socially and economically, it has negative environmental impacts. Grisa & Schneider (2015) state that in the municipality of Rio Grande do Sul, this program was predominantly oriented towards productive developments based on the use of chemical inputs. It also promotes a specialization in grain production and other agricultural commodities, which has led to the development of environmentally detrimental agricultural production models.

Finally, in Uruguay, internal policies regarding afforestation had a significant impact on the quantity and distribution of LULC changes (Cubbage et al. 2012). In 1987, Forestry Law (Nº 15,939), was approved as a commitment to supporting and growing the forestry sector. Its objective was to replace marginal and unprofitable farming and ranching on poor soils with afforestation and pulpwood production to supply mainly European markets (Snoeck et al. 2008). This law identified priority regions for afforestation and provided financial incentives such as subsidies, tax reliefs, and exemptions and targeted loans to investors (Cubbage et al. 2012). These incentives encouraged large-scale plantations and forest products manufacturing facilities (Mendell et al. 2007, Redo et al. 2012). Consequently, the tree plantations area in Uruguay increased rapidly, reaching the highest afforestation rate in Latin America between 1988 and 1998 (Mendell et al. 2007, Cubbage et al. 2012). However, in the early to mid-2000s, all incentives were revoked leading to a 24% decline in plantation areas between 2001–2009 (Redo et al. 2012). More recently forest companies are trying to promote joint ventures with cattle ranchers who own land by leasing their plantations to local farmers, forming silvopastoral systems (Cubbage et al. 2012).

Before the beginning of the century, soybean was not considered an essential crop within other agricultural staples in Uruguay. However, between 2000 and 2009, a soybean production boom exceeded the most dominant crop in the country, wheat, occurring at the expense of the country's herbaceous cover (Redo et al. 2012). Global demand and prices have played an essential role in driving soy expansion post-2002 (Oyhantçabal & Narbondo 2011). However, price alone cannot account for the sudden expansion, considering that the price was already relatively high in the mid-1990s. For this, it is essential to take into consideration external policies. The soybean export taxes in Argentina had a direct impact on the quantity and distribution of LULC changes in Uruguay (Redo et al. 2012). Between 2002-2013, the soybean area increased from 10,000 ha to 1.2 million ha (Souto 2012). On one hand, this increase was mainly due to the lower land prices and the lack of export taxes in Uruguay; and on the other, high land prices and high agricultural taxes in Argentina introduced in the early 2000s (Redo et al. 2012).

2.2. Conservation efforts in RPG at the international level

At an international level, there are two important initiatives focused on the RPG: (1) The Southern Cone Grassland Alliance (Alianza del Pastizal in Spanish) created in 2006 with the support of BirdLife International and in collaboration with NGOs (non-governmental organizations) from Argentina, Uruguay, Paraguay, and Brazil. This alliance seeks to protect the habitat of migratory birds and grassland diversity in general by working with different stakeholders (cattle ranchers, environmental NGOs, provincial and national governments, and researchers). In 2010, the Southern Cone Grassland Alliance developed a certification label for meat producers who protected 50% of their grasslands. In 2012, meat produced under this label became available to consumers (Alianza del Pastizal 2019). (2) The 'Official Incentives Project for the Conservation of Natural Grasslands of the Southern Cone of South America' that seeks to protect the BES in the region (Alianza Pastizal 2019). This project began in 2012, and its main goal was to promote an incentive system (payment for ES scheme) for cattle ranchers who carry out conservation management of natural grasslands on their lands (Parera et al. 2012). For this purpose, a technical tool (Grassland Conservation Index) was built to evaluate and quantify the rancher's contribution to grassland conservation, thereby enabling estimation of the amount of their economic compensation. However, objectives were only partially achieved, and in no case, the payments were done (Weyland et al. 2019). One possible reason for this result was that the scheme coincided with the end of the government's mandate and the change in the authorities (Weyland et al. 2019).

2.3. Conservation efforts in RPG at a national level

In each country, different policies or private initiatives have been attempted in order to protect biodiversity and the environment of the RPG (Table 2). To date, conservation initiatives in Argentina are mostly driven by NGOs in collaboration with researchers with the goal of boosting sustainable management practices as well as identifying areas for potential conservation (Table 2). Contrary, in recent decades, Brazil has made significant progress to link biodiversity conservation and economic development, which has played an essential role in international discussions related to conservation. The triggering within the Brazilian society of a specific concern regarding the Campos Sulinos appears to be related to two public discussions: the legal prohibition of burning as a practice of management of the fields in the Rio Grande do Sul (established under the State Constitution of 1989) and the debate surrounding the future of the Pampa biome alongside the announcement of extensive plantations of exotic trees for pulp production (Pillar et al. 2009). Finally, in Uruguay, conservation strategies promoted institutional strengthening, participatory research, and good management practices, by the government in an inter-institutional frame and international organizations (Table 2). All of them focus only on this environment, recognizing natural fields as one of the most important assets of the country in terms of biodiversity.

Based on these initiatives, different levels of conservation were reached in each country. Regarding the scientific community consideration, a natural region is adequately protected when at least 10-15 % of the area is protected by law (Burkart 1999, Bertonatti & Corcuera 2000) but this condition is not met in any country. Argentina protects 1.05% of the Pampas eco-region (Moreno et al. 2008, Burkart 2006, Sistema de Estadística Ambiental 2019), while Brazil protects 2.23% with the integration of federal level protected areas (Bilenca & Miñarro 2004). In Uruguay, the National System of Protected Areas (SNAP) constitutes approximately 0.98% of the national territory but with a high representation of specific species and ecosystems for conservation (Ávila et al. 2018, MVOTMA 2019). However, its low connectivity and surrounding landscapes (intensified production systems) are hostile to biodiversity and accentuating their biological isolation.

3. An approach to applying the IPBES conceptual framework to the RPG

It is important to note, that as the RPG extend into Argentina, Brazil and Uruguay, the associated values are affected not only by the spatial scale under analysis (local, regional, national or international), but also by micro and macro cultural, social, and political dynamics and complexities.

The conceptual framework we have developed for the RPG (Figure 2) has LULC changes as the main focal point and as the principal direct driver for the grassland BES. Based on our literature and policy review, there is a clear tendency to focus on the material contributions, which are traceable to the meat production history of the area (Viglizzo et al. 2001), as well as a distinct trend to increase crop production and afforestation with various incentives. The identification, valuation, and study of non-material values are scarce (such as learning and inspiration, physical and psychological experiences, and supporting cultural identities). Finally, the regulating contributions are becoming more relevant in the literature, especially in the face of climate change, but there is still a long way to go regarding policy application and implementation. However, in this framework, we emphasize the importance of all three of these interrelated components.

On one hand, LULC changes as the primary direct driver of change in the RPG includes three main elements: cattle grazing, crop production, and afforestation. The framework also articulates the values (NCP categories of IPBES framework) provided by these land uses, as a result of recognizing its social-economic importance. A relevant note regarding LULC changes is that the values provided, and the negative impacts on grasslands can profoundly differ according to the management applied. Traditional uses such as low-density cattle grazing or family farming will be more compatible with conservation concerns related to grasslands; intensive agriculture and afforestation, in turn, would be more detrimental to grassland's BES. Therefore, we assume that the transformations of this landscape are mostly to high-intensity LULC changes with inherent ecological consequences.

On the other hand, we organized the indirect drivers of LULC changes into two groups. The first one integrates technology, climate change, and international commodity prices. Technology, through technological advances, allows increasing productivity per unit area leading to less area needed. Climate change has the capacity to alter (un)suitable land uses and international commodity prices as market forces for higher or lower pressures from specific uses. Therefore, all these are affecting the weight that agricultural activities put on the remaining grasslands. The second group reflects the importance of highlighting the influence of politics and inherent political instability in the LULC changes, but also its integration in the remaining indirect drivers. Lastly, direct and indirect drivers' dynamics are viewed as a two-way relationship.

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Table 2. National policies and conservation initiatives in the Río de la Plata Grasslands (RPG). NA: not applicable, or information not available.

Country	Initiatives	Level	% Area protected or to be protected	Public/private promotion	Conservation goals	Year	Law	Outcomes	Other remarks and challenges	References
Argentina	National System of Protected Areas (PAs), and other preservation areas	National	1.05% of total grasslands within the national territory	Public	To conserve pristine grassland areas representative of the region for its biodiversity and scenic values	1980	Law Nº 22,351; other policies	493 PAs of different biomes at different levels (national, provincial)	To increase representation of at-risk ecosystems within the protected network. To increase budget for protected area management	Burkart 2006, Moreno et al. 2008, Sistema de Estadística Ambiental 2019, SAyDS 2020
	Sustainable livestock grazing	National	NA	Private: Fundación Aves Argentinas and Fundación Vida Silvestre Argentina	To generate knowledge on good management of natural grasslands to improve meat production and economic gains, without compromising grasslands sustainability	2012	NA	Several workshops and technical documents aiming at grassland management	To reach a greater number of local producers and stakeholders; replacement of input technology with process technology; to reach a sustainable development public-policy management	Aves Argentinas 2019
	Inventory of Important Birds Areas (IBAs)	National (based on regional initiative)	10.4% of the total RPG	Private: Fundación Aves Argentinas and BirdLife International	To identify and protect a network of critical sites based on the presence of globally threatened species, restricted distributions and/or confined to a singular biome, and/or congregating species	2000	NA	33 IBAs in Argentina; updated population data; monitoring and action plans were improved. Partnerships (Committee for the Conservation of Pampas Biodiversity, BIOPAMPA)	Some IBAs and Valuable Grassland Areas (VGAs) are overlapped	Bilenca & Miñarro 2004, Di Giacomo & Krapovickas 2005, Di Giacomo et al. 2007
	Valuable Grassland Areas (VGAs)	National (based on regional initiative)	3.5% of the Argentinean RPG	Private: Fundación Vida Silvestre Argentina (FVSA)	To define and identify well preserved natural grasslands, based on biodiversity, endemism, indicator species, land tenure and law, and cultural relevance	2002	NA	36 VGAs were identified in Argentinean Pampas and Campos	61% of VGAs overlapped total o partially with existing PAs; 47% on private lands, and most within areas with little agriculture aptitude. VGAs should be considered as “priority areas for protection by law” in future declarations (i.e. National Strategy on Biodiversity 2016-2020)	Bilenca & Miñarro 2004, Miñarro & Bilenca 2008, MAyDS 2017a
	Conservation strategy of Fundación Vida Silvestre Argentina (FVSA)	National (applied within regional approach)	NA	Private: FVSA	Creation of new PAs (public and private) and supporting existing ones; to promote policies and incentives for sustainable practices; conservation of flagship species; training, education and outreach for grassland conservation; partnership with entities experienced in grassland conservation.	2004	NA	Creation of public areas ("Campos del Tuyú") and private areas ("Refugio de Vida Silvestre Bahía Samborombón"), where the goals were undertaken.	NA	Miñarro & Bilenca 2008

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Brazil	National System of Conservation Unit (SNUC, in Portuguese)	Federal, state and municipal	3.24% of Pampas Biome in Brazil (0.7% within Full protection and 2.5% within sustainable use areas) in private and public lands	Public: Brazilian government	Regulation of PAs (federal, state and municipal areas)	2000	Law Nº 9,985	Land classification in two groups according to use and management strategy: fully protected and those that allow sustainable use.	To protect 17% of the area representative of the biome until 2020, under Convention on Biological Diversity (CONABIO 06/2013)	MMA 2019
	National Biodiversity Policy	National	Promote the conservation of 10% of the Pampa Biome (i.e. Campos)	Public: Brazilian government	Biodiversity conservation by promoting sustainable practices involving government and NGOs pertaining to resource use and valuations, considering economic, environmental, social and cultural values.	2002	Law Nº 4,339	Biodiversity valuation determined by its ecological, genetic, social, economic, scientific, educational, cultural, recreational and aesthetic contribution.	To link benefits of conservation to people wellbeing	MMA 2006
	Environmental Zoning plan for silviculture	State level (Rio Grande do Sul, Campos)	NA	Public: State Council	To conserve biodiversity (especially natural grasslands) and prevent expansion of agricultural frontier, particularly of large-scale industrial afforestation	2004	Resolution Nº 84/2004	Establishment of maximum plantation size buffering distances. Established of 3.5 million hectares as afforestation prone.	Disagreements between silviculture companies, activist groups and governmental institutions led to a reformulation with less restrictions	Gautreau & Velez 2011
	Legal Reserve law	National	Variable between biomes (20% in the case of the Campos)	Public: Brazilian government	To ensure the sustainable use of natural resources, assisting the conservation and rehabilitation of ecological processes that maintain biodiversity.	2012	Law Nº 12,727	Instrument applied on private land including Permanent Preservation Areas (protecting water resources, soil and biodiversity) and Legal Reserves (required on all private rural land, to preserve portions of native areas). Allowed alternative albeit compatible with conservation goals.	Effective implementation.	Silva & Ranieri 2014
Uruguay	National System of PAs(SNAP)	National	0.98% of the total territory are PAs along adjacency zones	Public: Uruguayan Congress	To harmonize planning and area management criteria; adoption of landscape level approach	2000	Law Nº 17,234	16 PAs identified. Strategic plans that articulate socio-economic and conservation aspects were generated; technical documents were produced for responsible land use and management.	To continue generating opportunities compatible with conservation (recreation, tourism, education, research and production) and increase native grasslands representation within PAs.	Ávila et al. 2018, Moraes Salvio & Ribeiro Gómez 2018, MVOTMA 2019
	Inventory of Important Birds Areas (IBAs)	National (based on regional initiative)	18% total IBAs area of the total territorial extension	Private: Aves Uruguay, Birdlife International	To identify and protect a network of critical sites for bird species based on the presence of globally threatened species, the existence of species with restricted distribution and the presence of species confined to a specific biome and/or species that form big bird congregations	2008	NA	22 IBAS proposed. Updated population data; monitoring and action plans were improved.	NA	Aldabe et al. 2009

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	Livestock Bureau in Natural Fields	National	NA	Public: Ministerio de Ganadería, Agricultura y Pesca (MGAP)	Cattle ranching management practices compatible with conservation and efficient use from an integral perspective; to identify and promote benefits obtained from native grasslands, and valuation regarding production and BES, especially resilience capacity to face climate change.	2012 to present	NA	Training workshops and meetings among ranchers to promote sustainable management and integrate research institutions with government sectors; GIS mapping of natural grasslands; institutional strengthening for conservation action; education and outreach; participatory research integrating farmer's knowledge.	NA	Pereira-Machín & Morales 2012, Jaurena et. al 2013, IICA 2017
	Climate Change Adaptation Development Project (DAAC)	National	NA	Public: MGAP	To support rural producers for the sustainable use of natural resources, while generating greater adaptation and resilience to climate change.	2012-2021	NA	Application of sustainable land management practices; project financing; strengthening capacities of farmer organizations; support for the Land Use and Management policy (National Agricultural Information System)	NA	Pereira-Machín & Morales 2012, Banco Mundial 2017
	National Plan for Adaptation to Variability and Climate Change for the Agricultural Sector	National	NA	Public and International: National System of Response to Climate Change and Variability (SRNCC); MGAP; Food and Agriculture Organization of the United Nations (FAO)	To guide public policies with a long-term vision (2025-2050) around the productive, environmental, social and institutional dimensions	2019	NA	Participative process involving different stakeholders	NA	OPYPA 2019
	Climate-smart Livestock Production and Land Restoration project (GCP/ URU/034/GFF)	National	4 Ecoregions with direct and indirect intervention	Public and International: Global Environment Facility; MGAP; MVOTMA; FAO	To mitigate climate change and restore degraded land through the promotion of climate-smart practices in cattle ranching	2019	NA	More efficient use of resources and lessen environmental impacts; reduction of greenhouse gas emissions; carbon sequestration in soil; positive impacts on biodiversity and other ecosystem services.	NA	OPYPA 2019

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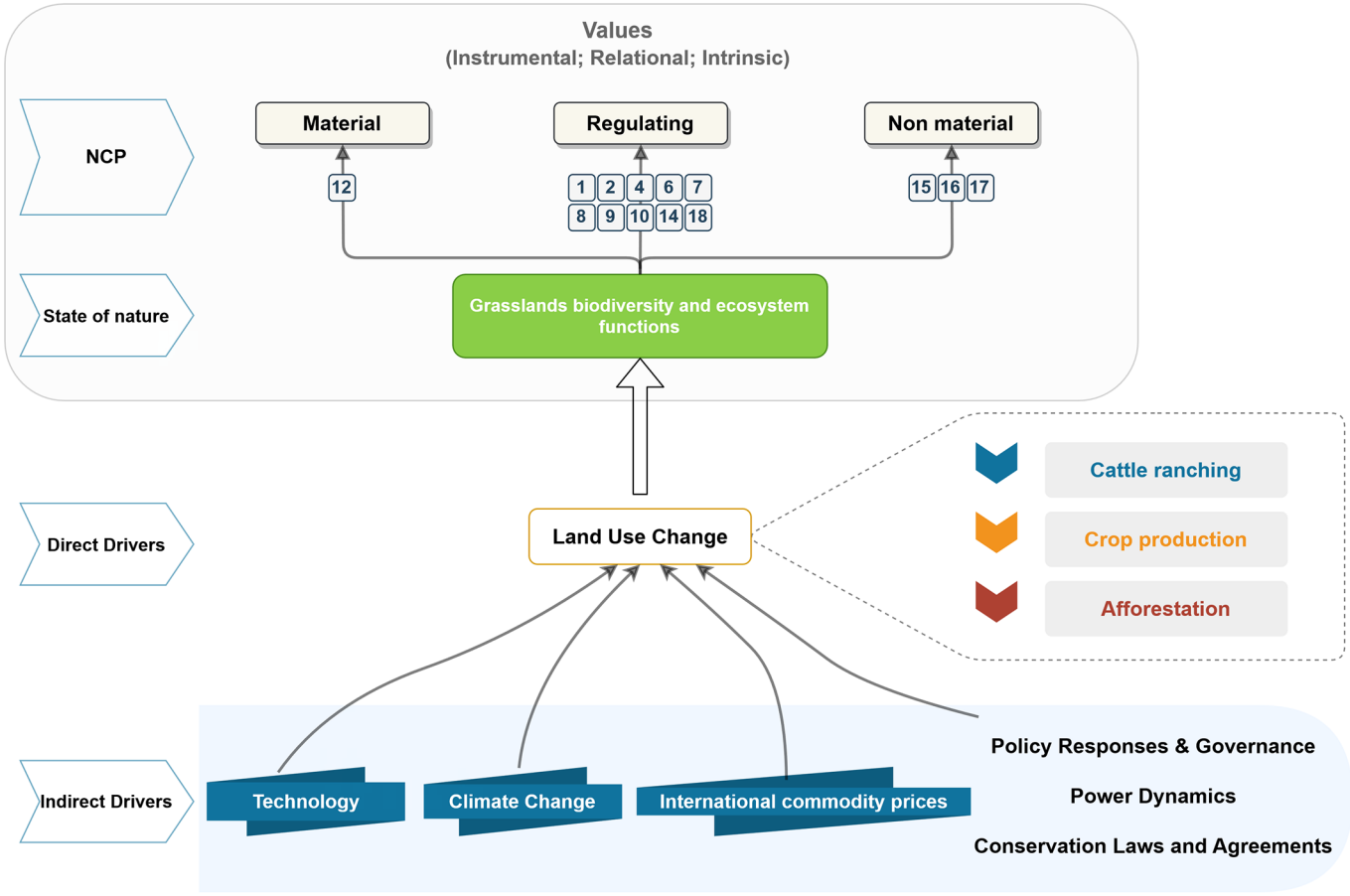


Figure 2. Conceptual framework for policy-based conservation of the Río de la Plata Grasslands (RPG) following the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) and Nature's Contribution to People (NCP) notion.

Discussion

The main goal of this study was to contribute to policy-based strategies for biodiversity conservation and ecosystem services provision for South America's Río de la Plata Grasslands, within a novel conceptual approach. From our review, we evidenced that the unsustainable practices that have resulted in negative consequences for BES over the RPG are currently still ongoing. We found that the different regions within the RPG share similar drivers of change (e.g. land-use change due to overgrazing, crop expansion, and afforestation, climate change, and invasive species) and are experiencing comparable negative consequences regarding the conservation of BES. Most studies highlighted regulating and material NCPs, while we found scarce information on non-material NCP. Similar results were evidenced by Mastrangelo et al. (2015), showing a tendency to focus on the biophysical processes and patterns of the ES rather than on assessing its cultural component and benefits to people. Thus, the LULC changes have occurred at the expense of the loss and degradation of natural environments, the system's sustainability, and cultural values (Mastrangelo et al. 2015, Modernel et al. 2016, Auer et al. 2017). Consequently, it is essential to develop a regional assessment of the RPG adapted to the cultural, social, political, and economic issues of the region. In addition, a transdisciplinary approach could help strengthen the interface between science and policy-makers while enhancing the participation of different stakeholders.

Current policy approaches for BES conservation differ between regions and countries. Based on our conservation-policy review, we found the pervasive and systemic grassland ecosystem degradation concerning. Although all countries recognize the importance of this biome and consequently express an interest in its conservation, the implementation and execution of plans and actions have been sparse. Lack of action is reflected in the limited inclusion of protection mechanisms in regional and local land planning strategies, as well as in the very low levels of protected-area coverage of native grassland within the RPG.

Policies for the conservation of BES in the study area are uncommon and incipient, particularly in Argentina and Uruguay (Azpiroz & Rilla Manta 2007, Modernel et al. 2016), while Brazil appears on the lead as far as current existing laws for grassland's BES conservation. To date, most conservation initiatives in Argentina are non-normative and territorial planning that includes grasslands is lacking. The Argentinian legislation considers only native forests as a priority for conservation when it regulates the promotion of productive developments. We propose that different types of biomes should be included, in order to reduce the potential threats to other vulnerable ecosystems. These could help increase the recognition of the grasslands´ ecological value and its conservation, from regional to national scales (Bond & Parr 2010, Overbeck et al. 2007). Thus, there is an urgent need to implement initiatives that establish a minimum proportion of grasslands to be

protected, with special emphasis on at-risk areas, along with strategic territorial planning initiatives. These could ensure that productive activities do not represent a threat to vulnerable ecosystems, especially where the most natural tracts of grasslands still remain. In Uruguay, a series of governmental initiatives were proposed in the last decades, which aimed at sustainable management of cattle ranching in natural fields and conservation of its BES (Bartesaghi et al. 2015, Ávila et al. 2018). Although there are concrete actions in the conservation of grasslands, it is necessary to create national legislation to regulate and enforce conservation policies. Contrary to these sustainable proposals, a recent law aims at intensifying agricultural production (Irrigation Law, Nº 19,553, 2017), which could negatively affect the grassland conservation.

In Argentina and Uruguay, conservation policies are more oriented towards the protection of a few threatened grassland species and their habitats (Di Giacomo et al. 2007, Soutullo et al. 2013, MAyDS 2017b). On the other hand, Brazilian policies for grassland conservation present a more optimistic perspective for the future. Expectations are on the enforcement of the Environmental Rural Registry code, which has the potential to constitute a reserve of preserved native grasslands. The possibility of linking the Permanent Preservation Areas and Legal Reserves should safeguard a minimum of 20% of the private grassland areas, and those within the governmental protected areas. However, grasslands in southern Brazil are considered a "neglected biome" (Overbeck et al. 2007), since it is not given adequate consideration and protection in comparison to other Brazilian biomes, and where policies focusing on farming intensification pose a significant threat to the BES sustainability of the grassland ecosystem.

We agree with Hoekstra et al. (2005) that conservation efforts should be addressed at large scales, as national and regional perspectives are the scales at which conservation policies will be more effective in halting habitat and biodiversity loss across the RPG (e.g. Di Minin et al. 2017). As previously mentioned, the management of the region has been mainly driven by national policies centered on rural economic development. Nevertheless, there are international initiatives that are applied to RPG conservation, mostly driven by NGOs actors. These initiatives are encouraging, but require institutional support enabled by national political approaches to reach a broad, transnational, and effective conservation outcome. There are several examples of successful multinational conservation efforts that transcend geographical boundaries and work together in pursuit of conservation, such as Natura 2000 network in the European Union through the EU's Birds (79/409/EEC), Habitats Directives (92/43/EEC) and the UN Convention on Biological Diversity. Regarding grassland management and conservation in the RPG, it is possible to address some similarities in comparison with European conservation approaches. Identified threats to European grasslands (Silvia et al. 2008) are in line with the ones found in our case study (EEA 2012). Concerning protected areas, different EU Member States define different approaches toward conservation. In effect, 25% of the 27 EU terrestrial lands are protected under either Natura 2000 (where human activities must be harmonious with the conservation of sites of natural importance), national designations, or a combination of both. Grasslands ecosystem share was 9.2% of the total area of protected sites in Europe, while for the total of areas included in Natura 2000, 11% were classified as grasslands (EEA 2012). Some of the policy proposals for these areas include the promotion of high nature value farmland or payments to farmers for the environmental services provided (Silvia et al. 2008).

Following the IPBES framework and the NCP concept, we sought to link scientific knowledge on biodiversity and ecosystem function, the values for society, and the policies that could promote conservation in the RPG. We concluded that the different regions in the RPG have in common not only the drivers but also the underlined negative consequences regarding the conservation of BES. Therefore, the conceptual framework built in this study is generalizable to the full extent of the RPG. This framework could be used as a tool to communicate the relevance and the benefits to society of preserving native grassland's BES in this region. Also, it could help to focus attention on the consequences of not applying sustainable management, which can result in the direct loss of the long-term productive capacity and resilience of this ecosystem (Foley et al. 2005, MEA 2005). Furthermore, this model would also aid in detecting the lack of information and policies in some areas, and serve as a base model to integrate new information. Lastly, the framework could be useful as a primary input in qualitative or quantitative modelling of relevant socio-economic scenarios and conservation outcomes (for instance, the Shared Socioeconomic Pathways; O'Neill et al. 2014), identification of policy options for future management (e.g. Anton et al. 2010, Paracchini et al. 2011), and to construct spatial models for synergies or trade-offs between different ecosystem functions and its conflicts (e.g. Zhang et al. 2019b).

1. Conservation policy proposal

Taking into consideration the "emerg[ent] biome crisis" (Hoekstra et al. 2005) that temperate grasslands face, and based on the threats identified in this study, we highlight a combination of policy mechanisms for conservation of the RPG. Based on the proposed framework, the following initiatives could enhance and/or maintain the existing biodiversity as well as increase connectivity throughout the RPG. In addition, we associate the different values and NCPs that these policies could enhance. However, we acknowledge that these efforts are not an end but a starting point to reach long-term conservation goals.

First and foremost, an expansion of the natural protected areas in the RPG is crucial. Dinerstein et al. (2019) state that there is a small window of opportunity of 10 years to halt climate change below 1.5°C and to prevent 'points of no return' in terms of habitat loss and species extinction. Following this idea, we concur that a higher percentage of the RPG should be under some form of protection. Protection here is understood as defined by the International Union for Conservation of Nature (Dudley 2008). In order to protect all subregions in the RPG, each country could use a combination of the following: (1) establish multiple protected areas through legal mechanisms in zones identified as hotspots for BES, including the creation of buffer zones and natural corridors within agricultural landscapes (e.g. Nin et al. 2016, Schröter et al. 2017) to increase interconnectedness throughout the RPG; (2) Create incentives (in the form of tax breaks or payments for ES) for landowners who allocate part of their properties to grassland conservation (Alianza del Pastizal 2019). (3) Argentina and Uruguay could adapt and implement similar measures to that of Brazil (Environmental Rural Registry) to protect 20% of each private property.

We are aware that effective grassland biodiversity conservation outcomes cannot be achieved through protected areas alone (Harlio et

al. 2019). Thus, it is important to take into consideration the connectivity of these conservation areas to minimize landscape fragmentation and its detrimental effect on biodiversity (Batáry et al. 2011). The connectivity of these natural areas is essential to dispersal success, persistence, and genetic diversity of species in fragmented landscapes (Schooley & Branch 2011). Some of the agri-environment schemes implemented by the European Union's Common Agricultural Policy did not have a positive effect on biodiversity and it was associated with the lack of regional and landscape conservation planning in farmlands (Batáry et al. 2011; Harlio et al. 2019). Looking at the trends of the RPG, there is an increase in cropland areas, so the maintenance of rural roadside could play an important role. Roadsides can host a diverse and representative flora and fauna of the region, supporting their importance as refuges and reservoirs of biodiversity (Saez et al. 2014; Arenas et al. 2017). Herrera et al. (2017) suggested a novel and simple index to assess the conservation status of roadsides that could serve as an initiative to implement in other areas and to take these landscape elements into consideration in decision-making.

Second, the regulation of LULC changes throughout the RPG is fundamental to the long-term conservation of this biome. Existing economic regional bodies such as MERCOSUR (Common Market of South America) could be used to establish biome-wide conservation goals, legislation, and control mechanisms that align with each country's economic growth models (Soutullo & Gudynas 2006). Such actions could include, but are not limited to, the establishment of national zoning and land use regulation schemes based on socio-economic information and BES hotspots identification (Nin et al. 2016; Di Minin et al. 2017). This process could be expanded to the entire RPG region, and even to larger spatial scales within a multi-biome land-use prioritization approach (i.e. the entire Del Plata Basin; Viglizzo & Frank 2006). These guidelines could help reach an agreement between countries about land-use policies focusing on particular areas that are crucial for the RPG's biodiversity and ecosystem services provision. This will require control mechanisms that can verify such activities are following and meeting national and regional agreements. Coordinated actions between the involved countries, along with well-defined management objectives and regulations, could represent a key strategy for developing an effective regional network of conservation strategies inside and outside of protected areas (Bicknell et al. 2017; Moraes Salvio & Ribeiro Gómez 2018).

Lastly, the inclusion of socio-cultural values into all management policies and plans is necessary. The identification and comprehension of the different nature values and worldviews are essential steps to link the NCP and their influence on human well-being. This approach is applicable to initiatives at the science-policy interface in order to obtain sustainable management of the environment (Pascual et al. 2017). Policies that consider stakeholder's welfare based on local and scientific knowledge and allow compatibility between different land uses could support long-term sustainable use of grassland ecosystems (see examples on Pillar et al. 2009). Effective conservation measures must be implemented with the full support of local communities (Modernel et al. 2016). Furthermore, Dujin et al. (2008) identified three major types of values related to protected areas: economic, social and environmental, which presents benefits that can be enjoyed at multiple levels: local, regional, cross-border, international or global benefits, including the public and private sectors (Kettunen et al. 2009).

Protected areas are the cornerstone of conservation, but taking into consideration the economic relevance of the region to each country, biodiversity conservation cannot rely only on those areas. Sustainable conservation also requires policies for managing the entire region, including areas dedicated to agricultural activities, within a regional perspective, and taking into consideration people's outlooks and values (Margules & Pressey 2000, Tscharntke et al. 2005, Harlio et al. 2019). Following IPBES' aim to promote the conservation and sustainable use of biodiversity, long-term human well-being, and sustainable development, our study addresses the main drivers of change in the RPG. Our conceptual framework can provide an approach to integrate international policies and increase the conservation level of this biome, connecting it with the different grassland values. We are aware of the complexity of these efforts and the implementation of international policies highlighted in this study. However, national and local governments should realize the importance of conserving the RPG and the consequences of not addressing the drivers affecting it.

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Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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A new species of freshwater amphipod (Crustacea, Amphipoda, Hyalellidae) from state of Rio Grande do Sul, Southern Brazil

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Abstract: The current study describes a new species of *Hyalella* found in a natural pond at the municipality of Palmeira das Missões, located in the northwestern region of state of Rio Grande do Sul, southern Brazil. The new species differs from other species found in state of Rio Grande do Sul (*Hyalella bonariensis*, *H. castroi*, *H. kaigang*, *H. imbya*, *H. georginae*, *H. gauchensis*, *H. montenegrinae* and *H. pampeana*) in the type and number of setae on uropods, on telson and on the inner face of gnathopod 1. Besides, *Hyalella palmeirensis* is morphologically similar to *H. curvispina*, especially in the shape and number of setae of uropods. However, *H. palmeirensis* differs from *H. curvispina* in having only two simple setae on telson, the inner face of gnathopod 1 with five serrate setae and only the posterior distal margin with denticles in comb-scales, and especially by the tubular sternal gills, present on segments 3 to 7. These new records increase from 11 to 12 the number of species known from state of Rio Grande do Sul.
Keywords: *Freshwater crustaceans, Hyalella, Peracarida, taxonomy.*

Uma nova espécie de anfípodo dulcícola (Crustacea, Amphipoda, Hyalellidae) do estado do Rio Grande do Sul, sul do Brasil

Resumo: O presente trabalho descreve uma nova espécie de *Hyalella* encontrada numa nascente no município de Palmeira das Missões, localizado na região noroeste do estado do Rio Grande do Sul, sul do Brasil. A nova espécie difere das outras espécies encontradas no estado do Rio Grande do Sul (*Hyalella bonariensis*, *H. castroi*, *H. kaigang*, *H. imbya*, *H. georginae*, *H. gauchensis*, *H. montenegrinae* and *H. pampeana*) especialmente com relação ao tipo e número de setas dos urópodos, télson e superfície ventral do gnatópodo 1. Além disto, *H. palmeirensis* é similar a *H. curvispina*, especialmente na forma e número de setas dos urópodos. Entretanto, *H. palmeirensis* difere de *H. curvispina* por possuir somente duas setas simples no télson, cinco setas serradas na superfície ventral do gnatópodo 1 e dentículos (comb-scales) somente na margem posterior do gnatópodo 1 e brânquias esternais presentes do segmento 3 ao 7. Esse novo registro aumenta para 11 o número de espécies de *Hyalella* conhecidas para o estado do Rio Grande do Sul.
Palavras-chave: *Crustáceo dulcícola, Hyalella, Peracarida, taxonomia.*

Introduction

Amphipoda is a successful group of peracaridan crustaceans known in several aquatic environments, including freshwaters where it exerts dominance of the benthic community of lakes (Ishikawa and Urabe 2002; Rodrigues 2016). The latest classification of the Order is shown by Lowry and Myers (2013), and these authors presented a new Suborder called Senticaudata, comprising almost all freshwater Amphipoda species and many marine species that previously belonged to the defunct Suborder Gammaridea.

The Family Hyalellidae is represented only by *Hyalella* Smith, 1874, which occurs throughout the Nearctic and Neotropical biogeographic regions, and it is endemic of the Americas (Baldinger 2004), presenting restrict distribution of species (Bousfield 1996). There are 74 limnic crustacean species of *Hyalella* (Marrón-Becerra et al. 2014; Colla and César 2015; Streck et al. 2017; Bastos-Pereira et al. 2018), however the highest diversity of species occurs in South America, where 56 species are currently described (Rodrigues et al. 2014, Colla and César 2015; Streck et al. 2017; Bastos-Pereira et al. 2018).

Brazil has the greatest number of *Hyalella* species described in the world, 27 in total (Bueno et al. 2013; Bueno et al. 2014; Cardoso et al. 2014; Rodrigues et al. 2014; Streck et al. 2017; Rodrigues et al. 2017, Bastos-Pereira et al. 2018). According to Bueno et al. (2014) and Streck et al. (2017) the state of Rio Grande do Sul (Southern Brazil) is the region with the highest species diversity in the country, counting 11 described species. With the finding of this specie the state of Rio Grande do Sul account now with 12 *Hyalella* species, the same number of species observed in all Southeast region of Brazil.

A new species of *Hyalella* is described from the municipality of Palmeira das Missões, northwest region of state of Rio Grande do Sul, southern Brazil.

Material and Methods

The municipality of Palmeira das Missões is located at the northwest region of state of Rio Grande do Sul, Southern Brazil. The specimens were collected in August/2012 and the sampling was made with the aid a hand net, with authorizations of the Instituto Chico Mendes de Conservação da Biodiversidade (MMA; ICMBio; SISBIO nº 32726-1).

Head length of the animals was measured through an optic microscope with a millimetric scale. Adult males and females were preserved in ethanol 70%, colored with Rose Bengal and dissected. A total of 15 individuals (10 males and 5 females) were dissected and the appendices were mounted on permanent slides. Illustrations were made using photos and the CorelDraw program.

The description was made based on main morphological characteristics such as the gnathopods, uropods and telson, according to González et al. (2003a, b), González et al. (2006), Cardoso et al. (2011), and Bastos-Pereira and Bueno (2012). The terminology used for the setae of the appendices follows Zimmer et al. (2009).

The description was based on male paratype and female allotype. The type material is deposited in the Museu Nacional do Rio de Janeiro (MNRJ).

Results

Taxonomy
Order Amphipoda Latreille, 1816
Suborder Senticaudata Lowry & Myers, 2013
Family Hyalellidae Bulycheva, 1957
Genus *Hyalella* S. I. Smith, 1874

***Hyalella palmeirensis* n. sp. Streck-Marx & Castiglioni**

Type material: Holotype male, total body length = 5.32 mm, head length = 0.50 mm (MNRJ 26584); Allotype female (MNRJ 26585). Brazil, state of Rio Grande do Sul, Palmeira das Missões municipality (27º 56.949' S – 53º 19.613' W), August, 24, 2012, Castiglioni, D.S. coll.

Paratypes: Mean total body length of male paratypes: 5.50 ± 0.78 mm and female paratypes: 5.00 ± 0.50 (20 males and 20 females) (MNRJ 26586), same date as holotype, Castiglioni, D.S. coll.

Type-locality. Brazil, state of Rio Grande do Sul (27º56.949'S 53º19.613'W), state of Rio Grande do Sul, Palmeira das Missões municipality, natural pond, 560 m, August, 24, 2012, Castiglioni, D.S. coll.

Diagnosis. Body surface smooth. Eyes round, pigmented. Antenna 1 shorter than antenna 2, flagellum with 11/12 articles and longer than peduncle, two aesthetascs occurring distally on flagellum after article 5. Antenna 2 flagellum with 10/11 articles and longer than peduncle. Maxilla 1 palp uniarticulate, short, longer than wide, inner plate shorter and slender than outer plate, with two long apical papposerrate setae, and some setules on the inner margin; outer plate with nine serrate setae. Maxilla 2 inner plate with only one long and strong papposerrate seta and several simple and serrate setae. Gnathopod 1 with inner face with five serrate setae, posterior distal margin with denticles in comb-scales, one cuspidate seta and some simple setae. Gnathopod 2 propodus longer than wide and with posterior margin of small lobe covered by denticles in comb-scales; palm smooth and sub-equal to posterior margin of propodus, slope oblique, palm margin convex; dactylus claw-like, short, not reaching the lobe of propodus; carpus wider than long, posterior lobe elongated, with pectinate border and one row of serrate setae, without polygonal pattern or comb-scales. Pleopods rami with long plumose setae. Uropod 1 inner ramus with a long-curved seta followed by a row of five small cuspidate setae with an accessory seta. Uropod 2 inner ramus apex with five cuspidate setae with an accessory seta and two cuspidate simple setae. Uropod 3 peduncle with three cuspidate setae with accessory setae apically, small cuspidate setae and simple setae distributed along the peduncle and ramus. Telson (male) longer than wide, with two apical simple setae, and three plumose setae close to each simple seta. Coxal gills sac-like present on segments 2 to 6 and sternal gills tubular, presents on segments 3 to 7.

Description of male. (Fig. 1a) Mean body length: 5.50 ± 0.78**,** mean head length: 0.52 ± 0.07 mm (n=20). Head longer than the first thoracic segment, rostrum absent. Eyes round, pigmented.

Antenna 1 (Fig. 1b) shorter than antenna 2, peduncle not surpassing head length, flagellum with 11/12 articles, longer than peduncle; aesthetascs occurring distally on flagellum after article 5.

Antenna 2 (Fig. 1c) peduncle less than half body length, with very few setae; flagellum with 10/11 articles and longer than peduncle.

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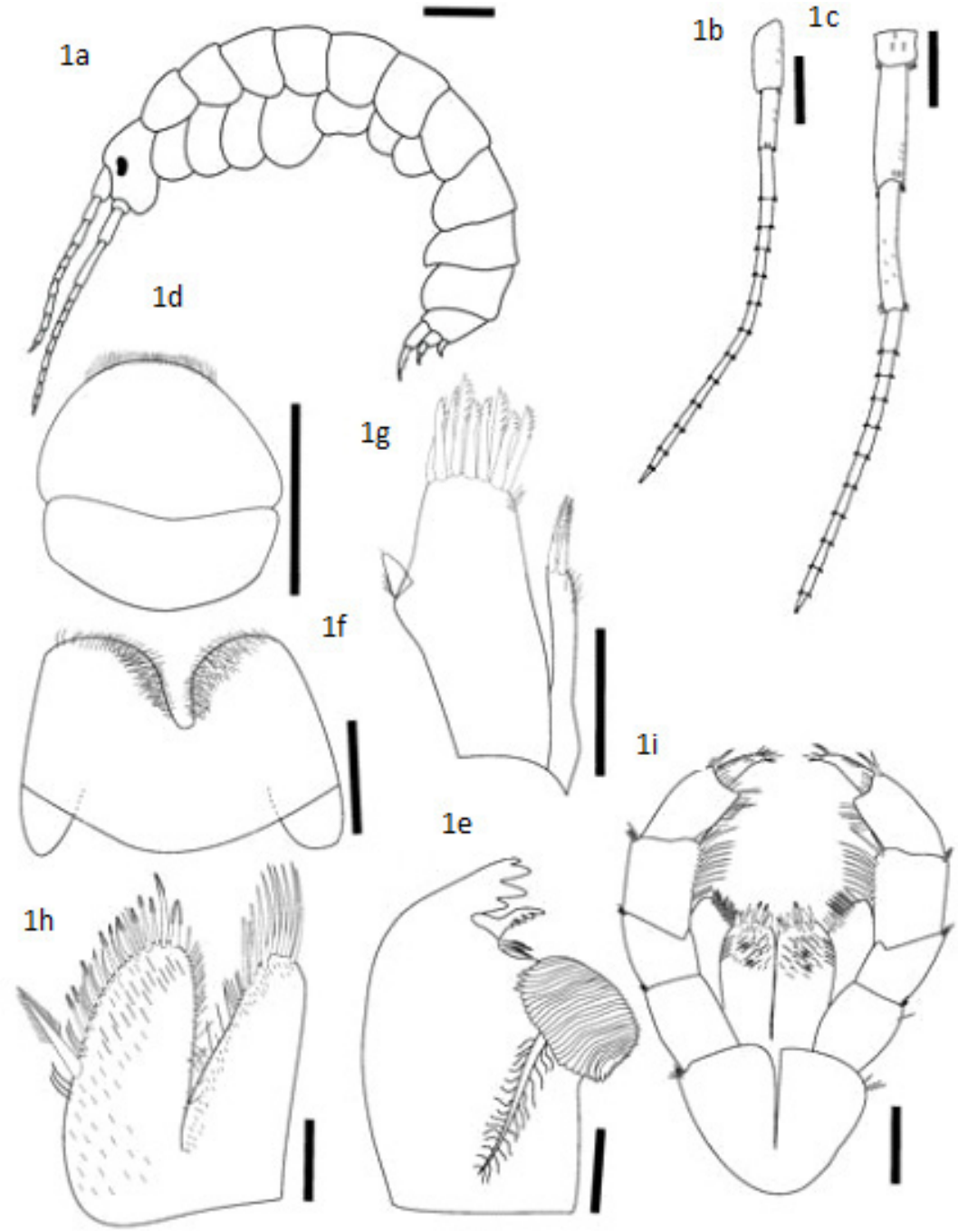


Figure 1. *Hyalella palmeirensis* n. sp. Paratype male (MNRJ 26586): (a) Habitus from holotype (MNRJ 26584), body length: 5.32 mm; (b) Antenna 1; (c) Antenna 2; (d) Upper lip; (e) Left mandible; (f) Lower lip; (g) Maxilla 1; (h) Maxilla 2; (i) Maxilliped; Scales: (1a-1c) represents 0.5 mm; (1d-1g) 0.2 mm; (1h) 0.05 mm; (1i) 0.2 mm.

Upper lip (Fig. 1d) margin rounded, distal border covered by several setules on dorsal and ventral faces.

Basic amphipodan mandible (Fig. 1e) (in sensu of Watling 1993), without palp; incisor toothed; left *lacinia mobilis* with five teeth and with three pappose setae; molar process large, cylindrical and with large accessory seta.

Lower lip (Fig. 1f) outer lobes rounded without notches or excavations, with several setules on dorsal and ventral faces.

Maxilla 1 (Fig. 1g) palp uniarticulate, short, longer than wide, reaching less than half length the distance between the base of the palp and tip of setae on outer plate; inner plate uniarticulate, shorter and slender than outer plate, with two long apical pappose setae. Outer plate uniarticulate, with 9 serrate setae.

Maxilla 2 (Fig. 1h) inner plate with one long and strong papposerrate seta, several simple and serrate setae; outer plate with one row of simple setae.

Maxilliped (Fig. 1i) inner plates apically truncated, with three connate setae and pappose and simple setae apically and medially; outer plates larger than inner plates, apically truncated, apical, medial, and facial setae simple. Palp of four articles with simple setae and few pappose setae; dactylus unguiform, shorter than propodus, with simple setae and comb-scales.

Gnathopod 1 (Fig. 2a) subchelate; dactylus claw-like, with denticles in comb-scales and one plumose seta dorsally; propodus longer than wide, width about 3⁄4 of maximum length (rectangular), hammer-shaped, palm slope slightly oblique and margin sinuose with several simple setae, posterior distal margins with comb scales, one cuspidate setae and some simple setae, anterodistal margin without comb scales, but with six or seven simple setae, propodus inner face (ventral) with five serrate setae; carpus longer than wide, slightly longer than propodus, with strong lateral distal lobe produced and forming a scoop-like structure, posterior lobe of carpus with one row of serrate setae and without comb-scales; basis, ischium and merus with simple setae dorsally, without comb-scales posterodistally; coxal plates longer than wide.

Gnathopod 2 (Fig. 2b) subchelate; dactylus claw-like, short, not reaching the lobe of propodus, with one plumose seta dorsally, without comb-scales; propodus longer than wide (ovate), propodus length 1.5 times the maximum width, posterior margin of lobe almost straight and covered with denticles in comb-scales; palm margin convex, with several cuspidate setae with accessory setae and simple setae, posterior distal corner with few simple setae; carpus wider than long, posterior lobe elongated, with pectinate border with one row of serrate setae and without polygonal pattern or comb-scales; ischium and merus with few simple setae on posterodistal margin; basis, ischium and merus without comb-scales on posterior margin; coxal plate wider than long.

Peraeopods 3 to 7 (Fig. 3a to 3e) dactylus, propodus, carpus, merus, ischium and basis with simple and cuspidate setae with accessory seta. All coxal plates with simple setae on the border.

Pleopods (Fig. 4a) not modified, peduncle slender, smaller than flagellum rami, and two distal coupling spines; both rami with long plumose setae.

Uropod 1 (Fig. 4b) peduncle slightly (1.2 times) longer than rami, with four cuspidate setae with an accessory seta dorsally; inner ramus longer than outer ramus; inner ramus with two dorsal cuspidate setae with an accessory seta, male with a curved seta followed by a row of five small cuspidate setae with an accessory seta, two cuspidate setae apically; outer ramus with three dorsal cuspidate setae with an accessory seta and four cuspidate setae apically (two of them with an accessory seta).

Uropod 2 (Fig. 4c) shorter than uropod 1; peduncle rectangular with similar size as rami, with four cuspidate setae with an accessory seta dorsally; inner ramus slightly longer than outer ramus, with two dorsal cuspidate setae with an accessory seta and seven cuspidate setae apically (five with an accessory seta); outer ramus with two dorsal cuspidate setae with an accessory seta and apex with four cuspidate setae (two with an accessory seta).

Uropod 3 (Fig. 4d) peduncle slightly longer than wide, wider than ramus, with three cuspidate setae with an accessory seta and one simple seta apically, two simple setae distributed along the peduncle; ramus with five simple setae and a short, strong cuspidate setae.

Telson (Fig. 4e) is longer than wide, with two long simple setae and three plumose setae close to each simple seta.

Coxal gills sac-like, present on segments 2 to 6. Sternal gills tubular on segments 3 to 7.

Female. Mean total body length: 5.00 ± 0.50, mean head length: 0.47 ± 0.05 (n= 20). Antenna 1 similar shape to male but with flagellum of 7–8 articles. Antenna 2 similar in shape to male, flagellum of 8–9 articles.

Gnathopod 1 (Fig. 5a) similar to male gnathopod 1, similar size to gnathopod 2; dactylus with comb-scales and plumose seta; propodus longer than wide, hammer-shaped, inner face with five serrate setae and two long simple setae and several short simple setae , anterior distal margin without comb-scales but two simple setae and distally with six or seven short simple setae, posterior distal margin with comb-scales and two simple setae and posterior distal corner with one strong cuspidate seta; carpus longer than wide, with lateral distal lobe produced and forming a scoop-like structure, posterior lobe margin with polygonal pattern and with serrate setae and without comb-scales; base, merus and ischium without comb-scales on posterior margin.

Gnathopod 2 (Fig. 5b) similar in size to gnathopod 1, but the propodus of gnathopod 2 is slightly longer than gnathopod 1; different to male gnathopod 2 in shape and smaller; dactylus with comb-scales and one plumose seta; propodus rectangular, longer than wide, inner face with four serrate setae and two long simple setae and several short simple setae, palm transverse, posterior distal corner with one strong cuspidate seta, posterior distal margins with comb-scales and two simple setae and anterior margin without comb-scales; base, merus and ischium without comb-scales on posterior margin. Telson similar in shape to male, with two long simple setae and three plumose setae close to each simple seta.

Habitat. Freshwater, epigean. *Hyalella palmeirensis* was found in a natural pond of shallow depth (around 40 cm) (Fig. 6a and 6b). The pond contains a large amount of macrophytes of the genus *Egeria* which were used as shelter for the specimens of *H. palmeirensis*.

Etymology. The specific name, *palmeirensis*, refers to native residents of Palmeira das Missões municipality, southern Brazil.

Remarks. We noted using the taxonomic key of Rodrigues et al. (2014) that *H. palmeirensis* differs from the other species of the genus in Brazil. *Hyalella palmeirensis* resembles *H. bonariensis*, *H. montenegrinae*, *H. curvispina*, *H. castroi*, *H. imbya, H. pseudoazteca*,

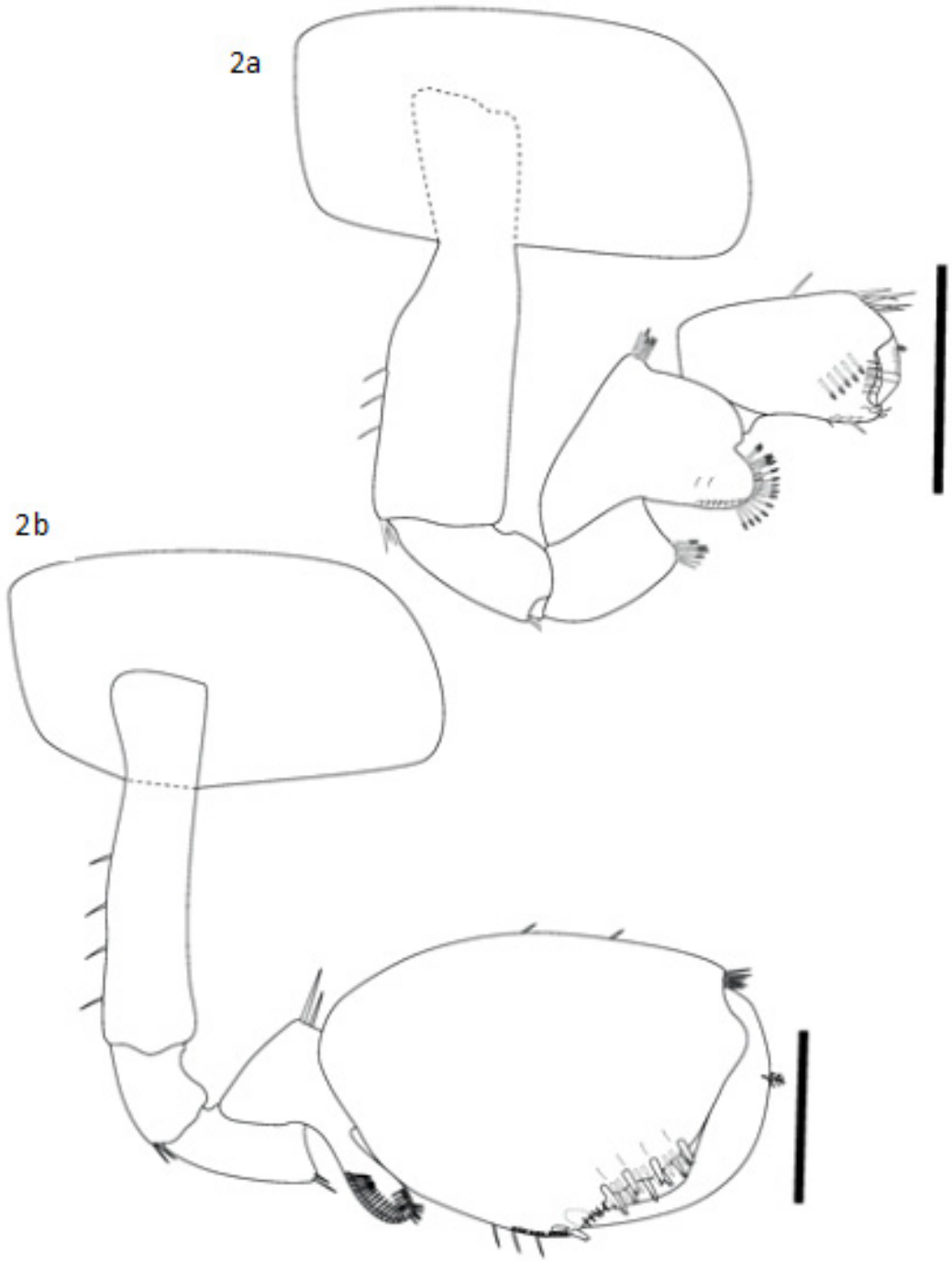


Figure 2. *Hyalella palmeirensis* n. sp. Paratype male (MNRJ 26586); (a) Gnathopod 1; (b) Gnathopod 2; Scales: (2a-2b) represents 0.5 mm.

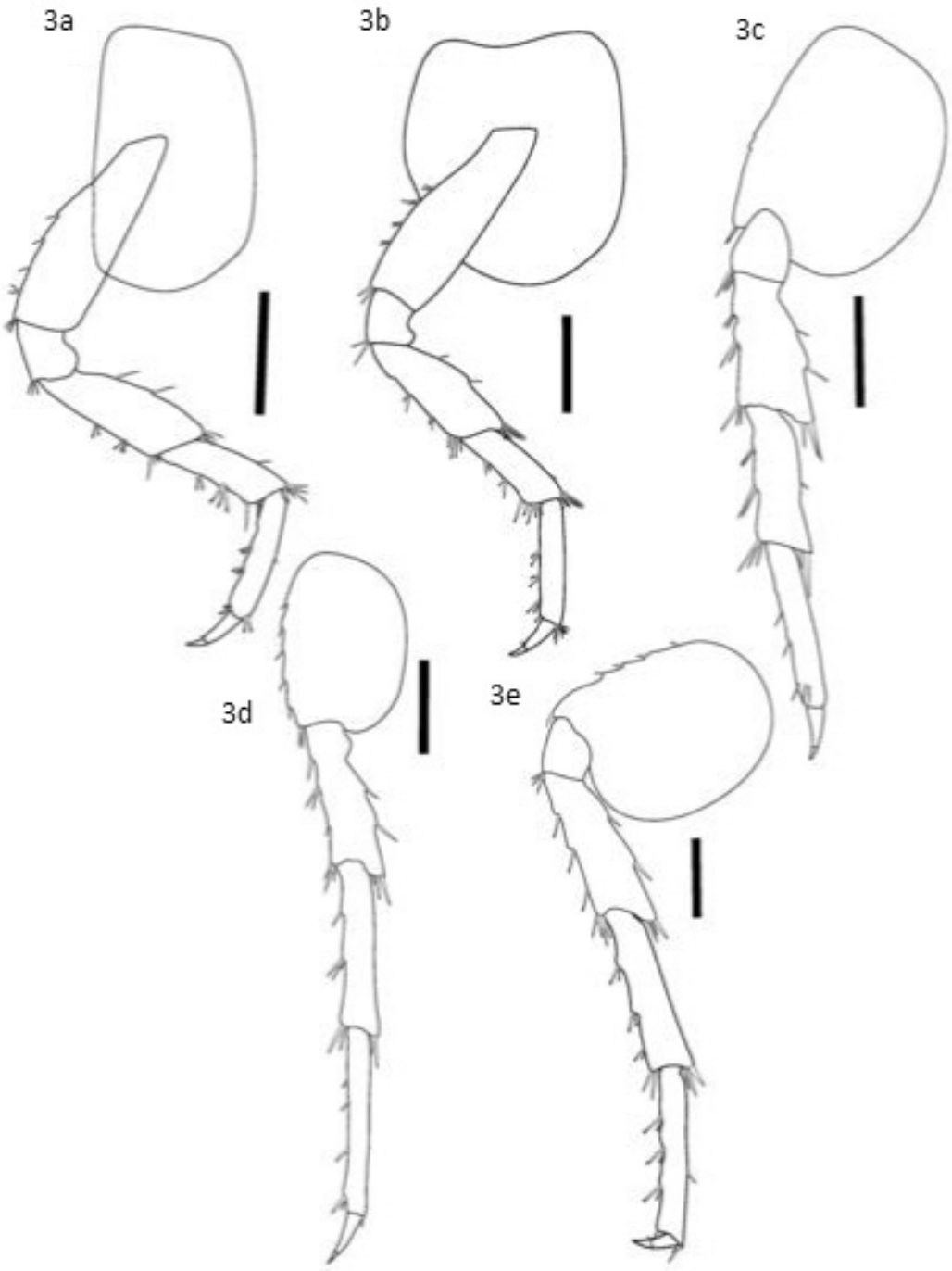


Figure 3. *Hyalella palmeirensis* n. sp. Paratype male (MNRJ 26586); (a) Peraeopod 3; (b) Peraeopod 4; (c) Peraeopod 5; (d) Peraeopod 6; (e) Peraeopod 7; Scales: (3a-3e) represents 0.5 mm.

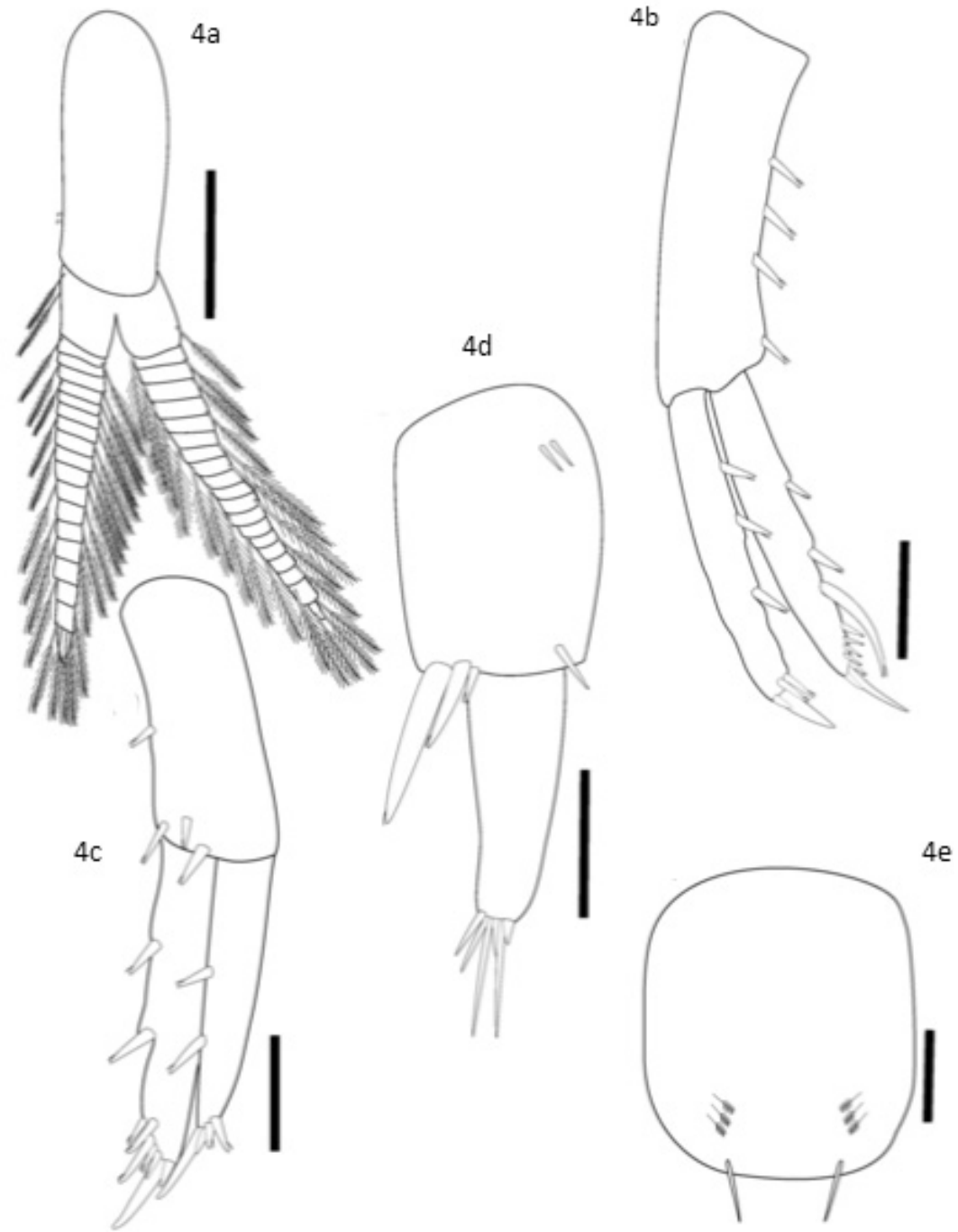


Figure 4. *Hyalella palmeirensis* n. sp. Paratype male (MNRJ 26586); (a) Pleopod; (b) Uropod 1; (c) Uropod 2; (d) Uropod 3; (e) Telson; Scales: (4a) represents 0.5 mm; (4b-4d) 0.2 mm; (4e) 0.05 mm.

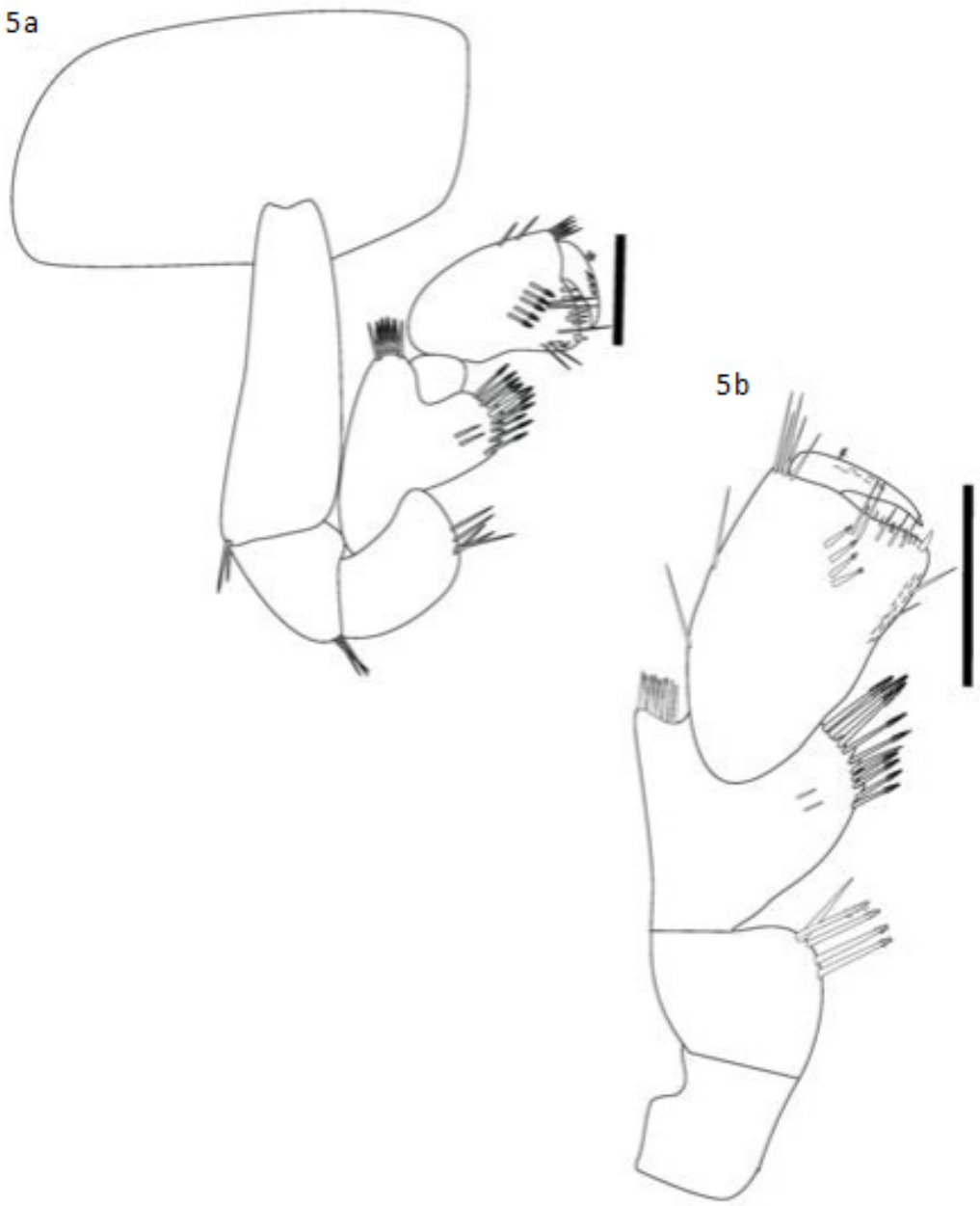


Figure 5. *Hyalella palmeirensis* n. sp. Allotype female (MNRJ 26585); (a) Gnathopod 1; (b) Gnathopod (2) Scales: (5a-5b) represents 0.2 mm.

H. kaingang, *H. pampeana, H. pleoacuta*, *H. carstica, H. xakriaba*, *H. georginae* and *H. gauchensis*, by having a curved seta on the inner ramus of uropod 1 of the males.

Besides, *H. palmeirensis* resembles *H. montenegrinae, H. carstica* and *H. montana* Rodrigues et al., 2017 in having sternal gills on segments 3–7. The new species resembles *H. curvispina, H. castroi*, *H. pseudoazteca*, *H. kaingang* and *H. pleoacuta* in having the dactylus of gnathopod 2 shorter than the propodus palm. Differs from *H. bonariensis, H. castroi*, *H. kaigang H. imbya, H. georginae, H. gauchensis, H. montenegrinae* and *H. pampeana* in the type and number of setae on uropods, telson and inner face of gnathopod 1. *Hyalella palmeirensis* is similar to *H. curvispina*, especially in the shape and number of setae of uropods. However, *H. palmeirensis* differs of *H. curvispina* in having only two simple setae on telson, inner face of gnathopod 1 with five serrate setae and only the posterior distal margin with denticles in comb-scales, and especially by tubular sternal gills present on segments 3 to 7.

The new species *Hyalella palmeirensis* resembles *H. misionensis*, from the Province of Misiones in Argentina, in the telson (male) with two long apical simple setae. However, it differs in the curved seta on the inner ramus of uropod 1, inner face of propodus of gnathopod 1 and sternal gills. The area where *H. misionensis* was found is geographically close to Brazil. Comparisons between morphological characters of *Hyalella* species of Rio Grande do Sul are presented in Table 1.

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Figure 6. Type-locality of *Hyalella palmeirensis* n. sp. Streck-Marx & Castiglioni; (a) Showing the natural pond of shallow depth (around 40 cm). Note the large amount of macrophytes of the genus *Egeria*, which are used as shelter for the specimens of the new species; (b) Showing the natural pond of shallow and surrounding cultivation of any type of crops, as soy and rice which could be considered a threat to this species as the pesticides used in these cultures can be harmful to the amphipods.

Discussion

The new species described here, improves the diversity of *Hyalella* in the Southern region of Brazil, increasing the number of species found in the region, to 14, whereas 12 of them are observed in the state of Rio Grande do Sul, the same number of all southeastern region of Brazil (Bueno et al. 2014; Cardoso et al. 2014; Rodrigues et al. 2014).

In addition to morphological differences, other evidence that *H. palmeirensis* is a distinct species from others of the genus comes from a matrix of pairwise nucleotide sequence divergences using concatenated genes 16 S (~650bps), 12 S (~550bps) and H3 (~375bps) (Rodrigues 2016). This analysis showed that *H. palmeirensis* (called *Hyalella* sp. 20 by Rodrigues 2016) diverge at least 15.3% to 25.4% from *H. curvispina*, (the closest species), and 16.2% from *H. gauchensis* (called *Hyalella* sp. 18 by Rodrigues 2016) and 17.6% from *H. georginae* (called *Hyalella* sp. 19 by Rodrigues 2016) (Rodrigues 2016). It should be noted that *H. gauchensis* and *H. georginae* are two species that occur in nearby areas where *H. palmeirensis* was sampled (Streck et al. 2017). Moreover, Rodrigues (2016) estimated the phylogeny of *Hyalella* reconstructed by Bayesian analysis and according to it, *H. palmeirensis* is statistically

Table 1. Main morphological differences between *Hyalella palmeirensis* n. sp. Streck-Marx & Castiglioni and 11 *Hyalella* species from nearby areas in the state of Rio Grande do Sul, Southern, Brazil.

Species	Body surface	Inner margin of maxila 2	Articles of flagellum of antenna 1	Articles of flagellum of antenna 2	Inner face of propodus of gnathopod 1	Setae on peduncle of uropod 3	Telson	Sternal gills	Tipe locality
H. bonariensis	Smooth	Two pappose setae	9–12	12–15	5 setae	6 setae	Quadrangular, with 2–3 cuspidate setae apically	2–7	Province of Buenos Aires, Salto, Argentina
H. castroi	Smooth	One pappose setae	10–17	14–18	More than 10 serrate setae	7 setae	Wider than long, with 8 setae	2–7	Vale of trout, Rio Grande do Sul, Brazil
H. curvispina	Smooth	Two plumose setae	11	13	5–7 setae	3 setae	Wider than long, with 3 simple spines	2–7	Lake Tramandai, Rio Grande do Sul, Brazil
H. georginae	Smooth	Two robust papposerrate apical setae	15	16	9 serrate setae	9 setae	Wider than long, with 7 apical cuspidate setae with an accessory seta, and 4 plumose setae laterally	2–7	Palmeira das Missões, Rio Grande do Sul, Brazil
H. gauchensis	Smooth	Two papposerrate apical setae	11	15	9–20 serrate setae	6 setae	Wider than long, with 6 apical cuspidate setae, and 6 plumose setae laterally	2–7	Palmeira das Missões, Rio Grande do Sul, Brazil
H. imbya	Smooth	Two papposerrate setae	18–23	14–16	7 serrate setae	1 seta	Two long simple apical setae	3–7	Roque Gonzales, Rio Grande do Sul, Brazil
H. kaigang	With dorsal flanges on pleonites 1-2	Two papposerrate setae	17–18	18–24	2 rows of serrate setae	6 setae	Wider than long, with 6–7 cuspidate seta with acessory setae	2–7	Garapiá stream, municipality of São Francisco de Paula, Rio Grande do Sul, Brazil
H. montenegrinae	Smooth	Two plumose setae	14–16	14–19	9–10 plumose setae	4 or 5 setae	Wider than long, 7 to 9 setae	3–7	São José dos Ausentes, Rio Grande do Sul, Brazil
H. pampeana	Smooth	Two bipectinada setae	11–12	Up to 18	5–6 setae	5 to 7 setae	As wide as long, apically rounded, with 2–5 spines	2–7	Province of Buenos Aires, Argentina
H. pleoacuta	With dorsal flanges on some segments	Two pappose setae	14	15	9 serrate setae	4 setae	As long as wide, with 2 simple setae	2–7	Vale of Trout, Rio Grande do Sul, Brazil
H. pseoudoazteca	With dorsal flanges on some segments	One pappose seta	10	8–9	1–3 pappose setae	1 seta	Wide as long, 2 closely spaced, long simple setae	3–7	Taim Ecological Reserve, Rio Grande do Sul, Brazil
H. palmeirensis	Smooth	One pappose setae	11–12	10–11	5 serrate setae	3 setae	Longer than wide, with 2 long simple setae and 6 plumose setae laterally	3–7	Palmeira das Missões, Rio Grande do Sul, Brazil

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well supported in a different clade from *H. curvispina*, *H gauchensis* and *H. georginae*, forming distinct groups which have divergence at 28.55 million of years ago.

The species *Hyalella palmeirensis* lives in association with macrophytes in a natural pond of shallow depth. The pond contains a large amount of macrophytes of the genus *Egeria,* which are used as shelter by *H. palmeirensis*. However, *H. palmeirensis* occurs in a natural pond surrounded by the cultivation of many types of crops, which could be considered a threat to this species as the pesticides used during cultivation can be harmful to the amphipods. Agricultural expansion, especially rice and soybean, is one of the main factors that affect and hinders conservation, because this activity not only remove the original vegetation for cultivation but also often bring out chemicals for soil remediation, pest control or fertilization, and cause fragmentation and deterioration of these ecosystems (Maltchik and Rolon 2010; Rodrigues et al. 2012).

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Authors Contributions

Morgana Taís Streck Marx: contribution to data collection, manuscript preparation, data analysis and interpretation.

Daniela da Silva Castiglioni: contribution to data collection and concept and design of the study.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

The sampling was made with authorizations of the Instituto Chico Mendes de Conservação da Biodiversidade (MMA; ICMBio; SISBIO nº 32726-1).

Data availability

The type material is deposited in the Museu Nacional do Rio de Janeiro (MNRJ).

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Inventory

Insect galls of the Reserva Biológica União, Rio de Janeiro, Brazil

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Abstract: Several inventories of insect galls have been performed in the Atlantic Forest of Rio de Janeiro, mostly in restingas, whereas the other phytophysiognomies remain poorly sampled. The present study inventoried the insect galls of Reserva Biológica União (RJ), a protected area comprising mainly Ombrophilous Forest. Field work was performed every two months from January to October, 2013. Insect galls were collected, photographed, characterized and transported to the laboratory. Adults were obtained by rearing and immature stages by gall dissection. The insects were deposited in the Cecidomyiidae Collection of the Museu Nacional. A total of 153 gall morphotypes were found on plants representing 37 plant families, 69 genera, 55 species and 53 morphospecies. Among them, two plant genera and five species were reported for the first time as host plants in Ombrophilous Forest. REBIO União showed little similarlity of host plant species and insect gall morphotypes when compared with other investigated Ombrophilous Forest areas. The leaf was the most attacked plant organ as expected. Asteraceae, Bignoniaceae, Fabaceae and Myrtaceae, and *Mikania* (Asteraceae) and *Myrcia* (Myrtaceae) were the richest host families and genera, respectivey, in number of gall morphotypes, all previously indicated as superhosts by other Brazilian Ombrophilous Forest inventories, except Bignoniaceae. Their great species richness may be related to their great gall richness, adding evidence in support of the taxon size hypothesis. Fusiform and globose galls were the most frequent, green was the predominant color, and most morphotypes did not present an indumentum. The highest gall richness was recorded in June and August. The gallers were distributed among Diptera (Cecidomyiidae), Lepidoptera, Hymenoptera, Hemiptera and Thysanoptera, with the first being predominant, following a global pattern. Eight gall-inducing species are recorded for the first time in REBIO União and four in Ombrophilous Forest. About 25% of the gall morphotypes were occupied by dwellers other than those that created the gall. They comprised parasitoids (Hymenoptera), inquilines (Diptera: Sciaridae and Muscomorpha, Hemiptera, and Lepidoptera) and successors (Psocoptera, mites, and Hymenoptera: Formicidae). Although these taxa were previously reported by Brazilian inventories of insect galls, 12 new association with plants are recorded. The amount of new records reinforces the importance of inventories.

Keywords: *Ombrophilous Forest, Atlantic Forest, insect-plant interaction, associated fauna.*

Galhas de insetos da Reserva Biológica União, Rio de Janeiro, Brasil

Resumo: Vários inventários de galhas de insetos vem sendo desenvolvidos no estado do Rio de Janeiro, principalmente em restingas, enquanto as outras fitofisionomias permanecem pouco estudadas. O presente estudo inventariou as galhas de insetos da Reserva Biológica União (RJ), uma área protegida ocupada principalmente por Floresta Ombrófila. Trabalhos de campo foram realizados a cada dois meses de janeiro a outubro de 2013. Galhas de insetos foram coletadas, fotografadas, caracterizadas e transportadas para o laboratório. Adultos foram obtidos por criação e os imaturos pela dissecção das galhas. Os insetos foram depositados na Coleção de Cecidomyiidae do Museu Nacional (MMRJ). Um total de 153 morfotipos de galhas foram encontrados em plantas de 37 famílias, 69 gêneros, 55 espécies e 53 morfoespécies. Dentre estas, dois gêneros botânicos e cinco espécies foram registradas pela primeira vez como plantas hospedeiras em Floresta Ombrófila. A REBIO União mostrou uma pequena similaridade de plantas hospedeiras e morfotipos de galhas quando comparada com outras áreas de Floresta Ombrófila. As folhas foram o órgão vegetal mais atacado, como o esperado. Asteraceae, Bignoniaceae, Fabaceae e Myrtaceae, e *Mikania* (Asteraceae) e *Myrcia* (Myrtaceae) foram as famílias hospedeiras e gêneros botânicos mais ricos em número de morfotipos de galhas, todos previamente indicados como superhospedeiros em outros inventários na Floresta Ombrófila brasileira, exceto Bignoniaceae. A grande riqueza de espécies destes táxons pode estar relacionada a sua grande riqueza de galhas, adicionando evidências para a hipótese do tamanho do

táxon. Galhas fusiformes e globoides foram as mais frequentes, a cor verde predominou e a maioria dos morfotipos não apresentou indumento. A maior riqueza de galhas ocorreu em junho e agosto. Diptera (Cecidomyiidae), Lepidoptera, Hymenoptera, Hemiptera e Thysanoptera foram as ordens indutoras encontradas, com predomínio dos Cecidomyiidae, seguindo o padrão mundial. Oito espécies galhadoras são registradas pela primeira vez na REBIO União e quatro em Floresta Ombrófila. Cerca de 25% dos morfotipos de galhas foram ocupados por outros artrópodes, que atuaram como parasitoides (Hymenoptera), inquilinos (Diptera: Sciaridae and Muscomorpha, Hemiptera, and Lepidoptera) e successores (Psocoptera, ácaros e Hymenoptera: Formicidae). Embora estes táxons já tivessem sido reportados em inventários de galhas de insetos do Brasil, 12 novas associações com plantas são registradas. A quantidade de novos registros reforça a importância dos inventários.

Palavras-chave: *Floresta Ombrófila, Mata Atlântica, interação inseto-planta, fauna associada.*

Introduction

Although several gall inventories have been developed in the state of Rio de Janeiro (RJ), Brazil, they have focused mainly on restinga ecosystems. Other physiognomies of the Atlantic Forest have been little investigated, including Dense Ombrophilous Forest, the focus of the present sudy. Dense Ombrophilous Forest is characterized by abundant phanerophytes, woody lianas and epiphytes, high rainfall distributed throughout the year and warm temperatures (annual mean of 25ºC) (Veloso et al. 1991). Due to the scarcity of studies, the insect galls of this physiognomy are poorly known.

Only two gall inventories have been developed in protected areas of Dense Ombrophilous Forest in Brazil, one in Santa Teresa, state of Espírito Santo (Maia et al. 2014) and the other in the Parque Nacional do Itatiaia (PNI), Southeast Brazil (Maia & Mascarenhas 2017). Other data can be found in various publications (Tavares 1915, 1916, 1917a, 1917b, 1918, 1920a, 1920b, 1922, Kieffer 1913, Gagné 1998, 2001). The main goal of this study was to provide a list of host plants, gall morphotypes and gallers of the Reserva Biológica União.

Material and Methods

1. Study site

This research was carried out in Reserva Biológica União (REBIO União), which has an area of about 2,500 hectares that encompasses parts of three municipalities in northern Rio de Janeiro State: Casimiro de Abreu, Macaé and Rio das Ostras (Figure 1). With about 250 tree species of 45 plant families, REBIO União hosts primary elements of the Atlantic Forest flora and fauna (MMA/ICMBio 2008a). Among these, Myrtaceae, Lauraceae and Sapotaceae exhibit the greatest species richness (Rodrigues 2004).

There are four official trails within REBIO União - Buracão, Interpretativa, Lavapé and Três Pontes - all of which were investigated during the present study. About 50% of Três Pontes and Lavapé trails are occupied by preserved forest, while the other two trails are more impacted, with the presence of roads, antropic fields, recuperating areas and exotic vegetation (MMA/ICMBio 2008b, c).

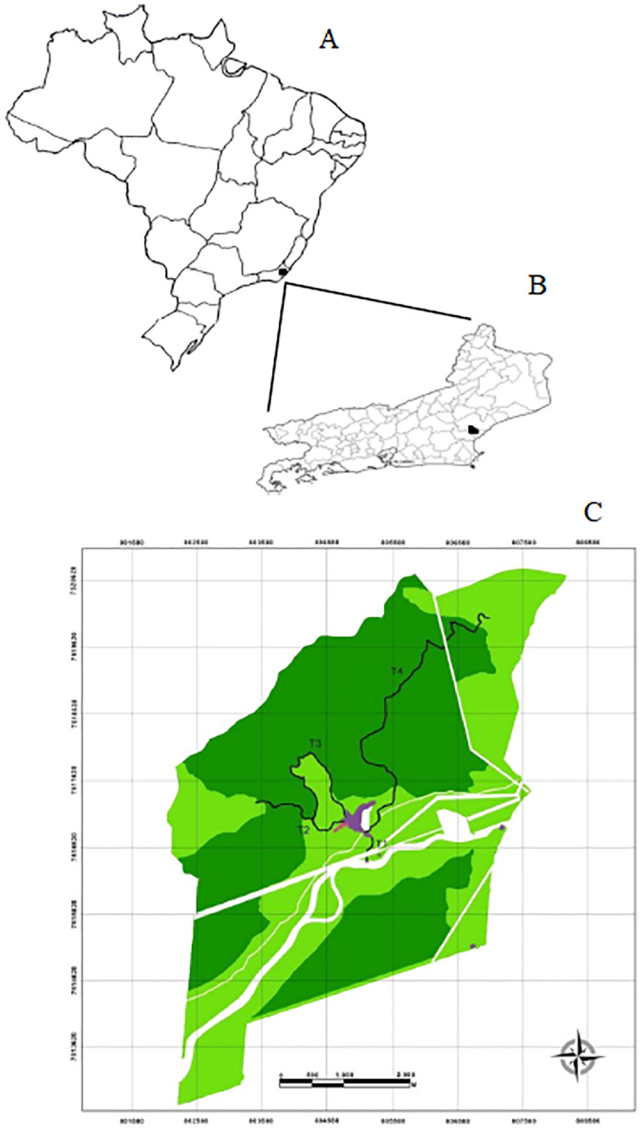


Figure 1. A) Map of Brazil, B) State of Rio de Janeiro and C) Reserva Biológica União. T1 – Buracão, T2 – Lavapé, T3 – Interpretativa, T4 – Três Pontes.

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2. *Field work*

Expeditions were undertaken every two months, from January to October, 2013, for a total of five. Each trail was investigated for insect galls for four hours by a single person per expedition, who obtained the geographic coordinates for each gall found using GPS.

Herbaceous, shrubby and arboreous plants were examined, the last up to 2 m high. Only aerial organs were investigated for galls. Branches (whenever possible with flowers and fruits) were removed from each host plant, labeled and pressed for preparation as exsiccates. The exsiccates were identified by Dr. Gracialda Costa Ferreira at Universidade Federal Rural da Amazonia, according to APGII, and deposited in the herbarium of the same institution. Galled branches were collected, packed and transported in labelled plastic bags. The galls were photographed and characterized according to their external morphology (shape, color, presence or absence of trichomes, and plant organ of occurrence).

3. *Laboratory work*

In the laboratory, samples of each gall morphotype were dissected to obtain the immature insects, observe the number of internal chambers and determine the food habit of the dwellers. They were classified into parasitoids (by observing parasitized galling larvae), inquilines (by observing different species cohabiting the same gall. In this case, early gall samples were examined to determine the galler) and successors (by observing dwellers in after dehiscent galls). To obtain adults, other samples were conditioned in labelled plastic pots lined with a layer of toilet paper. Each gall morphotype was kept in a separate pot to avoid mixing of the material. All pots were checked daily until newly emerged adults were encountered or the galls began to putrefy. When adults were found, the pots were placed in a refrigerator for some minutes to induced insect lethargy, at which time the adults were transferred to tubes with 70% ethanol. All insects were preserved in 70% ethanol and identified by the authors. Specimens of Cecidomyiidae were later mounted on microscope slides, following the methodology outlined in Gagné (1994), identified to genus, using the keys of Gagné (1994), and to species, based on gall morphology, host plant and original descriptions. Sciaridae (Diptera), Psocoptera and Hymenoptera were identified based on the keys of Steffan 1981, Aldrete and Mockford 2012 and Gibson et al. 1997, respectively. All insects were deposited in the Entomological Collection of Museu Nacional (MNRJ).

Botanical names and their respective authors, data on plant species distribution in Brazilian biomes, and origin (if exotic, native, or endemic) were obtained from Flora do Brasil 2018.

The geographic distribution of each gall morphotype in Brazil was updated based on the literature. New records of interactions between host plants and gallers were reported.

The similarity of gall composition among the investigated paths was measured using Sorensens´s index. We adopted this same index to evaluate the similarity among REBIO União and Santa Teresa and PNI, the two previous investigated areas of Dense Ombrophilous Forest in Brazil, using only the host plants which were identified to the species level.

Results

A total of 153 insect gall morphotypes (Figs. 2-6) were found in REBIO União on 108 plant species, 55 identified to the species level, 43 to genus and 10 to family, for an average of 1.42 gall morphotypes per plant species. The galled plants belonged to 37 families, of which Asteraceae, Bignoniaceae, Fabaceae, and Myrtaceae had the highest gall richness (the first three with 15 gall morphotypes each, followed by Myrtaceae with 13). *Mikania* Willd. (Asteraceae) and *Myrcia* DC. (Myrtaceae) were the genera with the greatest number of gall morphotypes (10 and 9, respectively) (Table 1).

Among the identified plant species, 51 were native — 16 of which were endemic — two naturalized, and one exotic; there were no data regarding origin for one of the identified species. The 153 gall morphospecies were distributed among 37 native genera and two endemic genera of plants. Native host plants (species and morphospecies) harbored 149 gall morphotypes, 27 of them on endemic plants, while exotic and naturalized species harbored one and three morphotypes, respectively. Twelve endemic species harbored a single gall morphotype, whereas *Mikania pilosa* Baker (Asteraceae), *Piper vicosanum* Yunck. (Piperaceae) and *Cupania racemosa* (Vell.) Radlk. (Sapindaceae) harbored two morphotypes, and *Myrcia splendens* (Sw.) DC. (Myrtaceae) three (Table 1).

Galls were found on both vegetative and reproductive plant organs (Table 2), and were most frequent on leaves (64.0%), followed by stems (30.7%), buds (9.1%), tendrils (1.3%), aerial roots (0.6%) and flower buds (0.6%). No galls were found on fruits. Nine gall morphotypes were observed on two or three plant organs simultaneously.

With regard to gall morphology, there was a predominance of globoid-shaped galls (49.0%), followed by fusiform (35.9%), lenticular (8.5%), marginal roll (4.6%), conical (3.9%), cylindrical (2.0%), imbricate (1.3%), toroid (1.3%), and amorphous (0.6%). Three morphotypes exhibited variation in shape, occuring as both globoid and fusiform. Green was the most frequent color (62.1%), followed by brown (34.0%), yellow (3.9%), red (1.3%), and purple (1.3%); greenish-yellow was also found (three morphotypes). A single morphotype exhibited color variation during development, changing from green to yellow. Additionally, all galls became brown when dried. Most of the galls were glabrous (81.7%), while trichomes were observed in just a few morphotypes (15.7%) (Table 2).

Concerning the trails, Três Pontes and Buracão had higher gall richness (65 and 56 morphotypes, respectively), while Lavapé and Interpretativa had lower (29 and 25, respectively). Thirty-eight morphotypes were observed exclusively along Três Pontes and 35 along Buracão, while the richness of exclusive morphotypes for the other two trails was considerably lower with 19 along Interpretativa and 18 along Lavapé. Sorensen's index revealed little similarity among paths; Buracão and Três Pontes were the most similar (0.28), followed by Lavapé and Três Pontes (0.19), Buracão and Lavapé (0.12), and Interpretativa and Três Pontes (0.11), with Interpretativa and Lavapé, and Buracão and Interpretativa being the most different (0.03 and 0.02, respectively) (Table 2).

Most galls were recorded in June and August, while the other months (January, April and October), the gall richness was lower (Table 2).



Figure 2. Insect galls of the Reserva Biológica União: A) On Acanthaceae, *Dicliptera mucronifolia*, stem gall, B-D) On Annonaceae, B) *Xylopia sericea,* marginal roll, C-D) Annonaceae (not determined), C) Leaf vein gall, D) Leaf gall, E-G) On Apocynaceae, E) *Aspidosperma* sp., stem gall, F) *Mandevilla* sp., stem gall, G) Apocynaceae (not determined), leaf gall, H-O) On Asteraceae, H) *Mikania gleasonii*, leaf vein gall, I-J) *Mikania glomerata*, I) Leaf vein gall, J) Leaf gall, K) *Mikania pilosa*, stem gall, L) *Mikania* sp.1, stem gall, M) *Piptocarpha lundiana*, stem gall, N) *Vernonia* sp., bud gall, O) Asteraceae (not determined), leaf vein gall, P-Z) On Bignoniaceae, P) *Adenocalymma subsessilifolium*, leaf vein gall, Q) *Adenocalymma validum*, stem gall, R) *Amphilophium* sp., leaf petiole gall, S) *Anemopaegma chamberlaynii*, leaf vein gall, T-U) *Fridericia conjugata*, T) Leaf gall, U) Leaf vein gall, V) *Fridericia* sp., leaf vein gall, W) *Lundia* sp., leaf vein gall, X) *Mansoa angustidens*, leaf gall, Y-Z) *Mansoa* sp., Y) Stem gall, Z) Leaf gall.

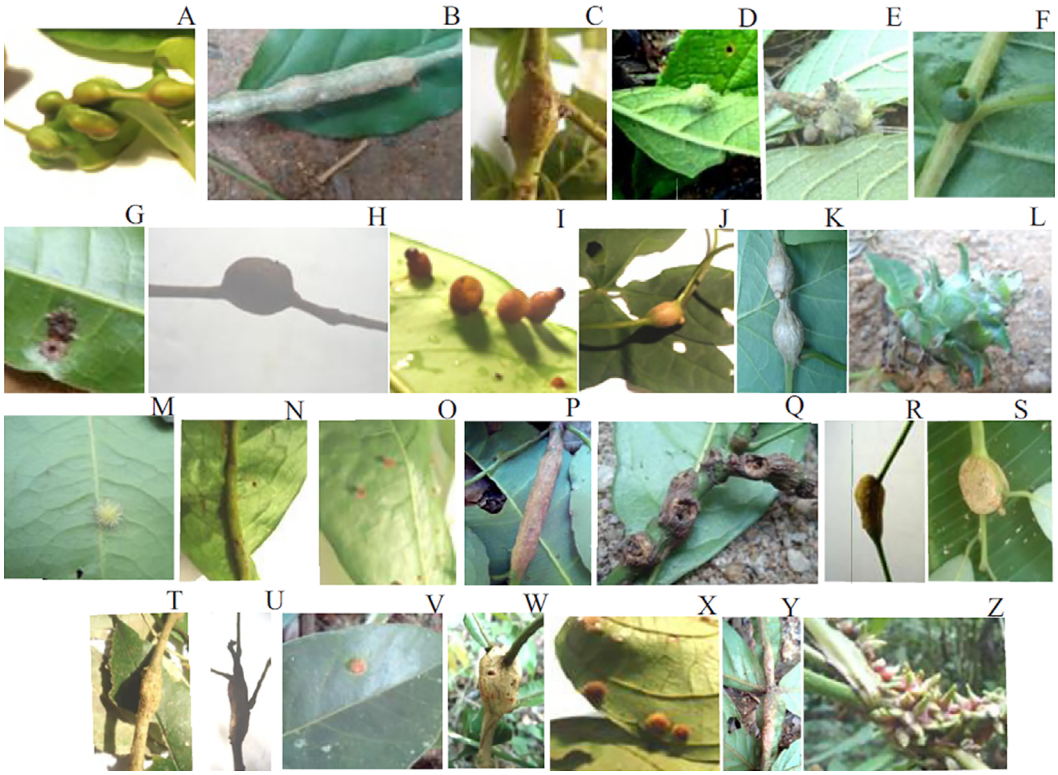


Figure 3. Insect galls of the Reserva Biológica União: A-B) On Bignoniaceae, *Pyrostegia* sp., A) Tendril gall, B) Stem gall, C-E) On Boraginaceae, C-D) *Varronia curassavica*, C) Leaf gall, D) Bud flower gall, E) Boraginaceae (not determined), bud gall, F) On Burseraceae, *Protium* sp., leaf gall, G) On Chrysobalanaceae, *Licania* sp., stem gall, H) On Combretaceae, *Combretum* sp., leaf gall, I-J) On Convolvulaceae, I) *Ipomoea hederifolia*, stem gall, J) *Ipomoea* sp., stem gall, K) On Dilleniaceae, *Davilla* sp., bud gall, L-N) On Erythroxylaceae, L-M) *Erythroxylum macrophyllum*, L) Leaf gall, M) Leaf vein gall, N) *Erythroxylum* sp., leaf gall, O-S) On Euphorbiaceae, O) *Dodecastigma* sp., leaf vein gall, P) *Mabea piriri*, stem gall, Q) *Mabea speciosa*, stem gall, R) *Mabea* sp., stem gall, S) Euphorbiaceae (not determined), stem gall, T-Z) On Fabaceae, T) *Bowdichia* sp., stem gall, U-V) *Inga alba,* U) Leaf gal, V) Stem gall, W-X) *Inga capitata*, W) Leaf gall, X) Stem gall, Y-Z) On Fabaceae, Y) *Machaerium* sp., leaf gall, Z) *Martiodendron* sp., stem gall.

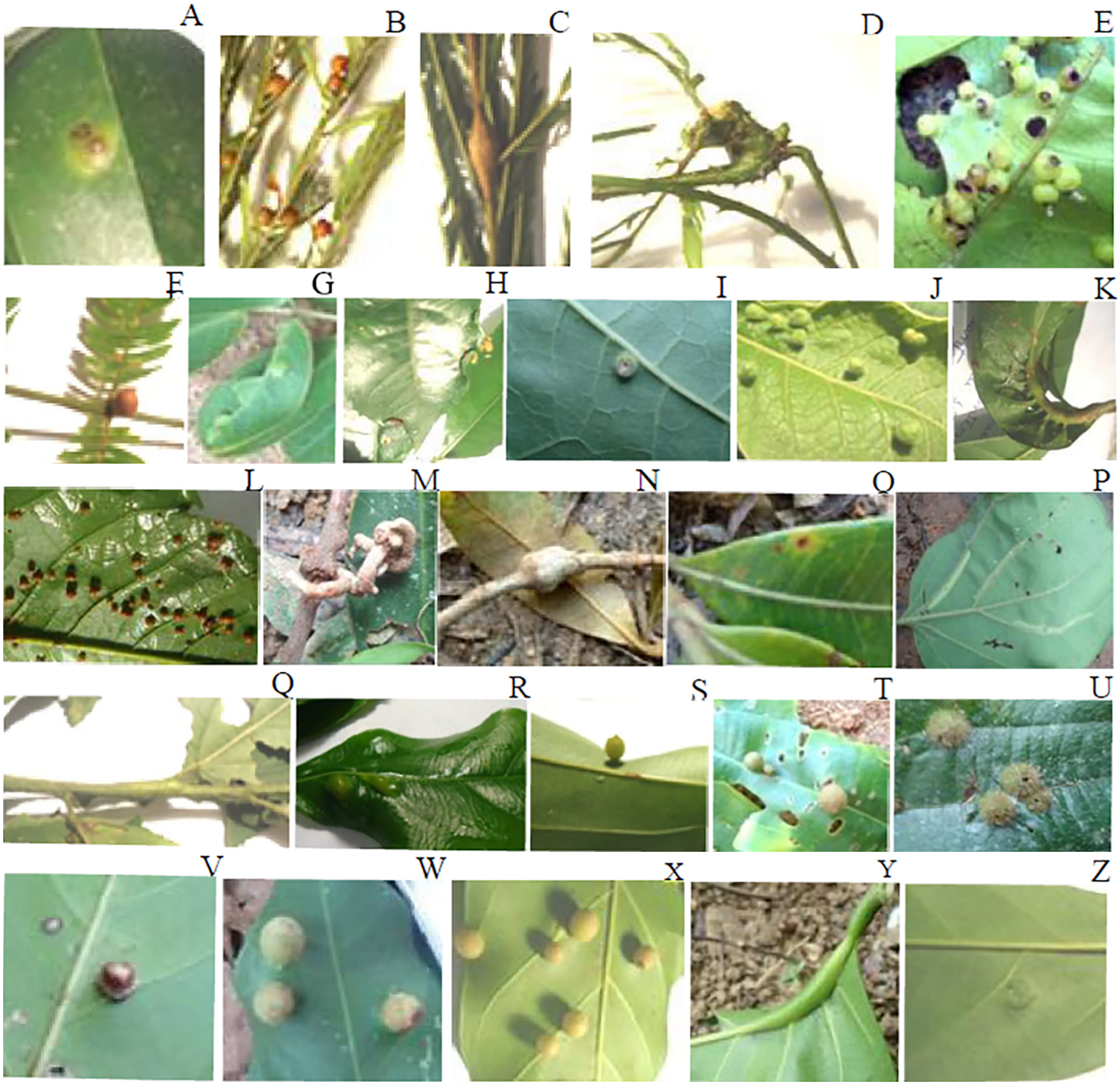


Figure 4. Insect galls of the Reserva Biológica União: A-I) On Fabaceae, A) *Myroxylon peruiferum*, leaf gall, B-D) *Parapiptadenia* sp., B) Leaf gall, C) Bud gall, D) Stem gall, E) *Pterocarpus* sp., leaf gall, F) *Senegalia serra*, leaf petiole gall, G) *Senna obtusifolia*, leaf gall, H) On Lacistemataceae, *Lacistema serrulatum*, leaf gall, I-J) On Lamiaceae, *Aegiphila integrifolia,* I) Leaf gall, J) Leaf gall, K) On Lauraceae, *Ocotea* sp., leaf vein gall, L) On Lecythidaceae, *Lecythis pisonis*, leaf gall, M) On Loranthaceae (not determined), aerial root gall, N-P) On Malpighiaceae, N-O) *Byrsonima sericea***,** N) Stem gall, O) Leaf gall, P) *Stigmaphyllon* sp., leaf vein gall, Q) On Malvaceae, *Sida acuta*, stem gall, R-U) On Melastomataceae, R) *Miconia prasina*, leaf gall, S-T) *Miconia pusilliflora*, S) Leaf gall, T) Leaf vein gall, U) *Tibouchina estrellensis*, leaf gall, V-Z) On Meliaceae, V-W) *Guarea guidonia*, V) Leaf gall, W) Leaf gall, X-Z) *Guarea kunthiana*, X) Leaf gall, Y) Leaf vein gall, Z) Leaf gall.

Galls were induced by Diptera (Cecidomyiidae), Lepidoptera, Hymenoptera, Hemiptera and Thysanoptera, the first being the most frequent gallers (49.0%). The other taxa were responsible for a single gall morphotype each. As several galls were found empty, parasitized or occupied by more than one insect taxon, we could not determined the gallers responsible for 48.4% of the morphotypes (Table 2).

Seven species of Cecidomyiidae were identified among the gallers: *Alycaulus globulus* Gagné, 2001, *Arrabiadaeamyia serrata* Maia, 2001, *Asphondylia cfr. cordiae* Möhn, 1959, *Brugmannia robusta* Maia and Couri, 1993, *Cordiamyia globosa* Maia, 1996, *Dasineura byrsonimae* Maia, 2010, *Liodiplosis conica* Gagné, 2001, and *Schismatodiplosis lantanae* Rübsaamen, 1908.

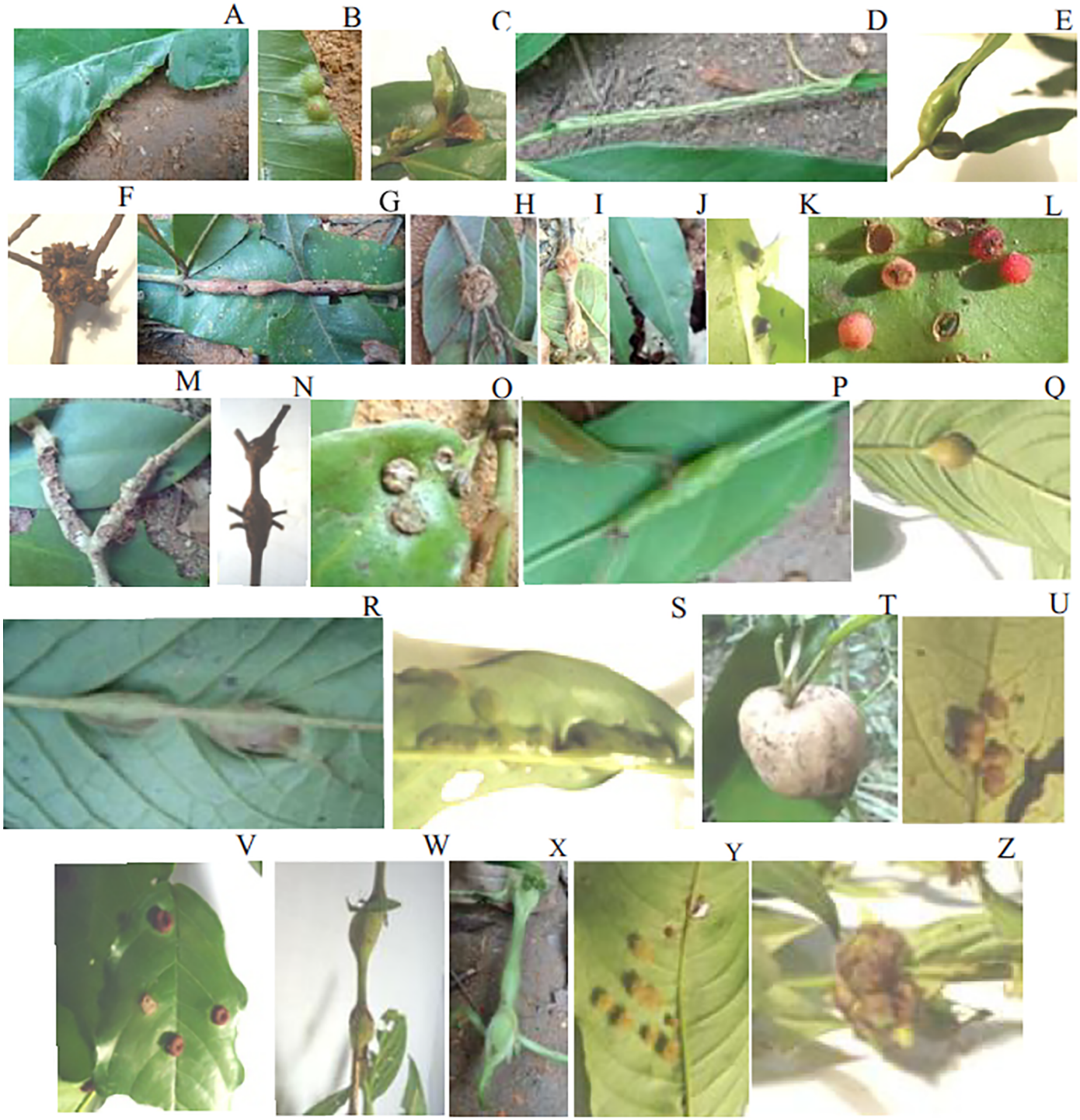


Figure 5. Insect galls of the Reserva Biológica União: A-J) On Myrtaceae, A) *Eugenia florida*, leaf gall, B-D) *Myrcia splendens*, B) Leaf vein gall, C) Bud gall, D) Leaf gall, E-G) *Myrcia* sp., E) Bud gall, F) Bud gall, G) Stem gall, H) *Psidium guineense*, stem gall, I) *Psidium laruotteanum*, stem gall, J) Myrtaceae (not determined), leaf gall, K-O) On Nyctaginaceae, K-L) *Guapira opposita*, K) Leaf gall, L) Leaf gall, M) *Neea acuminata*, stem gall, N-O) *Neea* sp., N) Stem gall, O) Leaf gall, P) On Olacaceae, *Chaunochiton* sp., stem gall, Q) On Onagraceae, *Ludwigia* sp., leaf vein gall, R-V) On Piperaceae, R) *Piper aduncum*, leaf vein gall, S) *Piper tuberculatum*, leaf gall, T-U) *Piper vicosanum*, T) Bud gall, U) Leaf gall, V) *Piper* sp., leaf gall, W-Z) On Rubiaceae, W) *Borreria verticillata*, stem gall, X) *Diodia* sp., stem gall, Y) *Psychotria nuda*, leaf gall, Z) Rubiaceae (not determined), flower bud gall.

Additionally, 11 cecidomyiid morphospecies were recorded distributed among seven genera: *Asphondylia* Loew, 1850, *Bruggmannia* Tavares, 1906, *Bruggmanniella* Tavares, 1909, *Clinodiplosis* Kieffer, 1894, *Lopesia* Rübsaamen, 1908, *Neolasioptera* Felt, 1908, and *Zalepidota* Rübsaamen, 1908. Among these genera, *Asphondylia* and *Clinodiplosis* were the most diversified, with nine and the five morphospecies, respectively, while the others were represented by a single morphospecies each.

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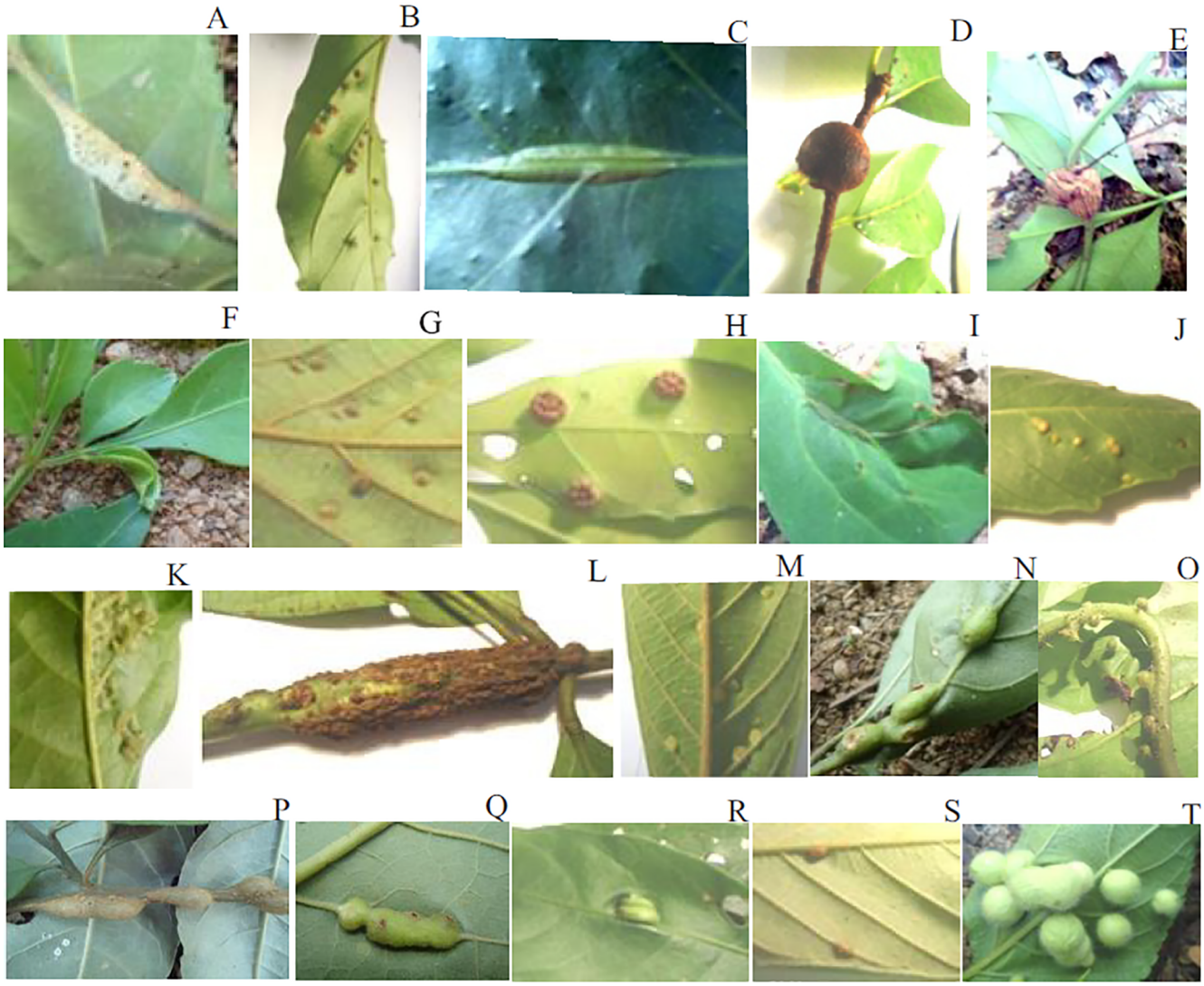


Figure 6. Insect galls of the Reserva Biológica União, A) On Salicaceae, *Casearia arborea*, stem gall, B-J) On Sapindaceae, *Cupania racemosa*, B) Leaf gall, C) Leaf vein gall, D) *Matayba* sp., stem gall, E-F) *Paullinia glomerulosa*, E) Stem gall, F) Leaf vein gall, G) *Paullinia* sp., leaf gall, H) *Serjania lethalis*, leaf gall, I-J) *Serjania* sp., I) Leaf vein gall, J) Leaf gall, K-M) On Siparunaceae, K-L) *Siparuna guianensis*, K) Leaf gall, L) Stem gall, M) *Siparuna* sp., leaf gall, N-R) On Solanaceae, N) *Solanum campaniforme*, leaf vein and petiole gall, O-Q) *Solanum* sp., O) Leaf and stem gall, P) Stem gall, Q) Leaf vein gall, R) Solanaceae (not determined), leaf vein gall, S) On Urticaceae, *Pourouma* sp., leaf vein gall, T) On Verbenaceae, *Lantana camara*, leaf gall.

Table 1. List of galled plants in the Reserva Biológica União (Rio de Janeiro, Brazil), their origin and number of gall morphotypes.

Host Plant		Origin	Number of gall morphotypes
Family	**Species**		
Acanthaceae	*Dicliptera mucronifolia* Nees	Endemic	1
	Thunbergia alata Bojer ex Sims	naturalized spe-cies	1
Total			2
Annonaceae	*Xylopia sericea* A.St.-Hil	endemic species	1
	Not determined	-	2
Total			3
Apocynaceae	*Aspidosperma* sp.	native genus	1
	Mandevilla sp.	endemic genus	1
	Not determined	-	1
Total			3

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Asteraceae	*Barrosoa organensis* (Gardner) R.M.King and H.Rob.	endemic species	1
	Mikania gleasonii B.L.Rob.	native species	1
	Mikania glomerata Spreng.	native species	2
	Mikania pilosa (Baker)	endemic species	2
	Mikania sp.1	native genus	1
	Mikania sp.2	native genus	1
	Mikania sp.3	native genus	1
	Mikania sp.4	native genus	1
	Mikania sp.5	native genus	1
	Piptocarpha lundiana (Less.) Baker	endemic species	1
	Vernonia sp.	native genus	1
	Not determined	-	2
Total			15
Bignoniaceae	*Adenocalymma subsessili-folium* DC.	endemic species	1
	Adenocalymma validum L.G.Lohmann	native species	1
	Amphilophium sp.	native genus	1
	Anemopaegma chamber-laynii (Sims) Bureau and K.Schum.	native species	1
	Cuspidaria sp.	native genus	1
	Fridericia conjugata (Vell.) L.G.Lohmann	native species	2
	Fridericia sp.	native genus	1
	Lundia sp.	native genus	1
	Mansoa angustidens (DC.) Bureau and K.Schum.	endemic species	1
	Mansoa sp.	native genus	2
	Pyrostegia sp.	native genus	2
	Tabebuia sp.	native genus	1
Total			15
Boraginaceae	*Tournefortia candidula* (Miers) Johnst.	native species	1
	Varronia curassavica Jacq.	native species	3
	Not determined	-	2
Total			6
Burseraceae	*Protium* sp.	native genus	1
Total			1
Calophyllaceae	*Calophyllum* sp.	native genus	1
Total			1
Chrysobalanaceae	*Licania* sp.	native genus	1
Total			1
Combretaceae	*Combretum* sp.	native genus	1
Total			1
Convolvulaceae	*Ipomoea hederifolia* L.	native species	1
	Ipomoea sp.	native genus	1
Total			2
Dilleniaceae	*Davilla rugosa* Poir.	native species	2
	Davilla sp.	native genus	1
Total			3

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continuation...

Erythroxylaceae	*Erythroxylum macrophyl-lum* Cav.	native species	2
	Erythroxylum sp.	native genus	1
Total			3
Euphorbiaceae	*Dodecastigma* sp.	native genus	1
	Mabea piriri Aubl.	native species	1
	Mabea speciosa Müll. Arg.	native species	1
	Mabea sp.	native genus	1
	Not determined	-	1
Total			5
Fabaceae	*Bowdichia* sp.	native genus	1
	Inga alba (Sw.) Willd.	native species	2
	Inga capitata Desv.	native species	2
	Inga edulis Mart.	native species	1
	Machaerium sp.	native genus	1
	Martiodendron sp.	native genus	1
	Myroxylon peruiferum L.f.	native species	1
	Parapiptadenia sp.	native genus	3
	Pterocarpus sp.	native genus	1
	Senegalia serra (Benth.) Seigler and Ebinger	endemic species	1
	Senna obtusifolia (L.) H.S.Irwin and Barneby	native species	1
Total			15
Lacistemataceae	*Lacistema serrulatum* Mart.	endemic species	1
Total			1
Lamiaceae	*Aegiphila integrifolia* (Jacq.) Moldenke	native species	2
Total			2
Lauraceae	*Ocotea* sp.	native genus	2
Total			2
Lecythidaceae	*Lecythis pisonis* Cambess.	endemic species	1
Total			1
Loranthaceae	not determined	-	1
Total			1
Malpighiaceae	*Byrsonima sericea* DC.	native species	2
	Stigmaphyllon sp.	native genus	1
Total			3
Malvaceae	*Sida acuta* Burm.f.	native species	1
Total			1
Melastomataceae	*Miconia prasina* (Sw.) DC.	native species	1
	Miconia pusilliflora (DC.) Naudin	native species	2
	Tibouchina estrellensis (Raddi) Cogn.	endemic species	1
Total			4
Meliaceae (N= 5)	*Guarea guidonia* (L.) Sleumer	native species	2
	Guarea kunthiana A. Juss..	native species	3
Total			5

continuation...

Myrtaceae	*Eugenia florida* DC.	endemic species	1
	Myrcia splendens (Sw.) DC.	endemic species	3
	Myrcia sp.	native genus	6
	Psidium guineense Sw.	native species	1
	Psidium laruotteanum Cambess.	native species	1
	Not determined	-	1
Total			13
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz	native species	2
	Neea acuminata Benth	no data	1
	Neea sp.	native genus	2
Total			5
Olacaceae	*Chaunochiton* sp.	native genus	1
Total			1
Onagraceae	*Ludwigia* sp.	native genus	1
Total			1
Piperaceae	*Piper aduncum* L.	native species	1
	Piper tuberculatum Jacq.	native species	1
	Piper vicosanum Yunck.	endemic species	2
	Piper sp.	native genus	1
	Not determined	-	2
Total			7
Rubiaceae	*Borreria verticillata* (L.) G.Mey.	native species	1
	Diodia sp.	native genus	1
	Psychotria nuda (Cham. and Schltdl.) Wawra	endemic species	1
	Not determined	-	1
Total			4
Salicaceae	*Casearia arborea* (Rich.) Urb.	native species	1
Sapindaceae	*Cupania racemosa* (Vell.) Radlk	endemic species	2
	Matayba sp.	native genus	1
	Paullinia glomerulosa Radlk	exotic species	2
	Paullinia sp.	native genus	1
	Serjania lethalis A. St.-Hil.	native species	1
	Serjania sp.	native genus	2
Total			9
Simaroubaceae	*Simarouba amara* Aubl.	native species	1
Total			1
Siparunaceae	*Siparuna guianensis* Aubl.	native species	2
	Siparuna sp.	native genus	1
Total			3
Solanaceae	*Solanum campaniforme* Roem. and Schult.	native species	1
	Solanum sp.	native genus	3
	not determined		1
Total			5
Urticaceae	*Pourouma* sp.	native genus	2
Total			2
Verbenaceae	*Lantana camara* L.	naturalized speci-es	2
Total			2

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Table 2. Host plant species, gall-inducing insects, gall characterization, sampled localities and dates of collecting in Reserva Biológica União (state of Rio de Janeiro, Brazil). BU - Buracão, IN - Interpretativa, LV - Lavapé, TP - Três Pontes. New records in Brazil are indicated by numbers: 1. new record of host plant genus, 2. new record of host plant species, 3. new record of gall morphotype.

Host plant spe-cies	Gall-inducing insect	Gall characterization				Locality/ Date of collect-ing	Fig.
		Plant organ	Shape	Color	Trichomes		
Dicliptera mu-cronifolia[1]	not det.	stem	fusiform	purple	absent	-/ VI.2013	2A
Thunbergia ala-ta[1]	not det.	stem	fusiform	-	absent	LV VIII.2013	-
Xylopia sericea[2]	not det.	leaf	marginal roll	green	absent	BU VIII/IX.2013	2B
Annonaceae (not det.)	not det.	leaf vein	fusiform	green	absent	TP, IN VI.2013	2C
Annonaceae (not det.)	not det.	leaf	conical	green	absent	IN VI.2013	2D
Aspidosperma sp.	Cecidomyiidae	stem[3]	fusiform	brown	absent	BU I.2013	2E
Mandevilla sp.	not det.	stem[3]	fusiform	green	absent	TP VIII.2013	2F
Apocynaceae (not det.)	not det.	leaf	globoid	greenish-yellow	absent	BU I.2013	2G
Barrosoa orga-nensis	Asphondylini (Cecidomyiidae)	leaf vein	globoid	-	present	BU I/VIII.2013	-
Mikania gleasonii	*Asphondylia* sp. (Cecidomyiidae)	leaf vein[3]	globoid	green	absent	TP I/VI.2013	2H
Mikania glomerata	*Alycaulus globulus* Gagné, 2001	leaf vein	fusiform	green	absent	LV IV.2013	2I
Mikania glomerata	*Liodiplosis conica* Gagné, 2001 (Cecidomyiidae)	leaf	conical	green	absent	LV IV.2013	2J
Mikania pilosa[2]	Cecidomyiidae	stem	globoid	green	absent	TP, BU VI.2013	2K
Mikania pilosa	Cecidomyiidae	leaf vein	fusiform	green	absent	LV VIII.2013	-
Mikania sp.1	*Asphondylia* sp. (Cecidomyiidae)	stem, leaf vein, petiole	globoid or fusiform	yellow, green or brown	present	BU VIII/X.2013	2L
Mikania sp.2	Cecidomyiidae	stem,	fusiform	green	present	BU/ IV/V/VIII. 2013	-
Mikania sp.3	*Asphondylia* sp. (Cecidomyiidae)	leaf vein	globoid	green	absent	BU, LV VI/X.2013	-
Mikania sp.4	Lasiopteridi (Ce-cidomyiidae)	stem	fusiform	brown	absent	TP VIII.2013	-
Mikania sp.5	*Asphondylia* sp. (Cecidomyiidae)	leaf vein petiole,	fusiform	green	absent	LV VIII.2013	-
Piptocarpha lundiana[2]	not det.	stem	fusiform	green	present	BU VI/VIII.2013	2M
Vernonia sp.	*Asphondylia* sp. (Cecidomyiidae)	bud	globoid	green	absent	BU, TP I/ VI.2013	2N
Asteraceae (not det.)	Lasiopteridi (Ce-cidomyiidae)	leaf vein	fusiform	green	absent	BU I.2013	2O
Asteraceae (not det.)	*Clinodiplosis* sp. (Cecidomyiidae)	leaf vein	globoid	green	absent	BU I.2013	-
Adenocalymma subsessilifolium[2]	not det.	leaf vein	fusiform	brown	absent	TP IV.2013	2P
Adenocalymma validum[2]	not det.	stem	globoid	green	absent	BU VIII.2013	2Q
Amphilophium sp.	Cecidomyiidae	leaf petiole[3]	fusiform	green	absent	BU IV/VI.2013	2R
Anemopaegma chamberlaynii	*Neolasioptera* sp. (Cecidomyiidae).	leaf vein	fusiform	brown	absent	BU, TP VI/ VIII.2013	2S
Cuspidaria sp.	not det.	leaf[3]	marginal roll	green	absent	BU VI.2013	-
Fridericia conjugata	*Arrabiadaeamyia* serrata, Maia 2001 (Ceci-domyiidae)	leaf	conical	green	absent	BU IV/VIII. 2013	2T

continuation...

Fridericia conjugata	*Neolasioptera* sp. (Cecidomyiidae)	leaf vein stem	fusiform	green	absent	BU VIII.2013	2U
Fridericia sp.	Cecidomyiidae	leaf vein	globoid	green	absent	TP VI.2013	2V
Lundia sp.	*Neolasioptera* sp. (Cecidomyiidae).	stem, tendril, leaf vein petiole[3]	globoid	green	absent	TP IV.2013	2W
Mansoa angustidens	not det.	leaf vein[3]	globoid	green	absent	LV/ IV.2013	2X
Mansoa sp.	*Neolasioptera* sp. (Cecidomyiidae)	stem leaf vein	fusiform	green or brown	absent	BU, TP IV/ VIII.2013	2Y
Mansoa sp.	not det.	leaf[3]	lenticular	green	absent	BU VIII.2013	2Z
Pyrostegia sp.	not det.	tendril	fusiform	brown	absent	BU I.2013	3A
Pyrostegia sp.	*Asphondylia* sp. (Cecidomyiidae)	stem	fusiform	brown	absent	LVIV.2013	3B
Tabebuia sp.	Cecidomyiidae	leaf vein	lenticular	green or yellow	absent	- VI.2013	-
Tournefortia candidula	not det.	stem[3]	fusiform globoid	green	absent	BU I.2013	-
Varronia curassavica	*Cordiamyia glo-bosa* Maia, 1996 (Cecidomyiidae)	leaf	globoid	green	present	TP IV/VI/X. 2013	3C
Varronia curassavica	*Asphondylia. cfr. cordiae* Möhn, 1959 (Cecidomyi-idae).	bud flower	globoid	green	present	TP VI.2013	3D
Varronia curassavica	Lepidoptera	leaf vein	fusiform	green	present	TP X.2013	-
Boraginaceae (not det.)	Cecidomyiidae	bud	globoid	green or brown	absent	BU, TP/ I/VI/ VIII. 2013	3E
Boraginaceae (not det.)	Cecidomyiidae	bud	globoid	green	present	LV IV.2013	-
Protium sp.	Hemiptera	leaf	lenticular	brown (dried)	absent	TP VIII.2013	3F
Calophyllum sp.	not det.	leaf	marginal roll	green	absent	IN IV.2013	-
Licania sp.	Cecidomyiidae	stem	globoid	brown	absent	BU I.2013	3G
Combretum sp	not det.	leaf[3]	globoid	brown	absent	BU I.2013	3H
Ipomoea hederifolia	Cecidomyiidae	stem	globoid	green or brown	absent	IN VIII.2013	3I
Ipomoea sp.	Cecidomyiidae	stem[3]	fusiform	green or brown	absent	LV/ IV.2013	3J
Davilla rugosa	Cecidomyiidae	leaf	lenticular	green	absent	TP VIII.2013	-
Davilla rugosa	*Clinodiplosis* sp. (Cecidomyiidae)	bud	imbricated	green	absent	TP X.2013	-
Davilla sp.	not det.	bud	imbricated	green	absent	TP VI.2013	3K
Erythroxylum macrophyllum	Cecidomyiidae	leaf[3]	globoid	yellow	present	BU, TP I/IV/VI/ VIII/X. 2013	3L
Erythroxylum macrophyllum	not det.	leaf vein[3]	fusiform	green	absent	BU VIII.2013	3M
Erythroxylum sp.	not det.	leaf[3]	cylindrical	reddish	present	LV I.2013	3N
Dodecastigma sp.	not det.	stem[3] petiole leaf vein	globoid	brown	absent	BU, TP I/VI/ VIII. 2013	3O
Mabea piriri	not det.	stem[3]	globoid	brown	absent	IN I.2013	3P
Mabea speciosa	not det.	stem[3]	fusiform	brown	absent	TP IV.2013	3Q
Mabea sp.	not det.	stem[3]	globoid	brown	absent	IN VIII.2013	3R
Euphorbiaceae (not det.)	not det.	stem	fusiform	brown	absent	IN VI.2013	3S
Bowdichia sp.	not det.	stem[3]	fusiform	brown	absent	BU I.2013	3T
Inga alba	Cecidomyiidae	leaf[3]	globoid	green	present	TP IV.2013	3U
Inga alba	not det.	stem	globoid	brown	absent	-/VI.2013	3V

continuation...

Inga capitata	Cecidomyiidae	leaf[3]	globoid	green or brown	present	LV, TP I.2013	3W
Inga capitata	Cecidomyiidae	stem	fusiform	brown	absent	- IV/VI.2013	3X
Inga edulis	Cecidomyiidae	leaf vein	fusiform	green	absent	IN VI.2013	-
Machaerium sp.	Cecidomyiidae	leaf	globoid	green	absent	BU I.2013	3Y
Martiodendron sp.	Schizomyiina (Cecidomyiidae)	stem[3]	conical	reddish or green	present	IN I/VI/VIII. 2013	3Z
Myroxylon peruiferum	not det.	leaf[3]	lenticular	greenish or yellow	absent	BU VIII.2013	4A
Parapiptadenia sp.	not det.	leaf[3]	globoid	green or brown	absent	IN VIII.2013	4B
Parapiptadenia sp.	not det.	stem[3]	fusiform	brown	absent	LV VI.2013	4C
Parapiptadenia sp.	not det.	bud[3]	globoid	green	absent	LV VI.2013	4D
Pterocarpus sp.	Cecidomyiidae	leaf[3]	globoid	green	absent	TP VI.2013	4E
Senegalia serra	not det.	petiole[3]	globoid	brown	absent	LV VIII/X.2013	4F
Senna obtusifolia	not det.	leaf	lenticular	green	absent	TP VI.2013	4G
Lacistema serrulatum	not det.	leaf[3]	marginal roll	green	absent	TP VIII.2013	4H
Aegiphila integrifolia	not det.	leaf[3]	globoid	green	absent	- VI.2013	4I
Aegiphila integrifolia	not det.	leaf[3]	globoid	green	present	BU VI.2013	4J
Ocotea sp.	not det.	leaf vein[3]	fusiform	green	absent	TP VIII/X.2013	4K
Ocotea sp.	not det.	leaf	globoid	brown	absent	TP VIII.2013	-
Lecythis pisonis	Lasiopteridi (Cecidomyiidae)	leaf[3]	globoid	brown	absent	BU I/VI/VIII. 2013	4L
Loranthaceae (not det.)	Cecidomyiidae	aerial root	fusiform	brown	absent	- VI.2013	4M
Byrsonima sericea	not det.	stem	globoid	brown	absent	TP IV/X.2013	4N
Byrsonima sericea	*Dasineura byrsonimae* Maia, 2010 (Cecidomyiidae)	leaf	lenticular	yellow or brown	absent	BU, TP VIII.2013	4O
Stigmaphyllon sp.	not det.	leaf vein[3]	fusiform	green	absent	- VI.2013	4P
Sida acuta	not det.	stem[3]	fusiform	green	present	IN VIII.2013	4Q
Miconia prasina	Cecidomyiidae	leaf vein	fusiform or globoid	greenish-yellow	absent	BU I/VI/VIII. 2013	4R
Miconia pusilliflora	Cecidomyiidae	stem, bud, leaf[3]	globoid	green	absent	BU, LV I/IV/ VIII. 2013	4S
Miconia pusilliflora	not det.	leaf vein[3]	globoid	green or brown	absent	TP VI.2013	4T
Tibouchina estrellensis	Cecidomyiidae	leaf[3]	globoid	green	present	BU, TP IV/ VI.2013	4U
Guarea guidonia	Cecidomyiidae	leaf	globoid	reddish	absent	BU VIII.2013	4V
Guarea guidonia	Cecidomyiidae	leaf	globoid	yellow	absent	BU VIII/2013	4W
Guarea kunthiana	Cecidomyiidae	leaf	globoid	green or brown	absent	BU, LV, I/VI/ VIII/X. 2013	4X
Guarea kunthiana	Cecidomyiidae	leaf vein	fusiform	green	absent	BU VI/VIII.2013	4Y
Guarea kunthiana	Cecidomyiidae	leaf[3]	lenticular	green	absent	BU VIII.2013	4Z
Eugenia florida	not det.	leaf[3]	marginal roll	green	absent	- VI.2013	5A
Myrcia splendens	Cecidomyiidae	leaf vein	globoid	green or brown	absent	IN, TP VI/ VIII.2013	5B
Myrcia splendens	not det.	bud	globoid	green	absent	IN VI.2013	5C
Myrcia splendens	Cecidomyiidae	leaf	marginal roll	green	absent	TP VI.2013	5D

continuation...

Myrcia sp.	not det.	bud	fusiform	green	absent	BU, TP I/ VIII.2013	5E
Myrcia sp.	not det.	bud	globoid	brown	abent	LV IVI.2013	5F
Myrcia sp.	Cecidomyiidae.	stem	fusiform	brown	absent	BU VIII.2013	5G
Myrcia sp.	not det.	leaf	marginal roll	green	and glabrous	IN, TP VIII.2013	-
Myrcia sp.	Lasiopteridi (Cecidomyiidae)	leaf	globoid	green	absent	BU, TP VIII.2013	-
Myrcia sp.	Thysanoptera	bud	amorphous	reddish	absent	TP VIII.2013	-
Psidium guineense	Hymenoptera	stem	globoid	green or brown	absent	LV, TP VI/X.2013	5H
Psidium laruotteanum	not det.	stem[3]	fusiform	brown	absent	BU, TP I/ IV.2013	5I
Myrtaceae (not det.)	not det.	leaf	lenticular	green	absent	TP IV.2013	5J
Guapira opposita	*Bruggmannia* sp. (Cecidomyiidae)	leaf	globoid	green	absent	TP I.2013	5K
Guapira opposita	*Bruggmannia robusta* Maia and Couri, 1993 (Cecidomyiidae)	leaf, petiole, stem	globoid	reddish	present	TP VIII.2013	5L
Neea acuminata[2]	Cecidomyiidae	stem bud[3]	fusiform	brown	absent	BU, TP I/ IV/X.2013	
Neea sp.	not det.	stem	fusiform	brown	absent	TP IV/X.2013	5N
Neea sp.	not det.	leaf	lenticular	brown	absent	TP VI.2013	5O
Chaunochiton sp.[1]	not det.	stem	fusiform	green	absent	- VI.2013	5P
Ludwigia sp.	not. det.	leaf vein petiole	globoid	green	absent	TP VIII.2013	5Q
Piper aduncum	Cecidomyiidae	leaf vein	fusiform	green	absent	TP VI.2013	5R
Piper tuberculatum	Cecidomyiidae	leaf	globoid	green	absent	LV, TP I/IV/VI. 2013	5S
Piper vicosanum[2]	*Zalepidota* sp. nov. (Cecidomyiidae)	bud	globoid	yellow or brown	absent	IN, TP IV/ VIII.2013	5T
Piper vicosanum	not det.	leaf	globoid	brown	absent	IN VIII.2013	5U
Piper sp.	Cecidomyiidae	leaf	toroid	green or brown	absent	BU, LV, TP I/ IV.2013	5V
Piperaceae (not det.)	not det.	leaf	lenticular	green	absent	- VIII.2013	-
Piperaceae (not det.)	not det.	leaf	conical	hairy	present	TP VIII.2013	-
Borreria verticillata	Cecidomyiidae	stem[3]	fusiform	green	absent	LV I.2013	5W
Diodia sp.	Cecidomyiidae	stem	fusiform	green	absent	- VI.2013	5X
Psychotria nuda[2]	not det.	leaf	globoid	green or yellow	present	IN I.2013	5Y
Rubiaceae (not det.)	not det.	flower bud	globoid	green or purple	present	LV IV.2013	5Z
Casearia arborea	*Lopesia* sp. (Cecidomyiidae).	stem	fusiform	brown	absent	- IV.2013	6A
Cupania racemosa	not det.	leaf[3]	globoid	green or yellow	present	IN I.2013	6B
Cupania racemosa	Cecidomyiidae	leaf vein	fusiform,	green	absent	IN, LV, TP IV/ VIII/X. 2013	6C
Matayba sp.	not det.	stem	globoid	brown	absent	BU I.2013	6D
Paullinia glomerulosa	not det.	stem	globoid	brown	absent	TP IV.2013	6E
Paullinia glomerulosa	not det.	leaf vein	fusiform	green	glabrous	TP VI/VIII.2013	6F
Paullinia sp.	not det.	leaf[3]	globoid	green	present	BU I.2013	6G

continuation...

Serjania lethalis	not det.	leaf[3]	toroid	brown	absent	LV I.2013	6H
Serjania sp.	Cecidomyiidae	leaf vein	fusiform	green	absent	BU, TP IV.2013	6I
Serjania sp.	Cecidomyiidae	leaf	globoid	green	absent	IN VIII.2013	6J
Simarouba amara	not det.	leaf	conical	green	absent	BU VIII.2013	-
Siparuna guianensis	Cecidomyiidae	leaf	cylindrical	green	absent	BU, IN I.2013	6K
Siparuna guianensis	*Bruggmanniella* sp. (Cecidomyiidae)	stem	fusiform	green	absent	IN IV/VIII.2013	6L
Siparuna sp.	Cecidomyiidae	leaf	lenticular	green	absent	LV I.2013	6M
Solanum campaniforme	*Clinodiplosis* sp. (Cecidomyiidae)	leaf vein petiole	globoid	green	absent	TP IV.2013	6N
Solanum sp.	*Asphondylia* sp. (Cecidomyiidae)	leaf stem	globoid	green or brown	present	TP IV/VIII.2013	6O
Solanum sp.	Cecidomyiidae	stem	fusiform	brown	absent	BU VIII.2013	6P
Solanum sp.	*Asphondylia* sp. (Cecidomyiidae)	leaf vein	globoid	green	absent	TP VI.2013	6Q
Solanaceae (not det.)	not det.	leaf vein	fusiform	green	absent	TP VIII.2013	6R
Pourouma sp.	Cecidomyiidae (Diptera)	leaf vein	fusiform	brown	absent	IN I.2013	6S
Pourouma sp.	not det.	leaf	lenticular	brown	absent	IN VIII.2013	-
Lantana camara	*Schismatodiplosis lantanae* Rübsaamen, 1907 (Cecidomyiidae)	leaf	globoid	green	present	TP, LV VI/ VIII.2013	6T
Lantana camara	*Neolasioptera* sp. (Cecidomyiidae)	stem	fusiform	green,	absent	BU, LV, TP IV/ VI/VIII. 2013	-

Other gall dwellers were found in 39 morphotypes (25.5%) (Table 3). They comprised parasitoids, inquilines (phytophagous insects that occupy galls when they are still being used by gallers), and successors. The first were the most frequent dwellers being obtained from 29 gall morphotypes, and represented by seven families of Hymenoptera: Braconidae, Eulophidae, Eurytomidae, Ichneumonidae, Pteromalidae, Scelionidae, and Torymidae. Among these, the families Torymidae, Eurytomidae and Eulophidae predominated, being found in seven, seven and four gall morphotypes, respectively. The other families occurred in a single gall morphotype each. Four parasitoid genera were identified: *Eurytoma* Illiger, 1807 and *Rileya* Ashmead, 1888 (Eurytomidae), *Horismenus* Walker,1843 (Eulophidae), and *Platygaster* Latreille, 1809 (Platygastridae). The first two were associated with two galled plants each (*Inga edulis* and *Varronia curassavica*, and *Guarea kunthiana* and *Piper vicosanum*, respectively), whereas the other two genera had a single galled plant each. As inquilines we recorded Diptera (Sciaridae and Muscomorpha), Hemiptera and Lepidoptera in 13 gall morphotypes. Among these Hemiptera and Diptera were the most frequent, being observed in six and five plant species, respectively, followed by Lepidoptera obtained from three plant species. Two genera of Sciaridae were identified: *Corynoptera* Winnerty, 1867 and *Pterothrix* Mohrig, 2004. Sucessores included Psocoptera (Caeciliusidae), Formicidae and Acari (mites), obtained from four gall morphotypes. No predators were found.

Discussion

One hundred and fifty-three gall morphotypes were found in REBIO União. Only two previous Brazilian inventories have been performed in areas of Ombrophilous Forest, the first in Santa Teresa, Espírito Santo (Maia et al. 2014), and the second in Parque Nacional de Itatiaia (PNI), Southeast Brazil (Maia & Mascarenhas 2017). The authors recorded 265 and 406 gall morphotypes in these areas, respectively. The average number of morphotypes per plant species was 1.42 in REBIO União, compared to 1.87 in Santa Teresa and 2.18 in PNI. Although the total number of gall morphotypes and the average number of morphotypes per plant were lower in REBIO União, it is important to emphasize that periodicity of field work and the size of the sampling area were very different among these sites. Parque Nacional do Itatiaia was investigated from February 2014 to December 2015 with a total of 13 trails in Ombrophilous Forest physiognomy, while Santa Teresa was investigated for two years — seasonally during the first year and monthly during the second year — and included surveys of three protected areas: Parque Natural Municipal São Lourenço (with a single trail), Estação Biológica de Santa Lúcia (with three trails), and Reserva Biológica Augusto Ruschi (single trail). Therefore, the sampling effort was higher in PNI and Santa Teresa than in REBIO União, which could have influenced the present results. The Sorensen´s index revealed little similarlity among these three areas both in terms of host plant species

(REBIO União X PNI = 0.05; REBIO União X Santa Teresa = 0.04; PNI X Santa Teresa = 0.03) and insect gall morphotypes (REBIO União X Santa Teresa = 0.06; REBIO União X PNI = 0.05; PNI X Santa Teresa = 0.03). Since these areas exhibited few galled plant species in common, the same was expected with respect to gall morphotypes due the galler specificity.

The botanical families with the greatest gall richness in REBIO União were Asteraceae, Bignoniaceae, Fabaceae, and Myrtaceae. All have been previously indicated as superhosts by other Brazilian Ombrophilous Forest inventories except Bignoniaceae. Asteraceae, Fabaceae, and Myrtaceae are three of the ten most speciose families of the Atlantic Forest (Jardim Botânico do Rio de Janeiro 2016), adding evidence in support of the plant species richness hypothesis, which predicts a positive correlation between galling insect richness and plant taxon (families or genera) size (Fernandes 1992).

Mikania (Asteraceae) and *Myrcia* (Myrtaceae) were the plant genera with the greatest richness of galls in REBIO União. Both were previously highligthed as superhosts in Santa Teresa and PNI. The former contains 450 species (Holmes 1996), 171 of which are recorded for Brazil (King & Robinson 1987), while the latter contains 753 species (Govaerts *et al.* 2015), with 282 recorded in Brazil (Flora do Brasil 2018). Their great species richness may be related to their great gall richness, again adding evidence in support of the taxon size hypothesis (Fernandes 1992).

Table 3. Host plant species, gallers, gall characterization and associated fauna in Reserva Biológica União (state of Rio de Janeiro, Brazil). 1. Parasitoid, 2.Inquiline, 3. Successor.

Host plant species	Galler	Gall characterization				Associated fauna
		Galled organ	Shape	Color	Trichomes	
Mikania gleasonii	*Asphondylia* sp. (Cecidomyiidae)	leaf vein	globoid	green	absent	*Platygaster* sp.[1] (Platygastridae, Hymenoptera)
Mikania sp.3	*Asphondylia* sp. (Cecidomyiidae)	leaf vein	globoid	green	absent	Hymenoptera[1]
Mikania sp.4	Lasiopteridi (Cecidomyiidae)	stem	fusiform	brown	absent	Hymenoptera[1]
Mansoa sp.	Neolasioptera sp. (Cecidomyiidae)	stem leaf vein	fusiform	green brown	absent	Torymidae[1] (Hymenoptera)
Varronia curassavica	*Cordiamyia globosa* Maia, 1996 (Cecidomyiidae)	leaf	globoid	green	present	Hymenoptera[1] Muscomorpha[2] Lepidoptera[2]
Varronia curassavica	Lepidoptera	leaf vein	fusiform	green	present	Hymenoptera[1] Caeciliusidae[3] (Psocoptera)
Boraginaceae (not det.)	Cecidomyiidae	bud	globoid	green brown	absent	*Eurytoma* sp.[1] (Eurytomidae) Eulophidae[1] Torymidae[1] (Hymenoptera)
Boraginaceae (not det.)	Cecidomyiidae	bud	globoid	green	present	Hymenoptera[1]
Ipomoea sp.	Cecidomyiidae	stem	fusiform	green brown	absent	Hymenoptera[1]
Dodecastigma sp.	not det.	stem petiole leaf vein	globoid	brown,	absent	Hymenoptera[1] Hemiptera[2]
Euphorbiaceae (not det.)	not det.	stem	fusiform	brown	absent	Braconidae[1] (Hymenoptera)
Inga capitata	Cecidomyiidae	stem.	fusiform	brown	absent	Hymenoptera[1]
Inga edulis	Cecidomyiidae	leaf vein	fusiform	green	absent	*Eurytoma* sp.[1] (Eurytomidae, Hymenoptera)
Martiodendron sp.	Schizomyiina (Cecidomyiidae)	stem	conical	reddish green	present	Sciaridae[2] (Diptera)
Myroxylon peruiferum	not det.	leaf	lenticular	greenishyellow	absent	Lepidoptera[2]
Senegalia serra	not det.	petiole	globoid	brown	absent	Pteromalidae[1] (Hymenoptera)
Aegiphila integrifolia	not det.	leaf	globoid	green	absent	Hemiptera[2]

continuation...

Ocotea sp.	not det.	leaf vein	fusiform	green	absent	Caeciliusidae[3] (Psocoptera)
Lecythis pisonis	Lasiopteridi (Cecidomyiidae)	leaf	globoid	brown	absent	Lepidoptera[2]
Miconia prasina	Cecidomyiidae	leaf vein	fusiform or globoid	greenish-yellow	absent	Hymenoptera[1]
Miconia pusilliflora	Cecidomyiidae.	stem, bud, leaf3	globoid	green	absent	Torymidae[1] (Hymenoptera) Hymenoptera[1]
Miconia pusilliflora	not det.	leaf vein	globoid	green or brown	absent	Eurytomidae[1] (Hymenoptera)
Guarea kunthiana	Cecidomyiidae. Associated fauna:	leaf vein	fusiform	green	absent	Rileya sp.[1] (Eurytomidae) Eulophidae[1] Torymidae[1] (Hymenoptera)
Guarea kunthiana	Cecidomyiidae	leaf	lenticular	green	absent	Hymenoptera[1]
Myrcia splendens	Cecidomyiidae	leaf vein	globoid	green or brown	absent	Hymenoptera[1]
Myrcia splendens	Cecidomyiidae	leaf	marginal roll	green	absent	Hymenoptera[1] Formicidae[3]
Myrcia sp.	Lasiopteridi (Cecidomyiidae)	leaf	globoid	green	absent	Torymidae[1] (Hymenoptera) Hemiptera[2]
Psidium guineense	Hymenoptera	stem	globoid	green or brown	absent	Hymenoptera[1] Sciaridae[2] (Diptera) Lepidoptera[2]
Piper tuberculatum	Cecidomyiidae	leaf	globoid	green	absent	Eurytomidae[1] (Hymenoptera)
Piper vicosanum[2]	*Zalepidota* sp. (Cecidomyiidae)	bud	globoid	yellow or brown	absent	Rileya sp.[1] (Eurytomidae) Torymidae sp.1[1] Torymidae sp. 2[1] Lepidoptera[2]
Piperaceae (not det.)	not det.	leaf	conical	hairy	present	Sciaridae[2] (Diptera)
Diodia sp.	Cecidomyiidae	stem	fusiform	green	absent	Ichneumonidae[1] (Hymenoptera)
Cupania racemosa	Cecidomyiidae.	leaf vein	fusiform,	green	absent	Hemiptera[2]
Siparuna guianensis	*Bruggmanniella* sp. (Cecidomyiidae)	stem	fusiform	green	absent	Eulophidae[1] (Hymenoptera)
Solanum campaniforme	*Clinodiplosis* sp. (Cecidomyiidae)	leaf vein petiole	globoid	green	absent	Eulophidae[1] (Hymenoptera Hemiptera[2] mites[3]
Solanum sp.	Cecidomyiidae	stem	fusiform	brown	absent	Hymenoptera[1]
Lantana camara	*Schismatodiplosis lantanae* Rübsaamen, 1907 (Cecidomyiidae)	leaf	globoid	green	present	Hemiptera[2]
Lantana camara	*Neolasioptera* sp. (Cecidomyiidae)	stem	fusiform	green,	absent	Scelionidae[1] Torymidae[1] (Hymenoptera) Sciaridae[2] (Diptera)

Most host plant species were native, and together they hosted more than 90% of the gall morphotypes. We expect that the gallers that are associated with these plants are also native, based on high host specificity.

In concordance with other Brazilian inventories in areas of Ombrophilous Forest, leaves were the most galled plant organ in REBIO União, which can be explained by the fact that leaves represent an abundant and common resource (Maia 2001). There was a predominance of globoid and fusiform galls at REBIO União, as was the case for Santa Teresa and PNI. Furthermore, most leaf galls were globoid, whereas most stem and vein galls were fusiform. These shapes are also highligthed in other Atlantic Forest physiognomies, such as Restinga (Maia 2001) and Tableland Forest (Maia & Carvalho-Fernandes 2016). According to Isaias et al. (2013), the high frequency of these shapes is related to the patterns of cell growth and differentiation of these plant organs. Most galls were glabrous, as in all other Brazilian inventories (Maia & Mascarenhas 2017). According to Inbar et al. 2010, trichomes can act as structural defenses against loss of water or against predators and parasitoids, as they impair their feeding and mobility. As the REBIO União is a mesic environment, and the frequency of parasitism was low, the presence of trichomes appears to be unnecessary. Green and brown galls predominated, being the same colors of the most frequent galled plant organs, leaves and stems, respectively, whereas yellow, red and purple galls were rare. Inbar et al. 2010 proposed that galls that exhibit a combination of high levels of defensive compounds with conspicuousness — size, shape, bright coloration and possibly odor — are aposematic. Galls are manipulated by gallers to form all the components of aposematism (chemical defenses and warning coloration or odor). The components of the aposematic phenotype are expressed externally in the gall tissue, protecting the galling insects and not the host plant that produces them, as the hosts have no interest in protecting their parasites. Advertisement of chemically-defended galls may reduce predation by mammalian herbivores, avian insectivores and frugivores and various arthropods. In contrast, galls that exhibit the same color of the host organ are cryptic and probably poor in chemical defenses. Cryptic coloration can also protect the galler against predation. In REBIO União, 57 plant species have been recorded as food sources for the golden-lion tamarin (*Leontopithecus rosalia* Linnaeus, 1766). Four of these plant species are known to host galls — *Inga edulis*, *Myrcia* sp., *Pourouma* sp., and *Simarouba amara* (Lapenta 2002) — all of which are cryptic, except for one morphotype on *Myrcia* sp., which is reddish. We observed color change in a single gall morphotype, which changed from green to yellow. According to Stone et al. 2002, some galls may change color during their development in association with exposure to light or plant defenses.

In the present study, the highest gall richness was recorded in June and August, the period when most plants are sprouting, which increases the availability of oviposition sites since new tissues have high differentiation capacity and plasticity (Gonçalves et al. 2005, Rohfritsch 1992).

We noticed that the longer trails had higher gall richness, while shorter trails had lower gall richness, indicating that the gall richness is positively related to trail length. This is probably a result of the longer paths encompassing a greater number of plant species and, consequently, a greater number of possible hosts. The Sorensen `s index revealed little similarity among the studied trails, so each contributes to the gall richness of REBIO União.

We recorded gallers of five orders: Diptera (Cecidomyiidae), Lepidoptera, Hymenoptera, Hemiptera, and Thysanoptera. Thus, all galling insect orders were represented at REBIO União with the exception of Coleoptera. Maia et al. 2014 and Maia & Mascarenhas 2017 found galls induced by other insect taxa in their inventories of Ombrophilous Forest, such as Tephritidae (Diptera) and Coleoptera. Cecidomyiidae were the most frequent gallers at REBIO União, following a global pattern. As several galls were found empty, parasitized or occupied by more than one insect taxon, we could not determined their gallers.

Among the gallers, *Alycaulus globulus* Gagné, 2001, *Arrabiadaeamyia serrata* Maia, 2001, *Asphondylia cfr. cordiae* Möhn, 1959, *Brugmannia robusta* Maia and Couri, 1993, *Cordiamyia globosa* Maia, 1996, *Dasineura byrsonimae* Maia, 2010, *Liodiplosis conica* Gagné, 2001, and *Schismatodiplosis lantanae* Rübsaamen, 1908 were recorded for the first time in REBIO União, thus expanding their known distribution. *Alycaulus globulus, Cordiamyia globosa*, *Liodiplosis conica* and *Schismatodiplosis lantanae* had been previously recorded from Ombrophilous Forest (Gagné et al. 2001, Maia et al. 2014, Maia & Mascarenhas 2017, Proença & Maia 2014), while *Asphondylia cfr. cordiae*, *Brugmannia robusta* and *Dasineura byrsonimae* were previously recorded from Restinga and Tableland Forest (Maia & Silva 2016, Maia & Carvalho-Fernandes 2016), and *Arrabiadaeamyia serrata* from just Restinga. So, the last four species were recorded for the first time in Ombrophilous Forest.

At least seven genera of gall midges were recorded in REBIO União in the present study, with those of the genera *Asphondylia* and *Neolasioptera* being the most diverse. These genera have been recorded in other Brazilian inventories, in restingas of the states of Rio de Janeiro and São Paulo (Maia 2001, Oliveira & Maia 2005, Maia & Oliveira 2010, Monteiro et al. 1994, 2004, Maia et al. 2008), in Ombrophilous Forest in Southeast Brazil (Maia & Mascarenhas 2017) and in Cerrado in Minas Gerais (Maia & Fernandes 2004), which is evidence of their adaptability to different environmental conditions.

The present study provided new data on insect-plant interactions, including: *Asphondylia* on *Mikania gleasonii* (Asteraceae) and *Pyrostegia* (Bignoniaceae); *Neolasioptera* on *Anemopaegma chamberlaynii*, *Lundia* and *Mansoa* (Bignoniaceae); *Bruggmanniella* on Siparunaceae; *Clinodiplosis on Davilla rugosa* (Dilleniaceae) and *Solanum campaniforme* (Solanaceae); and *Lopesia* on Salicaceae. These new data reinforce the importance of inventories.

About 25% of the gall morphotypes were occupied by dwellers other than those that created the gall. This rate is similar to that recorded in PNI (27.5%), but lower than the rates recorded for areas of restinga (50% in Bertioga, in the state of São Paulo; 56% in Maricá + Carapebus in the state of Rio de Janeiro; 40% in Mangaratiba also in the state of Rio de Janeiro). This finding is probably due to the harsh abiotic conditions of restingas, which include intense lumination and strong winds, which could favor gall formation and occupation as a protective strategy.

Parasitoids, being represented by seven families of Hymenoptera, were more frequent and diverse than inquilines and successors. Parasitoids were also reported in all other Brazilian inventories of insect galls as predominant. They are considered the main natural enemies of galling insects, and play an importan role in their populational control (La Salle 1993). These families of Hymenoptera have all previously been reported by Brazilian inventories of insect galls, among which Torymidae, Eurytomidae and Eulophidae are the most frequent families (Maia & Azevedo 2009).

Inquilines included Diptera (Sciaridae and Muscomorpha), Hemiptera and Lepidoptera, all of which have aready been recorded in other Brazilian inventories. Nevertheless, few records of inquilinous Sciaridae and Muscomorpha are known (Maia & Fernandes 2004, Maia et al. 2008, Maia et al. 2014, Rodrigues et al. 2014). Among Sciaridae, we identified two genera, *Corynoptera* Winnerty, 1867 and *Pterothrix* Mohrig, 2004, both reported for the first time as gall inquilines. The records of Sciaridae on *Martiodendron* sp. (Fabaceae), *Psidium guianeense* (Myrtaceae) and *Lantana camara* (Verbenaceae) are also new. Muscomorpha were reported for the first time on *Varronia curassavica* (Boraginaceae). Hemiptera and Lepidoptera are frequent inquilines, having been associated with several plants in Brazil, but the records of Hemiptera on *Dodecastigma* (Euphorbiaceae), *Aegiphila integrifolia* (Lamiaceae), *Myrcia splendens* (Myrtaceae), *Cupania racemosa* (Rubiaceae), *Solanum campaniforme* (Solanaceae), and *Lantana camara* (Verbenaceae) are new, as well as the record of Lepidoptera on *Piper vicosanum* (Piperaceae).

Successors were represented by Psocoptera, Hymenoptera (Formicidae) and Acari, all previously recorded in galls. Nevertheless, new associations were observed, namely: Caeciliusidae (Psocoptera) on *Varronia curassavica* (Boraginaceae) and *Ocotea* sp. (Lauraceae); Formicidae (Hymenoptera) on *Myrcia splendens* (Myrtaceae); and Acari on *Solanum campaniforme* (Solanaceae).

Comparing the galled plants of the REBIO União with those of other Brazilian inventories in the Atlantic Forest, we verified that two genera (*Xylopia* L. and *Thunbergia* L.), and five species (*Dicliptera mucronifolia*, *Thunbergia alata*, *Mikania pilosa*, *Adenocalymma subsessilifolium* DC., and *Adenocalymma validum*) were reported for the first time as host plants.

Conclusions

The REBIO União hosts particular insect gall richness with several galls on endemic plants, which showed the importance of this protected area for the conservation of the galling guild. Asteraceae, Fabaceae and Myrtaceae were confirmed as plant families with the greatest gall richness in Ombrophilous Forest areas, while Bignoniaceae was added as a super host. The predominant features of galls of REBIO União were in agreement with the morphological pattern previously observed in Brazil. The geographical distribution of eight gall midge species were expanded and new data on insect-plant interactions were provided. The new records reinforce the importance of such inventories for improving the knowledge of galling guild richness and distribution in Brazil.

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Author Contributions

Valéria Cid Maia: Substancial contribution in the concept and design of the study, contribution to data collection, analysis, interpretation and manuscript preparation.

Eick de Souza Siqueira: contribution to data analysis and interpretation.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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Inventory

Freshwater mollusks from three reservoirs of Piauí, northeastern Brazil

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Abstract: The pronounced dry season determines the characteristics of the semiarid region of Brazil. Numerous small reservoirs are built to overcome this condition, accumulating multiple uses and causing important changes in the landscape and the local biota. Considering the limited amount of information about the malacofauna of reservoirs, mainly in the Northeast region of the country, this inventory provides a list of mollusks from three important reservoirs located in the city of São Julião, state of Piauí. The collections were carried out monthly between May/2017 and April/2018, sampling a total of 11,149 mollusks, corresponding to the species *Melanoides tuberculata* (Müller, 1774) (n = 9,724), *Biomphalaria straminea* (Dunker, 1848) (n = 1,361) and *Pomacea lineata* (Spix, 1827) (n = 64). The richness of mollusks from the three reservoirs was low, similar to those described in studies conducted in other regions of Northeast Brazil. There was a significant difference in the abundance of *M. tuberculata* and *B. straminea* among the studied reservoirs. These environments are not connected and are installed in urban and rural areas, presenting different ecological conditions. The relationship between the human population and the reservoirs, associated with the lack of sanitation, increases the risks of spreading waterborne diseases besides the development of environmental imbalance by the introduction of exotic species.
Keywords: *Ampullariidae, Gastropoda, Planorbidae, species list, Thiaridae.*

Moluscos límnicos de três reservatórios do Piauí, nordeste do Brasil

Resumo: O período de seca pronunciado marca a região semiárida brasileira. Para superação dessa condição inúmeros reservatórios de pequeno porte são construídos, acumulando múltiplos usos e causando alterações importantes na paisagem e na biota local. Considerando as poucas informações sobre a malacofauna de reservatórios, principalmente na região nordeste do país, este trabalho apresenta o inventário das espécies de moluscos provenientes de três importantes reservatórios localizados no município de São Julião, estado do Piauí. As coletas foram realizadas mensalmente entre os meses de maio/2017 e abril/2018. Foi amostrado um total de 11.149 moluscos, correspondentes as espécies *Melanoides tuberculata* (Müller, 1774) (n=9,724), *Biomphalaria straminea* (Dunker, 1848) (n=1,361) e *Pomacea lineata* (Spix, 1827) (n=64). A riqueza de moluscos amostrados nos três reservatórios foi baixa, não diferindo daquelas descritas em estudos realizados em outras regiões do Nordeste do Brasil. Houve diferença significativa na abundância de *M. tuberculata* e *B. straminea* entre os reservatórios estudados os quais não são conectados e encontram-se instalados em áreas urbana e rurais, com condições ambientais distintas. A relação entre a população humana da região e os reservatórios, juntamente com a falta de saneamento representam riscos à propagação de doenças transmitidas pela água e desequilíbrio ambiental pela introdução de espécies exóticas.
Palavras-chave: *Ampullariidae, Gastropoda, lista de espécies, Planorbidae, Thiaridae.*

Introduction

The semiarid region covers a large part of the Northeast and a portion of the Brazilian Southeast (SUDENE 2017). This area is subject to recurrent and severe droughts periods (Ab'Sáber 2003) with spatial rainfall and temporal irregularity, providing edaphic high evapotranspiration and causing a serious water scarcity condition (Agostinho et al. 2007; Malvezzi 2007). Tundisi (2003) considers this scenario the main threat to the Brazilian Northeastern region biodiversity, driving to changes in natural environments dynamics and also in all communities that depend or live in freshwater.

Due to this ecological feature, a set of measures have been taken to reduce the impact of droughts in the Northeast and building dams has been an effective way to store water (Esteves 1998). Despite its intrinsic importance for the human population, the building of a reservoir severely changes local hydrology, moving streams from a lotic state to a lentic or semi-lentic condition (Agostinho et al. 2007, Tundisi et al. 2002). These changes produce considerable alterations in aquatic ecosystems, primarily due to variations in water residence time, habitat fragmentation and exotic species invasion (Tundisi 2008, Agostinho et al. 2005). These circumstances eventually promote the restructuring of the entire biota composition (Baxter 1977), allowing to species substitution and an increase on the abundance of more adapted species to the conditions of the new environment in opposition to the decrease of non-adapted ones.

Mollusca is an extraordinarily varied phylum, with estimates of 80,000-100,000 described species and the total diversity possibly as high as 200,000, they are behind only to arthropods in species richness (Strong et al. 2008). The mollusks have been successful in occupying most of all diverse freshwater habitats (Bogan 2008) with reports of phylogenetically distinct lineages and assemblages, of which Bivalvia and Gastropoda are cited as the most important classes (Lydeard et al. 2004). These animals participate in several ecological interactions within the community acting as filtering agents, herbivores, predators, ectoparasites, and commensal (Colley et al. 2012; Pombo 2016), besides carrying parasites intermediate forms.

Routinely and inadvertently, freshwater mollusks are introduced in new environments with aquatic plants, fish and anthropic action linked with aquaculture (Strong et al. 2008). Negative consequences of this introduction are diverse, including: (1) partial or total natural populations substitution (Freitas et al. 1987, Pointier 1999, Fernandez 2001); (2) health damage to both humans and other animals through the dissemination of larval stages of parasites (Pinto & Melo 2011); and (3) economic, causing damages to companies building structures because of the accumulation of these organisms (Santos et al. 2012, Vogler 2012).

There is no systematized information about native mollusk fauna nor exotic regarding Brazilian reservoirs, and the few existing reports about this group are restricted to large dams, mainly those related to hydroelectric plants (Thiengo et al. 2005, Fernandez et al. 2018, Rocha et al. 2011, Fernandez et al. 2014). Likewise, studies focused on mollusk fauna of small and medium-sized reservoirs in the Brazilian Northeast built for water storage are still scarce (e.g., Santos & Eskinazi-Sant'anna 2010, Almeida et al. 2018, Medeiros et al. 2018). Considering the importance of the malacofauna previously described and the fact that small reservoirs accumulate diverse uses by the populations, the knowledge of its composition is extremely important. Thus, this work presents a list of mollusks species derived from three important reservoirs located in the northeastern of Piaui state, semiarid region.

Material and Methods

1. Study area

This research is part of the long-term survey project about the malacofauna from Guaribas Valley territory. This territory comprises an area of 22,822 km² of Piauí state, reaching 23 cities (SEPLAN 2017). The studied reservoirs are in São Julião, a small city with 5,675 inhabitants, in the southeast of the state (IBGE 2019).

The sampling expedition occurred at São Julião reservoir, located in the urban area, Dona Maria Zeneide Viana de Andrade (former Piaus) and Emparedade reservoirs, both located in the rural area (Figure 1). Those survey points were chosen because they are perennial with massive presence of mollusks and accessible to the local human population.

2. Sampling and data analysis

Samplings were held monthly between May 2017 and April 2018 in three stations located 1.5 meters from the margin in each reservoir. The field procedures were done according to Silva et al. (2019). Sorting and identification of individuals were carried out at the Laboratory of Ecology, Parasitology and Neglected Diseases (LAPEDONE), at the Instituto Federal do Piauí.

The verification of normality in the data distribution occurred by applying the Shapiro-Wilk test. After not presenting normal distribution, there was the application of the Kruskal-Wallis nonparametric test to verify the differences in the abundance of mollusks between the reservoirs studied. The Kolmogorov-Smirnov test occurred *a posteriori*. All analyses used the SYSTAT® software, version 12.0.

The entire field procedure was authorized by Chico Mendes Institute for Biodiversity Conservation, through Biodiversity Authorization and Information System (SISBIO) permit number 60423-5. Voucher specimens are housed at Coleção de Moluscos do Instituto Oswaldo Cruz, Fundação Oswaldo Cruz, Rio de Janeiro, Brazil (CMIOC), Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP) and at the LAPEDONE collection as well (Table 1).

Results

During the sampling period, 11,149 alive mollusks were captured in the three reservoirs. These animals belong to three Gastropoda species: *Melanoides tuberculata* (Müller, 1774) (Thiaridae) (n = 9,724; min = 0; max = 795; mean = 30), *Biomphalaria straminea* (Dunker, 1848) (Planorbidae) (n = 1,361; min = 0, max = 74; mean = 4.2) and *Pomacea lineata* (Spix, 1827) (Ampullariidae) (n = 64; min = 0; max = 12; mean = 0.2) (Figure 2).

When comparing species abundance among the reservoirs, Dona Maria Zeneide Viana de Andrade Reservoir had the highest number of mollusks (n = 5,417; 48.6%). Emparedade (n = 4,619; 41.4%) was the second most abundant followed by São Julião (n = 1,113; 10%). Despite the species abundance being different between the analyzed reservoirs, their composition remained the same among them.

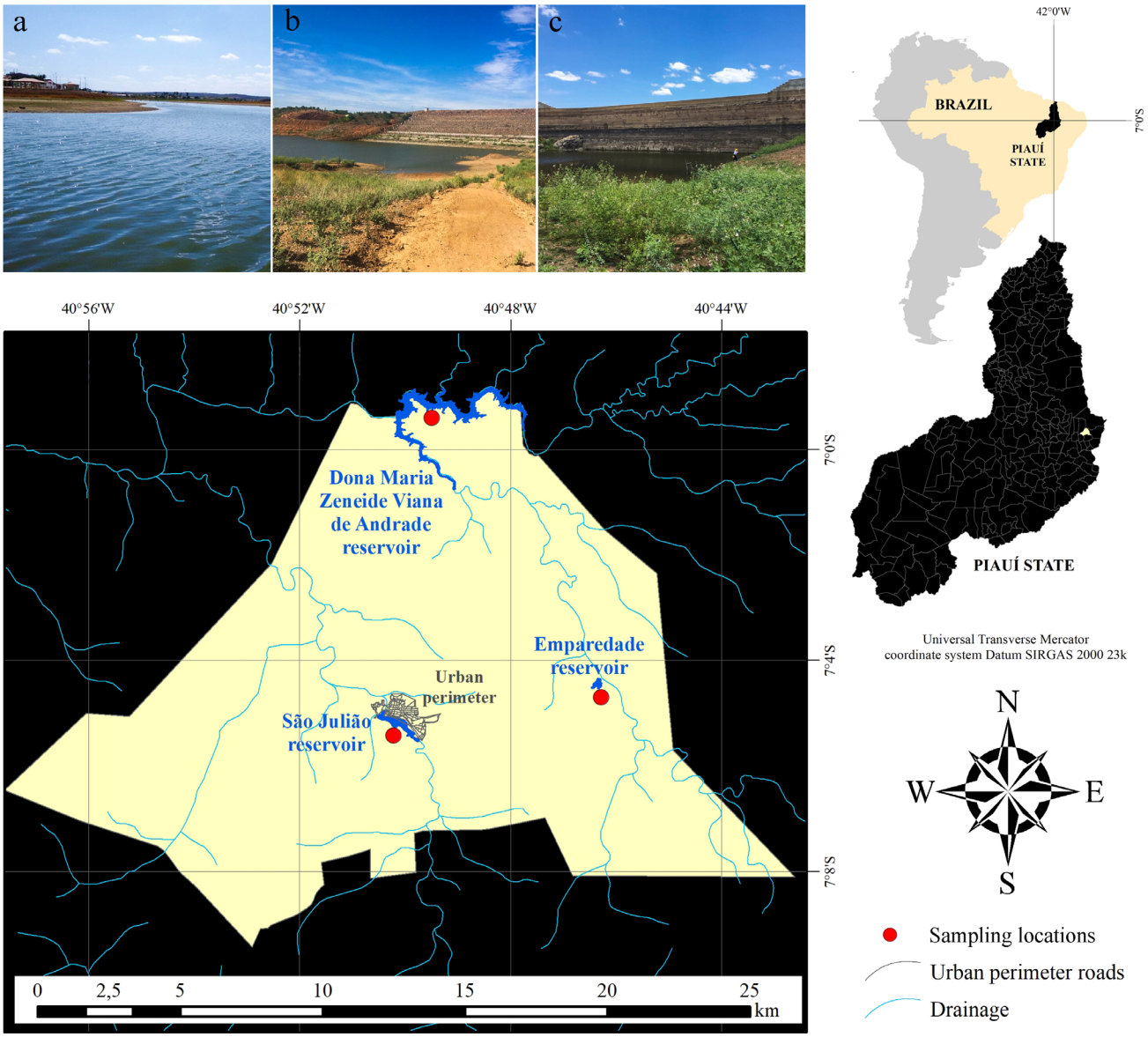


Figure 1. Sampling locations in São Julião, Piauí, Brazil. Details of reservoirs surveyed a: São Julião; b: Dona Maria Zeneide Viana de Andrade and c: Emparedade (Adapted from Silva et al. 2019).

Table 1. Gastropoda species sampled in the reservoirs of São Julião, Piauí, Brazil, between June 2017 and April 2018.

Order/Family	Species	Voucher number	Reservoir
Basommatophora/Planorbidae	*Biomphalaria straminea* (Dunker, 1848)	CMIOC 11598	São Julião Reservoir 7°05'02.6"S 40°50'29.0"W
Prosobranchia/Thiaridae	*Melanoides tuberculata* (Müller, 1774)	CMIOC 11599	
Prosobranchia/Ampullariidae	*Pomacea lineata* (Spix, 1827)	MZUSP 146748	
Basommatophora/Planorbidae	*Biomphalaria straminea* (Dunker, 1848)	CMIOC 11601	Emparedade Reservoir 7°05'02.6"S 40°50'29.0"W
Prosobranchia/Thiaridae	*Melanoides tuberculata* (Müller, 1774)	CMIOC 11602	
Prosobranchia/Ampullariidae	*Pomacea lineata* (Spix, 1827)	MZUSP 146750	
Basommatophora/Planorbidae	*Biomphalaria straminea* (Dunker, 1848)	CMIOC 11604	Dona Maria Zeneide Viana de Andrade Reservoir 7°05'02.6"S 40°50'29.0"W
Prosobranchia/Thiaridae	*Melanoides tuberculata* (Müller, 1774)	CMIOC 11605	
Prosobranchia/Ampullariidae	*Pomacea lineata* (Spix, 1827)	MZUSP 146751	

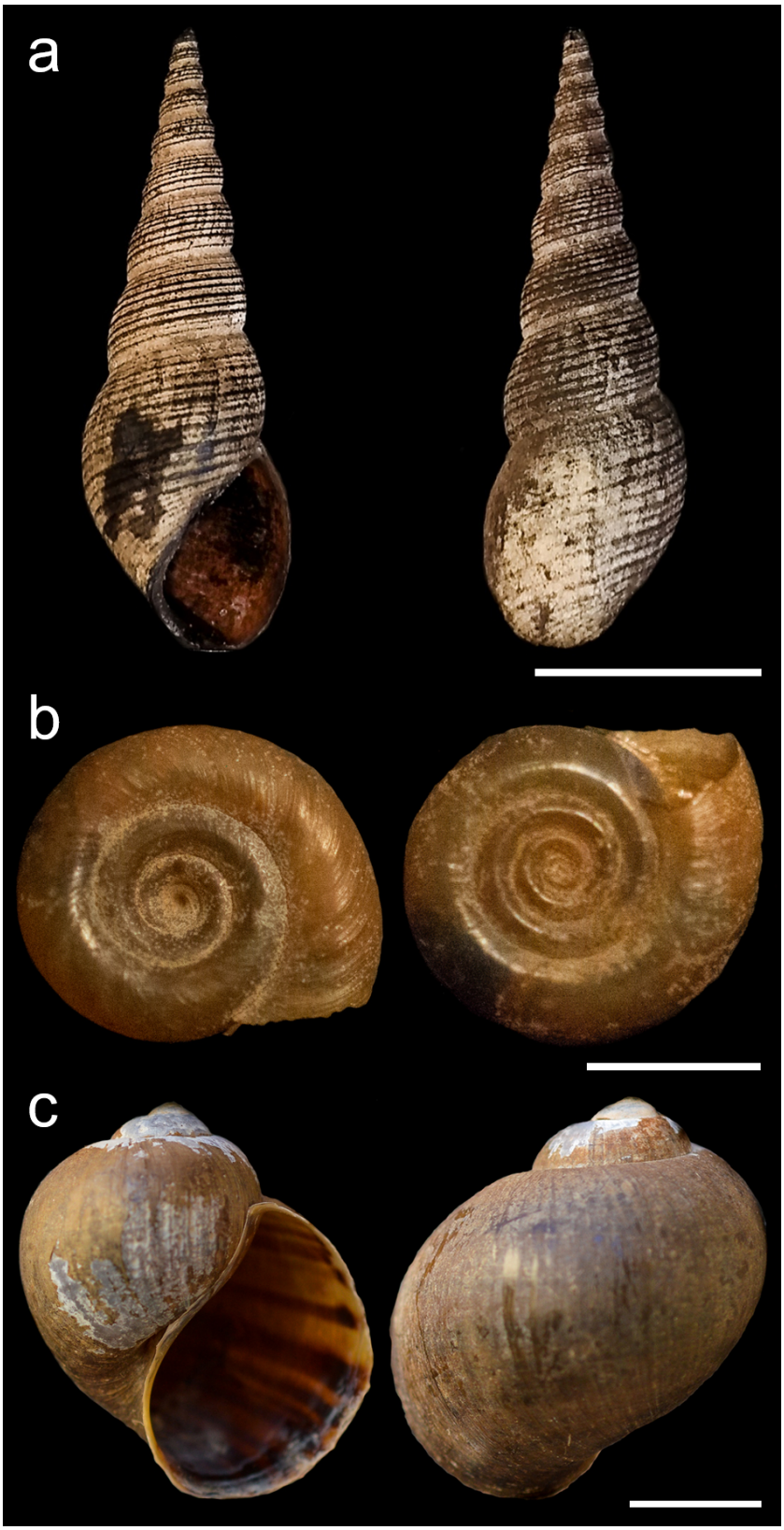


Figure 2. Mollusk species sampled in the reservoirs of São Julião, Piauí, Brazil. a: *Melanoides tuberculata*; b: *Biomphalaria straminea* and c: *Pomacea lineata*. Scale bars = a: 10mm, b: 5mm and c: 10mm.

Melanoides tuberculata was the most abundant species among the three reservoirs, corresponding to 9,724 individuals (87.2% of total sampled). This species had 4,894 specimens (50.3%; min = 0; max = 401; mean = 45.3) in Dona Maria Zeneide Viana de Andrade Reservoir, while in Emparedade there were 3,762 individuals (38.7%; min = 0; max = 795; mean = 34.8), and 1,068 in São Julião Reservoir (11%; min = 0; max = 111; mean = 9.9). It was verified a significant difference in the abundance of individuals among the studied dams, of which only São Julião Reservoir differed in its results ($P \leq 0.05$; d.f. = 2; $X^2 = 24.88$) (Figure 3a).

The second most abundant species in the study is *B. straminea,* corresponding to 1,361 individuals (12.2% of the entire sample). A total of 821 individuals were collected in Emparedade Reservoir (60.3%; min = 0; max = 74, mean = 7.7), 512 individuals (37.6%; min = 0, max = 64; mean = 4.8) in Dona Maria Zeneide Viana de Andrade Reservoir and 28 individuals (2.1%; min = 0; max = 4, mean = 0.3) in São Julião reservoir, the least abundant of all. There was a significant difference in the abundance of mollusks of this species among the studied reservoirs, of which São Julião differed from the others surveyed ($P \leq 0.05$; d.f. = 2; $X^2 = 78.79$) (Figure 3b).

Pomacea lineata was least abundant in all three reservoirs, comprising 64 individuals (0.6% of sampled animals). This species had 36 individuals in Emparedade reservoir (56.3%; min = 0, max = 12, mean = 0.3), followed by 17 individuals in São Julião (26.6%; min = 0; max = 5; mean = 0.2), and only 11 specimens in Dona Maria Zeneide Viana de Andrade Reservoir (17.2%; min = 0; max = 5; mean = 0.1). There was no significant difference in the abundance of individuals of this species among the reservoirs studied ($P = 0.06$; d.f. = 2; $X^2 = 5.54$) (Figure 3c).

Discussion

Similar to other freshwater and marine invertebrates, freshwater gastropods present an overall pattern of high diversity in tropics, with decreasing species richness as well as decreasing endemicity at higher latitudes (Strog et al. 2008). According to the latter author, the rivers and streams of South America are surprisingly species-poor, however, it is not yet clear if this is a sampling/study artifact or an actual pattern. The fauna of mollusks sampled in the three reservoirs of São Julião is, in fact, not diverse, consisting of three species from only three families of Gastropoda. These results are similar to those described by studies carried out in the Brazilian Northeastern, a region which accumulates a history of low species diversity (Abílio et al. 2007, Oliveira & Viana 2019).

Santos & Eskinazi-Sant'Anna (2010) attempted to explain the relatively low variety observed in semiarid tropical regions, attributing to prolonged dry periods a condition that selects to snail's community. Considering this assertion, in case of intermittent rivers dammed, the time of water residence is a factor that can play an important role in this phenomenon because drives the stratification processes and nutrient availability, causing considerably changes in water properties (Straškraba 1999, Londe et al. 2016). Bennion et al. (2005) described that retention periods longer than 30 days are very sensitive to enrichment, making the water more susceptible to eutrophication. According to the latter authors, shallow and completely mixed aquatic environments present a very low potential for recovery. These attributes are similar to the ones verified in the reservoir complex studied in São Julião.

Although geographically close, the studied reservoirs are not connected. This autonomy implies that each environment will present a peculiar response to environmental variations. Emparedade and Dona Maria Zeneide Viana de Andrade reservoirs are located in a rural area, far from urban influence. It is possible to verify a large deforested area along the reservoirs margin, which allows the exposure of water column to light, causing a consequent increase in primary productivity. Conversely, São Julião reservoir is in urban perimeter, having significantly more vegetation at its margin, and it receives a considerable amount of non-treated sewage. Thus, these particularities of each of the studied reservoirs may have been responsible for the significant difference in mollusks abundance.

Previous studies conducted in different regions of the country considered the species found in the three reservoirs of São Julião tolerant and very adapted to environmental diversity. *Biomphalaria straminea* is widely distributed in Brazil, as a result of their ability to adapt to different climates and ecological conditions (Paraense, 1986). According to Kotzian & Amaral (2013), *B. straminea* occurrence in water bodies of the semiarid region can be explained by their tolerance to dry periods, thus severe semi-arid conditions are not barriers to their survival. This species is the most important host of *Schistosoma mansoni* (Sambon, 1907) in Brazilian Northeastern. *Pomacea lineata*, in its turn, although less abundant, is quite resistant to desiccation. In a recent study, Glasheen et al. (2017) confirmed that the survival capacity of these animals to drought conditions, due to the behavior of fully burying itself in the substrate. Regarding *M. tuberculata*, this species has combined high tolerance to both salinities' levels (Farani et al., 2000, Silva & Barros 2015, Bolaji et al., 2011) and temperature variations (Pointier 1993), and it also supports longer desiccation periods. Allied to this, it has a high reproductive capacity through parthenogenesis (Jacob 1957) and sexual reproduction (Samadi et al. 1999).

In São Julião reservoir complex, the abundance of *M. tuberculata* is seven times higher than all other native species registered. The high number of individuals observed is a consequence of the set of biological traits mentioned, which allows *M. tuberculata* to become a successful competitor in new environments, capable of even suppressing the growth of native species population. The role of this invasive species in the reduction of native species have been described in different environments (Freitas et al. 1987, Pointier 1999, Fernandez 2001, Almeida et al. 2018). There are reports of the decline in *B. glabrata* and *B. straminea* densities from the Southeastern region (Giovanelli et al. 2003, Almeida et al. 2018), as well as it was responsible for the low diversity and density indices of native species in Northeastern reservoirs (Almeida et al. 2018). Although the effect of *M. tuberculata* on mollusk community of the São Julião reservoirs has not been evaluated, the expressive differences observed among abundances of this species, *B. straminea* and *Pomacea lineata*, suggest attention to a putative interspecific competition.

The history of severe droughts in the region of São Julião promoted a larger interaction between human populations and their reservoirs. However, without proper sanitation conditions that this interaction requires, the risk of spreading water-borne diseases and environmental imbalance through the introduction of exotic species is imminent. The

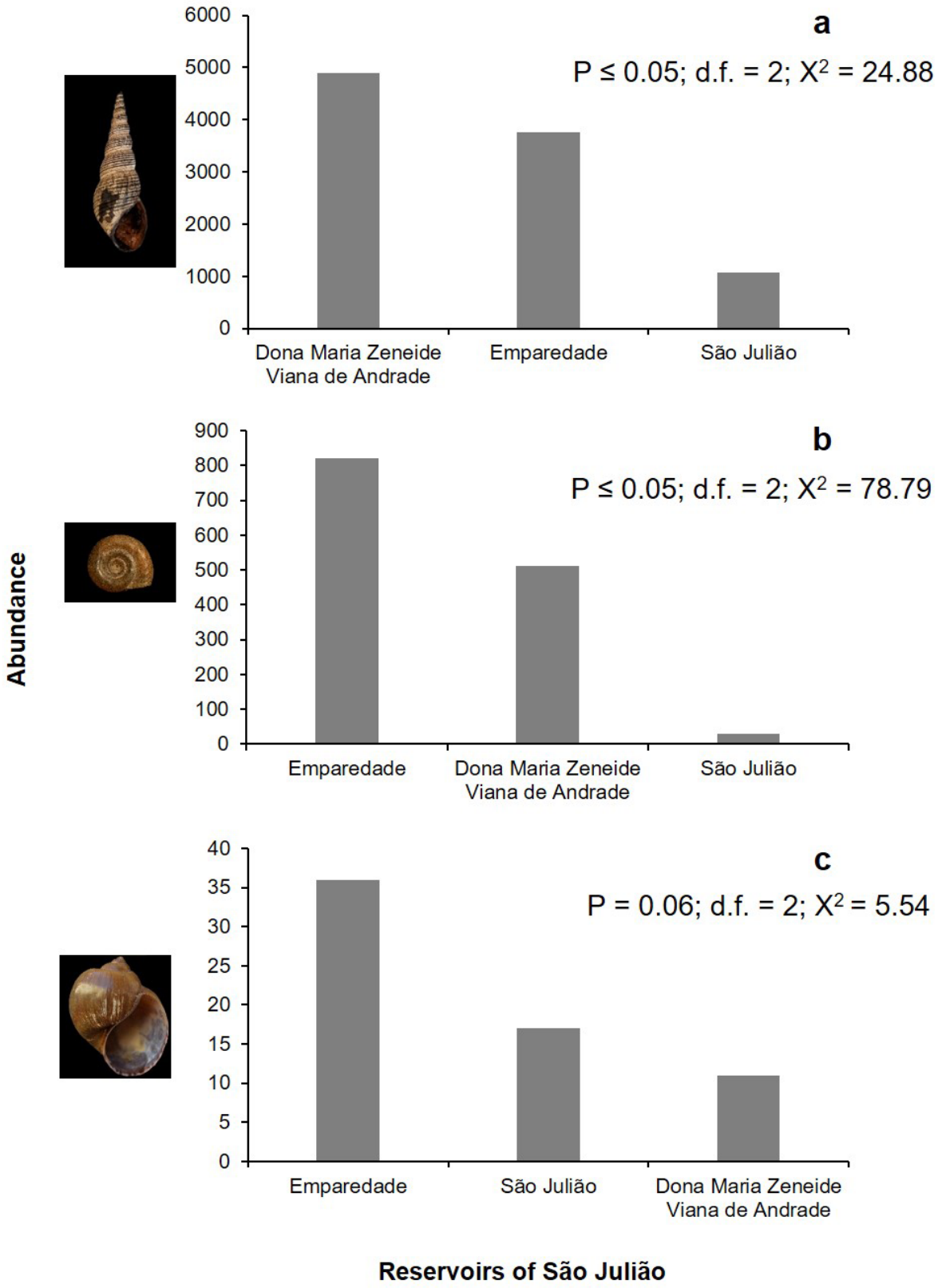


Figure 3. Abundance of Gastropoda species sampled in the three reservoirs of São Julião, Piauí, Brazil, between May 2017 and April 2018. Details of statistical tests in a: *Melanoides tuberculata*; b: *Biomphalaria straminea* and c: *Pomacea lineata*. Images of species out of scale.

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results obtained with this survey allowed us to make inferences about the influence of these water bodies on the malacofauna composition of the semiarid region as well as their interaction with the environment, besides recording the presence of *B. straminea*, which is the intermediate host of *S. mansoni,* in the studied region. This information is of paramount importance to local populations who depend on these water resources for a variety of activities.

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Author contributions

Edson Lourenço da Silva: Contribution to data analysis and interpretation.

Adriana Josefa da Rocha: Contribution to data collection.

Manuella Feitosa Leal: Contribution to data collection.

Orianna dos Santos: Contribution to data collection.

João Hemerson de Sousa: Contribution to data collection.

Antônia Rafaela Viana da Silva: Contribution to data collection.

Karina Ketelen Silva Dantas: Contribution to data collection.

Erika Maria Matos Rulim: Contribution to data collection.

Emerson Santos Castro: Contribution to data collection.

Ana Carolina Landim Pacheco: Contribution to critical revision, adding intellectual content.

Tamaris Gimenez Pinheiro: Contribution to critical revision, adding intellectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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Article

Scenario-modelling for the sustainable management of non-timber forest products in tropical ecosystems

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Abstract: Ecosystems degradation, and consequently biodiversity loss, has severe impacts on people around the world. The Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) is one of the international initiatives that have emerged to inform policy makers and aid decisions to prevent further global biodiversity loss, focusing on the interdependence between natural systems and human culture. IPBES promotes the use of scenarios and modelling approaches as a fundamental tool to advance the understanding of the relationships between drivers of change, Nature's Contributions to People (NCP), and social systems. Local-scale case studies with a system approach demonstrating how current knowledge can be used to inform decision-making are still scarce. Here, we present a comprehensive conceptual model and a series of four scenarios under different policies for shea tree species management, as a case-study of applying systems thinking and the NCP concept to a local-scale socio-ecological system. We first characterized the central processes, NCP, drivers and pressures affecting the shea tree system, to investigate the impacts of the multiple uses of the shea tree species on the system as a whole. We then described potential policy options, developed four scenarios, and evaluated them by a Bayesian Belief Network (BBN). We predicted qualitative outcomes of the proposed scenarios: Business-as-usual (BAU), "Conservation and fair trade", "Agroforestry and fair trade" and "Industrial development". We found that the scenarios focussing on conservation, fair trade and agroforestry, can improve the conservation status of shea trees, and enhance wellbeing in the local communities. In this case study, we demonstrate that the development of a comprehensive conceptual model at a local scale can be a useful exercise to identify opportunities for effective policy strategies and social innovation. The shea tree case study can provide an example for modelling non-timber forest products in other regions around the world that face similar drivers and pressures. Species for which this model could be adapted include Central and South American species such as the Brazilian nut (*Bertholletia excelsa*), cocoa (*Theobroma cacao*), andiroba (*Carapa guianensis*), *açai* (*Euterpe oleracea*) and the wax palm (*Ceroxylon quindiuense*). The model and workflow applied here may thus be used to understand similar socio-ecological systems with local and international economic value across the Neotropical region.

Keywords: *Biodiversity and Ecosystem Services; Conceptual model; Drivers of change; Shea tree; Tropical tree species.*

Modelagem de cenários para o manejo sustentável de produtos florestais não-madeireiros em ecossistemas tropicais

Resumo: A degradação dos ecossistemas e sua consequente perda de biodiversidade apresentam graves impactos sobre as pessoas em todo o mundo. A Plataforma Intergovernamental de Biodiversidade e Serviços Ecossistêmicos (IPBES) é uma das iniciativas internacionais que surgiram para informar tomadores de decisão e o desenvolvimento de políticas para evitar mais perdas globais de biodiversidade, com foco na interdependência entre sistemas naturais e a cultura humana. O IPBES promove o uso de cenários futuros e abordagens de modelagem como uma ferramenta fundamental para avançar no entendimento das relações entre fatores motivadores de mudança (vetores), as Contribuições da Natureza para as Pessoas (NCP) e sistemas sociais. Estudos de caso em escala local com uma abordagem de sistemas mostrando como o conhecimento atual pode ser usado para informar a tomada de decisão ainda são poucos. Neste trabalho, apresentamos um modelo conceitual abrangente e um conjunto de quatro cenários sob diferentes políticas para o manejo da árvore de karité, como estudo de caso para a aplicação de uma abordagem de sistemas e do conceito de NCP em um sistema socioecológico em escala local. Primeiro nós caracterizamos os processos centrais, os NCP, e os vetores e pressões que afetam o sistema da árvore de karité, para então, investigar os impactos dos múltiplos usos da espécie no sistema como um todo. Em seguida, descrevemos opções de políticas possíveis, a partir das quais desenvolvemos quatro cenários e os avaliamos por Redes Bayesianas baseadas em Crenças (BBN). Nós avaliamos os resultados qualitativos dos quatro cenários de manejo propostos: "*business-as-usual*" (BAU), "*Conservação e Fair Trade*", "*Agrofloresta e Fair Trade*", e "*Desenvolvimento Agroindustrial*". Verificamos que os cenários que incluíam medidas de conservação e comércio justo, assim como o que previa práticas agroflorestais indicaram potenciais melhorias no status de conservação das árvores de karité e aprimoramento do bem-estar das comunidades locais. Neste estudo de caso, demonstramos que o desenvolvimento de um modelo conceitual mais completo na escala local pode ser útil na identificação de oportunidades para a proposição de estratégias políticas efetivas e inovação social. O estudo de caso da árvore de karité pode fornecer um exemplo de modelagem de produtos florestais não-madeireiros para outras regiões do mundo que enfrentam vetores de mudança e pressões semelhantes. As espécies para as quais esse modelo pode ser adaptado incluem espécies da América Central e do Sul, como a castanha-do-brasil (*Bertholletia excelsa*), cacau (*Theobroma cacao*), andiroba (*Carapa guianensis*), açaí (*Euterpe oleracea*) e a palma da cera (*Ceroxylon quindiuense*). O modelo e a proposta de trabalho aplicados aqui podem, portanto, ser usados para entender sistemas socio-ecológicos semelhantes com espécies de valor econômico local e internacional em toda a região neotropical.

Palavras-chave: *Biodiversidade e Serviços Ecossistêmicos; Modelo conceitual; Vetores de mudança; Karité; Espécies de árvores tropicais.*

Introduction

Increasing human activities are responsible for ecosystem degradation, overexploitation of natural resources, climate change and introductions of invasive species (Brook et al. 2008, Morris 2010), which are considered the main drivers of biodiversity and ecosystem change. The impacts of these changes also directly affect the provision of services and benefits that people obtain from ecosystems (Díaz et al. 2015). The alteration of ecosystems and the resulting reduction of biodiversity are still accelerating in many places, with severe impacts on people around the world (Ceballos et al. 2015). Savannahs and tropical rainforests are among the world's major terrestrial ecosystems, and consequently experience marked impacts from human activities (Shackleton & Scholes 2011). Indeed, savannahs and tropical rainforest are subject to swift land-use changes due to rapid human population growth and the resulting growing interest in cash-crop production, infrastructure, grazing areas, and forest product harvesting (Wittig et al. 2007, Ouédraogo et al. 2010). The combined effects of these human pressures and climate change contribute to savannah degradation leading to biodiversity loss. Nonetheless, savannahs play enormous ecological, economic, and social roles throughout their distributional range. For instance, they are one of the most important ecosystems providing timber and non-timber forest products (NTFPs) in the West African Sudanian region (Nacoulma et al. 2011), where local people depend on these resources for meeting daily food, energy, medicinal, and cultural needs, as well as for deriving income. Among savannah species, those of higher socio-economic importance have been found to be declining faster as a result of overexploitation and unsustainable harvesting (Wezel & Lykke 2006).

The shea tree (*Vitellaria paradoxa* C. F. Gaertn.) is a tropical savannah species catalogued as threatened with extinction since 1998 (IUCN 1998). It is one of the most socio-economically and ecologically valuable species within its distribution area, providing numerous ecosystem services promoting human well-being and biodiversity conservation within the region. The shea tree is endemic to semi-arid sub-Saharan Africa and grows in 21 countries with the total number of trees estimated at 1.8 billion (Naughton et al. 2015). Growing naturally (neither planted nor cultivated), the shea tree is a "semi-domesticated" species growing in a wide variety of environments (Seghieri 2019). Farmers select and protect certain trees within their fields to benefit from the ecological and socio-economic value of the species (Elias 2012).

Within agroecological communities, shea trees improve soil fertility of croplands and make significant contributions to climate change mitigation through their potential for carbon sequestration and water regulation (Bayala et al. 2006, Sanogo et al. 2016, Dimobe et al. 2019, Seghieri 2019). Shea tree nectar, pollen, fruit pulp and seeds are important sources of nutrition for many faunal species, including pollinator insects, birds, and mammals (Stout et al. 2018). Shea trees therefore contribute greatly to biodiversity maintenance within their distribution area. The exploitation of shea products (both for local use and industrial processing) supplements the livelihoods of more than 80 million people across the sub-Saharan Africa region (Boffa 2015, Naughton et al. 2015). For instance, in Burkina Faso the market of shea kernels and butter contributes to 12% of the total income of the poorest households (Pouliot 2012). Because shea butter is frequently used in the food and cosmetic industries, the export of shea tree products also supports the national economies of shea-producing countries with annual contributions estimated at 49 and 30 million USD in 2011 in Burkina Faso and Ghana, respectively (APFNL 2012, Hatskevich et al. 2011, Bup et al. 2014).

Despite their ecological and socio-economic importance, shea tree populations are increasingly degraded, expressed through declining tree density, low regeneration, rates and ageing of existing shea tree populations (Okullo et al. 2003, Teklehaimanot 2004, Raebild et al. 2012). The Sudanian savannah zone, for instance, reached its largest shea tree density in the 1940s, with a population of 230 trees per ha (Chevalier 1946), but this has been reduced to 11 trees per ha on average in more recent years (Nikiema et al. 2003). This decline is mainly ascribed to (1) climate change; (2) habitat degradation due to land use change, mostly cropland expansion; (3) overexploitation of shea trees timber for firewood and charcoal production; (4) increasing international demand for shea butter, leading to high harvesting pressure on the species; (5) lack of clear policies for shea tree management; and (6) underestimation of the potential production of the species at local, national, and regional levels, as well as the associated economic opportunities (Teklehaimanot 2004, Raebild et al. 2012, Boffa 2015, Gaisberger et al. 2017, Bondé et al. 2019a). Two main sets of recommendations, based on scientific studies, have been formulated to develop sustainable strategies for the species' management. The first suggests changes in land-use and forest policies by developing local and national markets that break the long chain of middlemen to improve farmers' income, standardizing product quality at the national level, and legalizing farmers' access to market information (Teklehaimanot 2004). The second recommends the involvement of local people in shea tree management programs to ensure the inclusion of indigenous knowledge, such as gender-specific considerations on the species' management and its particular challenges (Boffa 2015, Diarassouba et al. 2008, Elias 2015). The implementation of the above recommendations should allow shea tree restoration and population recovery, but unfortunately, recent studies based on field data and expert knowledge have shown that the species is subjected to "severe threat levels" which led it to be among the most vulnerable food species in the region (Gaisberger et al. 2017).

These findings suggest the persistence of the drivers of change in the shea tree system and potentially signals the lack of implementation of effective policies for shea tree management. Indeed, the shea sector involves many actors affecting the species (Table 1). The weakness of the system lies in the low levels of connection between actors and decision-makers, which is one of the main constraints for the sustainable use of shea tree resources. Domestic use of shea trees as timber (for charcoal production and manufacturing of artisanal tools) is mainly connected to farmers, who are also responsible for most land use conversion from forest to croplands (Wittig et al. 2007). For the most part, men are in charge of the management of shea trees and the land, while women sell and locally process shea products. Neither of them, however, participate in decision-making processes such as fixing prices or developing management policies. These decisions are made at the industry-level, where exporters fix prices and ensure the quality of shea products. Lack of transparency hampers the ability of other actors and stakeholders to influence the shea market. Export data, including prices and potential of products exported by shea companies, are generally not accessible to other actors in the shea tree sector, as highlighted by Rousseau et al. (2015). Those authors indicated that many companies do not publish information on their export volumes and purchasing prices for economic reasons such as competition at the national level. This suggests that the shea sector is comparatively less well-organized than annual crop sectors such as cotton, for which purchasing prices are commonly known to producers.

Table 1. Key stakeholders in the shea sector.

Activities	Actors controlling decision making	Reference
Land and shea tree tenure, tree management, timber harvesting	Farmers	Boffa 2015; Seghieri 2019
Fruit and nut harvesting	Women and children	Elias et al. 2006; Boffa 2015; Seghieri 2019
Selling and local processing of shea products	Women at both individual and association level	Elias et al. 2006; Boffa 2015; Seghieri 2019
Trade system including price fixing and quality of products	Industries and exporters	Elias et al. 2006; Boffa 2015; Seghieri 2019
Knowledge generating	Scientists	Boffa 2015; Seghieri 2019
Species protection	Landowners (farmers) and Government (Ministry of Environment, Green Economic and Climate Change)	Boffa 2015; Seghieri 2019

Stronger connections between the various stakeholders and actors in the shea product sector are thus crucial for ensuring long-term species protection. Most studies and development activities involving the species have focused on specific aspects of the shea tree sector and have not employed a systems approach to address the sector as a whole. The development of an integrative model, linking all aspects of the shea tree social-ecological system has the potential to help understanding the system dynamics and could, therefore, be greatly beneficial in securing the sustainable use of shea tree resources as well as the ecosystems services and biodiversity values associated with the species.

The Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) promotes the use of scenarios and modelling approaches as a fundamental tool to advance the understanding of the relationships between drivers of change and social systems to inform decisions (Díaz et al. 2015, IPBES 2016). However, case studies showing how these approaches can be operationalized at the local level to identify opportunities for policy development or social innovation at the local level (Vohland et al. 2011, Liu et al. 2015, Kok et al. 2017) are still scarce. The IPBES highlighted the importance of integrating scientific disciplines (natural sciences, social sciences, engineering), diverse stakeholders (scientific community, governments, international organizations, and civil society at different levels), and different knowledge systems (science and indigenous knowledge, local and practitioners' knowledge) on conceptual models and scenario building (Díaz et al. 2015). Even though a systemic and participatory bio-economic modelling approach was already proposed to stimulate shea parklands' production (Seghieri 2019), the relationship between drivers of change and shea tree abundance was not clearly included in the model. Here, we detail a more comprehensive, integrative, modelling approach, including both social and ecological drivers of change in shea tree abundance to investigate how social-ecological modelling can contribute to improving the management of the shea tree system.

The objectives of this paper were to: (1) develop and model scenarios based on policy development for the sustainable management of the shea tree system using a conceptual model exploring the relationships of the different social-ecological elements affecting shea tree abundance; and (2) assess the qualitative potential future outcomes of these scenarios to inform policy decisions regarding the shea tree sector.

Material and Methods

The study presented here is the result of a workshop from the *São Paulo School of Advanced Science on Scenarios and Modelling on Biodiversity and Ecosystem Services to Support Human Well-Being*, a course organized by the Brazilian Platform on Biodiversity and Ecosystem Services (BPBES) and funded by the São Paulo Research Foundation (FAPESP) in July 2019. We developed a conceptual model for the use of non-timber forest products under the IPBES framework (Díaz et al. 2018), using the shea tree as case study. The conceptual model was based on existing literature and discussions during the workshop. First, we described the study system, framed its products and processes as Nature's Contributions to People (NCP), and derived a conceptual model. NCP are defined as all the contributions, both positive and negative, of living nature (diversity of organisms, ecosystems, and their associated ecological and evolutionary processes) to people's quality of life (Díaz et al. 2018). Subsequently, we proposed four scenarios for the system based on selected potential management options. Finally, we used a Bayesian Belief Network (BBN) to predict qualitative outcomes of the proposed scenarios to inform policies for the sustainable use of the shea tree.

1. Identifying pressures and drivers and building the conceptual model

As a first step in evaluating the shea tree socio-ecological system, we derived a conceptual model that included a focal component and the NCP it provides, four direct drivers or pressures, and three indirect drivers that modulate the intensity of those pressures (Figure 1). We selected shea tree abundance as the focal component in the system. We considered that shea abundance is a useful indicator because, (a) it has a direct relationship with shea productivity and shea use by local people, which makes it relevant to evaluate the contributions of the shea tree system to human well-being at the local level (Cissé et al. 2018), (b) it is easier to measure than alternative indicators such as tree age or fruit production. For instance, fruit production is highly variable and more difficult to estimate using the branch method (Bondé et al. 2019a). Based on literature review and discussions, we identified shea tree NCP that influence the state of the focal component of the system, and classified these into three categories: regulating, material, and non-material (Díaz et al. 2018). We also identified four different direct pressures that affect shea tree abundance. In addition to these, we recognized three main indirect drivers modulating the impact of direct pressures on shea abundance. Lastly, shea abundance, shea NCP, direct pressures and indirect drivers were integrated into a conceptual model, where elements were linked to represent how they influence each other.

2. From conceptual model to scenario modelling

2.1. Scenario development

We discussed policy options that countries within the shea tree distribution could implement and that have potential to influence shea abundance. These policies were later implemented as a set of scenarios based on alternative policy options with the potential to influence the state of shea tree abundance throughout the species distribution range (Figure 2). These scenarios were designed to present a broad overview of alternative outcome states of the system, and to investigate the likely outcomes for NCP, and human wellbeing. Scenarios illustrate how pressures and drivers can be modulated through a combination of selected policies and are useful to record the downstream effect on the system. These scenarios represent only a subset of the pool of possible scenarios and were selected for their potential contribution to illustrate the role of different policy management options over the shea tree system.

2.2. Scenario implementation

Modelling of outcomes of various scenarios was implemented as a Bayesian Belief Network (BBN) using the Netica software (version 3.07). BBNs are a stochastic modelling technique that uses probabilistic dependencies between components of a model as a common metric, allowing the integration of qualitative information. Netica uses the Lauritzen and Spiegelhalter algorithm (Lauritzen and Spiegelhalter 1988) to calculate binary pair-wise correlations of all possible combinations of linked variables.

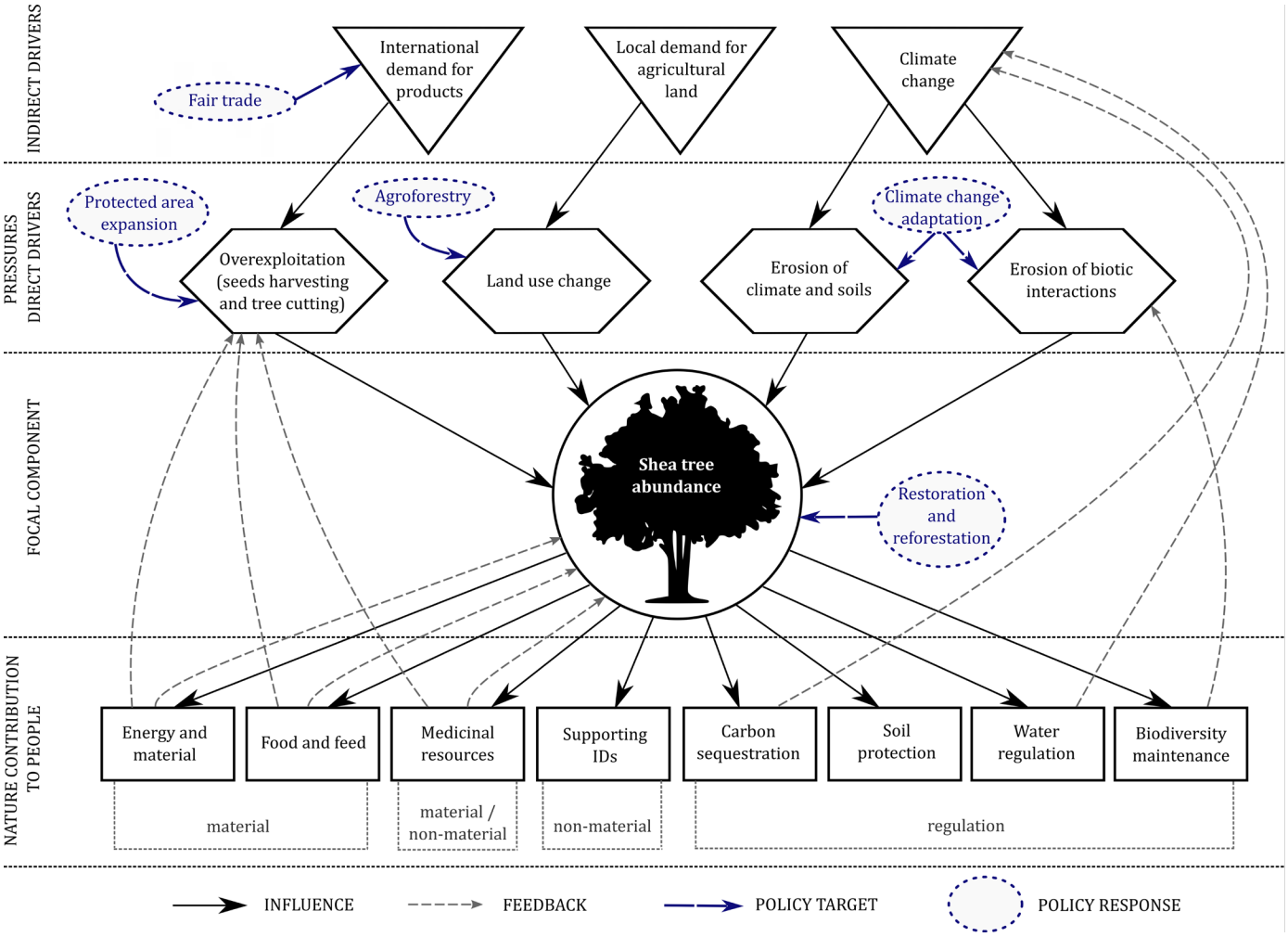


Figure 1. Conceptual model of the shea tree socio-ecological system including the focal component, drivers and Nature's Contributions to People. The relationships between system components are represented by arrows; a simple arrow implies an impact into the connected element, while a gray dashed arrow denotes a feedback relationship between the interconnected elements. Blue dashed circles illustrate the potential policies and are connected to their targets by blue dashed arrows.

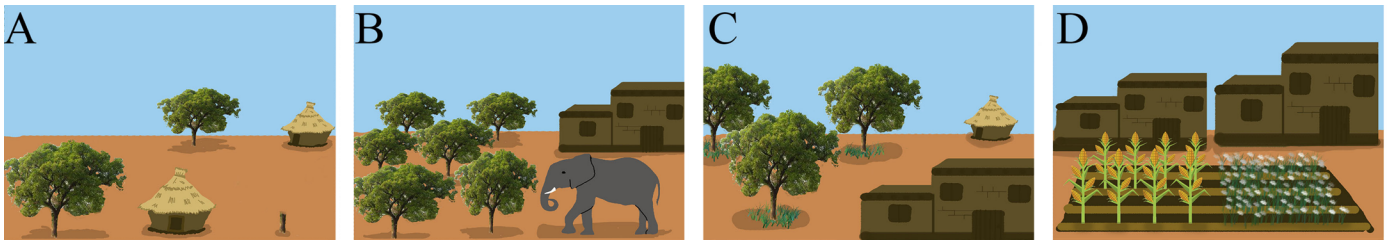


Figure 2. Visions of the four policy scenarios implemented in this paper. A) Business-as-usual, B) Conservation and fair-trade, C) Agroforestry, D) Industrial agriculture.

We used a BBN as a method of stochastic modelling to: (1) quantify the relationships between variables affecting the shea tree abundance and productivity and the potential scenario policies; (2) operationalise the model; and (3) assess the effects of alternative development pathways.

The BBN was based on the conceptual model. Each element in the conceptual model is included in the BBN as a node, and the relationships between elements were considered causal relationships represented as arcs between nodes. To reduce the complexity of the model, we did not include separate shea NCP in this exercise. Belief about variables are expressed as probability distributions that define the strength of the causal relationships. These probabilities were defined after group discussions, and are therefore qualitative estimations based on expert criteria and existing literature (Jensen 2001).

We first defined two discrete states for each variable (i.e. "low, high"). Secondly, for each node that is affected by one or more upstream nodes, we defined a conditional probability table to express the probability for the states of the child node given the states of its parent nodes (see Tables S1-S5). To decide these probabilities, the discussion group first ordered parent nodes from lower to greater impact on the child node, and classified them as small, medium or high (section 1, Tables S1-S5).

These impacts were identified either as positive or negative on the state of the child node. Impact order and relative magnitudes were set based on group discussions and the literature. Then, those qualitative impacts were translated into probabilities (section 2, Tables S1-S5), and these were finally used to build conditional probability tables for the node (section 3, Tables S1-S5). For instance, when a policy option is thought to have a relatively small downstream impact, the probability distribution for its two states was set to be relatively balanced (e.g. P(high) = 0.65 and P(low) = 0.35), while for policy options with a greater potential for downstream impact, the probabilities for its two states was set to be more diverging (e.g. P(high) = 0.80 and P(low) = 0.20).

Because policies are additive, we allowed for their impact to sum up to a P(high) ≤ 0.95 (in the example before, if both policies were applied simultaneously the resulting probabilities would be P(high) = 0.95 and P(low) = 0.05). Lastly, we defined the current initial status of the policy elements following a similar procedure: we first classified the level at which the policy is present across countries with shea as small, small-medium, medium, medium-large, large; and then translated these categories into unconditional probabilities (Table S6). After the BBN was characterised, we simulated the effect of the four scenarios by manipulating the marginal probability distributions of the policy elements.

Results

1. Conceptual model

1.1. Shea abundance and NCP

We compiled a comprehensive list of NCP provided by shea tree that are affected by its abundance (Table 2 and Figure 1). These contributions range from cultural uses in rituals or religion, to the consumption of fruits and nuts as food and feed, the use of the timber for energy, and as raw material for artisanal tools and construction.

Table 2. Principal nature's contributions to people (NCP) provided by shea tree.

NCP category	Specific NCP	Description
Regulating NCP		
Regulation of climate	Carbon sequestration	Parklands with high densities of shea tree can stock carbon comparable to native vegetation (Dayamba et al. 2016). Shea trees in the wild have high carbon storage (3.01 Mg ha^{-1}) (Dimobe et al. 2019).
Regulation of freshwater quantity, location and timing	Water regulation	Shea tree cover density influences groundwater recharge and superficial runoff improving water availability for people inhabiting seasonally dry tropics (Ilstedt et al. 2016).
Formation, protection, and decontamination of soils and sediments	Soil formation & protection	Shea trees improve deep soils by increasing macroporosity due to litter inputs and the combination of root, faunal activity, and microclimate. Soil fertility is enhanced by shea trees due to deposition of organic matter, i.e. the husk of the seeds improves soil fertility by forming mulch and fertilizer (Bayala et al. 2006, Bargués-Tobella et al. 2019).
Material NCP		
Energy	Fuel	Shea tree timber is used to produce coal and fuelwood. The wood has high burning capacity and efficiency, producing less smoke and ashes and a good amount of charcoal (Abdulrahaman et al. 2006).
Food and feed	Food	Fruit pulp constitutes an important source of nutrition for people living in the shea tree distribution area. It has high contents of energy, micronutrients and vitamins (Hall et al. 1996, Maanikuu & Peker 2017). Oil is used for cooking in the majority of households (Gwali et al. 2012).
	Feed	Shea trees provide fodder (Poudyal 2011, Noma et al. 2019).
Materials, companionship and labor	Construction	Timber is used as building material (Poudyal 2011). Butter is used as a fixative and waterproofing material in artisanal construction (Booth & Wickens 1988).
	Cosmetic	Butter is highly valued as an ingredient in luxury cosmetic (moisturizing creams, sun lotions, and soaps) (Boffa 2015).
Medicinal, biochemical and genetic resources	Medicinal resources	Several parts of the plant alone or in mixtures with other plants are used as a remedy for a range of diseases. Leaves are used for the treatment of stomach-ache, fevers and headache, and eye problems. The roots in combination with the bark are employed to treat jaundice, diarrhoea, and stomach pains. Bark infusion beverage are used to treat diabetes, leprosy, and as a child labour inductor (Maanikuu & Peker 2017). Derivatives of shea such as oil are used for facilitating childbirth (Gwali et al. 2012).
Non-material NCP		
Supporting identities	Cultural Heritage and Identity	Shea tree is considered sacred in numerous rural communities, is used in several cultural rituals and traditions, including enthronement, marriages and wedding ceremonies, funerals, and war rituals (Hall et al. 1996, Gwali et al. 2012, Ouédraogo et al. 2010). For example, Dagaaba people from West Africa countries celebrate the Bagre ancestral ceremony in which shea trees play an important role (Kuwabong 2004). Shea trees are also an important element in the cultural heritage of Sudano-Sahelian women. Knowledge about shea butter preparation is passed down from mothers to daughters (Elias & Carney 2007). Gwali et al. (2012) provides extensive information on additional traditional uses of the shea tree.

1.2. Drivers of change and pressures

We identified three indirect drivers (Figure 1) that influence the pressures that affect shea tree abundance, its survival and the type of NCP it provides to the local community. The first driver is climate change, which impacts biodiversity directly through effects of shifts in temperature and precipitation that affect the phenology of the tree, and its ability to grow and survive. In addition to the erosion of climate, climate change also has the potential to erode other abiotic properties of the environment of shea trees, including a role in the degradation of soils (Evans 1996). Climate change also affects the biotic interactions of the shea tree. These biotic interactions include pollinators and dispersers, which are needed to maintain shea tree production (seed production for regeneration) through effective pollination and increase the shea distribution area by seed dispersion in different habitats. They also encompass parasites and predators, which negatively affect shea tree abundance by reducing physiological and phenological events of the species, compromising seed production and their quality (especially their germinative ability). The second driver is the international demand for shea products, which influences shea tree abundance indirectly via the overexploitation of the tree and its products with economic value. This occurs through modulating local community decisions related to shea tree exploitation and land management. The third identified indirect driver of the shea tree abundance is the increasing demand for agricultural land by local communities. This driver promotes land conversion in areas previously covered by shea habitat into alternative land uses such as agriculture and urban areas. A list with indicators that can be used in the assessment of the elements of the conceptual model can be consulted in Table S7 in the Supplementary Material.

2. Scenarios

2.1. Policies and scenarios

We identified six policies with the potential to influence the drivers that have caused the current low abundance of shea tree: (1) climate change adaptation, (2) promotion of fair trade, including the development of more favourable commercialization options, (3) increasing efforts to restore and reforest shea habitat, (4) expansion of protected area networks, (5) promotion of agroforestry practices, and (6) policies towards a transition to more agro-industrial schemes. Climate change adaptation policies are those that seek to reduce the local effects of climate change on habitats and soils. Some examples of these policies include the use of nature-based solutions (NBS; Cohen-Shacham et al. 2016) to increase carbon sequestration and reduce soil degradation. Fair trade involves the arrangement of commercial practices to help producers in developing countries reach sustainable and equitable trade relationships. Despite its potential to enhance the sustainable use and trade of shea tree products by local communities, fair trade plays a small role on the trade of shea products. Restoration policies could also increase shea abundance through the direct plantation of trees and, indirectly, through the restoration of shea habitats. A similar impact could be achieved through the expansion of the protected area network, which could stop land transformation and overexploitation of shea within reserve borders. Moreover, an adequate management of protected areas could protect shea trees while permitting the sustainable use of its products by local communities. Finally, we included two policies linked to agricultural practices that have potential to influence shea abundance. The first of them is the promotion of agroforestry practices, where cultivated shea trees are combined with shade-tolerant crops. Lastly, agriculture practices could promote industrial agricultural development based on crops such as cotton, maize, and sorghum. These practices would displace shea and cause a decline of shea habitat if they become extensive.

We grouped the above policies into four scenarios (Figure 2). The first scenario is a "business-as-usual" (BAU) scenario, depicting developments that result from the projection of the current state of the system to the future. BAU is characterized by the unsustainable use of shea tree products at the local scale. The second is the "conservation and fair-trade scenario", where policy reinforces shea tree protection via enhanced area-based conservation of the species and its assisted regeneration and reforestation, which would provide means for climate change adaptation. The previous policies are combined in this scenario with the promotion of fair-trade certification of shea products. Third, in the "agroforestry and fair-trade scenario", policy focuses on promoting local-scale agriculture through agroforestry. We included climate change adaptation in this scenario because agroforestry is often recognized as a nature-based solution to combine food production and local adaptation to changing climate. This scenario is also associated with fair trade policies, because these trades are often associated to production approaches that can be coupled with sustainable practices, such as agroforestry. Fourth, the "industrial development scenario" prioritizes the expansion of industrial agriculture in spite of seeking the maintenance of the shea tree cover.

2.2. Scenario outcomes

In the "BAU scenario", the BBN model shows that the unsustainable use of shea leads to a general decrease of tree abundance and tree products ($P_{abundance}$ (high) = 0.282; Figure 3). Climate change is expected to continue the erosion of the climatic and soil requirements of the shea tree ($P_{erosion\ of\ climate\ and\ soil}$(low) = 0.77) and of its biotic interactions ($P_{biotic\ interactions}$(low) = 0.68). This negative impact will be reinforced by the continued reduction of shea cover as a result of agricultural expansion (P_{LUC}(high) = 0.597) and, most importantly, the unsustainable exploitation of the tree and its products ($P_{overexploitation}$(high) = 0.875), which would lead to further deterioration of the provision of traditional livelihoods. For the BAU scenario, we set the state of each scenario to the current state as estimated in the discussions. For the following scenarios we increased the level of all involved upstream policies to "high".

The "conservation and fair trade scenario" depicts a future where the combination of activated policies leads to an improvement of the shea tree abundance and the NCP it provides. Specifically, the BBN projects a doubling of the probability of reaching a high shea tree abundance ($P_{abundance}$(high) = 0.729; Figure S1), when compared to BAU. The promotion of fair trade shea products would lead to a more sustainable harvest of shea nuts ($P_{overexploitation}$(low) = 0.95), and the subsequent development of local communities that harvest them. This, combined with better conservation policies, would lead to a recovery of natural shea tree cover (P_{LUC}(high) = 0.485). In this scenario, there would be an enhancement of the NCP that the shea tree provides for local communities (Table 2).

For the "agroforestry and fair trade" scenario, the BBN indicates only a slight increase in the shea abundance ($P_{abundance}$(high) = 0.633; Figure S2). In this scenario, local communities' economies might benefit from the slightly increased shea abundance, products obtained from planted and managed shea trees, and also from alternative shade-tolerant crops cultivated alongside shea trees. The condition of the natural landscapes dominated by the shea tree would have the opportunity to partially recover as a result of reduced land use change (P_{LUC}(high) = 0.313). Changes in the use of shea products could lead to changes or losses in non-material NCP (e.g., cultural heritage and identity). However, policies only based on the promotion of agroforestry do not achieve an increasing in shea tree abundance comparable to the previous scenario, according to the BBN.

The "industrial development scenario" points to an impoverishment of shea tree ecosystems (Figure S3). These policies lead to a marked expansion of the land conversion, causing the loss of shea trees and reducing the accessibility of shea products for locals. It depicts the largest increase of land transformation (P_{LUC}(high) = 0.448) and decrease of shea abundance ($P_{abundance}$(high) = 0.322) of all analysed scenarios. As a result, most NCP provided by the shea tree would be reduced, including those related to cultural values of local communities (Table 2). Outcomes for all four scenarios are summarised in Table 3 and Figure 4.

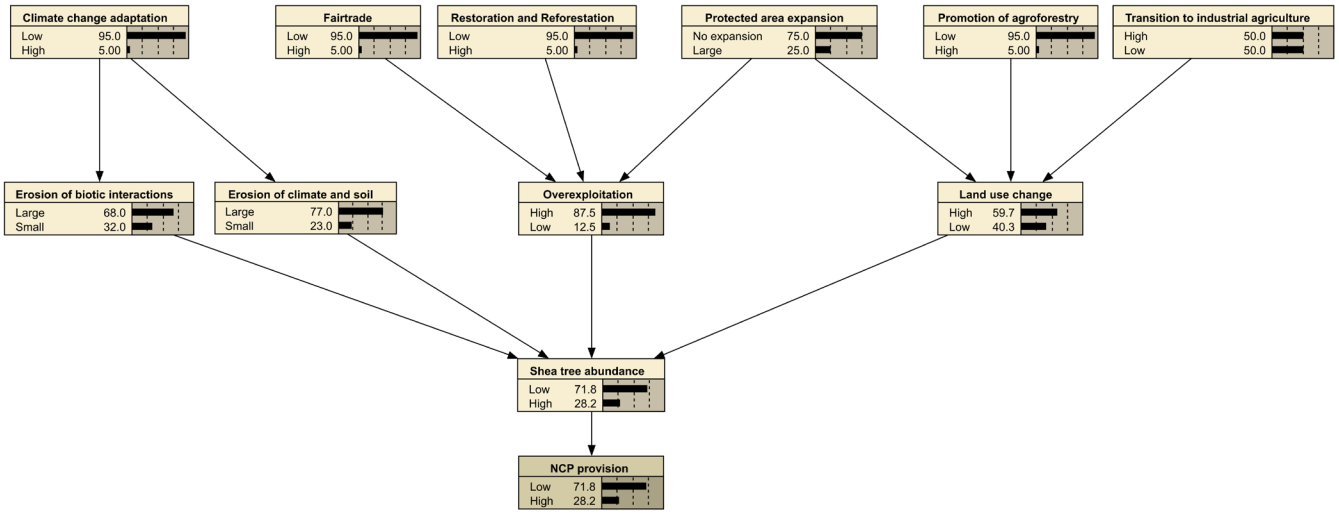


Figure 3. Bayesian Belief Network model structure of the BAU scenario. Nodes in the upper row represent policies, whereas nodes in the second row represent pressures. The probability distributions of policy nodes reflect the estimated current implementation of each policy.

Table 3. Summary of outcomes of four management scenarios for the shea tree system. Checkmarks represent the considerate policies for each scenario. The arrows are horizontal when the probabilities are distributed equally between "high" and "low" states (P = 0.50 ± 10). Arrows that point up have a distribution of probabilities biased towards "high" states, whereas arrows that point down have a distribution biased towards "low" states. Arrow colour indicates whether expected changes in pressures and states in each of the four scenarios can be considered positive or negative for the shea system: dark blue – strong increase; green – improvement; red – worsening. CC adaptation: Climate change adaptation.

	Scenarios			
	BAU	Conservation and fair trade	Agroforestry and fair trade	Industrialization
Policies				
Fair trade	–	✓	✓	–
Conservation	–	✓	✓	–
Reforestation	–	✓	–	–
CC adaptation	–	✓	–	–
Agroforestry	–	–	✓	–
Industrialization	–	–	–	✓
Pressures				
Overexploitation	↗	↘	→	↗
Land use change	→	→	↘	↗
Erosion of climate and soil	↗	↘	↘	↗
Erosion of biotic interactions	↗	↘	↘	↗
Abundance of shea tree	↘	↗	↗	↘

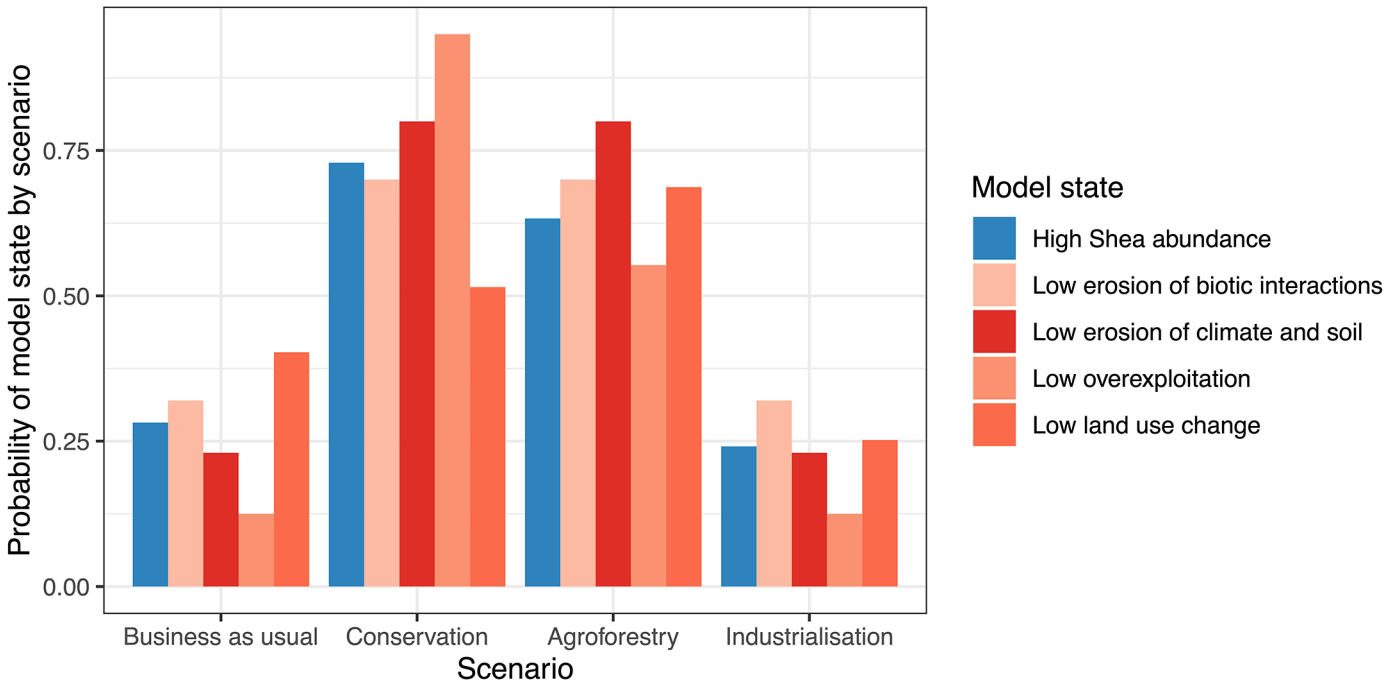


Figure 4. Summary of outcomes of four management scenarios for the shea tree system. Showing the probability that shea abundance will be high and pressures will be low in each of the four tested scenario. Note: showing $P_{abundance}$(high); $P_{erosion\ of\ climate\ and\ soil}$(low); $_{Pbiotic\ interactions}$(low); $P_{overexploitation}$(low); and P_{LUC}(low).

Discussion

The shea tree provides many NCP to the local community, being a fundamental resource to their cultural, economic and social development. However, only material NCP were connected with shea tree abundance through a mutual feedback relationship. This is because the supply of these NCP is linked with extractive processes that can diminish shea tree populations. For example, the nuts are used to obtain butter to produce cosmetics and personal care products, which are traded for high profits in the international cosmetic industry. Although some material parts of the shea tree are important for the supply of non-material NCPs, cultural uses of shea trees mainly exist at the local scale and are commonly associated with the implementation of traditional conservation practices (Gwali et al. 2012). Abiotic factors (such as climate variables, topography, and soil type) are other components influencing shea tree abundance, tree morphological traits and fruit yield (Lamien et al. 2008, Glèlè et al. 2011, Aleza et al. 2018, Bondé et al. 2019b). Shea tree requires specific environment characteristics such as warm temperatures (24-32 °C average), seasonal rainfall (600-1500 mm per year with a dry season period of 4 to 8 months), and elevations up to 1500 m (Godin & Spensley 1971). Additionally, shea tree is not compatible with some soil types, such as highly sandy and clayish soils, areas temporarily flooded, and alluvial hollows (Boffa 2015). Abiotic factors have been used to model the potential distribution of this species under climate change scenarios (Platts et al. 2010, Naughton et al. 2015), suggesting that the species could expand its distribution range northward and southward in response to predicted climate-change-induced increases in precipitation and temperature (Boffa 2015).

The growing demand for non-timber shea products on international markets offers an increasing source of foreign earnings to producer countries as well as an opportunity for agricultural development and the empowerment of their rural societies, especially women (Ingram et al. 2015). Therefore, international trade is an important socio-economic driver in the shea tree system, which not only relates to fluctuating international demand and prices for shea butter (and the possible resulting overexploitation), but also to speculation on the production of mixed crops (cotton, maize, sorghum, yam, cassava) in shea tree agroforestry parks (Noma et al. 2019). This speculation can lead to agricultural intensification that requires large-scale forest-clearings to create production areas, causing land-use to change and consequently affecting shea tree abundance. As described in this study, links between local actors in the shea tree system are weak, making effective conservation of the species difficult. In addition, there are gender and cultural issues that play a role at the local scale. Decisions to conserve and manage the shea tree are strongly gender dependent. Harvesting, processing and local selling of shea are locally considered as activities for women (Elias & Carney 2007), while men are a key component in the local-scale decision-making process. Men have the final decision regarding management and conservation of the shea tree due to the fact that they are considered the landowners (Poudyal 2011). Man can choose whether to plant alternative crops as a better source of income or implement management activities to enhance shea tree nut production and income for their families (Okiror et al. 2012). Opinions of women and direct management actions, such as planting trees, are considered in some places as a usurpation of male power (Okiror et al. 2012), because planting is traditionally done by men (Boffa 2015). Besides, local population growth drives urban expansion in the shea tree distribution area, causing not only land-use change and depletion of the species, but also the transformation of livelihoods in local communities (Dapilah et al. 2018). This can also entail potential reductions in the supply of NCP by the system, particularly in the non-material category.

Interaction with other species was identified as an important biotic factor affecting shea tree abundance. First, pollinators such as bees (*Hypotrigona gribodoi* (Magretti 1884) and *Apis mellifera adansonii* (Latreille 1804) (Stout et al. 2018) and dispersers such as flying foxes (Chiroptera: Pteropodidae) mammals (elephants, bats) (Djossa et al. 2008) and primates (Ontl 2017) were included in the model as a pressure with feedback to shea tree abundance due to their interdependence. Pollinators and dispersers play a crucial role in the species regeneration and distribution. Animal pollination is necessary in the life cycle of many plant species and play a crucial role in the long-term maintenance of biodiversity and natural ecosystems (Ratto et al. 2018), while seed dispersers significantly affect plant demography, dynamics and succession in tropical ecosystems (Petre et al. 2013). This emphasizes the need for the development of efficient strategies to ensure the conservation of pollinators and dispersers that support shea tree populations. Second, predators and parasites were linked as a pressure on shea trees because they gradually weaken the trees and can reduce nut yield. Caterpillars (*Cirina forda*) (Westwood 1849) and stemborers (*Neoplocaedaerus* sp) (N'Djolossè et al. 2012) primarily defoliate new leaves of shea trees, affecting all stages of the shea tree growth cycle, from seedlings to mature trees. Parasites like plants of the genus *Tapinanthus* (Boussim et al. 1993) and mistletoe (Loranthaceae) (Houehanou et al. 2011) heavily infest the trees, though at higher intensities in parklands compared to protected areas. In addition, larvae of *Mussidia nigrivenella* Ragonot 1888 and the Oriental fruit fly *Ceratitis silvestrii* Bezzi 1912 also affect mature shea trees by feeding on the pulp (Okiror et al. 2012). The biotic interactions affecting shea tree abundance are influenced by climate change. For instance, studies have suggested that climate change is one of the drivers behind the global decline of pollinators (Potts et al. 2010). However, more studies are needed to fully understand the actual impact of climate change on broader sets of species interacting on complex ecological networks. Moreover, its impact on the above described species that have a directly effect on the shea system is still largely unknown.

Our findings suggest that the integrative modelling approaches developed here can provide useful insights for non-timber forest products in other regions around the world that face similar drivers and pressures, such as low recruitment, slow growth, slow maturation, decreasing climate suitability, and high international demand. Examples of species in Central and South America that might be part of an equivalent system with similar unsustainable situation are the Brazilian nut (*Bertholletia excelsa* O. Berg), cocoa (*Theobroma cacao L.*), andiroba (*Carapa guianensis Aubl.*) açai (*Euterpe oleracea Mart.*) or the wax palm (*Ceroxylon quindiuense* (H. Karst)). The case of the wax palm is particularly similar to that of the shea tree, as this palm species is used not only as part of local economies but also for tourism, while also relevant for its cultural value. All these examples of plant species are to some extent threatened by land use change, fire rates, decrease of pollinators, international demand and fare exchange with local people (Bertwell et al. 2018, Porcher et al. 2018). As in the case of the shea tree, the sustainable use of these plant resources and their conservation should be sought through bold strategies that aim at addressing the different drivers that place pressure on them.

The four proposed scenarios are imagined to unfold over varying time horizons. The business-as-usual scenario might materialize over a shorter timeframe than the alternative scenarios. Following the nomenclature in Sardar and Sweeney (2016), this scenario is within the 'extended present' type of future. The conservation and fair-trade scenario is thought to be achievable within a 'familiar future' that is further into the future than BAU, but not by much. The transformations that substantiate this scenario are extensions of policies that exist today, but which have yet to take (large-scale) effect. The last two scenarios (agroforestry and industrial development) belong to the class of 'unthought futures', which lie in the unforeseeable future. These two scenarios require large-scale transformations that can only be achieved over a long timeframe.

Through scenario-analysis, we demonstrated how a variety of policy implementations could affect the shea tree system and highlighted a few potential management strategies that could contribute towards improving the sustainable management of shea tree habitats. First, we identified actions that the local population could implement to reduce the negative effects of land use change, and one of the main drivers of shea tree abundance declines. For instance, the plantation of shade-tolerant crops and the adoption of a culture of agroforestry could help mitigate the loss of shea tree abundance. Shea and other trees improve soil fertility and contribute to mitigate climate change effects at both, local (by regulating water flows and maintaining suitable microclimatic conditions) and global scales by increasing carbon sequestration (Van Noordwijk et al. 2014). The use of shea trees in agroforestry systems would benefit from the exploration of improved domestication practices (Seghieri 2019). The implementation of land tenure policies to ensure clarity on land (and tree) ownership could be a viable additional policy to implement to reach a sustainable planning for the local demand for agricultural land (Seghieri 2019). Second, to mitigate negative impacts of overexploitation and human population growth, policies related to assisted regeneration could be an important strategy. These include the promotion of tree-planting, and the improvement of seedling care practices. However, it is important to consider that the shea tree has a low growth rate (1-6 mm/year) (Serpantié et al. 1996), and that regeneration is a difficult long-term process that requires policy support. Finally, to adapt to growing international demand and international trade, a strategy to reinforce fair-trade certification could be implemented (Greig 2006). In order to achieve a better future for local communities and promote the sustainable use of the shea tree, pragmatic policy proposals may include not only fair-trade certification but also local legislation to regulate shea nut prices and support shea tree restoration. Indeed, in the use and management of commercial non-timber forest products, people are able to concentrate their efforts on management activities that provide the highest rewards (Belcher et al. 2005). Therefore, shea tree products need to be purchased at profitable price for local communities. Finally, the scenarios screened in this study showed that no single policy option might have the potential to restore high shea abundances on its own. Instead, multidimensional scenarios that address the different indirect drivers of the system seem to be required for a substantial recovery of shea habitats. In this regard, the "conservation and fair trade scenario", which combined addressing the problems of overexploitation (through fairer trade of shea products), accelerated land conversion (through protection and restoration of degraded lands) and decrease of environmental suitability (through climate change adaptation to restore and maintain biotic and abiotic systems supporting shea habitat), is predicted as the most likely to succeed at enhancing shea conservation and its provision of NCP to people.

The BBN developed here used a qualitative approach based on experts' criteria, since the lack of quantitative data on this system prevented the development of a more precise quantitative representation.

While the current approach can provide valuable insights and can constructively inform the discussion on alternative policy actions and their potential to influence the shea tree system, we emphasize the need to gather and systematize comprehensive, quantitative data to develop more sophisticated models to further our knowledge on this system in the future.

Conclusion

This study highlights the efficacy of a social-ecological modelling approach in shea tree management. Indeed, the conceptual model based on social-ecological drivers of change in shea tree abundance, enables deeper understanding of the relationship between these drivers and their effects on shea tree dynamics. The development of the four scenarios provided insight into the suitability of different policy options to improve shea tree management in the future. From this study, we conclude that the policy options enabled in the "conservation and fair trade scenario" might have most positive effects on shea tree abundance and local provision of NCP. Overall, we can highlight three main points from this study. First, we demonstrate that framing a case study at a local scale by identifying principal components and subsequently developing a conceptual model can be a useful exercise in identifying opportunities for effective policy strategies and social innovation. Such an approach can further guide IPBES in capturing the social-ecological dynamics of biodiversity and NCP at varying scales. Second, through the development of a conceptual model, and identifying key processes and products as NCP, we were able to generate a better understanding of potential policy options, which consequently allowed us to develop possible socio-ecological scenarios. Third, modelling scenarios can be a powerful tool to communicate with society more broadly, to raise awareness of current situations and potential futures, and to better explain the necessary interventions for a more sustainable future.

The model and workflow applied here may thus be used to understand similar socio-ecological systems with local and international economic value across the Neotropical region (Guariguata et al. 2017) in order to assess the qualitative potential future outcomes of the scenarios proposed, and could be useful to inform policy decisions for the sustainable management. We would like to stress that the presented alternative states represent broad generalisations of possible outcomes for the system. Before application of this model in practice, case-specific system states should be identified in collaboration with local stakeholders using appropriate social science techniques.

Supplementary material:

The following online material is available for this article:

Figure S1 - Bayesian Belief Network model structure of the "conservation and fair trade" scenario. Nodes in the upper row represent policies, whereas nodes in the second row represent pressures. The probability distributions of policy nodes reflect the estimated current implementation of each policy.

Figure S2 - Bayesian Belief Network model structure of the "agroforestry and fair trade" scenario. Nodes in the upper row represent policies, whereas nodes in the second row represent pressures. The probability distributions of policy nodes reflect the estimated current implementation of each policy.

Figure S3 - Bayesian Belief Network model structure of the "industrial development" scenario. Nodes in the upper row represent policies, whereas nodes in the second row represent pressures. The probability distributions of policy nodes reflect the estimated current implementation of each policy.

Table S1 - Overexploitation.

Table S2 - Erosion of climate and soil.

Table S3 - Erosion of biotic interactions.

Table S4 - Land use change (LUC).

Table S5 - Shea tree abundance.

Table S6 - Current policy.

Table S7 - Potential indicators for Nature's Contributions to People in the conceptual model of the shea tree social-ecological system.

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Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

The authors declare that the analysis detailed in this manuscript did not involve human beings and/or clinical trials.

Data availability

The authors declare that the analysis detailed in this manuscript involved conceptual models only. No data was used in the analysis.

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Article

Future scenarios of land-use-cover effects on pollination supply and demand in São Paulo State, Brazil

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Abstract: Rapid land-use/land cover changes (LULCC) have led to habitat loss and fragmentation in the natural forest areas, which are mainly due to the intense and rapid expansion of urban areas and intense agricultural management. These processes are strongly threatening biodiversity maintenance and the ecosystem services provided by them. Among the ecosystem services under threat, pollination has been widely studied since this service is essential to promote food production and, therefore, human well-being. In a scenario of increasing LULCC it is crucial to understand the interplay between these changes, pollination demand by insect-dependent crops and pollinator availability to ensure these ecosystem services meet the increased demand for food production. In this study, we developed a conceptual model to disentangle the relationships between human-nature, especially LULCC, and its consequences, to the delivery of pollination service. We also presented a case study in the Brazilian São Paulo state, where we modeled the effects of predicted LULCC associated to agriculture expansion between the years 2012 and 2030 on pollinator demand by crops and pollinator supply, for fourteen economically important crops. Additionally, we systematized an expert-based Ecosystem Service matrix to estimate the influences of LULCC on the provision of pollination. Our results showed that by 2030, the demand for pollination will increase by 40% on average, while pollinator supply, estimated using suitability values for the different land-use/cover classes, will show, on average, a 3% decrease. Our results highlight the importance of considering the dialogue among stakeholders, governments, institutions, and scientists to find alternatives and strategies to promote pollinator-friendly practices and safeguard the provision of pollination services in a future under LULCC.

Keywords: *bees; crop-dependence; Ecosystem services; human-nature interface; Tropical Forest.*

Cenários futuros de mudanças de uso e cobertura do solo e seus efeitos sobre oferta e demanda de polinização no estado de São Paulo, Brasil

Resumo: As aceleradas mudanças de uso e cobertura do solo levaram à perda e fragmentação de habitat das florestas naturais, principalmente devido a uma intensa e rápida expansão de áreas urbanas e ao intensivo manejo agrícola. Esses processos ameaçam fortemente a manutenção da biodiversidade e os serviços ecossistêmicos associados. Entre os serviços ecossistêmicos ameaçados, a polinização tem sido amplamente estudada, pois se trata de um serviço essencial para a produção de alimentos e, consequentemente, para o bem-estar humano. Em um cenário de crescentes mudanças no uso e cobertura do solo, é crucial entender a interação entre essas mudanças, a demanda de polinização por culturas dependentes de insetos e a disponibilidade de polinizadores para garantir que esse serviço ecossistêmico atenda o aumento da demanda produtiva de alimentos. Neste estudo, desenvolvemos um modelo conceitual para evidenciar as relações homem-natureza, especialmente as consequências das mudanças de uso e cobertura do solo sobre a prestação do serviço de polinização. Nós também apresentamos um estudo de caso no estado brasileiro de São Paulo, onde modelamos os efeitos de mudanças de uso e cobertura do solo associados à expansão de agricultura entre os anos de 2012 e 2030 e as demandas e oferta de polinizadores por cultura, para quatorze culturas economicamente importantes. Além disso, sistematizamos uma matriz de serviços ecossistêmicos baseada em conhecimento de especialistas para estimar as influências das mudanças de uso e cobertura do solo na provisão do serviço de polinização. Nossos resultados mostraram que até 2030, a demanda por polinização aumentará em média 40%, enquanto a oferta de polinizadores estimada, usando valores de adequação para as diferentes classes de uso e cobertura do solo, terá uma redução média de 3%. Nossos resultados destacam a importância do diálogo entre agricultores e outros importantes agentes impulsionando as mudanças de uso do solo, governos, instituições e cientistas para encontrar alternativas e estratégias para promover práticas favoráveis aos polinizadores e salvaguardar a prestação de serviços de polinização em cenários futuros de mudanças de uso e cobertura do solo.

Palavras-chave: *abelhas; dependência de culturas agrícolas; serviços ecossistêmicos; interface homem-natureza; floresta tropical.*

Introduction

Habitat loss and fragmentation are caused mainly by land-use/land cover changes (LULCC) resulting from the expansion of agricultural and urban areas demanded by human population growth and economic development (Kremen et al. 2004, Foley et al. 2005, Roberts 2011, Aizen et al. 2019). By LULCC we refer to human activities that alter land surface processes including biogeochemistry, hydrology and biodiversity and changes on the physical and biological cover over the surface of land (Mustard et al. 2004, Ellis & Pontius 2007). These changes occur at alarming rates in the Tropics which harbors the highest terrestrial biodiversity (Gaston 2000). Tropical regions are expected to face a dramatic agricultural expansion during the next decades (Laurance et al. 2014). Regarding to the negative impacts that LULCC can generate upon biodiversity (IPBES 2019), pollinator communities decline is one of the most widely studied (e.g. Klein et al. 2007, Vanbergen et al. 2013), mainly due to the importance of pollinators in maintaining biodiversity and world crop productivity (Bauer &Wing 2016).

In Brazil, pollination services mainly rely on wild pollinators since there is an incipient development of practices to increase crop production with managed bees (Imperatriz-Fonseca et al. 2006). The services of wild pollinators in natural habitats tend to decrease in scenarios of intensive LULCC resulting from increased human demands (Aizen et al. 2008, Garibaldi et al. 2014). Since wild pollinators require specific resources for nesting, feeding and reproducing as well as certain habitat conditions to ensure their survival, intensive LULCC can negatively affect the density of pollinators at different scales (Fahrig et al. 2011, Motzkea et al. 2016, Senapathi et al. 2017). For example, Ferreira (2015) found that above-ground nesting bees are more sensitive to forest loss induced by anthropogenic factors than ground-nesting bees. For social bees, the effect of changes in forest cover at local scale depends on the regional forest cover, with negative effects being detected when landscapes had at least 35% of forest (Ferreira et al. 2015). In addition, the usual agricultural practices, which still rely on the intensive use of pesticides and extensive monoculture, threaten pollination services (Park et al. 2015). These practices also affect stability and resilience of farming systems, which present lower capacity to adopt alternative strategies under stresses like climate change (Nelson et al. 2010). Therefore, to preserve the pollination services in Brazil, it is necessary to review environmental policies, socioeconomic system and crop management practices (Cunha et al. 2012).

Tropical forests, such as the Atlantic Rainforest, are examples of natural ecosystems threatened by high levels of degradation and reduction of forested areas as a result of urban development and crop expansion. This biodiversity hotspot (Tabarelli et al. 2005) originally comprised one of the largest rainforests in the Americas, covering around 150 million hectares under highly heterogeneous environmental conditions (Ribeiro et al. 2009). The agricultural and urban expansion throughout the Atlantic Rainforest over the past 500 years resulted in 80% of forest loss and a fragmented landscape composed of isolated patches of forest (Ribeiro et al. 2009, Rezende et al. 2018). Furthermore, these natural fragments are embedded into different matrices of pasture, agriculture, forestry and urban areas (Perfecto & Vandermeer 2010, Joly et al. 2014).

Studies have emphasized the importance of forest fragments in maintaining bee pollinators and consequently the pollination services provided by them (Carvalheiro et al. 2010, Saturni et al. 2016, Buchori et al. 2019). Thus, alternative conservation strategies are urgently needed in the Atlantic Rainforests, especially where insect-dependent crops are expected to increase. Such strategies should promote the reconciliation of the current restoration policies and pollinator-friendly practices (Dicks et al. 2016) leading to a socially equitable conservation scenario.

In this study, we developed a conceptual model based on the general framework elaborated by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) to assess key components and its relationships to guarantee the conservation and sustainable use of biodiversity, long-term human well-being and sustainable development (Díaz et al. 2015; IPBES 2016). Here, we described connections among drivers related to nature and social key elements supporting or constraining the provision of pollination services taking LULCC as one of the major direct drivers. We also presented a case study using the state of São Paulo as a model of large-scale landscape for which we projected a future scenario of pollination demand and supply and applied the general conceptual model. The modeling procedure included 14 economically important crops and LULCC scenarios from OTIMIZAGRO model (Soares-Filho et al. 2013, 2016). We asked the following questions: (1) Which land-use/cover classes favor the provision of pollination services? (2) How do LULCC influence the pollination demand of pollinator-dependent crops and (3) How do LULCC influence the pollination supply, considering differences in estimated availability of food and nest resources between land-use classes? By answering these questions, it is possible to understand how projected LULCC can potentially affect the flow of pollination services provided by wild pollinators.

Material and Methods

1. General conceptual model

Our conceptual model is based on the Assessment Report on Pollinators, Pollination and Food Production (IPBES 2016) in accordance with the IPBES conceptual framework (Díaz et al. 2015). This model illustrates the relationships between direct and indirect drivers influencing pollination services as well as the contributions of these services to people generating human well-being. The model also presents the role of institutions and governments in promoting conservation strategies at a national scale. Since bee pollinators are associated with more than 90% of economically important crops (Klein et al. 2007), we applied the IPBES conceptual model considering ecological requirements and conservation strategies related to this functional group of pollinators.

According to our conceptual model direct drivers, represented here by an anthropogenic factor (e.g., land-use changes), directly influence nature at local site (Arrow number 1 and Boxes A and B; Figure 1). For example, LULCC and the fragmentation process affect how landscapes support pollinator biodiversity and pollination services by constraining bee dispersal, occurrence and gene flow (Jha et al. 2015, Jaffé et al. 2019, Barbosa et al. 2019). Due to bee dispersal constraints, pollen flow should also be limited by the fragmentation process, resulting in low rates of cross pollination and endogamy (Hadley et al. 2012).

The mutual-effect relationship between nest availability, natural and semi-natural habitats, and diversity of floral resources directly affect the diversity of bees by reducing bee's ability to face diseases (Jones et al. 2018) and to persist in environments due to the lack of floral resources (Ricotta & Moretti, 2011). Therefore, the relationships with nature elements at local scale determine the habitat capacity to maintain biodiversity and deliver of pollination services (Arrow 2 leading to Box C).

Finally, the interactions and practices among farmers, land-use policies and environmental laws (Box D) can influence the maintenance of pollination services. At the same time, the pollination service can stimulate specific farming practices and guide the development of land use policies (bidirectional Arrow 3). LULCC is also influenced by the indirect drivers from Box D (Arrow 4). New market trends dictate farmers' decisions about investing in certain types of crops, especially because most of them are commodities and follow international trends. Land-use policies and environmental laws (such as the Forest Code and Atlantic Forest Pact) establish limits to deforestation and, in this way, limits to new cultivated areas.

At the end of the model, the pollination service delivers the nature's contributions to people (NCPs) (Arrow 5; Box E). The increment of crop productivity or even the assurance of crop production is resulted not only by biodiversity, but also from quantification of the relationships of stakeholders and anthropogenic assets, such as development of new agricultural systems based on local technologies.

2. Ecosystem Service matrix

In order to complement the conceptual model interpretation and evaluate pollination-related ecosystem services (ES) under different LULCC scenarios, we proposed a matrix from which the scores were determined according to expert knowledge for estimating capacity, supply, use and demand (Campagne & Roche 2018). This matrix relates ES categories to influences of promoting pollination services associated with broad land-use/cover classes (forest, urban area, pasture, crops, waterbodies, silviculture and savannah). Matrix scores indicate the supporting capacity of each land-use/cover class in the provision of ES (Campagne & Roche 2018). According to this approach, matrix scores range from 0 to 5, where "0 = no relevant capacity, 1 = low relevant capacity, 2 = relevant capacity, 3 = moderate relevant capacity, 4 = high relevant capacity, and 5 = very high relevant capacity" (Burkhard et al. 2009). To create the matrix, we searched for other studies that provide matrix scores describing the association between land-use/cover categories and ES. The studies were surveyed via the Web of Science repository (http://www.webofknowledge.com). Eleven studies developed in Tropical regions were selected. To obtain the final scores of our matrix, we calculated the mean scores considering the values representing the associations between each land-use/cover classes and ecosystems services, provided by these studies. We only considered land-use/cover classes relevant to our case study and ecosystem services related to pollination provision (habitat creation and maintenance, dispersion of pollen and other propagules, food security, medicinal and genetic resources, cultural heritage).

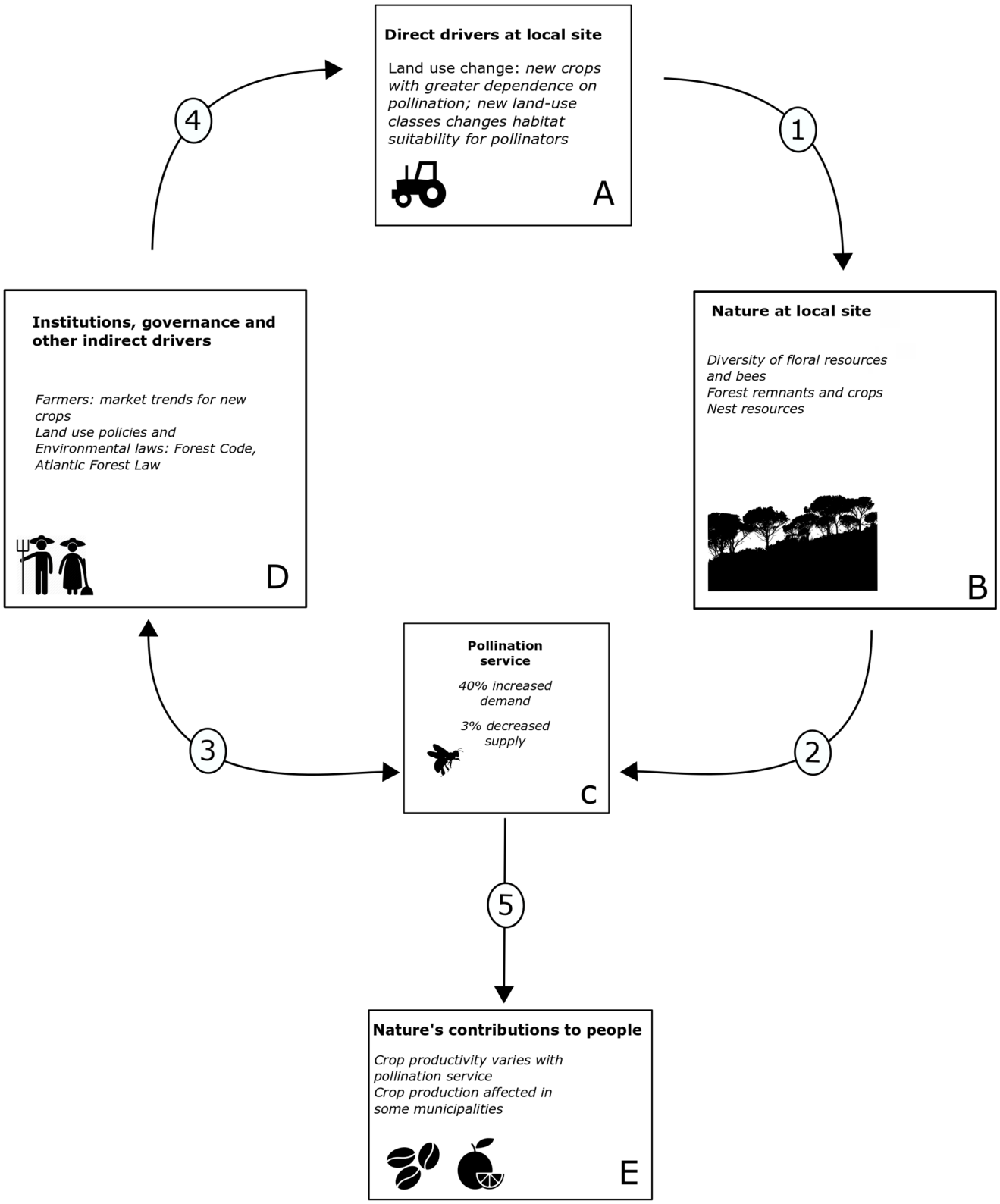


Figure 1. Study case conceptual model for achieving the increasing demand on pollination services in São Paulo State.

3. *LULCC model*

To predict future changes in land, we used outputs from the spatially explicit land-use/cover model provided by OTIMIZAGRO (Figure 2) (Soares-Filho et al. 2013, 2016). The model simulates future agricultural expansion for 14 economically important crops, considering the effects of transportation costs, climatic suitability and profitability: nine annual crops (soy, sugarcane, corn, cotton, wheat, beans, rice, manioc and tobacco), including single and double cropping systems; and five perennial crops (arabica coffee, robusta coffee, orange, banana and cocoa). The model also includes pastures, plantation forests, water surface, urban areas and native vegetation (Table S1). The future land-use/cover map of agricultural expansion is based on projections for 2024 (MAPA 2013) extrapolated to 2030 by using historical trends of agricultural production between 1994 and 2013 (IBGE 2013) and the modeled land cover changes considered deforestation within the limits established by the Brazilian Forest Code for Atlantic Forest and Cerrado Biomes.

To create a pollinator-dependence matrix comprising the 14 crops, we considered the pollination dependence rates estimated by the Brazilian pollination assessment (see Wolowski et al. 2019). The calculation of pollinator dependence rates provided by the assessment followed the methodology proposed by Gallai et al. (2009). The pollination dependence rates attributed to the crops included in the model were 0 (no dependence; e.g., rice and sugarcane), 0.25 (modest; e.g., soy and coffee) or 0.95 (essential; e.g., cocoa) (Table S1). The pollinator dependence matrix was spatialized using the OTIMIZAGRO Model maps of agricultural expansion for the years 2012 and 2030.

Mean dependence values were computed for each of the 645 municipalities São Paulo state considering the area covered by each category (crops, pasture, plantation forests, water, and urban area) and their respective pollinator dependence rate. Natural vegetation, urban area and water surface classes were not considered in the calculation. We used expert-based data on habitat suitability for bees synthesized by Kennedy et al. (2013) as a proxy for pollination supply in each land use/cover class (Table S1). Percentual changes in mean pollination demand and suitability values per municipality were computed for the period by subtracting the predicted value for 2030 and the value for 2012 and dividing the result by the 2012 value. Municipalities with null values for pollination demand in the year 2012 were not included in the calculations of percentage changes.

Associations between trends in pollination demand and supply were mapped by classifying each municipality in nine categories, representing all possible combinations of trends for both pollination supply and demand at the following three categorical levels: increases of more than 5% between 2012 and 2030, decreases of more than 5% between 2012 and 2030 and changes between +5% and -5% (see table S2 for the complete dataset).

The analyses were carried out in R version 3.6.1 (R Core Development Team 2019), using the packages *raster* (Hijmans 2019) and *rgdal* (Bivand et al. 2019). Maps were produced using the software QGIS (QGIS version 2.18).

Results

1. *Conceptual model case study*

We adapted the IPBES conceptual framework to our case study focusing on the effects of LULCC and the estimated demand for pollination services (Figure 1). We considered how land use changes affect pollination services and human well-being that were the focal components of our scenario modeling.

Land use change was the anthropogenic direct driver considered at local sites (Box A). Changes in land use and cover are known to impact significantly biodiversity and the delivery of ecosystem services.

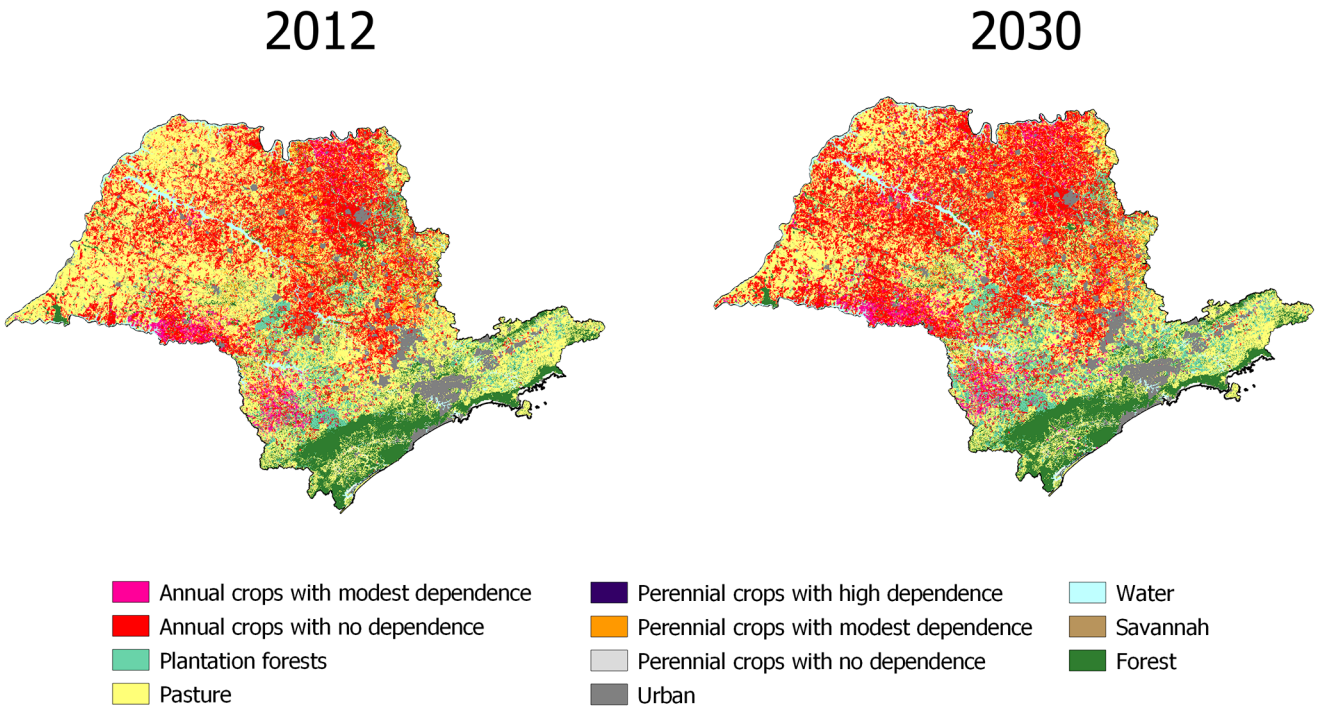


Figure 2. Land use changes scenarios for the state of São Paulo according to OTIMIZAGRO model.

The LULCC scenario modeling for São Paulo State projects a shift on the main dependence rate for pollination of croplands. It indicates a replacement of crops with low dependence rates on pollination by crops with higher dependence on pollinators. This change affects nature at a local site (Box B), since an increase of pollination dependent crops in semi natural habitats increases the demand for other floral resources used by bees in between crop season, which affects natural habitats, such as forest remnants that provide food resources for pollinators. These changes can also affect other factors, such as bee nesting resources, for example.

As a result of new cultivated crops and their specific dependence rates on pollination, we predict a 40% of increased demand for pollination service (see LULCC model effects on pollination section). This means that agricultural products will rely more on pollination service than they already do. Since the current scenario of bee conservation is not optimistic (see LULCC model effects on pollination section), productivity might be at risk in some municipalities.

Therefore, in order to ensure adequate pollination of these crops and safeguard productivity in these regions, strategic planning is needed. Involved actors, such as farmers and decision makers, should focus on spatial arrangements to improve bee's access to crops and to maintain resources and conditions for their survival.

This increased demand will directly affect nature's contribution to people (Arrow 5, Box E), as crops will provide different resources from those obtained in the past. It is expected that new products are more valuable than previous ones if farmers follow international market tendencies. Moreover, pollinator dependent crops also provide high quality and quantity products when pollinated, which add even more value to these products, both in intrinsic and extrinsic aspects (e.g. healthy foods and market prices, respectively).

2. *Ecosystem service matrix*

We evaluated eleven papers related to land use and different managements of landscape providing benefits to pollinator biodiversity and provision of pollination services. The resulting matrix showed that the land use types that contributed most with ES supply by pollinators were annual crops, native forest and forest plantations (Figure 3). On the other hand, pastures, constructed areas and water bodies contributed to a lesser extent.

3. *LULCC model effects on pollination*

The OTIMIZAGRO land use model predicts an increase trend for the demand on pollination services in São Paulo state considering the expansion of the modeled crops up to 2030 (Figure 4, Table S2). Comparing the present (2012) with the future scenarios, the mean demand for pollination services increases by 40%, considering predictions for future LULCC. The municipalities from the south of São Paulo state (such as Itapetininga, Itararã, Itapeva and Buri) show the highest mean crop dependence. This region and the northern region of the state comprise important agricultural areas and the crops under study, will expand on these regions in the future. Thus, these regions are more vulnerable and more likely to suffer from the implications of a decline in threatened pollinators.

The municipalities that currently do not have any pollinator-dependent crop will face the establishment and expansion of pollinator-dependent crops. As soybean expansion is predicted for the southwestern region, comprising Rosana and Presidente Prudente municipalities (Figure 4, Table S2), the demand for pollinators agents will rise. Most municipalities that do not have any crops dependent on pollinators will tend to remain so into the next decade.

Land Use Types/Average	Habitat creation and maintainance	Dispersion of pollen and other propagules	Food security	Medicinal, biochemical and genetic resources	Cultural heritage (Intrinsic value of biodiversity)	Pollination
Forest	2.4	2.76	1.02	2.22	2.66	4.36
Urban areas	0.6	0.36	0.26	0.22	0.68	0.76
Pasture	1.6	0.8	1	1	0.2	0
Crops	1.4	1.3	3.8	1	0.7	1.64
Water bodies	2.4	0.42	0.14	0.82	2.18	0.64
Forestry	2.6	2.9	1.4	2.82	2.66	0.6

Figure 3. ES assessment matrix illustrating the land use types capacities to provide pollination ecosystem service and other ecosystem service favoring wild pollinators.

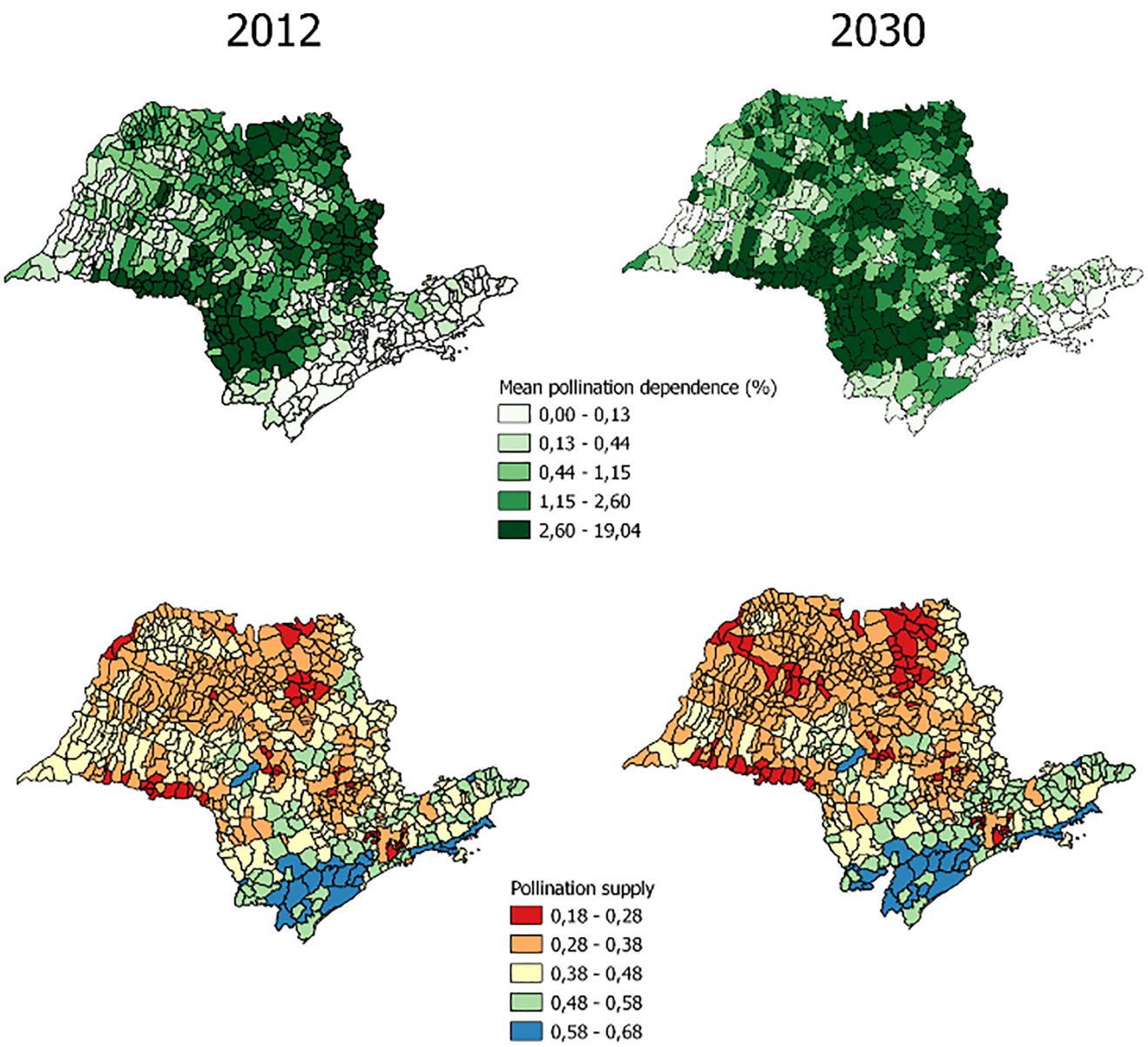


Figure 4. Present (2012) and future (2030) scenarios for the effects of land use change on pollination supply and demand of demands for pollination services in the state of São Paulo, Brazil. Top: Mean crop dependence on pollinators. Bottom: Mean pollinator supply.

Pollination supply is predicted to decline on average by 3% due to LULCC, represented mainly by expansion of annual row crops over areas that provide more suitable habitats to bees (such as native vegetation and pastures). These change will be more pronounced on the western municipalities (Figure 4, Table S2), with the higher percentage of changes expected to occur in Ipiguá, Bastos and São João do Pau d'alho, all with projected supply declines of over 20% (Table S2). The most common combined trend between pollination supply and demand was the increase in demand accompanied by a decrease in supply, observed in 195 municipalities, most of them located in the western portion of São Paulo State (Figure 5, Table S2). Only six municipalities showed the opposite trend (decrease in dependence and increase in suitability, Figure 5, Table S2) and the main pattern observed in this case was the replacement of crops by plantation forests (as observed, for example, in Pinhalzinho, SE São Paulo). Another 144 municipalities, also concentrated in the western region of the State, are expected to show an increase in dependence rate alongside a relatively stable pollination supply (changes between +5% and -5%; Figure 5, Table S2).

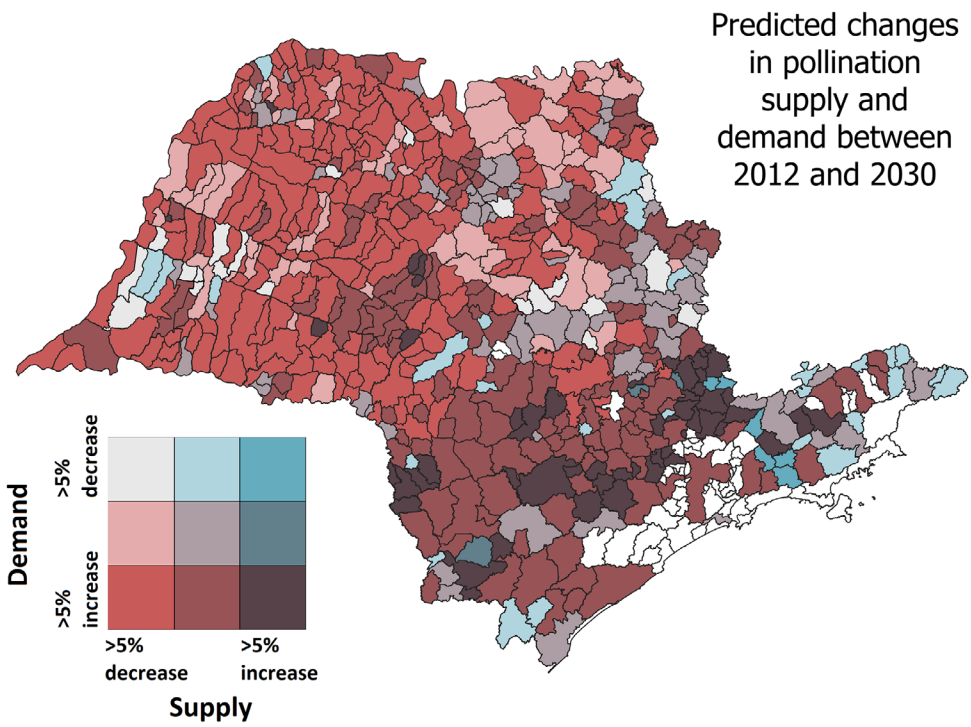


Figure 5. Changes in pollination supply and demand between 2012 and 2030. Municipalities in white had mean pollination dependence rate of 0 in 2012, and were not included in the percentage change calculations.

Discussion

In this study, we projected a future scenario that showed an increased demand coupled with a slightly reduced supply for pollination services in the state of São Paulo due to LULCC over the next twenty years. Population growth and the availability of suitable land for agriculture are major factors explaining present and historical LULCC in the state of São Paulo. These same factors can be considered as the major drivers of LULCC in a few years, suggesting an urgent need to reconcile environmental and economic policies.

The predicted increase in pollination demand up to 40% for São Paulo State was due to the expansion of areas with more pollinator-dependent crops, such as coffee, orange and cotton, replacing those that do not need pollination – mainly sugarcane, plantation forests and pastures. It is important to note that these results are probably an underestimation, since many of the crops not considered in the OTIMIZAGRO scenario have modest to high dependencies on pollinators (fruits and vegetables such as watermelon, tomatoes, strawberries, peppers etc.). Although the mean reduction in estimated pollination supply was not high, some municipalities are expected to show higher supply decreases simultaneously with increases in dependence. Thus, if this increasing demand is to be met, especially in those more affected municipalities, effective measures to conserve and promote the sustainable use of native and wild bees are needed, such as better allocation of areas for conservation units, pollinator-friendly management practices to improve the condition of the existing habitat and the adoption of better practices regarding agrochemical use (especially insecticides).

As indicated in the conceptual model, LULCC promotes loss of natural habitats and threaten pollinators, by affecting the quality and quantity of food resources and number of nesting sites. It is important to remark that our scenario approach only considers broad patterns in LULCC at the municipality level. At finer spatial scales, other effects have been demonstrated, such as the effects of fragmentation on biodiversity and gene flow of bees (Ferreira et al. 2015, Boscolo et al. 2017, Montagnana et al. 2018, Nery et al. 2018, Barbosa et al. 2019). The spatial configuration of crop fields and habitat patches can also be important, as exemplified by observed effects of the distance to the nearest native vegetation (Garibaldi et al. 2011). Nevertheless, the results shown here serve as a first step in describing the expected effects of LULCC in the considered scenario and are useful in defining research priorities and point directions for better management.

In order to reach the demand for pollination service in the future scenario, practices to maintain forest cover should be addressed, since this is the most important land-use class that supplies pollination ES. It has been widely reported that forest fragments can increase the diversity and abundance of pollinators with substantial gains in crop production (Campbell et al. 2017, Hipólito et al. 2019).This has been highlighted for orange (unpublished data) and coffee (Saturni et al. 2016) across the Atlantic Rainforest domain within the state of São Paulo. The role played by forest fragments in providing biodiversity of bees results in both an increase of crop productivity and improvement of nutritional composition of fruits (Brittain et al., 2014; Klatt et al., 2014). Therefore, maintaining, increasing and managing appropriate habitats for wild pollinators are profitable opportunities for species conservation and continuous crop production (Lautenbach et al. 2012).

Simulations have predicted that, depending on the magnitude and location of ongoing forest conversion, pollination services are expected to decline continuously and thus directly reduce coffee yields by up to 18% and net revenues per hectare up to 14% in other tropical forests (Priess et al. 2007). However, this scenario can be avoided if patches of forests (or other natural vegetation) are maintained in agricultural landscape,

which could be a viable near future option for local local farmers and regional land-use planners (Priess et al. 2007). This same approach may be applied for Brazilian tropical forests in order to prevent the reduction of crop pollination and attend the increased demand for future scenario in São Paulo state.

We observed a gap in Brazilian studies linking pollination services and different restoration contexts to promote crop yields. Filling this gap is urgent to inform and support land-use planners and decision makers to choose priority areas for restauration. This reflects not only on the delivery of the service in itself, but also to human well-being, since it may improve net revenues to small farmers. Among strategies that may contribute to the maintenance of natural habitat, the expansion of protected areas can act as reservoirs of pollinators and, therefore, provide pollination services for crops nearby. This gap might be fulfilled in order to provide information to land managers and obtain efficient provision of pollination considering future scenarios.

It is important to make a reservation about the results obtained by our model for the capacity of forest plantations on maintaining pollinators' communities. Even though in Kennedy et al. (2013) this land-use category was considered as suitable habitat as native broadleaf forest, we believe that there are some important differences between both habitat types in our study area. Plantation forests, typically consist of one or a few tree species, are grown as even-aged monocultures, intensively managed and harvested on relatively short rotations (Taki et al. 2011). These characteristics raise concerns that plantation forests may negatively impact forest biodiversity (Brockerhoff et al. 2008). However, moderate disturbances in native forests, including forest plantations, may help maintain pollinator abundance and diversity by expanding the cover of herbaceous plant species, thereby increasing nectar and pollen availability (Winfree et al. 2007). Nevertheless, for the sake of consistency, we opted to maintain the suitability value for plantation forests provided in Kennedy et al. (2013). In this way, the results driven by predicted changes in plantation forest should be interpreted with care in our case study and more specific information about the differences in floral resource and nesting site availability between native forests and plantation forests are needed for a better understanding of those trends.

From the perspective of crop management, Brazil has been adopting decisions in opposite directions that jeopardize biodiversity of pollinators and threaten pollination services. The consumption of insecticides in Brazil more than doubled (152%) in the last 15 years, from 2003 to 2018 (Santos et al. 2018). Besides increasing pesticide use, control policies by competent agencies are insufficient (SABESP 2019), which hamper monitoring for correct use of agrochemicals as required by the Brazilian Ministry of the Environment (Cham et al. 2017). Thus, to overcome this barrier and guarantee the delivery of pollination up to 2030 in São Paulo state, alternative strategies to regulate or diminish the use of chemicals products, should be adopted, such as agroecological systems, organic agriculture practices and integrated pest management (IPM). These strategies should be discussed with all parties involved including farmers, beekeepers, scientists, governments and decision-makers (Díaz et al. 2015, Wolowski et al. 2019).

Although we could not include in our case study the effects of urban expansion, since this process is beyond the OTIMIZAGRO land-use scenarios' scope (Soares-Filho et al. 2019), we consider that urban expansion may have important impacts on pollinators, especially in our study area. Even in a scenario of expansion of land use change, some degree of habitat and food resources for pollinators can be provided by urban areas. This supply may be enhanced by urban green environments that can help to maintain pollination service, particularly by habitat creation and dispersion of pollen and other propagules (Henning & Ghazoul 2011). These areas may be important to promote gene flow in native bee species, such as *Tetragonisca angustula* and those species with generalist habit that can nest inside urban pre-existing cavities, such as some solitary bees. Threlfall et al. (2015) suggest that established urban green areas that contain native flowering plants with lower surrounding impervious surface cover, support greater bee abundance and greater richness of bee species, especially ground-nesting and floral specialist bees. Future work considering these effects would be particularly useful for the better planning of urban development.

Practical application of ES knowledge enables integration of institutional organizations, governance, stakeholders and partnerships between them with small and large farmers, crucial to guide and elucidate the best directions and pollinator-friendly practices to crop management. Initiatives such as the pact to restore Atlantic Rainforest can compensate the loss of original habitats in agricultural areas located in the south region of the state. This can be observed by the prediction for the 2030, wherein planted forest and annual crops tends to increase. Following the ES approach, it is expected to achieve long-term results in the environmental, social, cultural, political and economic aspects of sustainable development in the respective area (Nedkov et al. 2018).

Guidelines and organizations promoting efforts to avoid pollinator crisis are increasing with a still incipient participation of the Brazilian government. For example, Brazilian Environmental Ministry published an assessment on the risks of insecticides to bees (MMA, 2018) and the Brazilian Network of Plant–Pollinator Interactions (REBIPP) brought up a National Report on Pollination, Pollinators and Food Production. This asset followed the IPBES conceptual assessment (IPBES 2016). Future studies that explore the relationships between the aforementioned drivers and the potential of pollination by native animals, taken together with spatially-explicit scenario analysis of future demand of these services, may better inform which are priority areas to focus on management actions in order to successfully reach future demand and ensure a higher productivity and sustainability of the agriculture. Mitigating indirect and direct drivers that impact pollinator communities is a general step for the conservation of pollination services under scenarios of increased demands. Indirect drivers represented mainly by governance and institutions, play an important role in guiding anthropogenic direct drivers, particularly in relation to management crop and land use.

Supplementary material

The following online material is available for this article:

Table S1 - Description, dependence rates (BPBES report) and suitability values (obtained from table S4_2 of Kennedy et al. 2013) for OTIMIZAGRO class

Table S2 - Mean dependence and suitability values for the years 2012 and 2030 and percentage change in dependence and suitability along the period, for each São Paulo State municipality.

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Laura Camilo Perez Giraldo: Contribution in the concept of the study; manuscript preparation; contribution to critical revision, adding intellectual content.

Conflicts of Interest

The authors declare no conflicts of interest related to this publication.

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Beta diversity patterns of Bromeliaceae growing on rocky cliffs within the Atlantic Forest in southern Brazil

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Abstract: In recent years there has been increasing attention in patterns of β-diversity and mechanisms related to variations in species composition. In this study, we evaluated beta diversity patterns of bromeliads growing on cliffs immersed in Atlantic Forest. We hypothesized that the species composition varies according to the spatial scale, inferring that there is a replacement of species influenced mainly by environmental factors. The study was carried out on sandstone cliffs included in contiguous but distinct vegetation formations: Evergreen and Seasonal forests. Twenty-four vertical rocky outcrops were sampled. The spatial variation in species composition was evaluated by two β-diversity components, turnover and nestedness. Multivariate analysis and variation partitioning were performed to distinguish niche and stochastic processes. We recorded 26 bromeliad species and a significantly higher contribution of turnover explaining beta diversity. Environmental factors affect β-diversity patterns of Bromeliaceae. However, individually, the environmental predictors do not explain the data variation. Environmental variations spatially structured, and spatial variables determinate the dissimilarity in the composition of bromeliads on cliffs. Thus, our results revealed that both environmental and spatial effects can act together to define the floristic composition of rock-dwelling bromeliad communities.

Keywords: *Sandstone outcrops, bromeliads, evergreen forest, seasonal forest, Niche Theory, Neutral Theory.*

Padrões de diversidade beta de Bromeliaceae crescendo em falésias rochosas dentro da Mata Atlântica no sul do Brasil

Resumo: Nos últimos anos tem havido uma crescente atenção em relação aos padrões de diversidade β e aos mecanismos relacionados às variações na composição de espécies. Neste estudo, nós avaliamos os padrões de diversidade beta de bromélias crescendo em escarpas rochosas imersas em matriz de Floresta Atlântica. Hipotetizamos que a composição das espécies varia de acordo com a escala espacial, inferindo que há uma substituição de espécies influenciadas principalmente por fatores ambientais. O estudo foi realizado em escarpas areníticas inseridas em formações vegetacionais contíguas, mas distintas: Florestas Ombrófila e Estacional. Vinte e quatro afloramentos rochosos verticais foram amostrados. A variação espacial na composição de espécies foi avaliada por dois componentes de diversidade β, turnover e aninhamento. Análise multivariada e particionamento da variação foram realizados para distinguir processos de nicho e estocásticos. Registramos 26 espécies de bromélias, com uma contribuição significativamente maior do turnover explicando a diversidade beta. Os fatores ambientais afetam os padrões de diversidade β de Bromeliaceae, no entanto, individualmente, esses preditores não explicam a variação dos dados. Assim, variações espaciais e variações ambientais espacialmente estruturadas determinam a dissimilaridade na composição de bromélias nas escarpas avaliadas. Desse modo, tanto os fatores ambientais determinísticos quanto os efeitos espaciais podem atuar em conjunto para definir a composição florística das comunidades de bromélias que se estabelecem sobre rochas.

Palavras-chave: *Afloramentos areníticos, bromélias, floresta ombrófila, floresta estacional, Teoria de Nicho, Teoria Neutra.*

Introduction

Investigating patterns of species distribution is one of the essential objectives of ecology and a challenge to understand the complex set of processes driving the structure of communities. The variation in species composition among communities (β-diversity) can be related to the influence of several biotic and abiotic conditions (Cottenie 2005). The use of beta diversity measures based on dissimilarity between samples or communities can clarify several questions about the distribution of species, allowing inferences on environmental effects, and the influence of spatial or random factors on the establishment of species (Baselga 2010).

Previous studies have identified that both deterministic and stochastic processes, widely discussed by the Niche Theory and the Neutral Theory, respectively, can act at different spatial scales to define species composition and diversity patterns (Ricklefs & Schluter 1995, Duarte et al. 2010, Segre et al. 2014). Niche-based processes assume that the establishment of a species is limited by environmental filters (Grinnell, 1917; Legendre & Legendre, 1998), while neutral processes assume that dispersion acts as one of the main mechanisms in determining the diversity patterns (Hubbell 2001). The structure of communities is thus determined by two distinct processes acting on the regional pool of species (Hubbell 2001, Gaston & Chown 2005).

Theoretical approaches related to the effects of spatial and environmental filters may also reveal interesting patterns when applied in plant communities growing on rocky cliffs associated with highly heterogeneous and diversified ecosystems. This is the case of the Brazilian Atlantic Forest, a well-known hotspot of biodiversity, and thus highly important for conservation purposes (Ribeiro et al. 2009, Mittermeier et al. 2015). There are many gaps in the understanding of how local and regional diversity on cliffs is maintained and the degree of connection between them along in the forest.

The Brazilian Atlantic Forest comprises noticeably heterogeneous vegetation, including several related ecosystems, such those occurring on rock outcrops (Scarano 2002, Leão et al. 2014). The vegetation on rock outcrops, including on cliffs, in general, differ from the surrounding forest matrix mainly due to absent or incipient soils, and microclimatic conditions resulting from high insolation and low water availability (Porembski & Barthlott 2000). In Southern Brazil, cliffs are embedded in different landscapes of the Atlantic Forest, which in this region is classified into three main types: Evergreen Forest (tropical rain forest), Araucaria Forest (subtropical Araucaria forest) and Seasonal Forest (tropical deciduous and semideciduous forest) (Veloso et al. 1991, IBGE 2012).

The Bromeliaceae family has been highlighted as one of the most frequent and important family in rocky environments, especially for the ecological role in the succession process, acting as nursery plants, forming islands that increase water availability and mechanical support for other species (Porembski et al. 1997, 1998, Porembski 2005, Rocha et al. 2014, de Paula et al. 2016). Furthermore, in Atlantic Forest, they present great ecological importance resulting from the many interactions with other organisms (Martinelli et al. 2008, Givnish et al. 2011, Machado et al. 2016).

The influence of the forest matrix on the composition and diversity of bromeliads growing on rocky outcrops has recently been described (Melo & Waechter 2018). However, patterns of species distribution and theoretical approaches related to the effects of spatial and environmental variables on the composition of these communities have not yet been addressed. Although studies evaluating plant communities on rocky outcrops have expanded in recent years, including in Brazil (Ferreira et al. 2014, Saraiva et al. 2015, do Carmo et al. 2016, Machado et al. 2016, de Paula et al. 2019), floristic composition and community structure on cliffs are still little known.

Here, we evaluated the effects of environmental and spatial variables in plant communities growing on rocky cliffs, identifying the variations in composition along in two distinct forest typologies: Evergreen Forest and Seasonal Forest. The objective of this study was to evaluate beta diversity patterns of bromeliads growing on cliffs immersed in Atlantic Forest and to identify the mechanisms that act in the structure of these communities. Thus, we investigate the following questions: (i) How do beta diversity of rock-dwelling Bromeliaceae vary in a transition zone between Evergreen and Seasonal Atlantic Forest? (ii) Which are the spatial and environmental variables affecting composition variations of bromeliads on rocky cliffs? (iii) What amount of variation in the floristic composition can be attributed to the environment (deterministic), space (stochastic), and both processes?

We expected that (i) the composition of species varies according to the spatial scale and between forest types, meaning that there is a substitution of species along with space, corroborating studies in rocky outcrop and with other vegetation components in this phytogeographic domain (Bergamin et al. 2017, Silva Mota et al. 2018); (ii) Species turnover is influenced by climatic factors related to transition zone, like the variation in temperature and precipitation, demonstrating that rocky outcrops also influenced by regional environmental filters, as is the distribution of epiphytic bromeliad species along the Atlantic forest (Fontoura *et al*. 2012). (iii) Beta diversity is explained mainly by spatially structured environmental variables so that both deterministic and stochastic processes are important in explaining the composition of epiplithic bromeliad communities, as has been observed in other studies conducted in rocky habitats (Sarthou et al. 2017, Silva Mota et al. 2018).

Material and Methods

1. Study Area

The study area is located in the Southern Region of Brazil, comprising the northeast of Rio Grande do Sul and the southeast of Santa Catarina states (roughly between latitudes 29º and 30ºS). Our study was conducted on cliffs, environments characterized as the exposed and steep face of the rocky outcrop (Larson et al. 2000). All the investigated cliffs are sandstone outcrops inserted in two different types of Atlantic Forest, the Evergreen and Seasonal physiognomies.

The studied rocky outcrops are located at low elevations (below 200 m) between the coastline of the Atlantic Ocean and the abrupt slopes of the Serra Geral Mountain Range, in a heterogeneous landscape now mostly comprising some disturbed habitats, like roadsides, meadows for cattle rise, or secondary vegetation.

The entire study area has a humid subtropical climate (Cfa), according to the Köppen classification system, with hot summers and abundant rainfall throughout the year. The regional climate has a mean annual temperature of around 18°C and a mean annual rainfall around 1750 mm (Alvares *et al*. 2013). The mean annual temperature varies between 18.4 ºC in the Evergreen forest region and 17.9 ºC in the Seasonal forest region while the rainfall in these regions may achieve an annual mean of 1660mm and 1850mm, respectively (Alvares et al. 2013).

The studied sandstone outcrops belong to the Botucatu Formation of the Paraná Sedimentary Basin, originated in the Mesozoic era and presently extending mainly in south-central Brazil (Bigarella & Salamuni 1961, Kaul 1990). Both the Evergreen and the Seasonal forests occur mostly on the slopes of the Serra Geral Mountain Range, but differing by their predominant exposition.

Besides the Atlantic Evergreen Forest and the Seasonal Forest, regional vegetation also includes the third major physiognomy of Atlantic Forest phytogeographic domain (IBGE 2012), the Araucaria forest, not included in this study.

2. *Sampling method*

It was selected 24 sample units, which consisted of cliffs isolated with a particular exposure. All sampled cliffs are composed of sandstone and have an essentially vertical slope. Among the 24 cliffs, 12 were immersed in the Evergreen Coastal Forest region and 12 were immersed in the semideciduous Seasonal Forest region (Figure 1). Data collection was performed two to three times, in each sample unit, considering different seasons and the flowering period of some species whose identification needed to be confirmed.

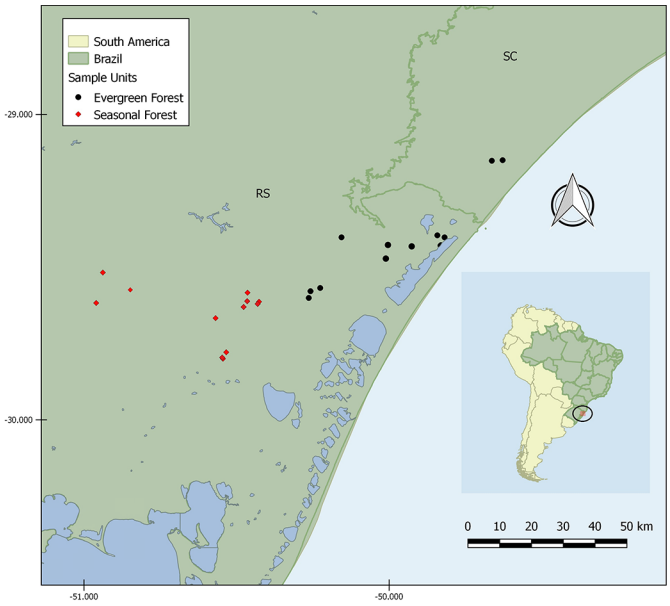


Figure 1. Study area and sampled sites. Black circles represent the cliffs immersed in Evergreen forest region and red squares those immersed in Seasonal forest region. RS = Rio Grande do Sul state; SC = Santa Catarina state.

Sampled cliffs in each forest region summed roughly the same area, 19,713m^2 in Evergreen forests and 19,277m^2 in Seasonal forest. We obtained solar radiation and the climatic variables for each site from the WorldClim Global Climate with a spatial resolution equivalent to 30" (~1 km): The bioclimatic variables selected represent annual trends (mean annual temperature, annual precipitation) and seasonality (temperature seasonality, annual temperature range, precipitation seasonality) (Hijmans *et al*. 2005). Additionally, continentality was obtained from the Envirem data set and is measured by the difference between the average temperature of the warmest month and the average temperature of the coldest month (Title & Bemmels 2018).

All species of bromeliads on cliffs were sampled, most of them are lithophyte plants, that is, arranged directly on rock or concavities. Some species also used cracks and small terraces on the rock, where a shallow substrate could to exist. Many species were grouped forming what the authors call Bromeliaceae mats. Only *Tillandsia usneoides* were using other herbaceous plants as support. Bromeliads species growing on the escarpments were registered employing of direct observations and with the aid of high-resolution binoculars, collected through climbing or pruning tools. Fertile specimens were collected and incorporated into the ICN Herbarium in the Federal University of Rio Grande do Sul.

3. *Data analysis*

We measured the spatial variation in species composition using beta diversity with its two components, turnover and nestedness, according to the methodology described by Baselga (2010). The first phenomena is related to species replacement by new species, caused by spatial or environmental constraints, for example (Qian *et al*. 2005); the last involves species loss in a community or along a gradient, when species found in one site represent a subset of another site, due to non-random processes, caused by circumstances that promote an orderly disaggregation of the assembly (Ulrich & Gotelli 2007, Baselga 2010).

For each forest type region, we calculated the Sørensen dissimilarity index (βSOR) and partitioned it into its turnover, i.e., Simpson dissimilarity index (βSIM) and nestedness (βSNE) components. Nestedness is defined as the difference between βSOR and βSIM. The estimations were performed with the package "Betapart" in R (R Development Core Team 2011, Baselga & Orme 2012). Despite being two antithetic phenomena, turnover and nestedness can occur simultaneously in communities, i.e., they are not mutually excluding (Baselga 2010).

We used PERMANOVA - Permutational Multivariate Analysis of Variance (Anderson 2001), to test the individual relationships between each of the environmental predictor matrices and the beta diversity metrics (βSOR, βSIM, and βSNE), in each study region. Beside the continentality and solar radiation, we had chosen the variables representing the climatic variation in the forest and seasonal transition zone: mean annual temperature, annual precipitation, temperature seasonality, annual temperature range, and precipitation seasonality. Thus, we analyzed whether areas with more dissimilar species compositions were associated with increasing environmental distances. These relationships were examined based on the partial R^2, and the significance was estimated using 999 permutations, in the R package "Vegan" (Oksanen *et al*. 2013).

The relative contributions of environmental and spatial factors in the structuring of communities were analysed by partitioning the variation from distance-based redundancy analysis (db-RDA) and variation partitioning based on the adjusted R^2 (Borcard et al. 1992, Legendre & Legendre 1998, Legendre & Andersson 1999, Smith & Lundholm 2010) Although there are critical issues in using statistical methods for variation partitioning, the approaches that divide environmental and spatial controls into community composition are recognized as important for ecological studies (Gilbert & Bennett 2010).

Initially, separate analyses were run for the set of spatial and environmental variables. The distance matrix of total beta diversity (βSOR) was used as the response variable. The environmental predictor matrix comprised bioclimatic variables, continentality and solar radiation, standardized through logarithmic transformations to homogenize the data distribution. A forward-selection procedure was applied to environmental dataset. The RDA with the selected variables (Temperature Seasonality - TS, Annual Temperature Range - TR, Solar radiation - SR) served as the model for the analysis of variance partitioning. We also test the multicollinearity in select variables to be used in the analyse (Borcard *et al*. 1992).

The spatial matrix (geographic overland distances) was obtained through of distance-based Moran's Eigenvector Maps (dbMEM, formerly called principal coordinates of neighbour matrices, PCNM). These filters are generated from a truncated Euclidean distance matrix between sample units based on their geographical coordinates and can be used as explanatory variables to model spatial relationships in community data (Dray et al. 2006, 2012). This procedure generated a total of 18 MEM filters, each of which corresponds to a specific spatial structure and scale: the first MEM variables model broader-scale patterns, whereas the subsequent variables progressively represent finer-scale patterns (Borcard *et al*. 2004). A forward-selection procedure was applied to spatial dataset. Only the significant spatial filters were retained for variation partitioning (MEM1, MEM2, MEM3, MEM 4, MEM16, MEM17, MEM18), corresponding to the first four and last three spatial predictors.

To perform variation partitioning, the three data matrix was required: Beta diversity matrix, environmental variables, spatial variables (Moran's Eigenvector Maps – MEM) (Dray *et al*. 2006). Thereafter, the variation in the matrix of the community was decomposed into components of explanation: purely environmental, both spatial and environmental, purely spatial and residual or unexplained (Borcard *et al*. 1992). The analysis was performed from three sets of multivariate linear regressions with the beta diversity matrix as the response. These regressions estimate the amount of variation explained by environmental and spatial predictors, alone and in combination (Peres-Neto *et al*. 2006). The significance of the environmental and spatial models generated by the dbRDAs was tested with a permutation test for constrained correspondence analysis.

The distance-based Moran's Eigenvector Maps were performed with the "adespatial" package (Dray *et al*. 2018). The RDA analysis, variation partitioning and Moran spectral randomization was executed with the "vegan", "adespatial", and "spdep" packages (Oksanen et al. 2013, Bivand & Wong 2018, Dray et al. 2018), all in the statistical program R (R Development Core Team 2011).

Results

We sampled a total of 26 bromeliad species, belonging to nine genera (*Aechmea, Bromelia, Billbergia, Dyckia, Edmundoa, Nidularium, Tillandsia, Vriesea*, and *Wittrockia*) and three subfamilies (Bromelioideae, Tillandsioideae, and Pitcairnoideae) (Table 1). The number of species per cliff ranged from one to 11 in Evergreen forest and from one to seven for Seasonal Forest. The total richness in each region was 23 species in Evergreen forest and 13 species in Seasonal Forest, and 10 species were shared between the two environments.

In assessing the proportion of each component of beta diversity, we observed a significantly higher contribution of turnover to nestedness, both when considering all the study area and those cliffs sampled in each forest type, with values ranging from 0.766 to 0.876 (pairwise βSIM). Total beta diversity (pairwise βSOR) was 0.851 for Evergreen forest, 0.900 for Seasonal forest and 0.925 for both forest types (Table 2).

Solar radiation was one of the factors that most influenced Bromeliaceae beta diversity, considering forest physiognomies separately and in an integrated manner. In Evergreen forest, the Annual Temperature Range (TR) also contributes to the variation in species composition, taking into account βSIM and βSOR. Beside this variable, Precipitation Seasonality (PS) also explained the total beta diversity (βSOR) in this forest type. In Seasonal forest, both βSIM and βSOR were influenced by the Mean Annual Temperature (AT), Temperatura Seasonality (TS), Temperature Annual Range (TR) and Continentality (CO). Considering both forest types, only Annual Precipitation (AP) and Continentality (CO) did not influence beta diversity of epilithic bromeliad communities. In general, the models revealed that the strongest environmental effects were on total beta diversity (βSOR), followed by the turnover component of beta diversity (βSIM) (Table 3).

The relationship between all sampled cliffs and the total set of selected spatial and environmental variables is represented in two dbRDA plots (Figure 2 and Figure 3). The permutation tests for these analyses were significant for spatial variables, for environmental variables and environmental variations spatially structured. However, if isolated, environmental predictors fail to explain the variation of the data. Essentially, our results showed that the distribution of rock-dwelling Bromeliaceae is limited both by spatial distances and by environmental variables acting within these limits. In variation partitioning, the spatial and environmental variables explained 62.0% of the variation found in the structure of the bromeliad communities.

The purely spatial component explained 26.5%, while the environmental fraction alone accounted for 3.40% of the variation. The percentage of the shared variation between spatial and environmental variables was 32.1%. However, 38.0% of the variation in beta diversity could not be explained by either of these variables (Table 4).

Discussion

This research provides ecological information on the Bromeliaceae inhabiting rocky cliffs in southern Brazil. Our results showed how the composition of bromeliads growing on this substrate varies at the boundary between evergreen and seasonal forest types, and how spatial and environmental factors influence the structuring of these communities. Beta diversity is arranged by spatial turnover reflecting climatic differences between sites. Thus, bromeliad composition is determined by both deterministic environmental factors and stochastic spatial effects.

The total beta diversity patterns showed a much stronger contribution of species turnover than species nestedness. This result was expected, considering that species turnover reveals the variation in community structure from one sampling unit to another along a spatial, temporal or environmental gradient (Anderson *et al*. 2011). The replacement of species along space is related to environmental difference throughout the study area, which comprises several climatic and landscape regimes, affecting the structure in forest communities of the Southern Brazilian Atlantic Forest (Oliveira-Filho & Fontes 2000, Bergamin et al. 2012). Contrary to nestedness, spatial turnover indicates the replacement of some species

Table 1. Bromeliad species sampled on sandstone cliffs in the South Brazilian Atlantic Forest, and their frequence in Evergreen (E) and Seasonal (S) forest types.

Subfamilies	Species	Author	Forest Type	
			E	S
Bromelioideae	*Aechmea comata*	(Gaudich.) Baker	2	5
	Aechmea gamosepala	Wittm.	9	0
	Aechmea nudicaulis	(L.) Griseb.	1	0
	Aechmea recurvata	(Klotzsch) L.B. Sm.	0	1
	Billbergia nutans	H. H. Wendl. ex Regel	0	5
	Billbergia zebrina	(Herb.) Lindl.	1	0
	Bromelia antiacantha	Bertol.	3	1
	Edmundoa lindenii	(Regel) Leme	2	0
	Nidularium innocentii	Lem.	1	0
	Wittrockia superba	Lindm.	6	0
Pitcairnioideae	*Dyckia maritima*	Baker	4	5
Tillandsioideae	*Tillandsia aeranthos*	(Loisel.) L.B.Sm.	2	3
	Tillandsia gardneri	Lindl.	2	1
	Tillandsia geminiflora	Brongn.	1	1
	Tillandsia mallemontii	Glaz. ex Mez	1	0
	Tillandsia polzii	Ehlers	2	5
	Tillandsia recurvata	(L.) L.	3	1
	Tillandsia stricta	Sol.	1	0
	Tillandsia usneoides	(L.) L.	8	2
	Tillandsia xiphioides	Ker Gawl.	2	0
	Vriesea carinata	Wawra	1	0
	Vriesea friburgensis	Mez	0	2
	Vriesea gigantea	Gaudich.	8	1
	Vriesea philippocoburgii	Wawra	4	0
	Vriesea platynema	Gaudich.	2	0
	Vriesea vagans	(L.B.Sm.) L.B.Sm.	1	0

Table 2. Total beta diversity, i.e., Sørensen dissimilarity (βSOR) and its two components, turnover (Simpson dissimilarity, βSIM) and nestedness (βSNE) in Evergreen Forest, Seasonal Forest and Both Forest Types.

Forest types	βSOR	βSIM	βSNE
Evergreen Forest	0.851	0.766	0.084
Seasonal Forest	0.900	0.847	0.053
Both Forests	0.925	0.876	0.049

by others, as a consequence of environmental arrangements or spatial and historical restrictions (Qian *et al*. 2005).

The similarity between species matrices was positively correlated with the similarity of local ecological conditions, evidencing the influence of environmental factors on the composition of Bromeliaceae growing on cliffs, particularly the βSIM diversity component. The degree of beta diversity for the two forest types found in our study is surprising because it is a transitional area, but corroborates with other studies applied to different forest components of the Atlantic Forest (Bergamin et al. 2012, Menini Neto et al. 2016). In addition, the changes in physiognomy are generally associated with higher values of β diversity (Pérez-García et al. 2009). The high turnover rates of species in each forest type also support other studies and reinforce the need to expand conservation areas of rocky habitats within each of these types (Bergamin et al. 2017).

Solar radiation was important variable in species' shifts in Evergreen forest, in Seasonal forest, and especially when considering the entire studied area. Variation in species diversity and composition on inselbergs in southern Brazil had already been associated with different exposures to solar radiation (Ferreira et al. 2014, Carlucci et al. 2015). The physiological sensitivity and performance of bromeliads are directly related to their thermal tolerances (Benzing 2000), which also corroborates the importance of this variable. Recently, studies have shown differences in the anatomy and morphology of epilithic species, reinforcing the existence of different adaptations in certain species to deal with drought in rocky environments (Hunter 2016, de Paula et al. 2019). Many bromeliads are adapted to environmental conditions with low water availability, being favoured by several functional attributes capable of efficiently capturing water and minimizing its loss. The CAM photosynthesis also

Table 3. Explained variation (R^2) of distance matrices representing effects of Solar Radiation (SR), Annual Mean Temperature (AT), Temperature Seasonality (TS), Annual Temperature Range (TR), Annual Precipitation (AP), Precipitation Seasonality (PS), and Continentality (CO) on total beta diversity (Sørensen dissimilarity, βSOR) and its turnover (Simpson dissimilarity, βSIM) and nestedness (βSNE) components of bromeliads on cliffs immersed in Evergreen Forest, Seasonal Forest and Both Forest Types.

	Evergreen Forest			Seasonal Forest			Both Forest Types		
	βSOR	βSIM	βSNE	βSOR	βSIM	βSNE	βSOR	βSIM	βSNE
SR	0.211**	0.299*	-	0.153*	0.150*	-	0.238**	0.292**	-
AT	-	-	-	0.259**	0.321**	-	0.093**	0.107**	-
TS	-	-	-	0.207*	0.185*	-	0.065*	0.072*	-
TR	0.152*	0.226*	-	-	-	-	0.057*	0.074*	-
AP	-	-	-	-	-	-	-	-	-
PS	0.029*	-	-	-	-	-	0.101**	0.002**	-
CO	-	-		0.099*	0.120*	-	-	-	-

Signif. codes: * P-value < 0.05; ** P-value < 0.01.

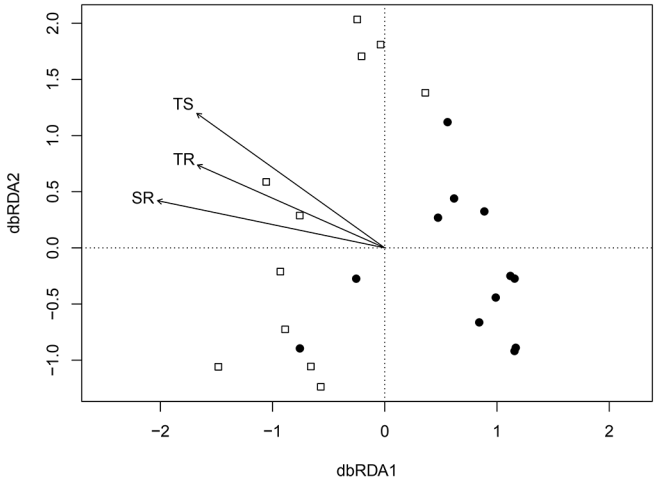


Figure 2. Distance-based Redundancy Analysis (dbRDA) of species assemblages and environmental variables in sandstone cliffs. (dbRDA, axis 1 = 24%, axis 2 = 13%). Temperature Seasonality (AT), Annual Temperature Range (TR), and Solar Radiation (SR). White squares correspond to cliffs in Seasonal Forest and black circles correspond to cliffs in Evergreen Forest.

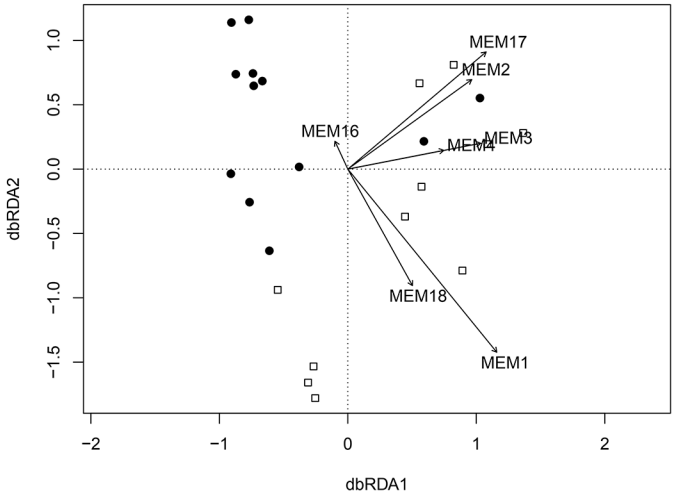


Figure 3. Distance-based Redundancy Analysis (dbRDA) of species assemblages and spatial variables in sandstone cliffs. (dbRDA, axis 1 = 31%, axis 2 = 18%). Selected spatial descriptors (forward selection): MEM 1, MEM 2, MEM 3, MEM 4, MEM 16, MEM 17, MEM 18. White squares correspond to cliffs in Seasonal forest and black circles correspond to cliffs in Evergreen Forest.

Table 4. Results of the partial dbRDA analysis (variation partitioning) for the composition of epilithic bromeliads growing on sandstone cliffs immersed in Atlantic Forest matrix.

Partition of variation	Adj.R^2	F	P-value
[a+b] = Spatial	0.586	5.644	0.001
[b+c] = Environmental	0.355	5.215	0.001
[a+b+c] = Spatial + Environmental Individual fractions	0.620	4.749	0.001
[a] = Only spatial	0.265	-	-
[b] = Environmental spatially structured	0.321	-	-
[c] = Only environmental	0.034	-	-
[d] = Residuals (Undetermined)	0.380	-	-

is significantly associated with increased diversification in Bromeliaceae in these habitats (Martin 1994, Reinert 1998, Quezada & Gianoli 2011). These adaptations are also effective in moist forests, for those bromeliad species growing on intermittently dry habitats, as rocky outcrops and the upper canopy of rainforests (Benzing 2000).

Temperature seasonality, annual range temperature and annual temperature influence the beta diversity patterns of rock-dwelling bromeliads, especially in seasonal forests and in the transition zone between the two forest types. This is probably because the coastal to inland climatic and topographic gradients affect several species even in areas with the same forest physiognomy, which is evidenced by lower temperatures, especially in winter, towards the Serra Geral Mountain Range (Alvares *et al*. 2013). Moreover, the richness of bromeliads in coastal Brazil shows strong latitudinal variations, that reflects a temperature gradient, decreasing both towards northern and southern from a central hotspot around Rio de Janeiro and São Paulo states (Martinelli *et al*. 2008).

Considering the studied region as a transition between two different forest types, differences in precipitation are less evident. However, seasonality precipitation was an important factor conditioning the turnover component of total beta diversity (βSOR) of the bromeliad communities. Analogous results were found for the tree component, being the differentiation between Ombrophilous (Evergreen) and Semideciduous (Seasonal) forests strongly correlated with rainfall regime and temperature variation (Oliveira-Filho & Fontes 2000). A similar situation has been recorded in studies performed on South American and African inselbergs, showing rainfall as the driver of floristic heterogeneity at regional scale (Parmentier et al. 2005, Sarthou et al. 2017).

Continentality was an important variable for species composition in seasonal forests, expressed by large proportions of variation explained in total beta diversity. Corroborating this assumption, the pattern of geographical distribution of bromeliads in Rio Grande do Sul and Santa Catarina has great longitudinal influence, mainly due to the effect of the Serra Geral Highlands (South Brazilian Plateau) and to the species irradiation of the more tropical Atlantic Forest into the southern of this mountains (Winkler 1982, Reitz 1983, Waechter 2007). Furthermore, the distance from the ocean, used as proxy for continentality, is considered an important variable in the composition of epiphytic bromeliads in South Brazilian Atlantic Forest (Fontoura *et al*. 2012).

Several supra-generic systematic groups of bromeliads are associated with different biogeographic regions or particular environmental conditions, thus promoting the replacement of species according to environmental characteristics (Benzing 2000, Givnish et al. 2011). In view of that environmental variables affected the floristic similarity of the communities, we can infer that vegetation is not exclusively influenced by local edaphic and hydrological factors, although these may also influence local vegetation (Hobohm 2014). In addition to having a clear relationship between climatic variables and species distribution, there is a sharing of species between the vegetation matrix and the rocky environment (Melo & Waechter 2018).

The detected variation in the structure of bromeliad communities is a result of spatial variables, as well as environmental variables structured along to the geographic space, which in fact had a major proportion in the explanation of data variation. A spatially structured gradient was also found in studies conducted in rocky outcrop in French Guiana and in south-eastern rock grasslands Brazil (Silva Mota et al. 2018, Sarthou et al. 2017). Similarly, floristic patterns of Bromeliaceae epiphytes in the Brazilian Atlantic Forest were mainly associated with space (Leitman *et al*. 2015). This result may also be related to the dispersion capacity of some species of bromeliads, or suggest the absence of some pollinators (bats, hummingbirds, bees and butterflies), indicating that environmental constrains positively correlate with spatial distances affect the floristic differences in this spatial scale (Brown & Lomolino 2001). Additionally, spatial distance has been used by researchers as a proxy for dispersion limitation (Zellweger et al. 2017). The percentage of variation in beta diversity that cannot be explained by either space or the environment predictors may be related to local environmental variations, biological interactions, and mainly to the degree of disturbance in the areas surrounding the cliffs, which were not measured.

In fact, neutral and niche processes can operate together to define the patterns of species diversity and distribution (Leibold & McPeek 2006, Segre et al. 2014), and our results clearly corroborate this premise, indicating that both are important in the structuring of epilithic bromeliad communities and the maintenance of local and regional biodiversity. Spatial filters and spatially structured environmental variations assume that species dissimilarity increases with increasing distance due to the relation between niche processes and environmental gradients (Bell *et al*. 2006). The high turnover values indicate that species occupy different spaces, and that the sites differ in environmental characteristics, selecting bromeliad species. In order to conserve this diversity of species, it is important to maintain the present environmental characteristics and identify habitats where species are restricted. In addition, if beta diversity is the result of spatial and environmental processes, the conservation of landscape organization and species-space-environment relationships is highly necessary to maintain species diversity.

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Authors' Contributions

Edilaine Andrade Melo: Substantial contribution in the concept and design of the study; contribution to data collection; contribution to data analysis and interpretation, contribution to manuscript preparation and Contribution to critical revision, adding intellectual content.

Jorge Luiz Waechter: Substantial contribution in the concept and design of the study; contribution to data collection; contribution to data analysis and interpretation, contribution to manuscript preparation and Contribution to critical revision, adding intellectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

This study did not involve humans and /or clinical trials, following all applicable guidelines.

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Article

Uses of wild vertebrates in traditional medicine by farmers in the region surrounding the Serra do Conduru State Park (Bahia, Brazil)

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Abstract: Wild and domestic animals and their by-products are important ingredients in the preparation of medicines traditionally used in folk medicine, present in various human cultures since antiquity. However, the decline in the number of species in neotropical regions as a result of hunting for various purposes, including food, medicine and magico-religious use, has placed some species – especially endemic species - at risk of extinction. In this context, the present study aimed to identify the wild vertebrate species used in folk medicine in five communities in the region surrounding the Serra do Conduru State Park (PESC), Bahia, Brazil. Forty-five hunter-farmers were interviewed, citing 23 species, from which 17 raw materials are extracted for prevention and/or treatment of 19 illnesses. Mammals were the most cited taxon followed by birds and reptiles. Among the species mentioned, *Cuniculus paca* is the most used for zootherapy purposes, followed by *Salvator merianae* and *Sphiggurus insidiosus*. There was dissimilarity between the communities in relation to the diversity of species used for zootherapy. Ten categories of body systems were classified for which the therapeutic resources are recommended. Disorders related to the middle and inner ear were the most cited. Some of the species mentioned are endangered, such as *Bradypus torquatus* and *Lachesis muta*. This research demonstrated that zootherapy is a traditional practice embedded in these communities. Further studies are needed to broaden knowledge of other species that may have important cultural value for these families, as well as to evaluate the potential implications of the uncontrolled use of these species in traditional medicine in an ecological context, since the practice of zootherapy can excerpt pressure on critical animal populations and threaten biodiversity.
Keywords: *Ethnozoology, zootherapy, conservation, Serra do Conduru.*

Usos de vertebrados silvestres na medicina tradicional por caçadores-agricultores da região do entorno do Parque Estadual Serra do Conduru (Bahia, Brasil)

Resumo: Animais silvestres, domésticos e seus subprodutos são ingredientes importantes na preparação de medicamentos tradicionalmente utilizados na medicina popular, presentes em várias culturas humanas desde a antiguidade. No entanto, a diminuição do número de espécies nas regiões neotropicais, por meio da caça para diversas finalidades, como uso alimentar, medicinal e mágico-religioso tem colocado espécies em risco de extinção, especialmente as endêmicas. Nesse contexto, o presente estudo objetivou identificar as espécies de vertebrados silvestres utilizadas na medicina popular em cinco comunidades na região do entorno do Parque Estadual Serra

do Conduru (PESC), Bahia, Brasil. Foram entrevistados 45 caçadores-agricultores que citaram 23 espécies os quais são extraídas 17 matérias-primas para prevenção e/ou tratamento de 19 enfermidades. Os mamíferos foi o táxon com maior número de citações, seguido pelas aves e répteis. Dentre as espécies citadas a *Cuniculus paca* é a mais utilizada para fins zooterápicos, seguido por *Salvator merianae* e *Sphiggurus insidiosus*. As comunidades apresentaram uma dissimilaridade em relação a diversidade de espécies de uso zooterápicos. Foram classificadas 10 categorias dos sistemas corporais para os quais os recursos terapêuticos são recomendados. Transtornos relacionados ao ouvido médio e interno foram os mais citados. Algumas espécies citadas encontram-se ameaçadas de extinção, como a *Bradypus torquatus* e *Lachesis muta*. A pesquisa mostrou que a zooterapia é uma prática tradicional inserida nas comunidades. Estudos adicionais são necessários para ampliar o conhecimento sobre demais espécies que possivelmente desempenham importante valor cultural às famílias, bem como avaliar em um contexto ecológico às implicações que pode acarretar com o uso descontrolado dessas espécies na medicina tradicional, uma vez que a prática da zooterapia pode causar pressão sobre populações animais críticas e ameaçar a biodiversidade.
Palavras-chave: *Etnozoologia, zooterapia, conservação, Serra do Conduru.*

Introduction

Humans have always used nature as a source of survival resources, including disease and illness treatments, with traditional medical practices including the use of plants, animals and minerals to produce remedies (Alves & Rosa 2012, Alves & Souto 2010, Souto et al. 2000). Traditional forms of medicine have been strongly incorporated into contemporary societies, including phytotherapy and zootherapy, which are among the various therapeutic alternatives used throughout the world (Alves & Rosa 2005). In modern societies, zootherapy is an important alternative alongside the many other known therapies that are practiced (Adeola 1992). Wild and domestic animals and their by-products are important ingredients in the preparation of traditionally-used medicines (Anageletti et al. 1992) and have been present in various human cultures since antiquity (Gómez-Ulla 1983, Lev 2003).

Worldwide, studies on zootherapy have increased in the last years, demonstrating that this practice is common in various parts of the world (Alves & Rosa 2007a,b, Alves 2007, Kakati et al. 2006, Lev 2003, 2006, Mahawar & Jaroli 2006, Mahawar & Jaroli 2007, Negi & Palyal 2007, Pieroni et al. 2002). In Latin America, many cultures still resort to animal-derived remedies as part of their traditional medicine practices, most of them deeply rooted in a long-standing tradition of wild fauna use, including many endangered species, to treat all kinds of diseases (Martínez 2013). In México the use of 18 species was recorded in Mapimi, Durango (Jacobo-Salcedo et al. 2010), 24 species in San Luis Potosí (Alonso-Castro et al. 2011), and 74 species in the state of Chiapas (Enriquez Vazquez et al. 2006). More than 20 species used by the Izoceño-Gurani from the South East Bolivia (Bourdy et al. 2004) and 14 species traded in the Bolivian rain forest (Apaza et al. 2003) were also reported.

In Brazil, publications containing quantitative data on zootherapy have recorded that about 290 species of animals are used in Brazilian traditional medicine (Almeida 2007, Alves 2008, Alves et al. 2007, Alves & Rosa 2006, 2007a,b). Specifically in Northeast Brazil, zootherapy is a very common practice (Alves 2009, Alves & Rosa 2005, Costa-Neto 2002), evidenced, for example, by the use of about 95 animal species in folk medicine in the state of Bahia (Costa-Neto 2011), 36 species in the semiarid region of Pernambuco (Alves et al. 2009) and 51 species in the Caatinga Biome in the state of Paraiba (Alves et al. 2011). However, the decrease in the number of species, especially in neotropical regions, through hunting, structural changes to ecosystems and varied uses has led to the extinction of species before science has even had a chance to study them (Costa-Neto 2011).

In recent years, studies have shown that the link between traditional medicine and the loss of certain species has become apparent (Alves et al. 2007, Call 2006) showing that zootherapeutic use has an additional impact on wildlife populations (Alves et al. 2013, Rosa et al. 2011). This follows the tendency already observed in other countries, especially in Asia, where some species have been heavily targeted for traditional medicine (Kikuchi 2012, Zhang et al. 2008). Thus, studies of zootherapy and its significance for human communities should be conducted in order to determine the best way to exploit natural resources, leading to the long-term sustainable use of animals used culturally for this purpose (Alves & Rosa 2006). In addition to providing information about the species utilized for traditional purposes (medicinal, religious, food, etc.), which can contribute to the development of actions that allow the maintenance of faunistic resources (Almeida & Albuquerque 2002, Alves 2009, Alves & Rosa 2010).

In this context, the present study aimed to identify and characterize the wild vertebrate species used by hunter-farmers in traditional medicine in the region surrounding the Serra do Conduru State Park (PESC), located in the Atlantic Forest (*Mata Atlântica*) of the state of Bahia, Brazil. The following questions were addressed in the field study: which species are used for medicinal purposes? What body parts are used for the preparation of these remedies? What diseases are treated by these remedies?

Materials and Methods

1. Study area

The Serra do Conduru State Park (14º 26' 53" S; 39° 05' 36" O) (Figure 1) is a full protection Conservation Unit (CU) with a total area of 9,275 hectares, created by State Decree Nº. 6,227 of February 21, 1997, in exchange for the perpetuation of a highway (BA 001) (Bahia 2005). It is located within the Costa de Itacaré/Serra Grande Environmental Protection Area (APA). Both have the conservation of the remnants of the Atlantic Forest and the biodiversity of southern Bahia as one of their objectives (Bahia 2005, MMA 2004).

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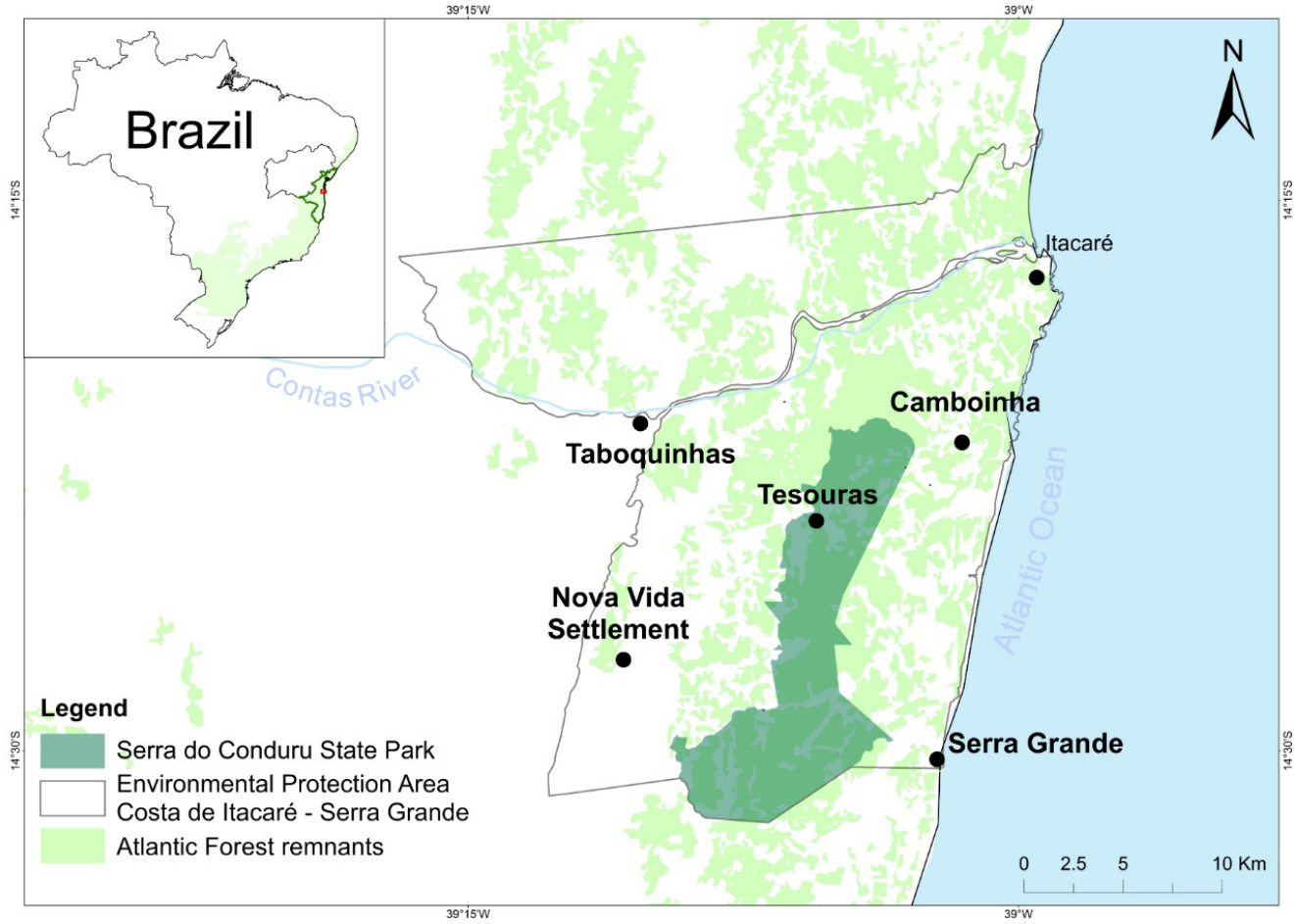


Figure 1. Map of the study area identifying the Serra do Conduru State Park; Costa de Itacaré/Serra Grande Environmental Protection Area; the municipality of Itacaré and the communities in which the field study was carried out with hunters: Camboinha Settlement (AC), Community of Tesouras (CT), Nova Vida Settlement (NV), District of Serra Grande (SG) and District of Taboquinhas (DT).

In the inventory of the PESC management plan, 39 species of mammals were recorded, eight endemic to the Atlantic Forest and four endemic to the Atlantic Forest of southern Bahia (Bahia 2005). Previous studies conducted in the region during the "South Bahia corridor" (IESB/PROBIO/MMA) project in 1999/2002 identified at least 45 amphibian species, including endemic and endangered species; 175 species of birds, 27 endemic and 6 endangered; 9 species of small mammals and 30 species of medium and large mammals, some of which are endangered (Silvano & Pimenta 2003, Cordeiro 2003, Moura 2003).

For this reason, the Atlantic Forest of southern Bahia is indicated as a priority area for conservation. It is here that the most important remnants of Atlantic Forest in the Northeast of Brazil are found, rich in biodiversity and endemic species, considered to be of high biological importance (Alger & Caldas 1994, Leol-Galindo & Câmara 2003, Martini et al. 2007, MMA, 2000).

The study was undertaken in five communities in the region: District of Serra Grande (SG), District of Taboquinhas (DT), Nova Vida Settlement (NV), Camboinha Settlement (AC) (located within the Costa de Itacaré/Serra Grande APA and in the region surrounding the PESC) and the Community of Tesouras (CT) (within the limits of the PESC) (Figure 1). Hunting is prohibited in all of the communities (Instituto Ynamata, 2008).

Serra Grande (14º 27' 53" S; 39º 02' 24" W) is a district of the municipality of Uruçuca in the south of Bahia. It was founded in 1941 and is located almost 40km from the municipality's center. It has an estimated population of 3,585 inhabitants, 74% residing in the urban area and 26% in rural areas (Instituto Ynamata, 2008).

The district of Taboquinhas (14º 21' 24" S; 39° 10' 30" W) is located 28 km from the municipality of Itacaré. Before tourism the economy was based on the cultivation of cacao, but with the fall of the crop and the advance of tourism the district began to value its natural wealth more. The Camboinha Settlement (14º 21' 35" S; 39° 02' 12" W), located between the district of Serra Grande and Itacaré, is made up of small farmers who dedicate themselves to agriculture and local handicrafts (Instituto Ynamata, 2008, Sema 2005).

The Nova Vida Settlement (14° 29' 45" S; 39° 12' 14" W) consists of small farmers who were expropriated during the implementation of the PESC and who came from the communities of Serra Azul and Tesouras, alongside the old residents of the community itself. The community is made up of 44 families whose income is based on family farming (Ribeiro & Schiavetti 2009, Sema 2005).

Tesouras is a community (14° 23' 41" S; 39° 05' 21" W) composed of 8 families residing within the PESC. Even though human presence is prohibited within the full protection CU, these families still reside

inside the park due to the slow process of land regularization (Ribeiro & Schiavetti 2009, Sema 2005). In view of this, the major problems related to the implementation of the PESC at present are the presence of residents inside the park who continue to carry out agricultural and hunting activities, and the constant removal of timber from the area of the Park (Sema 2005).

2. *Data collection*

Data collection took place between September 2016 and July 2017. Only farmers who had been engaged in hunting in the region for at least two years or who have hunted for at least a two-year period of their lives and who use animal by-products for zootherapeutic purposes, participated in the study. As such, 45 informants (44 men and 1 woman) aged 18 to 90 participated in the study. Each informant was interviewed only once.

The respondents were selected by the criterion of native experts, i.e. those who recognize themselves and are recognized by the community as culturally competent (Hays 1976) and by the snowball sampling technique (Bailey 1982). These two techniques made it possible to interview all hunters who use zootherapeutic products in the region. Sampling was non-random intentional, in which the interviewees were pre-defined (Albuquerque & Paiva 2004). Thus, only hunters who use zootherapeutic products participated in the research.

Information was obtained through open and semi-structured interviews, complemented by informal conversations (Huntington 2000). During the interviews questions about the animal species used for medicinal purposes, their respective uses, preparations and parts utilized. The free-listing technique was used to record the names of the animals used by the respondents, based on the principle that the most culturally important elements appear in many of the lists in order of cultural importance (Albuquerque et al. 2008). In order to overcome the existing limitations of free-listing, non-specific induction prompting and reading back were performed (Albuquerque et al. 2008).

To respect intellectual property rights, we adopted the following protocol in the field: before the survey, we introduced ourselves, explained the nature and objectives of our research and asked the respondents for permission to record the information. Prior to each interview, a Free and Informed Consent Form (TCLE) and an authorization term for the use of images were submitted to the respondents, according to the norms established by Resolution No. 196 of the National Health Council of 10/1996 and approved by the Committee of Ethics in Research with Human Beings (CEP) of the State University of Santa Cruz (Caae 61683516.2.0000.5526).

The vernacular names of the medicinal specimens were recorded as denominated by the respondents and identified according to the specimens, or parts thereof, donated by the respondents; photographs of the animals taken during the interviews and/or photographs shown to the interviewees; and with the help of taxonomists familiar with the fauna of the study area (Alves & Rosa 2006), and based on zoological and ethnozoological studies carried out in the study area (Argôlo 2004, Castilho et al. 2013, Lobão 2011, Pereira & Schiavetti 2010, Ribeiro & Schiavetti 2009, Sema 2005, A. E. Encarnação, dados não publicados).

The classification and nomenclature used followed the specifications of the Brazilian Ornithological Records Committee for birds (CBH 2014) and the Brazilian Society of Herpetology (SBH 2016) for reptiles. For mammals, the 2nd edition of the Annotated Mammalian List of Brazil was consulted (Paglia et al. 2012). The Red Book of Endangered Brazilian Fauna (Machado et al. 2008), the IUCN Red List (International Union for Conservation of Nature) (IUCN 2014) and the official list of endangered species of the state of Bahia (SEMA 2017) were consulted to ascertain the conservation status of the species recorded. All material collected in the field was registered and deposited in the Alexandre Rodrigues Ferreira Mammalian Collection (CMARF) of the State University of Santa Cruz (UESC).

3. *Data analysis*

The results were analyzed qualitatively, according to the unified model of individual competence, according to which all information regarding the research subject is considered (Marques 1991). The diseases treated with zootherapeutic resources cited by the interviewees were distributed into 10 categories, based on the tenth revision of the International Statistical Classification of Diseases and Related Health Problems (CID, 2008) as follows: (1) chronic diseases; (2) sexual dysfunction; (3) skin and subcutaneous tissue diseases; (4) neoplasia (5) problems in the skeletal system; (6) middle ear and inner ear disorders; (7) disorders of the circulatory system; (8) disorders of the teeth and their supporting structures; (9) disorders in the respiratory system; (9) disorders in the urinary system and (10) indefinite diseases.

The influence of the five communities surveyed on the species composition cited by the interviewees was tested using a permutational multivariate analysis of variance (Anderson 2005). We used Jaccard distance and 1000 permutations. PERMANOVA uses the "Adonis" procedure in the vegan package for R (Oksanen 2011). We also used non-metric multidimensional scaling (NMDS) to represent the results of the PERMANOVA analyses. In the NMDS, we also used the Jaccard for the ordination of species composition. All analyses were performed in the software R (Development Core Team R 2017).

Results

1. *Species of medicinal use*

In the present study, 23 wild vertebrate species from 21 families were identified from which 17 raw materials were extracted to prevent or treat 19 traditionally recognized illnesses (Table 1). Only two families are composed of two species: Canidae (*Nasua nasua* and *Cerdocyon thous*) and Dasypodidae (*Dasypus novemcinctus* and *Euphractus sexcinctus*), the other families are represented by a single species. All species mentioned are native to the regionand are caught within the hunter's residence limits. Mammals were the taxon with the highest number of species mentioned, followed by reptiles and birds (Table 1). The paca *Cuniculus paca*, the tegu *Salvator merianae*, the Bahia hairy dwarf porcupine *Sphiggurus insidiosus*, the six-banded armadillo *Euphractus sexcinctus*, the nine-banded armadillo *Dasypus novemcinctus*, the South American bushmaster *Lachesis muta*, the coati *Nasua nasua* and the sloth *Bradypus sp*. were the species with the highest number of mentions.

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Table 1. Species of wild animals used in traditional medicine in the PESC region.

ANIMAL CITED	SPECIES	PART OR PRODUCT	FUNCTION	POPULAR PRESCRIPTION
MAMMALIA = 56.5% (Nº = 13 species/11 families/6 orders)				
Agouti	*Dasyprocta leporina* (Linnaeus, 1758)	Fur	CVA*	*"Toast the fur and smell the smoke"*
Bahia hairy dwarf porcupine	*Sphiggurus insidiosus* (Olfers, 1818)	Quills	CVA*	*"Toast and drink in hot water"* *"Burn the quills and inhale"*
Bat	Chiroptera (Order)	Whole animal	Nasal discharge	*?*
Big-eared opossum	*Didelphis aurita* (Wied-Neuwied,1826)	Lard	Nasal discharge	*"Drink it in warm water"*
Coati	*Nasua nasua* (Linnaeus, 1766)	Penis	Male impotence	*"When the person is no longer good for anything, when the guy gets disarmed (laughs), those old people"* *"Scrape from the bottom up saying that you want it to go up, throw the powder in warm water and drink it"*
Crab-eating fox	*Cerdocyon thous* (Linnaeus, 1766)	Liver	Fatigue Asthma Bronchitis	*"Fry it or roast it and eat it without salt"*
Golden-headed lion tamarin	*Leontopithecus chrysomelas* (Kuhl, 1820)	Liver	Cancer	*"Roast the liver and eat it"*
Kinkajou	*Potos flavus* (Schreber 1774)	Fur	Nasal discharge	*"Toast them, make the powder and put it in water"*
Nine-banded armadillo	*Dasypus novemcinctus* (Linnaeus, 1758)	Tail Shell	Earache Dogs bad at hunting	*"Scratch the ear [with it] when it's hurting"* *"Throw the shell on the fire and leave the dog tied up nearby smelling the smoke"*
Paca	*Cuniculus paca* (Linnaeus, 1766)	Gallbladder Bile	Kidney disease Any tip of pain Diabetes	*"Conserve with alcohol and drink"* *"put the gall in white wine, bury it and after 8 to 15 days you can drink it"* *"For men it has to be the gall of the female paca and for the woman the gall of the male paca"* *"conserve with alcohol and drink"*
		Gallbladder Bile Lard	Snake bite	*"With a snake bite, take the paca's gall, put it in water and drink it"*
		Visceral peritoneum of the liver "oroma"	Snake venom	*"Eat the roasted 'oroma' of the liver"*
Six-banded armadillo	*Euphractus sexcinctus* (Linnaeus, 1758)	Shell Tail Stomach "tripe"	Fatigue Earache Wounds	*"Toast the shell and put it in water, then drink it"* *"Take off the tail of the armadillo before it dies, if you take it once the animal is dead it's no good..., put it to dry and scratch your ear with it when it hurts"* *"Take the tripe, toast it, put it to dry and step on it and put it on top [of the wound]"*
Sloth	*Bradypus* sp.	Fur Fur Leather	Spiritual illness Hemorrhoids Back pain	*"For people who have "caboco", those dogs that bite, its only with smoke that you can get them out" (use of smoke as a cure)* *?* *"Dry the leather and put it on top of the mattress and sleep straight"*

Continuation Table 1.

ANIMAL CITED	SPECIES	PART OR PRODUCT	FUNCTION	POPULAR PRESCRIPTION
Southern tamandua	*Tamandua tetradactyla* (Linnaeus, 1758)	Stomach "tripe" Claws	Bronchitis Dogs bad at hunting	*"Toast it, put it in warm water and give it to someone when they have nasal discharge"* *"Burn the claw and give it for the dog to smell"*
REPTILE = 26.1% (Nº = 6 species/6 families/3 orders)				
Broad-snouted Caiman	*Caiman latirostris* (Daudin, 1802)	Lard	Bronchitis	*"Put it in warm water and drink it"*
Lava lizard	*Tropidurus* sp.	Heart	Spots on the skin; Pityriasis versicolor	*"Roast it and eat it without seasoning, toasted"*
Boa constrictor	*Boa constrictor* (Linnaeus, 1758	Lard	Back pain; Rheumatism	*"Fry the lard and rub it on the back"*
Red-footed tortoise	*Geochelone carbonaria* (Spix, 1824)	Whole animal	Back pain	*"Put it to sleep under the bed."*
Tegu	*Salvator merianae* (Duméril & Bibron, 1839)	Lard Lard Lard Lard Lard Lard Lard Lard	Snakebite prevention Rheumatism Cough Back pain Pityriasis versicolor Spots on the skin Earache Toothache	*"Fry the lard and throw drops on the site and drink a little as well"* *"Fry the lard and put it on and rub on top"* *"Put it in warm water and drink it"* *"Fry the lard and put it on and rub on top"* *"Rub the fried lard at the site"* *"Rub the lard at the site of the pain"* *"Rub the conserved lard on the site of the spot"* *"Conserve the lard and when you use it you just heat it up and put it in the ear"* *"Rub the lard at the foot of the tooth, the tooth will rise, rise rise… in no time it falls"*
South American bushmaster	*Lachesis muta* (Linnaeus, 1766)	Liver Liver Venom Liver Liver	Terminal disease in dogs Snakebite prevention Cancer Rheumatism Back pain	*"Make the dog eat it raw"* *"Eat it roasted, if a snake bites you, you don't feel anything"* *?* *"Toast the lard and conserve it in alcohol, rub it on the site every night"* *"Toast the lard and conserve it in alcohol, ask someone to rub it on the spine"*
BIRDS = 17.4% (Nº = 4 species/4 families/3 orders)				
Black vulture	*Coragyps atratus* (Bechstein, 1793)	Feathers	CVA*	*"The person has to smell the burned feathers"*
Red-rumped cacique	*Cacicus haemorrhous* (Linnaeus, 1766)	Nest	CVA*	*"Cook the nest, drink one part and take a shower with the other"*
Solitary tinamou	*Tinamus solitarius* (Vieillot, 1819)	Feathers	CVA*	*"Burn the feathers of the animal and stay close to the smell"*
Southern house wren	*Troglodytes musculus* (Naumann, 1823)	Nest	CVA*	*"Throw the nest in fire and breathe in the smoke"*

Wild vertebrates used in traditional medicine by hunter-farmers in the Serra do Conduru State Park region. Recorded: June/16 to June/17. (?) Did not know how to respond. (*) Cerebrovascular accident. Source: research data.

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The Bile (secreted by the liver and stored in the gallbladder, traditionally recognized as "gall") was the main raw material used from the paca, which hunters regarded as "a holy remedy" and with therapeutic powers for various diseases, usually taken in warm water, white wine or alcohol (Figure 2). Tegu lard was the only by-product extracted from the species and used as a medicinal resource in the region to treat various illnesses such as rheumatism, back pain and toothache.



Figure 2. (A) Gallbladder of the paca *Cuniculus paca* (Linnaeus, 1766) preserved by smoking in a wood stove at the hunter's residence. (B) *Cuniculus paca* (Linnaeus, 1766) captured by a hunter from the region of the Serra do Conduru State Park. Recorded: June/16 to June/17. Photo: Author.

The thorn of the Bahia porcupine is used as a medicine to treat cerebrovascular accidents, a condition known to hunters as "stroke". The tail of the armadillo species *Euphractus sexcinctus* and *Dasypus novemcinctus* is used to treat diseases related to the auditory system where the raw material serves as an instrument to scratch the ear at the time of earaches. In addition to their use for zootherapy, the use of wild species for food was also observed.

There was dissimilarity between the five communities regarding the composition of species used medicinally (PERMANOVA, p = 0.04). Eleven species were mentioned exclusively by one of the communities; three species were mentioned by two of the communities; two species were shared by three of the communities; five species were of common medical use in four of the communities and only two species (*Cuniculus paca* and *Salvator merianae*) (Figure 3) were shared by all five communities, with similar preparation of the raw material extracted from the two species in all the communities.

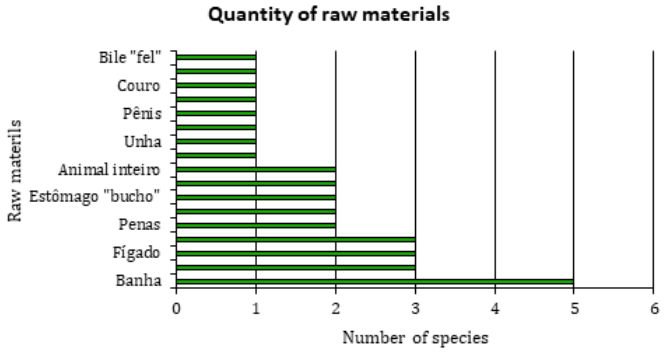


Figure 3. Quantity of raw materials from wild vertebrates used in traditional hunter farmer medicine in the region of Serra do Conduru State Park. Recorded: June/16 to June/17.

The zootherapeutic item cited with the greatest frequency was animal fat, a product that can be extracted from the following animals: *Didelphis aurita, Caiman latirostris, Cuniculus paca, Boa constrictor and Salvator merianae*. It is collected from five species that form part of the local prescription resource (Figure 4). Besides lard, other by-products such as claws, leather, fur, penis, tail, shell, feathers and liver are also used. The number of parts or products obtained from each animal varied from one to three; however, some species are used in their entirety, as is the case of the red-footed tortoise *Geochelone carbonaria* and bats (*Order Chiroptera*).

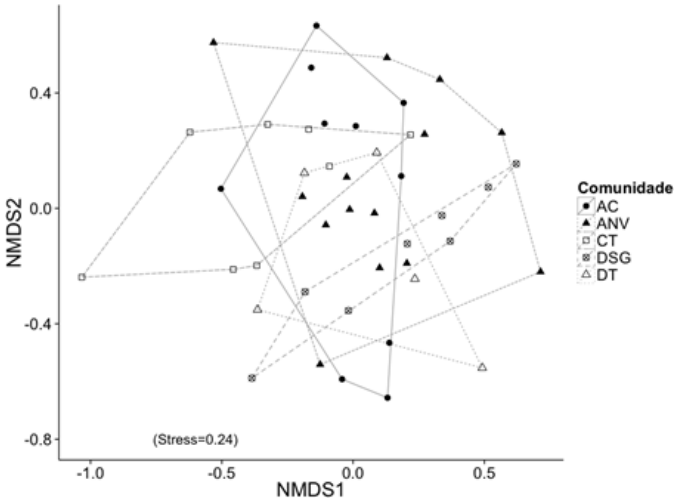


Figure 4. NMDS analysis showing the dissimilarity of the composition of wild animal species used as medicinal resources by hunter farmers in the five localities (communities) studied in the Serra do Conduru State Park region.

In the communities studied, animal by-products are roasted and processed into powder to be preserved or taken with warm water, teas, wine and/or other liquids, depending on the illness. Some parts, such as the liver of the crab-eating fox *Cerdocyon thous* are ingested directly, roasted or fried, without using seasoning or salt, locally termed "eating it bland." Some religious beliefs and rituals have also been mentioned: the red-footed tortoise, for example, is placed under the bed of people who experience back pain and the fur of sloth species is used to keep bad spirits away from people.

2. *Categorization of body systems*

Ten categories were classified for which therapeutic resources are recommended. Some diseases were listed in the category "indefinite diseases" due to characteristics that did not fit into the other categories (Table 2). Disorders related to the middle and inner ear, such as earache, were the most cited, with two therapeutic resources for their treatment: six- or nine-banded armadillo tails or tegu lard. Respiratory disorders (asthma, fatigue, cough and bronchitis) was the category with the second highest number of mentions, using eight therapeutic resources for treatment, followed by chronic diseases (diabetes), using only one zootherapy resource (paca "gall") for its treatment (Table 2).

Table 2. Categorization of body systems (ICD-10 2008).

Body system	Treatable problems	Number of raw materials	Nº of mentions	(%) Mentions
Chronic diseases	Diabetes	1	22	14.8
Sexual dysfunction	Male impotence	1	21	14.1
Skin and subcutaneous tissue diseases	Pityriasis versicolor; spots on the skin; wounds	3	10	6.7
Neoplasia	Cancer	2	2	1.3
Problems in the skeletal system	Rheumatism; back pain	6	14	9.4
Middle and inner ear disorders	Earache	2	29	19.5
Circulatory system disorders	CVA*, hemorrhoids	4	12	8
Disorders of the teeth and their support structures	Toothache	1	4	2.7
Respiratory tract disorders	Asthma; fatigue; cough; bronchitis	8	27	18.1
Disorders in the urinary system	Renal pain	1	3	2
Indefinite diseases	Protection from snake venom; any type of pain; any type of disease; dogs bad at hunting; terminal illness in dogs, spiritual problems	6	22	14.8
Total mentions			149	100

Categorization of body systems in accordance with the International Statistical Classification of Diseases and Related Health Problems (ICD-10 2008) from which raw materials are used by hunter farmers in the PESC region for traditional medicine. Register: June/16 to June/17. (*) Cerebrovascular accident. Source: research data.

Some species of vertebrates mentioned are used for the treatment of more than one disease, such as tegu lard which is used to treat diseases like rheumatism, cough, back pain, Pityriasis versicolor and earache. On the other hand, some different species are indicated to treat the same disease, such as CVA, for which therapeutic resources from 6 species are used for treatment.

3. Conservation status

Of the recorded species, four are included in the endangered species categories established by the IUCN: Critically Endangered (CR), Endangered (EN), Vulnerable (VU) and Near Threatened (NT) (IUCN, 2014, Machado et al. 2008, Sema, 2017). The maned sloth *Bradypus torquatus* and the South American bushmaster *Lachesis muta*, which provide two and three raw materials for disease treatment respectively, are considered to be vulnerable in the wild. The solitary tinamou *Tinamus solitarius*, the feathers of which are used in the treatment of diseases, and the golden-headed lion tamarin *Leontopithecus chrysomelas*, the roasted liver of which is used for cancer treatment, are considered to be endangered (IUCN, 2014, Machado et al. 2008, Sema, 2017).

Discussion

1. Species of medicinal use

As in the present study, several publications have shown the importance of zootherapy in different rural communities in Brazil (Alves 2008, 2009, Alves & Pereira-Filho 2007, Alves & Rosa 2007a,b,c, Barboza et al. 2007, El-Kamali 2000, Kakati & Douto 2002, Mahawar 2006, Vázquez 2006). For example, Branch & Silva (1983) reported 33 species in Alter do Chão in the state of Pará; Begossi (1992) reported the use of 10 species on Ilha de Buzios in São Paulo. Marques (1995) noted the use of 56 species in Varzea de Marituba in the state of Alagoas, while Seixas & Begossi (2001) reported 16 species used on Ilha Grande in Rio de Janeiro. Rodrigues (2006) reported the use of 29 species in Parque Nacional de Jau, Amazonas, while Alves & Rosa (2006, 2007a,b) described the use of 74 species in Mamanguape in Paraiba, 57 species in Raposa in Maranhão, 54 species on Ilha do Marajo, and 46 species in Cajueiro da Praia in Piaui.

In the state of Bahia, there was a report of 23 species in the municipality of Remanso (Costa-Neto 2000a) and 34 species in the city of Tanquinho 34 (Costa-Neto 2000b). In larger sphere, Costa-Neto (2004) pointed to the use of 180 animals in traditional medicine throughout the state. In the Atlantic Forest region of south Bahia specifically, the use of 14 species as medicinal resources by indigenous Tupinambá hunters from the district of Olivença (Ilhéus) has been described (Pereira & Schiavetti 2010) and 11 species used by the residents of the Serra do Conduru State Park (Ribeiro & Schiavetti 2009). This study demonstrates the importance of zootherapy for families in the Region Surrounding the PESC.

The fact that the mammals are the taxon with the highest number of species cited, followed by reptiles and birds corroborates the results obtained by previous authors, which show that, after fish, mammals and reptiles present the greatest number of species used as medicine in Brazil (Almeida & Albuquerque 2002, Alves 2008, Begossi & Braga 1992, Branch 1983, Silva et al. 2004). In line also with the catalogue of 584 species of animals of medicinal use in Latin America, which reveals that mammals are the group with most medicinal animals (Alves & Alves 2011). As in this study, other research has indicated widespread use of the family Canidae in Latin America, Africa and Asia, and describe their use for treating 28 ailments, such as asthma, arthritis, and backache (Alves et al. 2010).

In addition to their use for zootherapy, the use of wild species for food was also observed. This indicates another anthropic disturbance that acts in conjunction (synergistic effect) with medicinal use and entails an impact on the conservation of the vertebrates mentioned here. According to Alves and Rosa (2006) the multiple use of wild animals, which includes medicinal and food aspects, should be properly evaluated to understand the pressure that target species are subject to.

Historical studies indicate that the paca, species with the highest number of mentions for medicinal use in the study region, has suffered from the pressure of hunting for some time (Cardim 1925, Gândavo 1956, Silva 1898), in addition to studies published in several regions that describe the capture of the species in the last years (Canale 2012, Chiarello 2000, Freitas et al. 2005, Peres 1990, Peres & Nascimento 2006, Varnhagen 1860). Fernandes-Ferreira and Alves (2014) in their work on the historical and current panorama of hunting in Brazil affirmed that the paca was cited by respondents from all biomes, allowing its identification as the preferred mammal for hunting in Brazil. In south Bahia the species was indicated the vertebrate that plays a major role in hunting for local communities (Castilho et al. 2018). However, due to their high demand, their population number may have been reduced in regions where they have been exploited excessively (Chiarello 2000, Deutsch 1990, Fernandes-Ferreira 2014). According to Alves and Souto (2010) in the Northeast region, mainly in the Caatinga Domain, the paca has already gone extinct in much of its original area of distribution. Fernandes-Ferreira (2011) documents reports of hunters from the Northeast stating that the species has been extinct locally for more than 40 years.

The tegu *Salvator merianae* was identified as the lizard of greatest importance to the zootherapeutic practices of the region, a fact also described by Alves et al. (2012) in a study carried out in two municipalities of Paraíba. The species was also cited by other researchers as a species of zootherapeutic use (Begossi 1992, Fernandes-Ferreira 2011, Klemens 1995, Oliveira et al. 2010, Souto et al. 2011). Fitzgerald (1994) states that lizards of this genus are also heavily hunted for consumption in Argentina, Paraguay, and parts of Bolivia. The review by Alves et al. (2008) describes that reptiles are among the most commonly used species in traditional folk medicine and have been since ancient times. In this aspect, the popularity of the use of tegu fat, a widespread natural medicine, has been the motive of one of the few studies on the clinical efficacy of animal products for medicinal purposes (Ferreira et al. 2010). The Bahia porcupine also referred to by other ethnozoological studies (Castilho 2013, 2018, Oliver 1991) as well as species *Euphractus sexcinctus* and *Dasypus novemcinctus* (Almeida & Albuquerque 2002, Alves et al. 2012, Moura 2003).

The differences in medicinal use of species between the five surveyed communities is possibly related to the cultural beliefs rooted in each family. Traditionally, certain communities have the habit of using different species for the treatment of diseases and illnesses. This use is often restricted to only one or a few communities and is not widespread throughout the region. Another factor that may justify this dissimilarity is the varying frequency of occurrence and/or abundance of species in each community, since they are spatially distant from one another and some are close to urban centers or more urbanized areas, which implies a smaller number of species in these areas. According to Alves et al (2007) and Alves (2009), the use of animal-based medicines is closely associated with local beliefs in different regions of Brazil. Different uses and combinations of hunting techniques may also influence composition of species. Some hunters may be more specialized or like to hunt only one species and others are more generalist, capturing more species.

Other authors have reported the use of similar raw materials as medicines in other Brazilian communities (Alves 2008, 2009, Costa-Neto 1999, 2004), which indicates that their use is widespread in the country. The preference for animal lard is common in zootherapy, described in different world reports (Castilo & Ladio 2019, Filipov 1997, Bourdy et al. 2004; Martinez 2013, Medrano 2016, Moura & Marques 2008) and in the northeastern Brazil (Alves et al. 2008, 2009, Costa-Neto, 1999, Ferreira et al. 2009a,b,c). Silva et al. (2004, 2010) indicated lard as the main by-product of wild animals for medicinal purposes in three public markets in Recife (PE) and in the semi-arid Paraíba. Ribeiro and Schiavetti (2009) also described the lard as the most commonly used animal part by the residents of the Serra do Conduru State Park, also located in southern Bahia state.

Medrano (2012) suggests that the fat holds the greatest potential of desirable attributes, and the possibility of transmission, amplifying this concept to include use/ingestion/contact with diferente animal parts. For Alves et al (2008), the wide utilization of lard can be attributed to the fact that the main medicinal animals utilized are vertebrates which have a large quantity of body fat. Another possible explanation for the marked use of body fat for medicinal purposes can be due its chemical composition. Body fat consists mainly of fatty acids, which have an extensive proven medicinal applicability (Ferreira et al. 2009a, 2010, 2011).

Just like in this research, links between popular beliefs and zootherapy have also been found in other Brazilian communities (Alves 2008,2009, Begossi & Braga 1992, Branch 1983, Costa-Neto 1999, 2004, Marques 1995). The use of armadillo tail (*Euphractus sexcinctus and Dasypus novemcinctus*) to scratch and cure earaches has also been reported in the city of Santas Cruz do Capibaribe, state of Pernambuco (Alves et al. 2008) and in the city of Crato and Juazeiro do Norte, state of Ceará (Ferreira et al. 2009b). Whereas in Brazil, different animal species are used in magical-religious practices of Afro-Brazilian cults (Alves et al. 2009, Alves et al. 2010, Alves & Pereira Filho 2007, Leo Neto et al. 2010, Leo Neto & Alves 2010) in the context of rituals that emphasize the holistic nature of traditional medicine and that are designed to address spiritual, physical, and social-psychological problems (Alves & Rosa 2010).

According to Zweber (2002), cultural issues are recognized as important components of the provision of health care services. The sociocultural and mythical-religious meaning of the species involves symbolic healing actions, or using animals as shamanistic auxiliaries that send and/or heal diseases by the transgression of taboos (Martínez 2010a,b). The zootherapy phenomenon is part of a complex medical system, which includes, among other folk practices of healing and disease prevention, rituals and magic prophylaxis, including mojos (*patuás*), scapulars (*bentinhos*), amulets, talismans, gestures and transfers (Araújo 1977, Vuoto 1999). The use of animals in native medicine transcends mere zootherapy (Vuoto 1999) and for being organized as cultural systems the use of animal substances must be understood from a cultural perspective (Costa-Neto 1999, 2004).

2. *Categorization of body systems*

Wild animals and their parts and products are considered to be important ingredients for preparing curative and preventative medicines (Anyinam 1995). In the context of zootherapy, products of animal origin have been recorded as resources used in the treatment and attenuation of symptoms of various health problems in humans and domestic animals (Coutinho 2010). In this research, the zootherapy products are prescribed for the treatment of common diseases or illnesses in people's day-to-day lives, such as "fatigue" and back pain, however, some recommendations were made for more serious diseases, like CVA and cancer. To the hunters, the use of a particular raw material as a medicine in the region depends on the nature of the illness, and how people understand it culturally.

An analogous trend in relation to medicinal animals was found in cities in the north and northeast of Brazil (Alves & Pereira-Filho 2007, Alves & Rosa 2006, 2007a, Costa-Neto 1999, 2004). According to Alves and Rosa (Alves e Rosa 2007b), the two most frequent categories of use are gastrointestinal and respiratory diseases. Alves (2009) and Costa-Neto (2004) observed that the treatments most cited in Pernambuco and Bahia, respectively, are for the respiratory system, mainly related to the treatment of asthma. In total, 132 wild species used for the treatment of diseases related to the respiratory system were listed in all Brazilian territory (Alves & Rosa 2012). Second Costa-Neto (2004) the animal-based remedies are frequently used to treat respiratory diseases (asthma, cough and bronchitis) (Costa-Neto 2004). Almeida and Albuquerque (2002) indicated that digestive problems represented the highest-use category, followed by respiratory diseases, diseases of the musculoskeletal system, and of connective tissue.

The literature shows that ethnobiological research on traditional medicines from natural resources is a valuable resource in the growing art of bioprospecting for compounds with pharmacological potential (Costa-Neto 1999). However, even with the high number of citations to illnesses treated with animal products commercialized in Brazil, there are few laboratory studies testing its efficacy (Ferreira et al. 2012). Some animals have been methodically tested by pharmaceutical companies as sources of drugs for modern medical science, with the discovery of active principles for the treatment of certain diseases (Kunin & Lawton 1996). For Pieroni et al. (2002) the chemical constituents and pharmacological actions of medicinal products of animal origin are known and ethnopharmacological studies focused on this type of medicine are important in order to clarify their possible therapeutic usefulness.

For example, Ferreira et al. (2011) indicate that the body fat of *Boa constrictor* does not present a clinically relevant bacterial activity, but when combined with antibiotics, the fat demonstrated a significant synergistic activity. Similar results are reported to the decoction of the lizard *Tropidurus hispidus* and the termite *Nasutitermes corniger*. But et al. (1990) report the antifever activity of the preparations using the horn of *Bos taurus*. Murari et al. (2005) and Ferreira et al. (2010) report that extracts of *Pavo cristatus* and the body fat of *Tupinambis merianae* demonstrated anti-inflammatory activity. Tempone et al. (2008) showed that steroids from the skin of *Rhinella jimi* are active against leishmaniasis and trypanosomiasis.

Even with many species commercialized with medicinal uses in Brazil, studies about the improved biological activity of theses products are still preliminary and insufficient. Therefore care must be taken to use wild animals and their by-products for medicinal purposes. Smet (1991) draws attention to the fact that some sideeffects of traditional medicines have proven to be more severe than the disease that they are treating. Zootherapies recommended to treat a specific disease may not contain any active principle capable of producing such an effect or, if present, there may not be an effective concentration after preparation, leading to damage and health risks to those who believe in the efficacy of the product (Costa-Neto 2011). The development of more studies is necessary to understand, evaluate, and validate the traditional and medicinal knowledge associated with the use of animal products (Ferreira et al. 2012). Such considerations must be taken into account, further highlighting the need for clinical studies of traditional remedies (Alves & Alves 2011).

There is also a concern for public health as some species of wild animals may be vectors of some infectious diseases. Diseases and infections that are naturally transmitted between vertebrate animals and humans are known as zoonoses (Bell et al. 1988, Krauss 2003, Van Vliet 2017) and have been known to affect human health throughout history (Kruse et al. 2004) and responsible for 75% of emerging infectious diseases (Chomel et al. 2007; Taylor et al. 2001). Several organs and tissues including bones and bile can be a source of Salmonella infection causing chronic diarrhoea and endotoxic shock. The possibility of transmission of other serious and widespread zoonoses such as tuberculosis or rabies should be considered whenever animal tissues from unknown sources are handled and used as remedies (Schnurrenberger & Hubbert 1981). Another example deserving mention is Avian influenza (Influenza A) viruses; these are responsible for highly contagious acute illness in humans, pigs, horses, marine mammals and birds, occasionally resulting in devastating epidemics and pandemics (Bengis et al. 2004).

However, Ngokwey (1995) strengthens that the possibility of using several remedies for diseases, as quoted in this research, is an adaptation to the availability/accessibility of the animals that can be used and that depending on this factor, it is possible to use several remedies for the same disease. The use of various zootherapeutic resources to treat the same disease demonstrates a utilitarian redundancy, a model proposed by Albuquerque and Oliveira. (Albuquerque & Oliveira 2007). According to these authors, the idea of utilitarian redundancy is based on the theory of ecological redundancy, the notion of functional redundancy relies on the presumption that some species are utilized for the treatment of more than one disease and/or symptom, such that the inclusion of more than one species within a disease category can be a mechanism of reducing the impact on the animals sold for medicinal purposes (Albuquerque & Oliveira 2007).

Ferreira et al. (2009) indicated the use of more than one species for the treatment of some diseases in public markets in the cities of Crato and Juazeiro do Norte, Ceará state, Brazil. The fat from *C. durissus*, for example, is used to treat rheumatism, osteoporosis, leprosy, back-aches, ear-aches, and fissures on soles of the feet; while the rattle from this same snake is used in *simpatias*. The fat of *T. merianae* is used to treat rheumatism, inflammations, fissures on sole of the feet, and ear-aches (Ferreira et al. 2009).

3. *Conservation status*

Studies have estimated that, respectively, 25% and 53% of canids and reptiles used in zootherapy are listed in some degree of extinction

threat according to the IUCN (Alves et al. 2010, Alves et al 2008). Costa-Neto (1999) estimated that 30% of all animal pharmacopoeia in northeastern Brazil is threatened with extinction. With regards to conservation, the use of traditional animal-based medicines can threaten biodiversity (Costa-Neto 2011). As argued by Martínez and collaborators (2013), many species play a key role in local ecosystems and their reduction and disappearance would cause environmental changes. For Marques (1997), the medical potential of the Brazilian fauna and flora allows for exhaustion or extinction of species due to their overexploitation. However, although medical use is relevant because it implies additional pressure on critical animal populations, it should be emphasized that many factors affect vertebrate populations in the PESC region, such as hunting for food and commercial purposes.

In this case, zootherapy should be considered along with other anthropogenic pressures, such as loss of habitat, human activities such as agriculture, domestic animal husbandry, and subsistence hunting (Alves 2009, Leal 2005). It is also necessary to consider where these species are being used, in the case of this study these are environmentally protected areas where it is prohibited to hunt without authorization from the competent organs, regardless of the purpose.

According to Andriguetto-Filho and collaborators (1998), zootherapeutic practices, if properly managed, can be compatible with environmental conservation programs, where the use of natural resources can occur in such a way that human needs and biodiversity protection are guaranteed. This demonstrates the need for further studies to determine the extent to which medicinal use in the region may be causing problems for local vertebrate fauna. Therefore, it is necessary to understand the biology and ecology of species commonly used as remedies to better evaluate the impacts of this use on populations of local species (Alves et al. 2007). The medicinal value of species represents an important link between human society and biodiversity that therefore needs to be recognized in efforts aimed at sustainable use of ecosystems (Alves et al. 2009).

Final Considerations

The results obtained showed that hunter-farmers in the area surrounding the PESC traditionally use wild vertebrates as a medicinal resource in the treatment of diseases and illnesses that are culturally recognized in the communities studied. A total of 23 species were identified from which 17 raw materials are obtained for the treatment of 19 local illnesses. Some of these species are endangered.

Although two species are commonly used for medicinal purposes in all the communities, the research demonstrated a dissimilarity regarding the composition of the species with cultural use in each community. This can also be justified by the frequency and abundance of the species, hunting techniques and their combinations, and the influence of the local culture.

Zootherapy products are used to treat diseases common in the region, such as problems in the skeletal system, middle and inner ear disorders, and circulatory and respiratory system disorders. However, additional studies are needed to broaden knowledge of other species that may exist in the region and which have an important cultural value to families, as well as to evaluate in an ecological context the implications that can result from the uncontrolled use of these species in traditional medicine.

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Author Contributions

Joanison Vicente dos Santos Teixeira: substantial contribution to the design and design of the work; contribution to the acquisition of data; contribution in the analysis and interpretation of data; contribution in the writing of the work.

Jade Santos: contribution to the acquisition of data; contribution in the writing of the work.

Deyna Hulda Arêas Guanaes: contribution to the acquisition of data; contribution in the writing of the work.

Wesley Duarte da Rocha: contribution in the analysis and interpretation of data.

Alexandre Schiavetti: contribution in the writing of the work; contribution in the critical review adding intellectual contente.

Conflicts of Interest

The authors declares that they have no conflict of interest related to the publication of this manuscript.

Availability of Data and Material

The data used to support the fndings of our study are available from the correspondences upon request.

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Article

Urban expansion in the Atlantic Forest: applying the Nature Futures Framework to develop a conceptual model and future scenarios

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Abstract: The Atlantic Forest is an important *hotspot* of biodiversity and ecosystem services that contributes to the well-being of its 125 million human inhabitants, about three quarters of the Brazilian population. In the coming decades, forecasts show that urban areas in the Atlantic Forest will grow at the expense of natural ecosystems, leading to increasing pressure on biodiversity and ecosystem services. We used the Nature Futures Framework (NFF) for envisioning positive scenarios for cities in the Atlantic Forest. First, we developed a conceptual model based on the Driver-Pressure-State-Impact-Response (DPSIR) approach to describe consequences of urban growth for the three NFF perspectives: Nature for Society, Nature for Nature and Nature as Culture. Second, we proposed scenario storylines that encompass multiple social-ecological values of nature and could be used by policy makers to plan desirable futures for the Atlantic Forest. Then, we discussed the impact of distinct policies on these values, identifying the different ways in which the management of urban green and blue spaces, natural ecosystems, and urban densities can lead to different social-ecological outcomes. We further detail the complexity, trade-offs, and synergies regarding city development, nature conservation, and human well-being in this tropical *hotspot*. Applying NFF can contribute to the ongoing debate regarding urban sustainability, by providing an interdisciplinary and integrative approach that explicitly incorporates multiple values of nature and the visualization of positive futures.
Keywords: *Biodiversity; Ecosystem Services; Human well-being; Urban planning; Connectivity.*

Expansão urbana na Mata Atlântica: aplicando o "Nature Futures Framework" para desenvolver um modelo conceitual e cenários futuros

Resumo: A Mata Atlântica é um importante hotspot de biodiversidade e serviços ecossistêmicos que contribui para o bem-estar de seus 125 milhões de habitantes, cerca de três quartos da população brasileira. Nas próximas décadas, a previsão é de que as áreas urbanas na Mata Atlântica crescerão às custas de ecossistemas naturais, conduzindo a um aumento na pressão sobre a biodiversidade e os serviços ecossistêmicos. Nós usamos a perspectiva do *Nature*

Futures Framework (NFF) para visualizar cenários positivos para as cidades na Mata Atlântica. Em primeiro lugar, desenvolvemos um modelo conceitual baseado na abordagem *Driver-Pressure-State-Impact-Response (DPSIR)* para descrever as consequências do crescimento urbano para as três perspectivas do NFF: Natureza para a Sociedade, Natureza para a Natureza, e Natureza como Cultura. Em seguida, propusemos cenários na forma de narrativas que abrangem múltiplos valores socioecológicos para a natureza, e que pudessem ser usados por tomadores de decisão para planejar futuros desejáveis para a Mata Atlântica. Posteriormente, discutimos os impactos de distintas políticas sob esses valores, identificando como diferentes maneiras de gerenciar os espaços urbanos verdes e azuis, os ecossistemas naturais, e as densidades urbanas podem conduzir a diferentes contextos socioecológicos. Ainda, nós detalhamos a complexidade, os *trade-offs* e as sinergias relacionados ao desenvolvimento de cidades, conservação da natureza e bem-estar humano neste *hotspot* tropical. A aplicação do NFF pode contribuir para o debate em andamento sobre sustentabilidade urbana, por meio do fornecimento de uma abordagem interdisciplinar e integrativa que explicitamente incorpora múltiplos valores da natureza e a visualização de futuros positivos.
Palavras-chave: *Biodiversidade; Serviços ecossistêmicos; Bem-estar humano; Planejamento urbano; Conectividade.*

Introduction

Brazil is a highly urbanized country — 90% of the gross domestic product (GDP) is created in cities, which harbour approximately 80% of the country's population (DaMata et al. 2007), mostly located in the Atlantic Forest Domain (Cincotta et al. 2000). This biodiversity hotspot originally covered about 17% of the country's territory and most of its coastal area, and nowadays the region is responsible for 70% of the GDP, 2/3 of the industrial economy, and is home to more than 125 million Brazilians (Rezende et al. 2018, Joly et al. 2014). This biome is already severely affected by human activities - only 28% of its original vegetation remains, 30% of which is inside protected areas (Rezende et al. 2018). Pressures are likely to increase: estimates by the UN Population Division for Brazil indicate that 92% of the population will live in cities by 2050, and the total urban population will be over 215 million (UN 2019). In the Atlantic Forest specifically, a 160% increase in urban area is predicted from 2000 to 2030 (Seto et al. 2012). Besides, it is likely that more than 20% of the expansion of cities located along the Atlantic coast of Brazil will occur within areas currently supporting natural habitats (McDonald et al. 2018a), turning it into one of the most affected regions of the world in terms of natural habitat and biodiversity loss due to urban growth (McDonald et al. 2018b).

Although most of the Atlantic Forest has been converted to other uses (Rezende et al. 2018), forest remnants still provide important biodiversity and ecosystem services to about three quarters of the Brazilian population, such as water supply for human use and power generation; food and feed; climate regulation; protection against floods and landslides; pollination; and cultural services such as supporting identities of traditional peoples and providing recreational opportunities (Joly et al. 2014). However, human activities such as the conversion of forest in urban spaces, crop areas, and industrial uses threaten the quantity and quality of biodiversity and ecosystem services provided by the Atlantic Forest (Ditt et al. 2010).

Many studies target the impact of urban expansion on natural habitats (Seto et al. 2011, Seto et al. 2012, Guneralp and Seto 2013; McDonald et al. 2018a, 2018b). Limiting the sprawl as well as planning the spatial pattern of urbanization is important to minimize the impacts on ecosystems (UNCCD 2017) since the negative impacts of urban expansion transcend the limits of cities. In tropical forests, for instance, it may increase habitat fragmentation, decrease biodiversity (Fahrig 2003), and potentially hamper the delivery of ecosystem services provided by forests (Mitchell et al. 2014). In parallel, there can be significant impacts inside cities as well, such as the intensification of urban heat islands and human well-being impairment (Krüger et al. 2011). Unplanned or inadequately managed urban growth may result in uneven access of city dwellers to biodiversity and ecosystem services provided by the Atlantic Forest (Krüger et al. 2011). In contrast, well-planned urbanization informed by an understanding of population trends, climate change, and biodiversity scenarios can help maximize benefits while minimizing environmental degradation (UN 2019).

The coupled nature of societal and environmental dimensions regarding urban expansion in the Atlantic Forest requires a social-ecological systems approach, which recognizes people as part of nature, as well as considers the complexity and uncertainty that emerge in those systems (Berkes & Folke 1998). Therefore, interdisciplinary tools to navigate this complexity are needed and models and scenarios can be useful in this regard. Models are qualitative or quantitative descriptions of key components of a given system and the relationships between those components. Scenarios are representations of possible futures for one or more components of a system (IPBES 2016). Models and scenarios can contribute to policy making by addressing relationships and feedbacks between environmental drivers, biodiversity and ecosystem services, and socioeconomic dynamics (Pereira et al. 2010).

It is important to stress that although urban growth affects biodiversity and ecosystem services in the Atlantic Forest, those impacts are not perceived in the same way by different stakeholders. People differ in how they value nature depending on local, cultural, socioeconomic, and ecological contexts, and the recognition of this plurality of values can improve policy-making by practitioners (González-Jiménez et al. 2018). Pascual et al. (2017) and Díaz et al. (2018) recognized those differences and proposed assigned values to nature that can be intrinsic, instrumental, or relational. In parallel, the concept of Nature's Contributions to People (NCP) has been introduced within the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) as a more comprehensive way to address ecosystem services, while taking into account all contributions of living nature for people's quality of life and the cultural context present in all nature-society relationships (Díaz et al. 2018).

More recently, new frameworks to assess the impacts of changes in biodiversity and ecosystem services considering different worldviews have been proposed, such as the Nature Futures Framework (NFF), which was developed by IPBES as a strategy to formulate scenarios

centred on our relationship with nature to inform decision-making at multiple scales (PBL 2018, Rosa et al. 2017). NFF can be used to model impacts of drivers and policy responses while recognising multiple dimensions of three perspectives of nature: Nature for Nature, Nature for Society, and Nature as Culture. In Nature for Nature, nature is regarded as having a value in and of itself without human intervention, and the preservation of nature's diversity and functions is of primary importance; Nature for Society relates to nature being primarily valued for the benefits or uses people derive from it, which could lead to an optimisation of multiple uses of nature; Nature as Culture considers humans as an integral part of nature and its functions (PBL 2018). These three perspectives form a continuum, or gradient, that is represented by a triangular framework, which can be viewed across different scales and sectors (Figure 1). The process of applying NFF to develop possible futures for nature produces multiple, stakeholder-defined endpoints. Once alternative nature futures are identified, qualitative and quantitative approaches (for example, modelling, empirical studies, and expert knowledge) can be used to identify potential pathways for reaching these endpoints, including specific policy alternatives and feedbacks between biodiversity and ecosystem services, human well-being, and decision-making (Rosa et al. 2017).

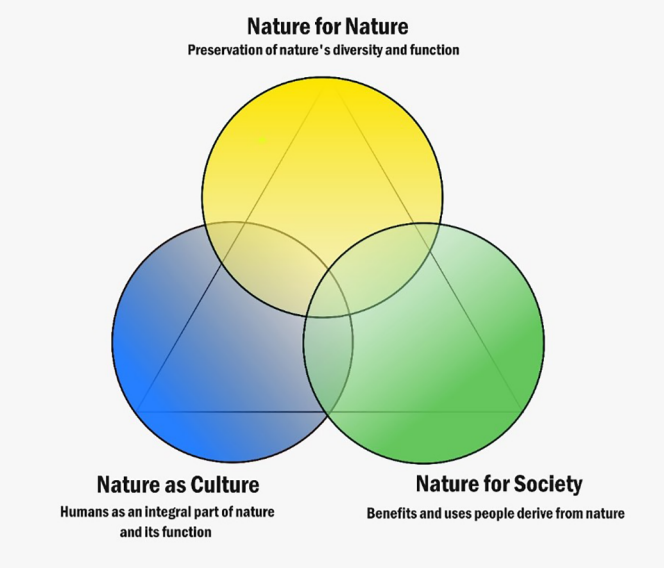


Figure 1. Conceptual framework of the Nature Futures Framework (Adapted from PBL 2018).

This paper is the result of a group exercise from the São Paulo School of Advanced Science on Scenarios and Modelling in Biodiversity and Ecosystem Services to Support Human Well-Being (SPSAS Scenarios), a 120-hour course developed by the Brazilian Platform on Biodiversity and Ecosystem Services (BPBES) and funded by the São Paulo Research Foundation (FAPESP) in July 2019. We aimed to (i) develop a conceptual model describing drivers and impacts of urban growth in the Brazilian Atlantic Forest, considering the complex relationship between nature and people by employing the NFF; (ii) propose three nature future scenarios for urban expansion, analyze and compare the impact of distinct policies on multiple social-ecological values of nature. We do not intend to thoroughly debate the issues involved, but instead to contribute to developing a better understanding and appreciation of the complexities, trade-offs, and synergies which need to be considered in reconciling city development, nature conservation, and human well-being.

Material and Methods

1. Study area

The Brazilian Atlantic Forest (Figure 2) is a biome that originally covered around 150 million ha, encompassing a wide latitudinal, longitudinal, and altitudinal range of the territory. The heterogeneous environmental conditions of precipitation and temperature, for instance, promoted high species diversity and endemism (Rezende et al. 2018). Severe habitat fragmentation threatens the fauna and flora present in this biome (Silva & Casteleti 2003).

2. Conceptual model and scenarios

For our conceptual model, we used a *Driver-Pressure-State-Impact-Response* (DPSIR) framework, given its interdisciplinary approach that enables the assessment of the links between economic, social, physical, and biological features of a system (Rousenvell et al. 2010). This framework has been widely applied to demonstrate the causal-effect relationships in human-environmental systems (Rousenvell et al. 2010, Hou et al. 2014) and is considered an effective approach for linking science to policy (Tscherning et al. 2012).

'Driver' refers to a social, demographic and/or economic development leading to 'Pressure' on the environment. Drivers can be distinguished into direct and indirect ones. Indirect drivers derive from demography, economy, policy, culture, religion, science, and technology, and may influence the amount of land that is converted and allocated to food crops, energy crops or urban sprawl (Hou et al. 2014). Direct drivers, in turn, include the land use changes that directly pressure the nature-human systems (Díaz et al. 2015). 'Pressure' is related to emissions of substances, introduction of physical and biological agents, use of resources, and the use of land by human activities that provokes changes on the 'State' of environment. 'State' consists of the physical, biological, and chemical conditions in a specific area. Changes in environment 'State' culminate in 'Impact' on human and environmental systems (e.g., human health, ecosystems, climate, and materials) that may elicit a societal or government 'Response'. 'Response' corresponds to actions and policies which may feed back on the driving forces, pressures, states, or impacts (Smeets & Weterings 1999, Hou et al. 2014).

The 'impacts' represented in the DPSIR model may have different effects on different stakeholders, depending on who they are and how they value nature. In order to couple those different views into our conceptual model, we described each component of the DPSIR framework and identified its respective connections. Regarding 'impacts', specifically, the components of NFF were attached to express values of nature associated with our case study (i.e., Nature for Nature, Nature for Society, and Nature as Culture).

After creating our conceptual model, we used it to develop the scenarios based on the NFF perspectives. According to each perspective, scenarios were designed to represent the different ways cities can grow and the consequences this could have for the future of biodiversity, ecosystem services and human well-being. In order to do that, we decided to work with the amount and spatial distribution of urban

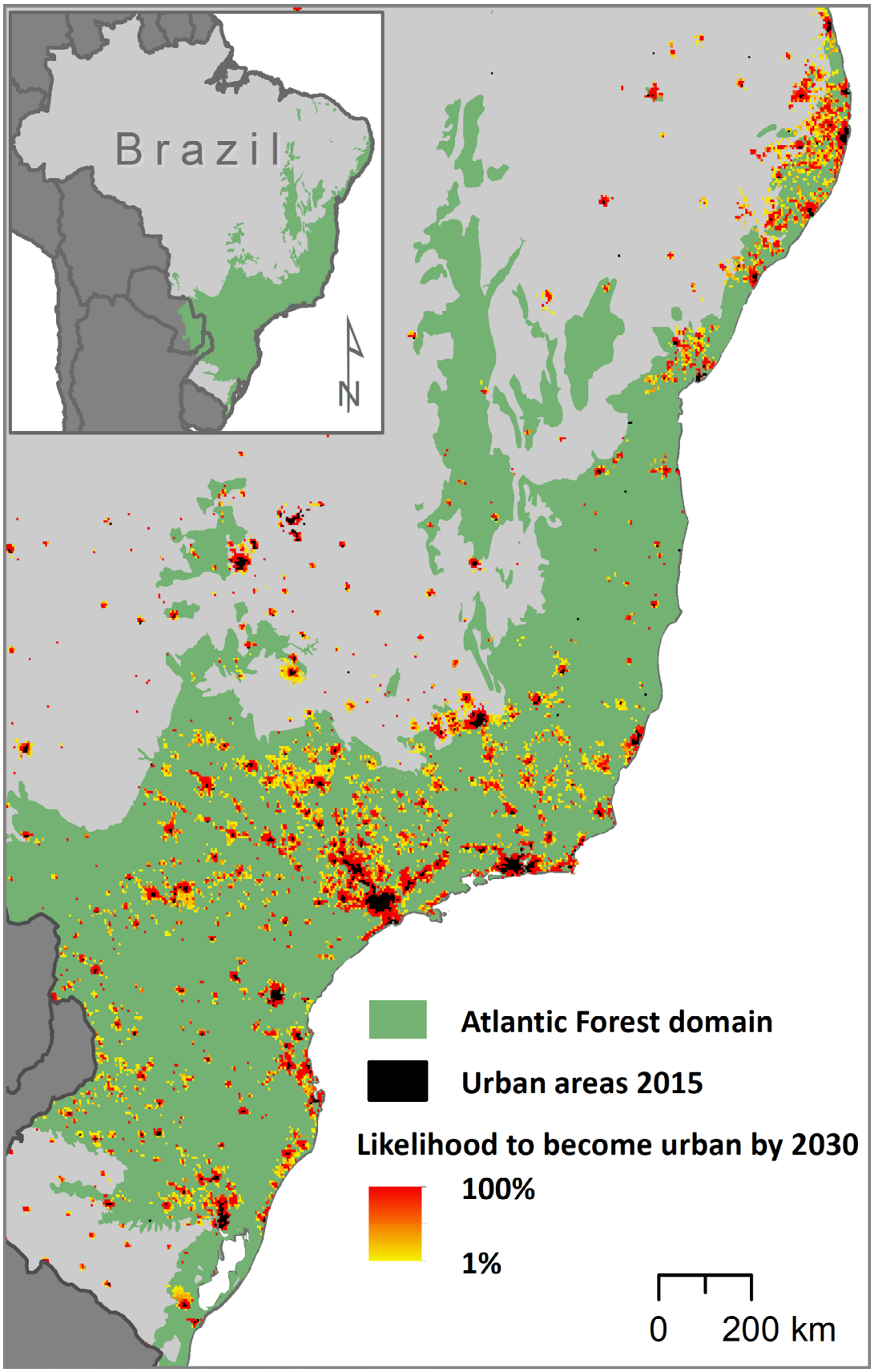


Figure 2. Urban land extent in 2015 and probability of urban expansion by 2030, based on the spatially explicit global forecasts of probability of urban expansion from Seto et al. 2012, in the Atlantic Forest domain in Brazil according to delimitation proposed by Muylaert et al. 2018. Data source: Urban land 2015 (Global Human Settlement Layer, available at https://ghsl.jrc.ec.europa.eu/); Urban expansion (Seto et al. 2016); Atlantic Forest domain (Muylaert et al. 2018).

green and blue spaces, as well as urban densification policies, and the way these two policies may interact at different scales and affect the connectivity of urban green and blue spaces, and between such spaces and natural habitat fragments at local and regional scales. Urban green and blue spaces are understood here as elements of the green infrastructure, which are a hybrid of built infrastructure and human-made ecosystems that provide multiple biodiversity and ecosystem services (Kettunen et al. 2014). The scenarios presented here are theoretical and do not represent all the possible ways a city can grow. In accordance with the NFF, only positive scenarios for biodiversity and ecosystem services were represented. We developed our conceptual model using 'draw.io' digital platform and used Inkscape free software (Harrington 2004) to design the future scenarios.

Results

1. Conceptual model and Nature Futures Framework

In our case study, economic and population growth are considered the indirect drivers boosting urban expansion, which is the direct driver. Those drivers are translated into pressures on the environment and we represented these pressures as the loss of natural ecosystems (e.g., primary forests, mangroves, altitude grasslands) linked to the creation and expansion of urban forms. Urban forms refer to the aggregation of spatial patterns of city development such as block size and form, street patterns, lot configuration, parks, and public spaces design (Jabareen 2006). A compact city, for example, aims at increasing the density of inhabitants and recycling spaces within the city instead of expanding its borders (Jabareen 2006).

The loss of natural ecosystems and the increase of urban forms might alter landscape permeability, microclimate, and quantity and quality of the remaining natural ecosystems, as depicted in Figure 3. For our conceptual model, those features were selected as 'states', because changes in them result in impacts on different dimensions of the three perspectives of the NFF. Therefore, such features can be used as a proxy to understand 'impacts' of urban expansion in a multiple value perspective. In the diagram, changes in permeability of the landscape and the quantity and quality of natural ecosystems may impact values across the three NFF perspectives, while changes in microclimate will only affect values of the 'Nature for Nature' and 'Nature for Society' perspectives.

Changes in landscape permeability may affect water supply due to changes in water table rechargeability. A direct impact in cities is the occurrence of floods, which are a critical problem for the cities in the Atlantic Forest, especially during the rainy season. Water quantity and quality in turn are also affected (Pires et al. 2019), since riparian forests are often removed causing soil erosion.

Regarding microclimate alterations, urban expansion is associated with temperature increase and heat island formation in the most urbanized and sealed part of the cities (Cortinovis & Geneletti 2018), as well as with the loss of green areas inside the cities (Gómez-Baggethun & Barton 2013). Consequently, higher temperatures can negatively affect citizen's health and well-being, mostly the children and elderly people who are more vulnerable to heat

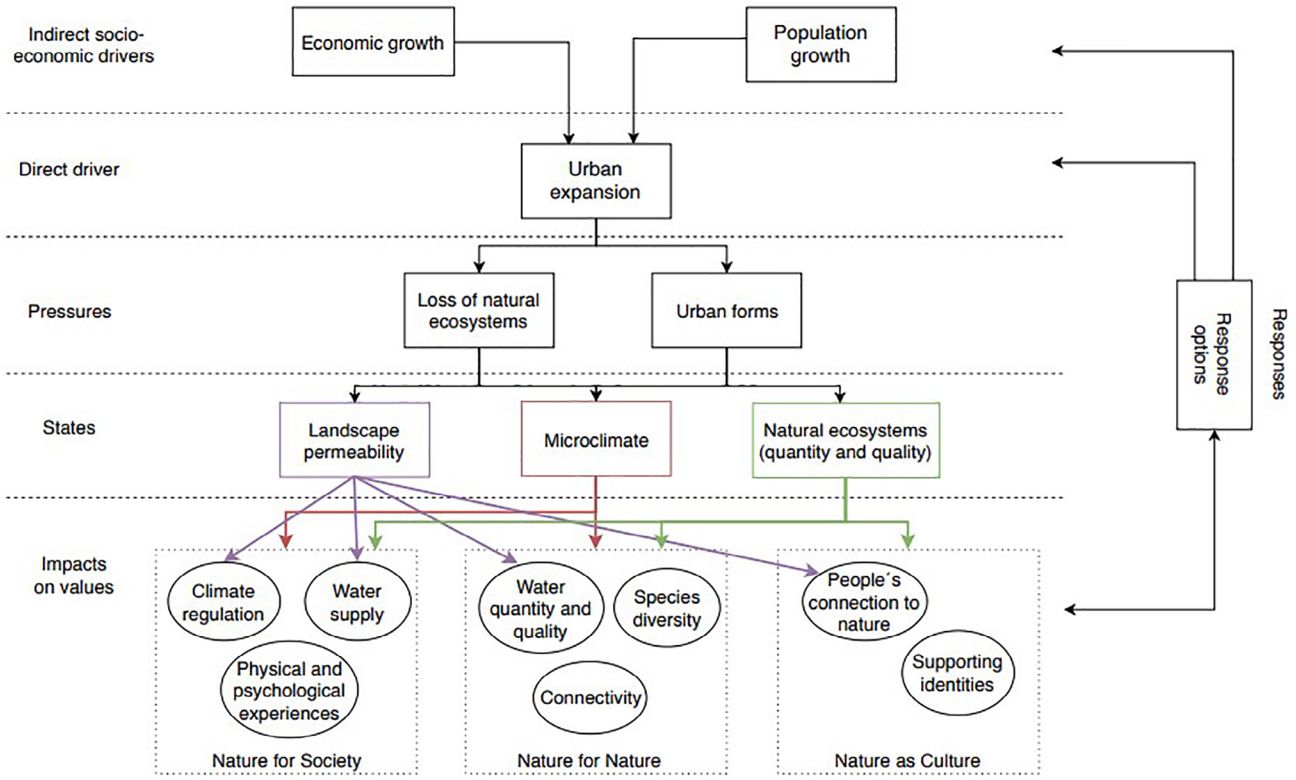


Figure 3. Conceptual model describing drivers and impacts of urban growth in the Atlantic Forest, following the DPSIR approach. Impacts were described for values of nature according to the NFF, which encompasses multiple social-ecological perspectives.

stress (Cortinovis & Geneletti 2018). At a larger scale, urban expansion can also increase carbon emissions due to land clearing, reduction in primary productivity, and even higher per capita greenhouse gas emissions, thus contributing to global warming (Seto et al. 2012).

The modifications of quantity and quality of natural ecosystems will potentially impact values across the three NFF perspectives, having effects, for instance, on the amount of available water for human populations, but also for biodiversity (McDonald et al. 2011). The conflict regarding the maintenance of natural ecosystems and the amount and distribution of urban green areas will be a determinant of the available habitat for native biodiversity and how connectivity among remnants will be maintained. The loss of green spaces may also affect the emotional and affective connection that people have with the natural environment (Gómez-Baggethun & Barton 2013, Chan et al. 2016), as well as may lead to impacts on social and cultural identities of local communities (Sampson & Goodrich 2009). In this sense, the amount and proximity of urban green and blue spaces available for city dwellers will directly affect people's connection to nature. When taking into account areas outside city limits, natural ecosystems play an important role for the maintenance of a sense of place for some local communities, thus supporting their identities (Masterson et al. 2017). In the context of the Atlantic Forest, those communities can be *caiçaras*, *quilombolas*, rural, indigenous people, among others (as established on Federal Decree 6040/07). Therefore, the amount of natural ecosystems, as well as their quality and location, may affect supporting identities.

Finally, impacts on values influence response options in the same way response options influence impacts on values, thereby resulting in feedback mechanisms. Such responses can include statutory regulation and fees, voluntary market-based schemes, spatial and integrated planning, management structures and monitoring, technical arrangements, protected areas, education and knowledge exchange, and private subsidies (Tscherning et al. 2012, Brown & Everard 2015). Response options can influence socioeconomic driving forces through modifying development and population growth policies.

As mentioned before, one of the main purposes of the DPSIR framework is to connect science to policy. For this reason, the establishment of an indicator set is crucial to represent the causal-effect relationships of DPSIR components. Indicators reflect trends and changes in the environmental-human systems; therefore, they can help inform the formulation of policy targets, and the subsequent tracking of their progress (Smeets & Weterings 1999, Hou et al. 2014). We propose a set of indicators that could be measured and modeled according to our conceptual model (Table 1). The selection of these indicators took into account their representativeness, data availability (or a proxy), and the geographic scale (local or regional).

2. *Conceptual model to scenarios*

In our conceptual model, the impact on values is expected to produce a feedback acting mainly on the direct driver (Figure 3), which would then promote changes in loss of natural ecosystems and urban forms. This is expected to occur mainly through different response options and here we focus on creation and changes in public policies regarding urban growth and city planning. To compare different strategies that policy makers could implement, we created three scenarios and inferred the impact of the proposed policies on each of the NFF value perspectives (Table 2).

The proposed scenarios feature different ways urban green and blue spaces, connectivity between fragments, and urban densification policies can be planned at both local and regional scales. This framework allows modelling how different urban densification thresholds affect the future size of cities or how different size and spatial distribution patterns of urban green and blue spaces affect microclimate regulation (i.e. heat islands), physical and psychological well-being (through different accessibility to these spaces), and connectivity between urban green and blue spaces and natural habitat fragments.

Scenario 1 focuses primarily on Nature for Society values, and how we can better use urban green and blue spaces to improve biodiversity, ecosystem services and city dwellers' livelihood (Figure 4 - S1).

Table 1. Set of variables and associated indicators regarding the different components of the conceptual model for urban growth in the Atlantic Forest and scales in which they can be measured.

	Variable	Indicator	Scale
Driver	Urban expansion	Urban area extent	local/regional
Pressure	Loss of natural ecosystems	Area of natural habitat lost	regional
	Population density	Number of inhabitants per m^2	local
States	Species diversity	Number of species per pixel	regional
	Connectivity	Functional connectivity index	regional
	Urban green space	Area of green spaces per person (m2/person)	local
	Heat island effect	Temperature range (max/min)	local
		Humidity	local
	Drought and floods	Precipitation regime	local
	Air quality	Air quality index (PM 2.5)	local
	Extreme weather events	Sea level rise	local
		sand/hail storm intensity	local
	Water recharge	Percentage of impervious surface	regional
Values	Human well-being	Quantity of green spaces within 300 m radius	local
		Frequency of mental disorders	local

Table 2. Comparative description of three scenarios of urban expansion in the Atlantic Forest regarding policies at the local and regional scales and the impact of those policies on the assessed NFF values. The symbols indicate the expected impact on each value, whether positive (+) or negative (-). The number of symbols indicate the magnitude of the predicted impact, allowing comparisons among scenarios.

Scenario	Policies			Nature Futures Framework							
				Nature for Society			Nature for Nature			Nature as Culture	
	Local scale - urban green spaces	Regional scale - natural habitats	Densification	Climate regulation	Physical and psychological experiences	Water supply	Connectivity	Species diversity	Water quantity and quality	Supporting identities	People's connection to nature
1	Several Small Scattered	Loss of natural habitats	Moderate	++	++	+	++	+	+	+	++
2	Single Large Concentrated	Loss of natural habitats Natural habitats integrated with urban area	High	+	+	+	+	++	++	++	+
3	Without significant urban green spaces	High priority for conservation - minimum loss of natural habitats	Very high	-	-	++	+++	+++	+++	+++	-

Together with a moderate densification policy, this city planning would also result in urban sprawl and loss of natural habitats. In this scenario, policy regulates the minimum area of green spaces per person (WHO 2012 defines a minimum of 9 m² per person) and the maximum distance from local residences (300 m is defined as an acceptable distance - WHO Regional Office for Europe 2016). These areas are scattered throughout the city, thereby aiming to maximise access in order to improve non-material ecosystem services such as physical and psychological experiences and people's connection to nature. Spatial distribution of urban green and blue spaces can also influence microclimate regulation through the borders of heat islands and improve connectivity between these areas and other natural habitats on the city outskirts. However, since such spaces are scattered, they become smaller in area, which means they are not able to provide suitable habitat for many species. While urban green and blue spaces would reduce the proportion of impervious surface at the local scale, increasing water rechargeability, the reduction of natural ecosystems at the large scale would result in loss of water-related services, causing an overall positive but moderate effect on water supply and water quantity and quality. This scenario also benefits supporting identities of local communities located outside city limits, by means of providing and maintaining opportunities to develop cultural links to nature. Equity in access to urban green and blue spaces is valued within this scenario, as well as diversity of uses in these areas.

On the other hand, if city planning focuses more on Nature for Nature values, and the main goal is to keep urban biodiversity high, policies could prioritize urban green and blue spaces with larger sizes and good connectivity between these areas and natural habitat outside the city center (Figure 4 - S2). By increasing in area, the number of these spaces would be lower and densification would be higher than in the previous scenario. In Scenario 2, accessibility to urban green and blue spaces is unequal, resulting in an uneven response in physical and psychological experiences and people's connection to nature, favouring city dwellers that live in proximity to them. This inequality could provoke an erosion in the social and cultural link to nature where the loss of green spaces has been most intensified. Microclimate regulation may also be unevenly distributed throughout the city, allowing the creation of heat islands. Although urban expansion would cause loss of natural habitat, large areas of natural ecosystems would still be preserved in this scenario, resulting in an improvement in water supply, water quantity and quality. At a regional scale, the improvement of connectivity can benefit the maintenance of biodiversity as well as local identity of indigenous peoples and traditional communities, especially because large areas of natural ecosystems are maintained.

Scenario 3 also focuses on Nature for Nature values, however only minimal loss of natural ecosystems is allowed (Figure 4 - S3). Urban densification is thus very high, following a compact city model and leaving almost no urban green and blue spaces because of high values of properties. Biodiversity and connectivity between habitat fragments outside the city centers is high, but biodiversity and ecosystem services inside city nuclei are low. Since natural ecosystems are preserved in this scenario, water supply and water quality will be improved, even though inside cities impervious surfaces are dominant. Given the absence of urban green and blue spaces and distance to natural areas, climate regulation, physical and psychological experiences, as well as cultural values are negatively impacted at local scale. On the other hand, this scenario maintains the largest area of natural habitat, thus improving and maintaining the support of identities of people living outside the cities, especially traditional communities. Theoretically, if city patches are of adequate size, built with adequate materials, and green infrastructure is included (e.g., green roofs), there can still be some biodiversity and ecosystem services of microclimate regulation, physical and psychological experiences, and people's connection to nature. However, the tendency is that the inhabitants of the downtown areas would be the most affected by heat islands and the difficulty to access urban green and blue spaces. In this scenario, because the cities are compact, transportation may be more efficient (if emphasis is given to public rather than individual transport) and there may be a lesser impact over microclimate coming from greenhouse gas emissions from vehicles.

Discussion

Our conceptual model revealed the main relationships between urban growth processes and impacts on biodiversity, ecosystem services and other social-ecological values embedded in the NFF. By coupling the DPSIR model with this innovative framework, we were able to depict how these multiple values interact and identify possible responses to guide urban growth. The comparison of our three scenarios showed potential trade-offs and synergies among values, highlighting the complexity of urban expansion impacts on a biodiversity hotspot. Different policies could be derived from the scenarios, leading to alternative outcomes, depending on the main interests of the public administration, stakeholders, and especially the targeted values. In this regard, we discuss possible policies to build pathways for achieving a sustainable urban expansion, especially by managing natural areas, densification, and urban green and blue spaces. This discussion is focused on the planning of new development areas and the retrofitting adaptation of established urban centers, both at local and regional scales.

For the planning of new development areas in Brazil, a few existing policies are of particular relevance: (i) the city master plans ("Planos Diretores Municipais", first established by Brazilian Federal Constitution of 1988), which are the main instrument to guide city growth; (ii) Ecological-Economic Zonings ("Zoneamento Ecológico-Econômico", first established by Federal Law 6938/1981), which refer to state or regional-level planning; (iii) Municipal Atlantic Forest Plans ("Planos Municipais da Mata Atlântica", established by the Federal Law 11428/2006), which are plans for the protection and recovery of Atlantic Forest remnants in local level including inside urban areas (these plans are mandatory to access conservation and restoration funds - Dutra et al. 2013); and (iv) Water Resource Plans ("Planos de Recursos Hídricos", established by the Federal Law 9433/1997), which focus on water resource in three levels: watershed, state, and national. All these instruments consider the division of the territory in zones with different purposes (Lopes et al. 2017). They can complement each other in a way to formally establish and implement urban densification and urban green and blue spaces rules (city master plans), and promote connectivity among natural areas at local (Municipal Atlantic Forest Plans) and regional scale (Ecological-Economical Zonings and Water Resource Plans).

Despite the existence of distinct planning instruments, their implementation is not guaranteed (Pinheiro 2016). In this case, the main challenges are: funding and implementation of the planning instruments,

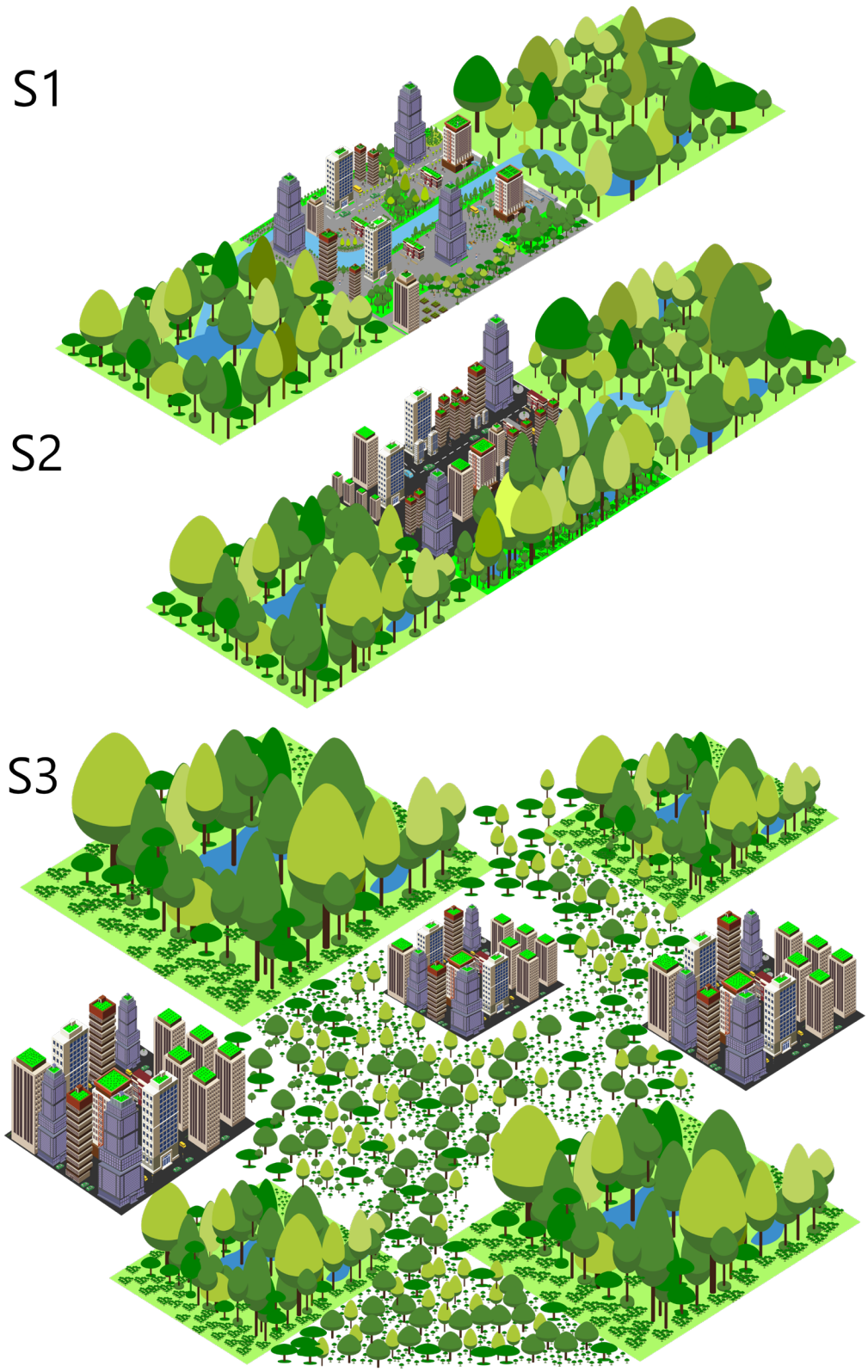


Figure 4. Scenario 1 (S1) - Nature for Society. In this scenario, urban planning prioritizes urban green and blue infrastructure, promoting physical and psychological experiences and increasing people's connection to nature. Scenario 2 (S2) - Nature for Nature. In this scenario, cities grow in a dense way, prioritizing urban green infrastructure, protecting biodiversity by conserving urban forests, and increasing habitat connectivity. Scenario 3 (S3) - Saving land for nature. This scenario is also based on Nature for Nature values, conserving as much forest outside cities as possible and ensuring biodiversity protection. However, biodiversity and ecosystem services inside cities would be low due to a hyperdense cityscape, with almost no urban green and blue infrastructure.

integration of different plans, and the capacity of the municipalities to offer planned habitation options and urban services versus the high demand created by population growth and migration (Nagendra et al. 2018). Housing needs in Brazil, as in most developing countries, are largely satisfied by informal solutions, such as favelas, which are usually built over, or are adjacent to highly biodiverse ecosystems such as forests or mangroves (Puppin de Oliveira et al. 2011). Although national laws dealing with Ecological-Economical Zonings have been effective since 1981, the current situation is that only nine out of the 27 Brazilian states have finished their respective planning processes (MMA 2018), and 37,6% of all Brazilian municipalities that should have a master plan by 2008, still did not have one in 2015 (IBGE 2016). Moreover, there is no national database that stores all the cities master plans, state and regional Ecological-Economical Zonings, and other plans, making the integration among them a major challenge.

The development of new areas allows the planning of the spatial distribution and area of urban green and blue spaces. However, adapting existing cities poses a different set of challenges. One of these challenges is to promote retrofitting adaptations and to preserve remaining natural habitats with scarce financial investments, especially if we consider that most natural areas that are going to be affected by urban growth are located in countries with moderate to low average incomes (McDonald et al. 2008). For the retrofitting adaptation of established urban centers, policy options include small credit lines or tax compensation to stimulate green roof adaptations, promoting urban gardening, provision of tree saplings for backyards and sidewalks, or greening of vacant lots. Cortinovis & Geneletti (2018), for instance, discussed alternative scenarios for creating urban parks from regeneration of brownfields and examined the effect of these policies on microclimate regulation and nature-based recreation opportunities. There are some examples of successful city green adaptations around the world, but they are all very costly (Russo & Cirella 2018) and therefore are not widely applicable. Nevertheless, green solutions for tropical urban centers have been proposed, such as low-cost and low-maintenance green roofs (Silva et al. 2018). Planting trees in cities is also a possible low-cost response option, requiring an annual investment of 8 US dollars per person, on average (McDonald et al. 2017).

Restoration and regeneration strategies are also important to be considered in order to avoid further loss of natural ecosystems, a focal component of our conceptual model. Considering that the area covered by the Atlantic Forest is highly urbanized, natural ecosystems remnants are an important provider of habitat for native biodiversity, enhancing connectivity between fragmented areas. However, planning connectivity between fragments is still a great challenge, since it demands ecological studies of species requirements, investment in a large number of linkages to form corridors (Rudd et al. 2002), and coordinated efforts among multiple municipalities (Seto et al. 2012). Despite those difficulties, connectivity between fragments should be a high priority policy as Atlantic Forest remnants are highly fragmented (Rezende et al. 2018).

Green areas in cities can offer benefits to citizens, including aesthetics and scenic views, a place for socializing and relaxing, and opportunities for physical exercise (Campbell-Arvai 2019, Cortinovis & Geneletti 2018). Studies have shown associations between the amount of vegetation cover and better outcomes to mental health and well-being such as lower prevalence of anxiety, depression, and life satisfaction and happiness (Cox et al. 2017, Houlden et al. 2019). In this regard, we argue that impaired access to green spaces may be related with depression and nostalgia in individuals. Cultural and social values must be explicitly included in urban green and blue spaces and densification policies, and NFF provides a working framework for this. It is also noteworthy that green areas contribute to microclimate regulation, even though tropical urban environments require a larger extent of green spaces to reduce warming (Manoli et al. 2019).

Another challenge decision-makers face regarding urban policies implementation lies in finding appropriate indicators to express benefits and associated values across the whole range of ecosystem services. For example, the development of indicators for measuring the expected outcomes of planning actions in terms of changes in human well-being and cultural values is still a challenge, often demanding qualitative assessments (Gómez-Baggethun & Barton 2013). In this regard, the use of our conceptual model, which is a qualitative model, could be the foundation for an evaluation of multiple values regarding urban expansion. A further step would be to develop a quantitative modelling system, and the indicators here proposed could support the development of such models (Table 1). Data on most of these indicators can be obtained either from public databases (e.g. climate variables), scientific literature (e.g. biodiversity) or from local government (e.g. green spaces coverage). However, there are aspects that would require future research, such as the ones related to human well-being and mental health. By translating our model into a more quantitative form, scientists could better inform stakeholders about different pathways to achieve multiple scenarios of urban expansion. The plurality of response options and set of indicators here discussed reveal how different solutions are feasible to address sustainable urban growth in the Atlantic Forest. However, given the complexity of this issue, such policies will only serve the purpose of reconciling conservation, development, and human well-being if designed and applied considering multiple values for nature. As previously stated, people value and acknowledge the services provided by nature and its uses and benefits in different ways, which has implications for environmental management and policies (Gómez-Baggethun & Barton 2013, Campbell-Arvai 2019). Decisions that take this into account have a better chance of being more sustainable, legitimate, and effective (Jacobs et al. 2016). From a scenarios perspective, not considering such plurality might lead to undesirable futures (Chan et al. 2016). In our case study, the different perspectives that emerged by employing the NFF allowed us to identify synergies between different values. For instance, enhancing urban green and blue spaces seems to be a strategy that is positive to all three NFF's perspectives. For the Nature for Society values, such spaces are important for temperature regulation and recreation opportunities; for Nature for Nature values, they are important for habitat creation and maintenance to support biodiversity; and for Nature as Culture, they serve to promote people's connection to nature and support local identities. Depending on the size, location, and connectivity of the urban green and blue spaces, they may enhance one value more than others, but it is feasible to model a solution that captures the most of the three values for each specific city situation.

Even though the proposed scenarios pose major implementation challenges, they are not far from reality. Sustainable Development Goal 11, proposed by the 193 members of the United Nations, is a commitment to make cities inclusive, safe, resilient, and sustainable (UN 2015). The World Health Organization has recognized the

importance of urban green and blue spaces in promoting human health (WHO Regional Office for Europe 2017b) and corporations have publicized the benefits of green and blue infrastructure to increase business resilience to external economic and environmental stressors (Dow et al. 2013). Furthermore, the United Nations have declared the period from 2021 to 2030 as the Decade on Ecosystem Restoration, helping to raise awareness and funds towards this issue (UNEP & FAO 2020).

Regarding this perspective, the use of NFF enabled our conceptual model and scenarios to envision positive futures for nature. Envisioning the future is a difficult task, with inherent associated errors, since the different individual and collective choices are always shaping it on the present. Nevertheless, once a possible scenario is developed, people may act and organise themselves collectively in ways unlikely to happen outside this circumstance, potentially leading to transformative change (Bai et al. 2016). In doing so, the necessary processes to achieve such positive futures can be then discussed, meaning that the creation of new visions for the world can also change how the world currently is (Costanza & Kubiszewski 2014). However, in order to successfully achieve such world, people should collectively work on a wanted future, shared values, and the plan to achieve this goal (Costanza & Kubiszewski 2014). This is why urban planning, as well as scenarios development, should be conducted in a participative manner, involving several stakeholders, and considering each city's particularities (geography, demography, budget, priorities, etc). Thus, participatory tools in planning and management of land use can help decision makers to design effective policies, minimizing the risk of competing interests among stakeholders at multiple scales.

Applying the NFF value perspectives can contribute to disentangle complexities and to better understand and navigate urban growth problems, by offering a multiple value perspective that enables the visualization of positive and desirable futures for nature and our world. As Costanza (2003) stated, in order to achieve a better world, we must first envision it. We strongly believe that the integrative and interdisciplinary approach used in this work could lead to better planning and problem-solving of future challenges on urban sustainability in the Brazilian Atlantic Forest.

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Author contributions

All authors have contributed in the following aspects:
- Substantial contribution in the concept and design of the study;
- Contribution to data collection;
- Contribution to data analysis and interpretation;
- Contribution to manuscript preparation;
- Contribution to critical revision, adding intellectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

The authors declare that the study complied with ethical guidelines, and did not require the approval of an ethics committee.

Data availability

The study does not provide data to be archived in public data repositories.

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Article

Feeding strategy and morphology as indicators of habitat use and coexistence of two loricariid fishes from a Brazilian coastal stream

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Abstract: We aimed to evaluate the relationship between form and function of two Loricariidae species (*Hypostomus punctatus and Parotocinclus maculicauda*) from a Neotropical coastal stream. We performed morphological-dietary analysis and discussed their coexistence strategies, as well. We hypothesized that both species use similar food resources according to their morphology but differences in habitat use facilitate their coexistence. In order to test this hypothesis, morphology, diet and habitat use were analyzed for both species. Trophic variance and the Pianka Niche Overlap index were calculated to explore the differences in trophic niche. Correlations between species abundance and water flow were applied to test habitat use. Principal Component Analysis and one Permutational Multivariate Analysis of Variance were applied to test differences between morphology and diet of both species. Morphological-dietary relationships were tested with Mantel test correlations. Total abundance of *H. punctatus* was higher in the stream channel with higher water flow. The dominant food items were sediment and organic matter for both species, and high trophic niche overlap was revealed. Additionally, morphology did not explain feeding habits for both species. Morphological characteristics were significantly different, especially for intestine length, relative area of the dorsal fin, ventral flattening and mouth attributes. The study site was rich in sand sediment, mud, and clay that are not considered good substrates to the establishment and growing of periphyton, which is an important trophic resource to Loricariidae species. Here, low consumption of periphyton can provide a possible explanation for the feeding similarity and the weak morphological-dietary relationships for both species. Thus, the environmental conditions can be more important for diet composition when compared to the similar and specialized morphology of loricariids.
Keywords: *ecomorphology, trophic niche overlap, stream-dwelling fish, Atlantic rainforest.*

Estratégia alimentar e morfologia como indicativos do uso do habitat e da coexistência de dois loricarídeos em um riacho costeiro do Brasil

Resumo: Nós tivemos como objetivo avaliar a relação entre forma e função em duas espécies de Loricariidae (*Hypostomus punctatus e Parotocinclus maculicauda*) de um riacho costeiro neotropical. Nós testamos as relações entre morfologia e dieta e também discutimos suas estratégias de coexistência. Nossa hipótese é de que as duas espécies utilizam os mesmos recursos alimentares de acordo com sua morfologia, porém diferenças no uso do habitat facilitam sua coexistência. Para testar essa hipótese, a morfologia, a dieta e o uso do habitat foram analisados em ambas as espécies. A variância trófica e o Índice de Sobreposição de Nicho de Pianka foram calculados para explorar as diferenças no nicho trófico. Correlações entre a abundância das espécies e velocidade da água foram aplicadas para testar o uso do habitat. Análises de Componentes Principais e Análises de Variância Multivariada Permutacional foram aplicadas para testar as diferenças entre morfologia e dieta para ambas as espécies. As correlações entre morfologia e dieta foram testadas a partir de correlações com teste de Mantel. A abundância total de *H. punctatus* foi maior no canal do riacho com maior velocidade no fluxo da água. Os itens alimentares dominantes foram detrito/sedimento e matéria orgânica em ambas as espécies e uma alta sobreposição de nicho alimentar foi encontrada. Adicionalmente, a morfologia não explicou os hábitos alimentares para ambas as espécies.

As características morfológicas foram significativamente diferentes, em especial o comprimento do intestino, área relativa da nadadeira dorsal, achatamento dorsoventral e atributos da boca. A localidade de estudo é rica em substrato de areia, lodo e argila, que não são consideradas superfícies propícias para o estabelecimento e crescimento do perifíton, um recurso alimentar importante para as espécies de Loricariidae. Neste estudo, o baixo consumo de perifíton pode explicar a similaridade trófica e a baixa correlação entre morfologia e dieta em ambas as espécies. Dessa forma, as condições ambientais podem ser mais importantes para definir a composição da dieta quando comparadas a morfologia similar e especializada desses loricarídeos..

Palavras-chave: ecomorfologia, ecologia trófica, sobreposição de nicho, peixes de riacho, Mata Atlântica.

Introduction

Fish coexistence, in special the one involving close related species, is an important point in the understanding of natural community organization (Wooton 1990). Information about diet and feeding strategies can reveal fundamental aspects of fish life history traits that enable species to coexist (Schoener 1974, Silva et al. 2019) and maintain viable populations in the community. Feeding strategies reflect morphology and individual foraging performance (Douglas & Matthews 1992, do Carmo et al. 2015) and are frequently described by those corporal characters related to fish movement (Celestino et al. 2017, Conde-Saldaña et al. 2017) as well as feeding tactics (Ramírez et al. 2015). The synergy of those aspects, of fish form and function, can be well described by the ecomorphological approach (Oliveira et al. 2010, Feilich & López-Fernández 2019) and explain habitat occupation (Sabino & Castro 1990, Wood & Bain 1995, Tulli 2012) and coexistence of some close related species (Villares-Junior et al. 2016).

Coexistence of close related species is normally mediated by spatial, feeding and/or morphological segregation (Wikramanayake 1990, Jackson et al. 2001, Abilhoa et al. 2016). In this context, studies on feeding habit and resource partitioning contribute to the understanding of species interactions in aquatic systems (e.g. Ross 1986, Lowe-McConnell 1987, Esteves & Aranha 1999, Mazzoni et al. 2012, Leitão et al. 2015). In scenarios of high abundance and diversity of resources, coexistence can occur without negative interaction between species (Pianka 1973, Hurlbert 1978) and feeding overlap does not necessarily imply the existence of direct competition (Lawlor 1980, Frehse et al. 2015). It is expected that when close related species coexist, niche breadth is narrowed and feeding specialization reduce competition chance (MacArthur 1972, Young et al. 2010).

Siluriformes is one of the most abundant order of fish from South America, especially in waters with high turbidity and large amounts of suspended sediment (Barbarino Duke & Winemiller 2003). Loricariidae is the largest and most specialized family of the order and is distributed throughout South America (Burgess 1989). Loricariidae species are highly specialized and have adaptations related to morphology, feeding habits, and digestive processes, including processing of debris, sediment, algae, and periphyton (Gerking 1994, Mazzoni et al. 2010, Lujan et al. 2011). For example, the suctorial oral disc, larger fins and the shape of caudal fins are structures that help these species to attach to stream bottom, to hold position in faster waters and as indicators of swimming and propulsion ability (Buck & Sazima 1995, Casatti et al. 2005).

The relationship between morphology and ecological functions have been described for loricariids (e.g. Delariva & Agostinho 2001, Lujan et al. 2011, Leitão et al. 2015), revealing the importance of feeding and habitat use specialization in the segregation of ecological niches between co-existing species. For stream fish species, analyses involving ecomorphology are considered as a valid assay within-family species comparisons (Douglas & Matthews 1992) and morphology can explain feeding habits for some species (Maldonado et al. 2009, Ramírez et al. 2015). However, dietary-morphological relationships are not well defined for all fish assemblages and morphology was not considered as a good descriptor of diet in other species (Manna et al. 2019). Stream-dwelling fish have high plasticity and versatility in their diet on Neotropical environments (Lowe-McConnell 1987, Svanbäck & Persson 2004) which can improve this weak correlation between morphology and diet (Labropoulou & Eleftheriou 1997, Boyle & Horn 2006). Thus, it seems important to test this relationship, especially between co-existing species with similar ecological requirements.

Parotocinclus and *Hypostomus* species are normally classified as grazers or herbivores with benthonic behavior, inhabiting the bottoms of streams and/or submerged vegetation (Costa 1987, Casatti 2002, Mazzoni et al. 2010, Villares-Junior et al. 2016). We present here a comparative analysis of morphology, diet and habitat use of two of these Loricariidae species, namely *Parotocinclus maculicauda* (Steindachner, 1877) and *Hypostomus punctatus* Valenciennes, 1840. These species were the only loricariids inhabiting the studied stream and coexisting in all collected sites (Miranda & Mazzoni 2015). Knowing that these closely related Loricariidae species have specialized similar morphology (Lujan et al. 2011, Borzone Mas et al. 2019), we predicted that morphology will explain dietary habits, but differences in habitat exploration should be the strategy to facilitate their coexistence.

Material and Methods

1. Data collection

Fishes were sampled at Mato Grosso stream that drains the northwest of Saquarema municipality in the State of Rio de Janeiro, southeastern Brazil (22°52'S, 42°40'W and 22°53'S, 42°34'W). This stream is a third order stream with its headwaters 500 m above sea level. The stream is 11 km long and discharges into the Saquarema Lagoon. It is a typical coastal stream with water levels regulated only by rainfall (~1.500 mm yr^{-1}) and run-off. Sampling sites from which data of total abundance and habitat use were sampled are located along Mato Grosso stream and in Roncador stream, one tributary of Mato Grosso stream (Figure 1). The sampling site which diet and morphology were analyzed (22°52'24,7''S and 42°39'06,4''W) is located in the lowlands of the Mato Grosso stream in a grassland area with gravel and sand substrata, an absence of canopy and scarce riparian vegetation. Total abundance and data of habitat use were also sampled in this site.

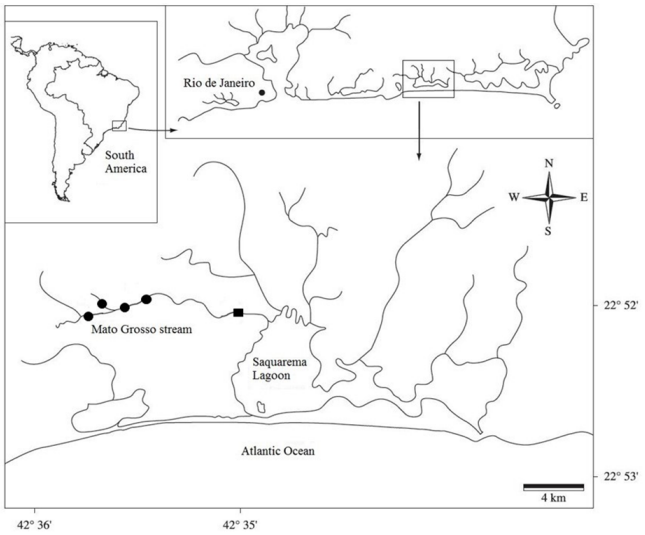


Figure 1. Map of the study area with all sampled sites. Black circles represent the sites that habitat use and morphology were sampled and black square represents the site that morphology and diet were sampled.

Physical characteristics were quantified in the two types of habitats that both species occur, classified as "stream channel" and "stream bank" along a 100 m stretch. Total depth, water flow and substrate were measured on both habitats. We marked 50 transverse transects along the 100 m stream stretch with five meters apart. Along each transect we measured the depth (cm), water flow (m/s) and substrate type at five equidistant points (spaced according to the transect width). The two points closer to stream bank represented the measurements of the habitat "stream bank". Depth measurements were taken with metric rulers and water flow with a digital flow meter (Global Water FP101). Substrate types were classified as mud, sand, gravel, boulder and bedrock following Manna et al (2014). Proportion of each substrate type were calculated using quadrats of 20 cm^2 in the same five points along each transect.

For habitat use, fish were sampled by electrofishing (Mazzoni et al. 2000) through successive removals, following the Zippin method (Zippin 1958). We achieved the premises of constant electrofishing effort and capturability expected by the Zippin method in all sites. Sampling was conducted bimonthly from March 2006 to February 2007 in daytime. Fish for diet analysis were sampled in the same period of the year with seines (mesh size 0.5 mm) in both habitats along 100 m stretch of downstream site (Figure 1). Each sampled fish was anesthetized with a dilute solution of MS222, in accordance with the applicable Brazilian environmental legislation (collecting permit IBAMA/MMA 02022.002475/2006-10, authorization number 118/2006 – DIFAP/IBAMA). Voucher specimens were placed in the ichthyological collection of the National Museum of Rio de Janeiro (*Hypostomus punctatus* - MNRJ 29993, 30008, 30013; *Parotocinclus maculicauda* - MNRJ 29957, 29981, 30023). For morphology, 20 preserved specimens of each studied species were randomly selected from all sampled months and all other specimens were used for dietary analysis. Specimens for diet and morphology analyses were not the same individuals.

2. *Laboratory procedures*

Sampled fish were conditioned in ice for transportation; total weight (WT, g) and standard length (SL, cm) were determined in the laboratory. Morphological data (Table 1) were taken by a caliper (0.01 mm), whereas fin areas were calculated on a graph paper. Sample size were determined following Gatz (1979). Based on these data, 16 ecomorphological traits, listed on Table 2, were calculated (Gatz 1979, Watson & Balon 1984, Casatti & Castro 2006). These traits are calculated with ecomorphological indices that are able to remove allometric effects in posterior analyses (Gatz 1979). Additionally, all analyzed specimens were adults. Specimens with more than 4.6 cm of standard length for *Hypostomus punctatus* and 2.5 cm for *Parotocinclus maculicauda* were considered adults (Lima 2012, *unpublished data*).

The intestine of each specimen was removed through a longitudinal abdominal incision, distended, and measured (gut length = GL, cm). The first third of the intestine was fixed in formalin (5%) and kept in alcohol (70%) for subsequent analysis. Intestine contents were diluted and analyzed in a Sedgewick-Rafter counting camera, under an optical microscope, according to procedures described by Mazzoni et al. (2010). Diet items were identified to the lowest feasible taxonomic level (Bicudo & Bicudo 1970, Mugnai et al. 2010). Food items were grouped into eight broad categories: diatoms, filamentous algae, cyanobacteria, plant debris, insects, scale, organic matter and sediment (the classification of food items was adapted from Teresa et al. 2015 and Manna et al. 2019). Plant debris were identified as any fragment of allocthonous plants, such as leaves, seeds or litter. Organic matter was identified as autochthonous animal or vegetal fragments with unknown taxonomic classification. Sediment was identified as sand particles. A total of 62 specimens of *H. punctatus* and 117 specimens of *P. maculicauda* were used for diet analysis.

3. *Data analysis*

An analysis of similarity (ANOSIM) was applied to test the physical differences between the two sampled habitats (stream channel vs. stream bank). ANOSIM was performed using data from stream depth, water flow and substrate type. The units from stream depth and water flow were transformed to the same unit (i.e. meters), and the unit from substrate type was transformed using arcsine square root transformation. After that, we scaled each variable to a null mean and a standard deviation of 1, to give them the same weight, and we then computed Euclidean distance between sampled points using the scaled values. ANOSIM was applied using this distance matrix.

To test the relationship between species and habitat use (i.e. water flow) we ran Pearson correlation test between number of individuals (total abundance) and water flow values. These correlations were applied using data from sites along the stream, including the site that diet and morphology were analyzed (details on sampling sites in Figure 1). The two habitats that fish occurred were classified as stream bank with lower values of water flow (<0.1 m/s) and as stream channel with higher values of water flow (>0.1 m/s). We tested the existence of correlation between water flow and stream depth using Pearson correlation and these variables were highly correlated. Thus, we decided to use water flow as the only habitat variable on this relationship. Furthermore, the morphology of loricariids is adapted to explore habitats with a higher range of water flow when compared to other habitat variables, providing high stability in riffles (Webb et al. 1996, Oliveira et al. 2010, Pagotto et al. 2011), justifying the higher influence

of this variable in habitat exploitation by loricariids. The other habitat variables were used to test the differences between stream bank and stream channel as mentioned above.

Diet items were quantified through Volumetric (*Vo*) and Frequency of Occurrence (*Fo*) methods (Hyslop 1980). Alimentary index for each food item, *AI* (*i*), designed to express the relative importance of different food items, was obtained by combining the volumetric occurrence with the frequency of occurrence (Kawakami & Vazzoler 1980, Hahn et al. 1997).

A principal component analysis (PCA) was applied based on the correlation matrix of morphology and diet data to illustrate the differences between species. One PCA was performed for morphological data and another PCA for diet data. Before performing the PCA, we transformed each morphological and diet trait to the same unit (millimeters in morphology and relative abundance of food items in diet). To test differences in diet composition between sampled months we performed an analysis of variance (ANOVA) using relative abundance of food items.

Differences in morphology and diet between species were tested with a permutational multivariate analysis of variance (PERMANOVA) for each group of traits, with 999 permutations, using dissimilarities among species in their respective distance matrices. One PERMANOVA was applied for morphology and another one for diet. The variance of morphology and diet was calculated using morphological data and relative abundance of food items to test the niche width for each species. The Pianka Niche Overlap Index (Krebs 1989) was also calculated using relative abundance of food items in order to evaluate the overlap in the partitioning of the food resources.

To evaluate the relationship between morphology and diet, a Mantel test correlation was applied on Euclidean distances between individuals in the morphological and dietary 4-dimensional PCA spaces (Manna et al. 2019). Positive correlation with significant relationship reveals that morphology explains feeding niche, so a graphical example with hypothetical data was developed to facilitate the comparisons with our results (Figure 4a). All analyses were performed in the R statistical and programming environment (R 3.1.0., R Development Core Team 2014), with the "vegan" (Dixon 2003), "ade4" (Dray & Dufour 2007), and "spaa" (Zhang 2013) packages.

Table 1. Morphological data of twenty specimens of *H. punctatus* (HP) and *P. maculicauda* (PM) from Mato Grosso stream, Saquarema, Rio de Janeiro, Brazil. SD = standard deviation.

Character	Range							
	Minimum		Maximum		Mean		SD	
	HP	PM	HP	PM	HP	PM	HP	PM
Body measurements (mm)								
Standard length (Sl)	53.85	33.38	91.03	39.75	71.07	37.34	12.879	1.867
Body height (Bh)	8.90	4.92	18.14	6.67	12.36	5.93	2.926	0.486
Body width (Bw)	14.20	6.2	25.30	8.95	18.15	8.13	3.114	0.745
Body area (Ba) (mm^2)	479.27	164.22	1602.13	256.79	914.01	222.17	389.188	22.520
Midline height (Mh)	4.94	2.8	8.36	4.38	6.19	3.85	1.110	0.436
Head measurements (mm)								
Head length (Hl)	13.67	8.09	20.73	10.23	16.98	8.98	2.511	0.621
Head height (Hh)	7.65	3.24	14.21	5.01	10.38	4.42	2.029	0.401
Eyes midline height (Emh)	6.25	2.6	10.96	3.25	8.17	3.02	1.607	0.155
Fin measurements (mm)								
Pectoral fin length (Pfl)	15.55	9.18	29.48	11.12	20.77	10.24	4.130	0.624
Pectoral fin width (Pfw)	8.57	4.35	14.54	6.51	11.77	5.34	2.382	0.672
Pectoral fin area (Pfa) (mm^2)	86	25	310	43	160.35	32.1	65.13	5.035
Caudal fin length (Cfl)	18.97	8.86	36.06	12.88	26.16	11.46	4.372	1.225
Caudal fin height (Cfh)	15.87	8.29	33.90	12.27	23.21	10.69	4.193	1.188
Caudal fin area (Cfa) (mm^2)	185	48	720	76	353.1	64.85	143.526	8.028
Dorsal fin area (Dfa) (mm^2)	165	27	708	40	338.8	32.65	152.404	4.356
Caudal peduncle measurements (mm)								
Caudal peduncle length (Cpl)	17.35	10.04	31.90	12.90	23.29	11.80	4.37	0.897
Caudal peduncle width (Cpw)	3.25	1.6	9.11	2.67	4.97	2.39	1.887	0.268
Caudal peduncle height (Cph)	4.63	2.43	9.43	3.9	6.18	1.93	1.601	0.234
Mouth measurements (mm)								
Mouth width (Mw)	4.8	2.27	8.72	3.05	6.16	2.66	1.087	0.248
Mouth height (Mh)	3.95	1.68	8.03	2.46	5.21	1.93	1.233	0.234

Results

1. Habitat use

The ANOSIM revealed significant differences in the physical characteristics between the two studied habitats "stream channel" and "stream bank" (R = 0.712; p < 0.001). Sand and mud were the most abundant substrate types registered in both habitats totalling 97.4% in stream channel and 84.5% in stream bank. The mean values of water flow and depth were 0.37 m/s and 30.6 cm in stream channel and 0.2 m/s and 24.1 cm in stream bank, respectively. Water flow and stream depth were highly correlated (t = 5.379; df = 308; p < 0.001) revealing that habitats with higher water flow were also the habitats with higher depth. Relationship between habitat use and fish abundance revealed a positive correlation for *Hypostomus punctatus*, indicating that a high number of individuals was using habitats with higher values of water flow (Figure 2a) and no correlation for *Parotocinclus maculicauda* was found (Figure 2b).

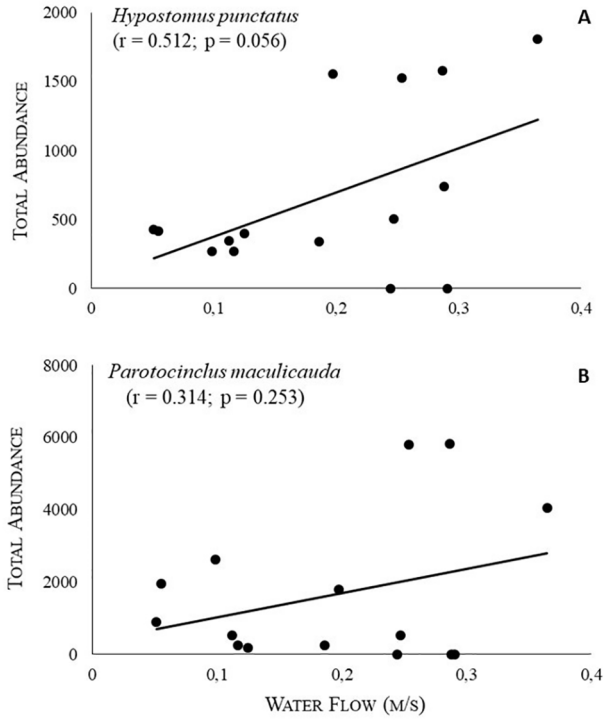


Figure 2. Correlations between total abundance and water flow for (A) *H. punctatus* and (B) P. *maculicauda.*

2. Morphology and feeding ecology between studied species

The intestine content analysis showed nine types of food items for *P. maculicauda* and seven for *H. punctatus*. Sediment and organic matter were the main items for both species, whereas plant debris, diatom and filamentous algae showed a high frequency of occurrence but low volumetric values (Table 3).

PCA showed morphological differences between the species (Figure 3a). The first axis explained 57.24% of the total variance and the second axis 15.21%. Intestine length, the relative area of the dorsal fin, the relative mouth height, the index of ventral flattening, and the relative mouth width were the principal attributes responsible for the separation of the species (Table 2). For diet, PCA showed feeding similarity between species (Figure 3b and Table 4) and values of diet traits did not vary between sampled months for both species (*H. punctatus* – F = 2.612; p = 0.111 and *P. maculicauda* – F = 0.8; p = 0.373).

PERMANOVA results revealed significant differences between species for morphology (F = 112.64; p < 0.001) corroborating PCA results. However, as the opposite from PCA results, diet was significantly different between species (PERMANOVA – F = 6.553; p < 0.001). Finally, the variance in the use of food resources was higher for *H. punctatus* (9.567) than for *P. maculicauda* (0.037) and niche overlap tended to 1 (0.981) showing an overlapping trend between the studied species.

3. Morphological-dietary relationships

Mantel test correlations between morphological dissimilarity and diet dissimilarity among individuals were not significant for *H. punctatus* (R = -0.213; p = 0.76) (Figure 4b) and for *P. maculicauda* (R = -0.2005; p = 0.964) (Figure 4c). Both correlations were weak and revealed that morphology did not explain the diet in both studied species.

Discussion

The physical differences between stream channel and stream bank observed in this study allowed two different habitats to be explored by both loricariid species, corroborating the high diversity of habitats previously registered in Neotropical streams (Manna et al. 2017). Our results revealed that total abundance of *H. punctatus* was higher in stream channel confirming that this species used the stream channel with more frequency. Species of the same family (close-related species) generally present niche segregation (MacArthur 1972, Kirchhof et al. 2010), and this was one of our initial hypotheses when the habitat use by the two studied species was considered. However, *Parotocinclus maculicauda* and *Hypostomus punctatus* from Mato Grosso stream explored similar food resources in both of them. Many studies in the literature have shown that the species of Loricariidae consume mainly vegetal items (e.g. Menezes 1949, Nomura et al. 1975, Casatti & Castro 2006, Casatti et al. 2005) but diet composition in the Loricariidae species is variable (Garavello & Garavello 2004). Some species have been classified as iliophagous, with a low frequency of algae and high values for detritus and sediment in the diet (Buck & Sazima 1995, Albrecht & Silveira 2001, Mazzoni et al. 2010) and even with a variable diet composed by detritus, sponges, bryozoans, and bryophytes (Delariva & Agostinho 2001). Vegetal items, such as diatoms and filamentous algae, and periphyton colonize various types of substrate in aquatic environments, especially composed by hard structure (e.g. stones and gravel) (Azim et al. 2005). Our results revealed that "stream channels" and "stream banks" were composed mainly by sand and mud, which are soft substrates, affecting the availability of periphyton to be consumed by fish and explain the high amount of sediment consumed by the studied species. Diet in stream-dwelling fish can be largely dependent of the environment where the individuals inhabited in the moment of fish sampling (Lobón-Cerviá et al. 2016, Dias et al. 2017) explaining the diet composed by a large amount of sediment in the two studied Loricariidae species.

Loricariidae species are specialized in the way they explore the environment and frequently present morphology adapted to explore specific resources like detritus or periphyton (Agostinho et al. 1997,

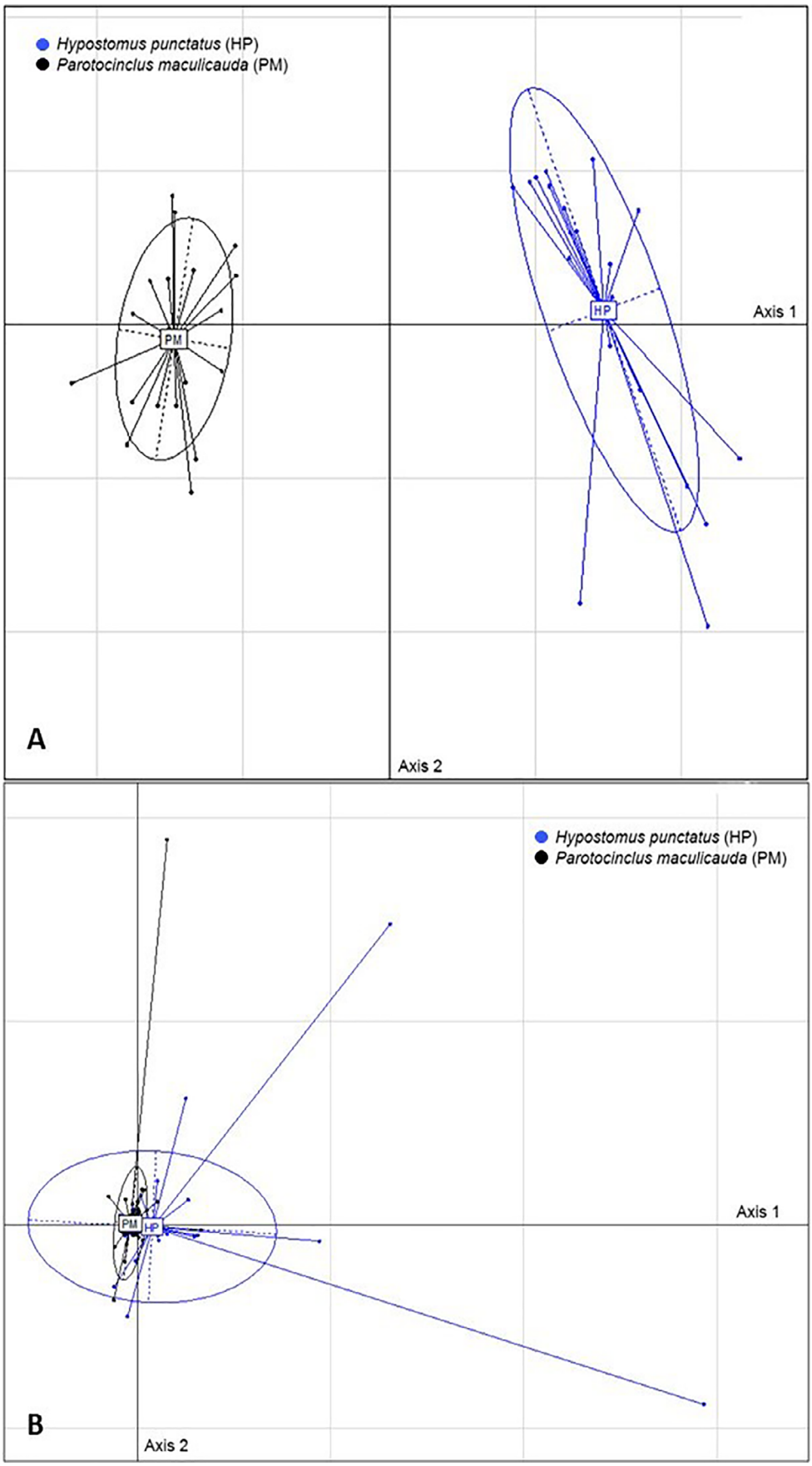


Figure 3. Principal component analysis (PCA) for *H. punctatus* (HP; blue circles) and P. *maculicauda* (PM; black circles) from the Mato Grosso Stream according to (a) 16 ecomorphological traits identified in Table 2 and (b) diet traits identified in Table 4.

Table 2. Percent of total variance explained by components and scores, and average values of 16 ecomorphological attributes for 20 specimens of *H. punctatus* and 20 of *P. maculicauda* from the Mato Grosso Stream, Saquarema, Rio de Janeiro, Brazil.

Ecomorphological	**PCA**		**Average value (mm)**	
Attribute (mm)	**Factor 1**	**Factor 2**	***Parotocinclus maculicauda***	***Hypostomus punctatus***
Relative head length (= Sl / Hl)	-0.212	0.622	0.240	0.238
Caudal fin aspect ratio (= Cfh^2 / Cfa)	-0.386	0.417	1.768	1.603
Compression index (= Bh / Bw)	-0.436	-0.795	0.724	0.676
Pectoral fin aspect ratio (= Pfl / Pfw)	-0.587	-0.366	1.929	1.768
Relative caudal peduncle length (Cpl / Bl)	0.633	0.091	0.316	0.327
Relative eye position (= Emh / Hh)	0.689	-0.225	0.685	0.777
Relative depth (= Bh / Bl)	0.723	-0.485	0.159	0.172
Relative area of pectoral fin (Pfa / Ba)	0.801	0.431	0.142	0.177
Caudal peduncle compression index (Cph / Cpw)	-0.801	0.464	1.513	1.287
Mouth aspect ratio (= Mh / Mw)	0.806	-0.363	0.725	0.837
Relative area of caudal fin (= Cfa / Ba)	0.826	0.370	0.293	0.390
Relative mouth width (= Mw / Bl)	0.902	0.272	0.071	0.087
Index of ventral flattening (= Mh / Bh)	-0.914	0.165	0.648	0.508
Relative mouth height (= Mh / Bl)	0.955	-0.061	0.052	0.072
Relative area of dorsal fin (= Dfa / Ba)	0.958	0.192	0.147	0.376
Intestine length	0.968	-0.028	3.960	12.476
Predicted Eigenvalues (Broken-stick)	**9.159**	**2.435**		
Percent of Total Variance Explained	**57.24**	**15.21**		

Table 3. Volume (Vo), Frequency of Occurrence (Fo), and Alimentary Index (AIi) of each food item registered for *H. punctatus* and *P. maculicauda* from the Mato Grosso stream, Saquarema, Rio de Janeiro, Brazil.

Standard Length (minimum-maximum)	***Parotocinclus maculicauda*** **(N = 117)** **2.5 ± 4.8 cm**			***Hypostomus punctatus*** **(N = 62)** **2.2 ± 6.5 cm**		
Item	***Vo***	***Fo***	***AIi***	***Vo***	***Fo***	***AIi***
Aquatic larvae	0.07	0.85	0.001	0.00	0.00	0.00
Cyanobacteria	0.01	2.56	<0.001	0.003	3.23	<0.001
Scale	0.14	2.56	0.004	0.00	0.00	0.00
Unidentified	0.01	2.56	<0.001	0.01	6.45	0.001
Filamentous algae	0.47	48.72	0.23	0.32	29.03	0.09
Plant debris	1.24	63.25	0.79	1.94	80.65	1.58
Diatom algae	0.99	88.89	0.89	1.69	96.77	1.65
Detritus	41.06	100	41.49	38.32	100	38.58
Organic matter	56.01	100	56.60	57.72	100	58.11

Hahn et al. 1997) playing an important role for nutrient cycling in aquatic ecosystems (Capps & Flecker 2013, Santos et al. 2016). Large dorsal fins and maneuverability to sustain in the rapids is one of their main ecomorphological features and was also registered in the studies developed by Pagotto et al. (2011). The mouth position and shape can allow the species to explore benthonic microhabitats by grazing (Casatti 2002, Garavello & Garavello 2004). Microscopic algae grow on stones, twigs, or submerged vegetation (Bicudo & Bicudo 1970), and the physical parameters of the streams can influence the composition and structure of the diatom communities (Sinitean et al. 2012). The stream site has suffered strong environmental changes resulted from sand extraction and presented a lot of sand, mud substrata, and an absence of stones in stream bank (Mazzoni et al. 2010, Lobón-Cerviá et al. 2016). These changes could be influencing the availability of algae and hence explain the low volume of algae in the diet of the two studied species. We suggest that the environmental changes have forced changes in the natural feedings habits and caused the similar diet of the two studied species with high amount of sediment in their diet composition.

Although the two studied species are morphologically closely related, the results of the present study revealed significant differences in the morphological attributes between them. *Hypostomus punctatus* showed higher values for its mouth characteristics and a lower value

Table 4. Percent of total variance explained by components and scores, and average values of seven diet traits for 117 specimens of *Parotocinclus maculicauda* and 62 of *Hypostomus punctatus* from the Mato Grosso Stream, Saquarema, Rio de Janeiro, Brazil.

Diet traits (V%)	PCA		Average value (Volume - mm³)	
	Factor 1	Factor 2	*Parotocinclus maculicauda*	*Hypostomus punctatus*
Aquatic larvae	0.001	-0.511	0.005	0.000
Cyanobacteria	0.009	0.011	<0.001	<0.001
Scale	0.013	0.052	0.010	0.000
Unidentified	0.014	0.185	<0.001	0.002
Filamentous algae	-0.053	-0.788	0.035	0.059
Plant debris	-0.451	-0.225	0.092	0.365
Diatom algae	-0.501	0.119	0.073	0.318
Detritus	-0.514	0.088	3.065	7.216
Organic matter	-0.524	0.077	4.182	10.869
Predicted Eigenvalues (Broken-stick)	**3.478**	**1.154**		
Percent of Total Variance Explained	**36.65**	**12.82**		

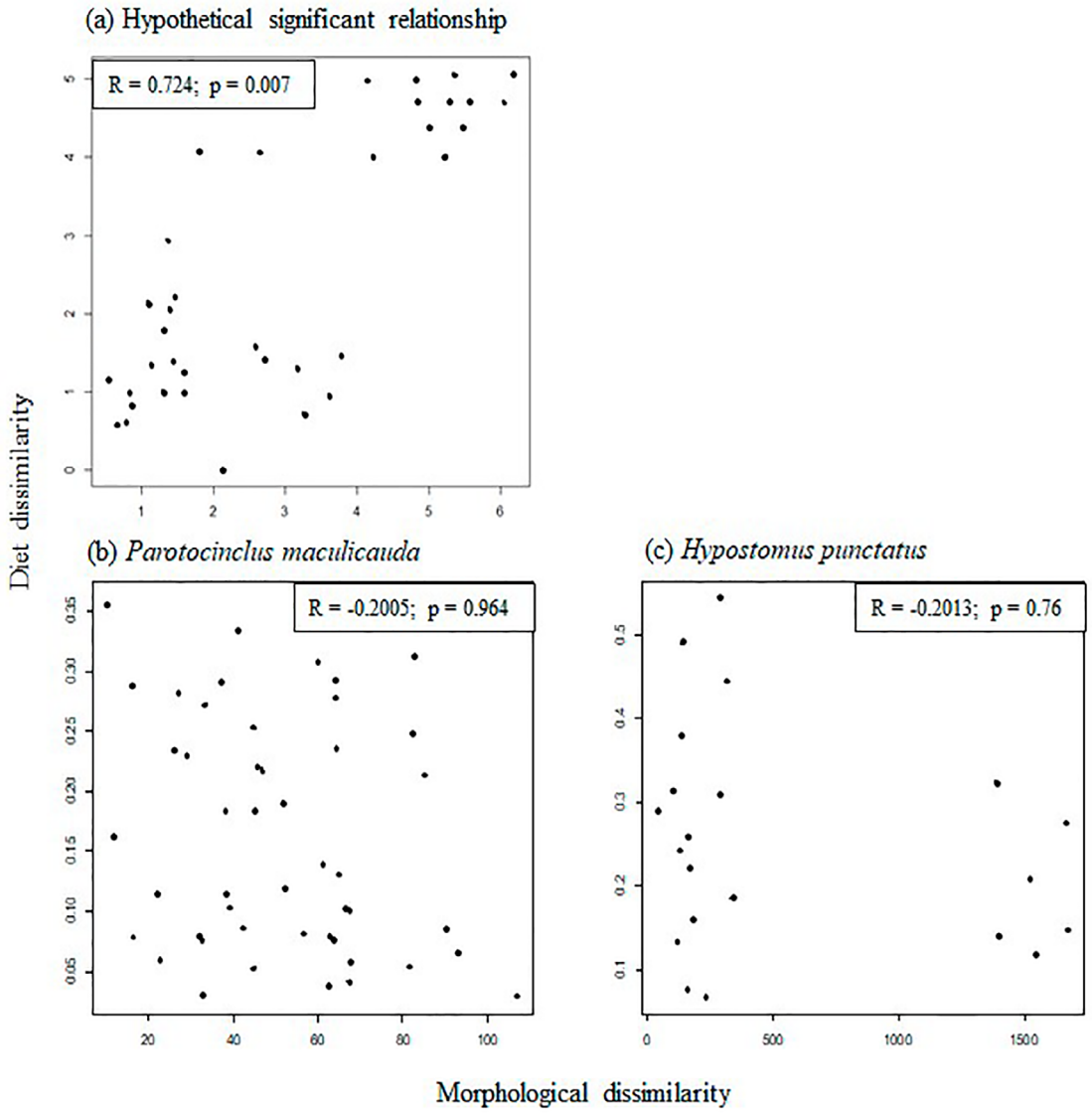


Figure 4. Correlation between dissimilarity in morphology and diet for the two studied species. The top panel show a significant correlation computed on with hypothetical data (a). Bottom panels show results computed on individual's data for *P. maculicauda* (b) and *H. punctatus* (c). Values of Mantel's correlation test are provided at the top of each panel.

for ventral flattening, whereas *P. maculicauda* presented a lower value for the relative area of the dorsal fin. A larger mouth with modified oral lips is used for temporary substrate attachment (Casatti et al. 2001) and provides better foraging performance in turbulent water (Casatti et al. 2005). Furthermore, low ventral flattening is an important factor that indicates a better ability to remain fixed on the river bed (Mahon 1984). The larger size of the dorsal fin on *H. punctatus* enables faster movement and is used for propulsion, braking, and stabilization in turbulent waters (Breda et al. 2005). These differences between the two studied species can explain the higher frequency of *H. punctatus* in the stream channel when compared to *P. maculicauda*. Thus, despite their use of similar food resources, we suggest that these loricariids are spatially segregating in the studied stream, facilitating their coexistence, as it has been reported in other studies (Leitão et al. 2015, Celestino et al. 2017).

The weak correlation between morphological variability and diet dissimilarity registered for both species suggests that specialized morphology described for Loricariidae species (Schaefer & Lauder 1986, Delariva & Agostinho 2001) was not enough to explain feeding habits of the studied species. Correlations between diet and morphology were already related as weak relationships revealing that morphology is not a good proxy for diet (e.g. Ibañez et al. 2007, Manna et al. 2019). Versatility in the diet for Neotropical fishes can explain this absence of significant relationship between morphology and diet, since fish are able to change feeding habits according to environmental conditions (Manna et al. 2012, Lobón-Cerviá et al. 2016). Additionally, some studies revealed the morphological adaptation of the digestive system (e.g. intestine length) to process detritus during digestion in loricariid species (Agostinho et al. 1997, Hahn et al. 1997) which can explain the consumption of sediment and organic matter by studied species. Moreover, our results revealed that feeding overlap was high and that morphology did not explain feeding habits. The studied site is impacted with siltation along the entire stream bank, which seems to explain why studied species do not have a high range of prey to capture and consequently, showed high feeding overlap and weak dietary-morphological relationships.

Intraspecific variability in trophic morphology between related species has been frequently documented in the literature (Binning & Chapman 2010, Griffen & Mosblack 2011). Trophic variance was higher for *H. punctatus* which reflect higher individual variation in the use of food resources when compared to *P. maculicauda*. This difference can be explained by the larger body size of *H. punctatus* that allows it to explore a larger spatial area and different microhabitat types, especially the stream channel, where there is high turbulence (personal field observations). Buck & Sazima (1995) have previously proposed that Loricariidae species exploit the same type of substrata and present similar foraging habits. Although PERMANOVA revealed significant differences in the diet between studied species, these observations reflect our results, as *H. punctatus* and *P. maculicauda* in the Mato Grosso stream displayed almost complete trophic niche overlap. Furthermore, the high consumption of sediment and organic matter seems to explain the higher feeding overlap between species (Abilhoa et al. 2016) while the differences in the consumption of algae and plant debris are driving the differences detected in PERMANOVA. These variations in trophic resource utilization can be also explained by the differences in how species are exploring their foraging habitats (Pagotto et al. 2011). These results may be explained by certain physical characteristics of the study site, such as high amount of sand and mud (Mazzoni et al. 2010, Lobón-Cerviá et al. 2016).

The differences in morphological traits, expressed by the differences in ventral flattening should be causing species segregation according to habitat use. However, the morphology did not explained trophic similarity revealed between species, which is probably reflected by the high consumption of sediment and organic matter in both species' diet. Thus, our results suggest that the environmental conditions were more important for the diet composition when compared to the similar and specialized morphology of studied loricariids, and that studied species are segregating in habitat use to facilitate their coexistence.

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Author contributions

Luisa Resende Manna: conceived the ideas and designed methodology; collected the data; analyzed the data; led the writing of the manuscript.

Jean Carlos Miranda: collected the data; analyzed the data;

Carla Ferreira Rezende: conceived the ideas and designed methodology;

Rosana Mazzoni: conceived the ideas and designed methodology; led the writing of the manuscript.

All authors contributed critically to the drafts and gave final approval for publication.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

This study was performed in strict accordance with the recommendations of the Ethical committee of Rio de Janeiro State University (CEUA/012/2013) and sampling was compiled with current Brazilian laws (collecting permit IBAMA/MMA 02022.002475/2006-10, authorization number 118/2006 – DIFAP/IBAMA).

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Taxonomic Distinctness of the subterranean fauna from Peruaçu Caves National Park, state of Minas Gerais, eastern Brazil

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Abstract: Limiting factors of subterranean environments, high relative air humidity and, especially, permanent darkness, represent ecological filters for organisms and biodiversity patterns of surface and subterranean communities display wide disparities. Subterranean diversity and singularity are, thus, better expressed when the common presence of rare and endemic species are considered. Our study aimed to describe the diversity of the cave fauna from 14 caves from Peruaçu Caves National Park (PCNP), eastern Brazil. We analyzed the regional diversity using the index that includes the average taxonomic distinction (TD - Δ+, AvTD). We recorded 1,674 individuals belonging to 10 Classes and 237 morphotypes, 11 troglobitic and two troglomorphic and possible troglobites. Greatest species abundance (N=330) and richness (s=76) were recorded at Lapa do Cipó cave, followed by Gruta Olhos d'Água (N=330, s=71), which shows the highest TD value (Δ+ = 90.18) in relation to the others, including the richest Lapa do Cipó (Δ+ = 85.24), consequence of the several taxonomic units with large number of species. The below-expected values of TD (Δ+ = 87.70) may indicate anthropic impacts on these communities. Our results demonstrate that Gruta Olhos d' Água and Lapa do Cipó caves are the most important sites for the occurrence of endemic and troglobitic species and may be part of a complex system that should be considered for a more efficient conservation planning.
Keywords: *Diversity, Gruta Olhos d'Água cave, troglobites, subterranean environment.*

Distinção Taxonômica da fauna subterrânea do Parque Nacional Cavernas do Peruaçu, estado de Minas Gerais, leste do Brasil

***Resumo*:** Fatores limitantes dos ambientes subterrâneos como alta umidade relativa do ar e, principalmente, a falta de luz, representam filtros ecológicos para organismos e padrões de biodiversidade de comunidades superficiais e subterrâneas, nas quais mostram grandes disparidades. Diversidade e singularidade subterrâneas são, portanto, mais bem expressas quando os presença de espécies raras e endêmicas. Nosso estudo teve como objetivo descrever a diversidade da fauna da caverna de 14 cavernas do Parque Nacional das Cavernas de Peruaçu (PCNP), leste do Brasil. Analisamos a diversidade regional usando o índice que inclui a distinção taxonômica média (TD - Δ+, AvTD). Registramos 1,674 indivíduos pertencentes a 10 classes e 237 morfotipos, 11 troglóbios e dois troglomórficos e possíveis troglóbios. A maior abundância de espécies (N = 330) e riqueza (s = 76) foram registradas na caverna da Lapa do Cipó, seguida por Gruta Olhos d´Água (N = 330, s = 71), que mostra o maior valor de DT (Δ+ = 90,18) em relação aos outros, incluindo a Lapa do Cipó mais rica (Δ+ = 85,24), consequência das várias unidades taxonômicas com grande número de espécies. Os valores abaixo do esperado de TD (Δ+ = 87,70) podem indicar impactos antrópicos nessas comunidades. Nossos resultados demonstram que as cavernas Gruta Olhos d 'Água e Lapa do Cipó são os locais mais importantes para a ocorrência de espécies endêmicas e troglóbias e pode fazer parte de um sistema complexo que deve ser considerado por mais planejamento eficiente de conservação.
Palavras-chave: *Diversidade, Gruta Olhos d'Água, troglóbios, ambiente subterrâneo.*

Introduction

Subterranean or hypogean environments have striking features which represent environmental filters, because selective regimen contrasts sharply with those of surface environments. Permanent darkness at deeper zones is the main difference (Hoenen 2005, Hervant et al. 2000, Poulson & White 1969), leading to the dependence of allochthonous energy inputs because photoautotrophic organisms do not thrive there (Poulson & Lavoie 2000). Environmental stability is other noteworthy aspect of subterranean ecosystems. Unlike surface communities, little variation occurs in parameters such temperature and air humidity, due to the isolation caused by the surrounding rock (Juberthie 2000, Culver & Pipan 2009). Such contrasts between subterranean and superficial environments are related to processes of colonisation and reproductive isolation of subterranean species (Trajano 2012).

Subterranean communities are formed by populations which present distinct ecological-evolutionary relationships with the environment and, consequently, may be classified at three categories (Racovitza 1907, Trajano 2012), according to its degree of specialisation to the subterranean realm: trogloxenes are those who need to leave the cave periodically in order to complete its life cycle because subterranean resources are insufficient (Racovitza 1907). Troglophiles are those capable of completing its life cycle inside as well as outside subterranean environments. They represent the majority of the taxa found at subterranean communities (Racovitza 1907). Some species only live at subterranean environments (Racovitza 1907), not being able to colonise surface environments anymore, because they evolved isolated at subterranean environments and, during this period, accumulated specialisations that hampers survival or reproduction in surface environments. They are called troglobites (Racovitza, 1907). This condition is recognised by the presence of autapomorphies acquired throughout evolutionary process, known as troglomorphisms (Holsinger & Culver 1988, Holsinger 1988, Trajano & Bichuette 2010). Even though the term troglomorphism (*sensu* Christiansen 1962) had been originally proposed for morphological characteristics, it has been applying to behavioural and physiological characteristics as well (Barr 1968). This classification has been extended and discussed by Trajano and Cobolli (2012) to include source-population concept and, thus, population characteristics has been included for recognizing the troglobitic status of a given species.

Diversity patterns of subterranean and superficial communities show significant disparities. Even though richness of subterranean communities is much lower when compared to superficial communities, it can be considered high on a global scale (Gibert & Deharveng 2002). In addition, when lineages that colonised both habitats at the same geographical area are compared, subterranean communities have much higher proportion of endemic species than superficial communities (Gibert & Deharveng 2002). Recognition of such patterns is essential to support conservation proposals (Trajano 2010).

Knowledge about Brazilian subterranean fauna has been broadened at the last two decades. The first faunistic lists were produced for the karst area of Ribeira Valley (Trajano & Gnaspini 1991), states of São Paulo and Paraná (Trajano & Bichuette 2010). Later, other regions had their diversity assessed, including karst areas at the states of Minas Gerais, Bahia, Mato Grosso do Sul, Goiás and Rio Grande do Norte (Gnaspini & Trajano 1994, Pinto-da-Rocha 1993, Trajano & Bichuette 2010, Ferreira et al. 2010, Gallão & Bichuette 2018).

Some are important because they have high species richness, presence of phylogenetic indicators or high genetic diversity. (Trajano et al. 2016). High genetic diversity is based on the degree of specialisation of individual species, with accumulation of autapomorphies, that may evolve into a troglobitic species, while phylogenetic indicators are related to the presence of biogeographical relicts (Trajano et al. 2016). Exclusively subterranean populations are generally fragile and represent one of the main arguments in favour of the conservation of caves and its systems (Trajano 2010, Trajano et al. 2016, Gallão & Bichuette 2018). For this reason, to understand the evolutionary processes and patterns that occur in underground environments, faunal studies are needed to identify high diversity spots and to propose actions and political for conservation. (Trajano et al. 2016).

We investigated the biodiversity of caves located at Peruaçu Caves National Park (PCNP), northern state of Minas Gerais, taking into account not only the number of species, but its identity as well. The region has 140 caves registered so far, of which, Gruta Olhos d' Água cave is the largest one, with approximately 9,100 m of conduits and passageways, and harbors the highest number of troglobites (Trajano et al. 2016, Gallão & Bichuette 2018). For this, two main questions were considered: 1) Do the PCNP caves have high phylogenetic diversity? 2) Does Gruta Olhos d 'Água cave present higher diversity compared to the other caves of the PCNP?

Materials and Methods

1. Study Area

We conducted the study herein presented in 14 caves located at Peruaçu Caves National Park (PCNP), municipalities of Itacarambi and Januária, northern of Minas Gerais state (Figure 1). The region has outcrops composed by carbonate rocks from Bambuí Group, more precisely laminated limestone and dolomites from Januária-Itacarambi Formation (Piló & Kohler 1991). Inside the limits of PCNP, Peruaçu river traverses about 17 Km of its valley surrounded by enormous rocky walls, channels and dolines, forming the Peruaçu river, left tributary of the upper-middle São Francisco River.

Peruaçu Valley, where PCNP is located, occurs in a transition zone between Cerrado and Caatinga morphoclimatic Domains (Ab'Saber 1977). Climate covering Peruaçu, according to Köppen-Geiger, is tropical humid with dry winters ("Aw") (Peel et al. 2007), characterised by dry winters, between March and October, and rainy summers, between April and November, with annual average temperature of 24°C and average annual rainfall of 800 mm (INMET 2010).

2. Samplings

We conducted field campaigns between the years along the years of 2013 and 2015 at the following caves: Lapa da Onça, Lapa d' Água, Lapa do Branco I, Lapa do Branco IV, Toca do Pedrinho, Toca Mina d'Água, Gruta Olhos d' Água, Lapa do Cipó, Lapa do Mogno, Gruta Troncos, Caverna dos Cascudos, Caverna Janelão, Caverna Boquete and Caverna Bonita (Figure 2). During this period, we visited Gruta Olhos d' Água seven times, Lapa do Cipó four times and only once the other caves.

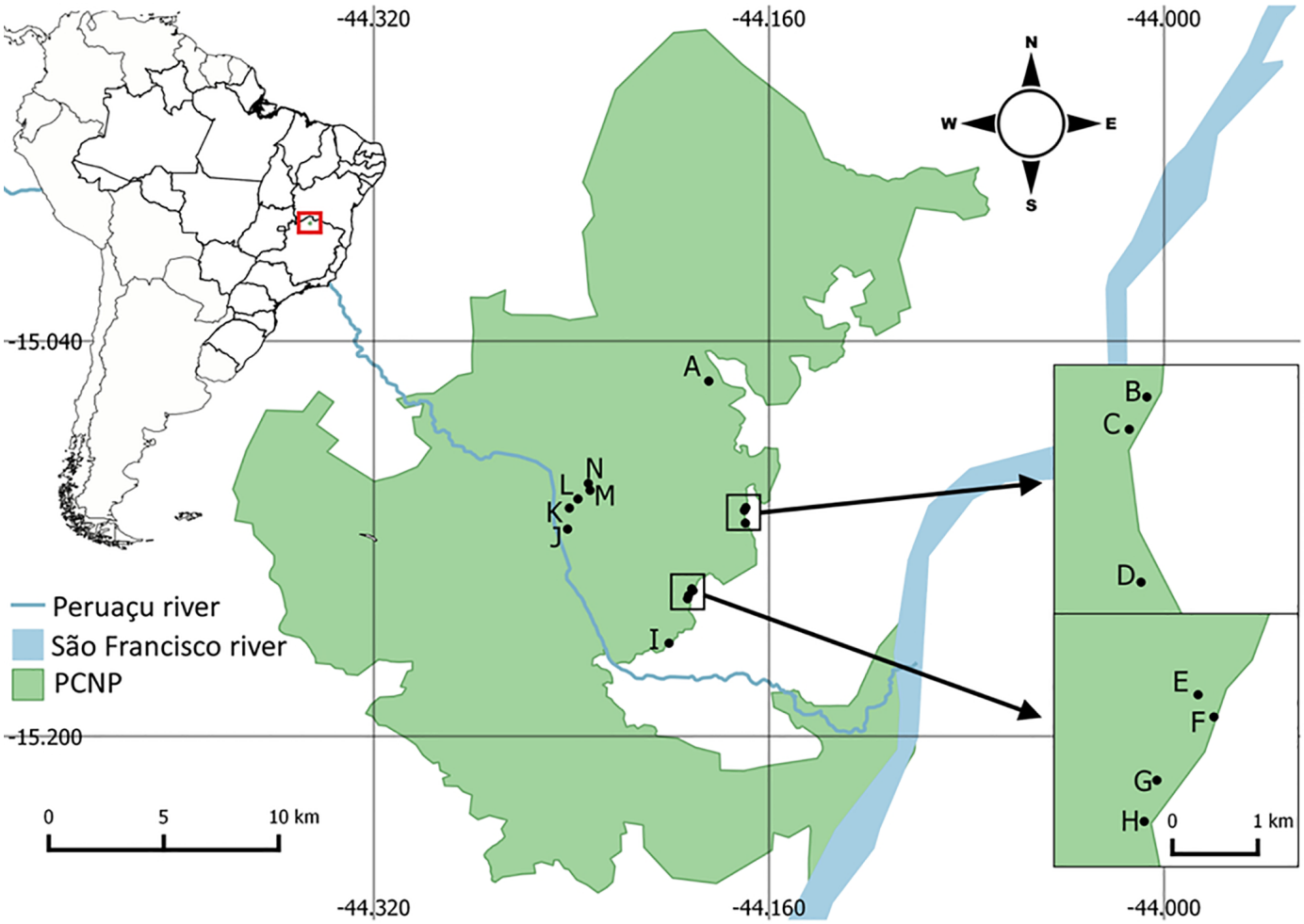


Figure 1. Study area. Peruaçu Cave National Park (PCNP), Itacarambi municipality, state of Minas Gerais, Brazil. A = Lapa do Cipó; B = Gruta Mina d' Água; C = Toca do Pedrinho; D = Gruta Olhos d' Água; E = Lapa da Onça; F = Lapa do Branco I; G = Lapa do Branco IV; H = Lapa dos Sonhos; I = Lapa do Mogno; J = Gruta Janelão; K = Gruta Bonita; L = Caverna Boquete; M = Gruta dos Troncos and N = Caverna dos Cascudos.

We sampled potential microhabitats by active search and then the collected specimens were euthanized and preserved in 50% and 70% alcohol. We then identified morphotypes at the least inclusive taxonomic level we could reach using specialised literature (Borror et al., 1989; Adis, 2002; Costa et al., 2006). In addition, we consulted specialists in order to refine identification: Bolfarini, M.P. (Orthoptera - LES/UFSCar), Brescovit, A. (Ctenidae – Instituto Butantan), Carvalho, L.S. (Pholcidae - UFMG), Chagas-Jr, A. (Chilopoda - UFMT), Fernandes, C.S. (Isopoda – LES/UFSCar), Gallão, J.E. (Scorpiones - LES/UFSCar), Gallo, J.S. (Diplopoda - LES/UFSCar), Prado, L.P. (Formicidae – Museu de Zoologia/USP), Cizauskas, I. (Araneae - Museu de Zoologia/USP), von Schimonsky, D.M. (Pseudoscorpiones - LES/UFSCar) and Salvador, R.D. (Gastropoda - State Museum of Natural History Stuttgart, Germany).

3. Data analysis

We used Taxonomic Distinctness index (TD) (Δ+, AvTD) for diversity analysis, defined as the mean distance between two randomly chosen species, traced by means of a Linnean or phylogenetic classification of all the species in the data-set (Warwick & Clarke 1998, Clarke & Warwick 2001).

Differently of a traditional diversity index, the Taxonomic Distinctness TD (Δ+, AvTD) take into account the abundance of rare and common species by giving them different weights (Warwick & Clarke 1998, Cianciaruso et al. 2009). Besides considering the relative contribution of each species at a given community by using the number of species and the distribution of individuals, TD also includes the taxonomic value of each species.

Taxonomic distinctness is, thus, estimated by the expected number of nodes between any two individuals of different species randomly drawn from the full species set. The biggest number of nodes or links among them, the higher will be the distinctness of a given species (Warwick & Clarke 1998, Cianciaruso et al. 2009). Also, Taxonomic Distinctness index is a robust measure, when compared to traditional indexes of diversity, because it is independent of sampling effort (Warwick & Clarke 1998). We used PRIMER 7 statistical package to calculate TD (Δ+, AvTD) (Clarke & Gorley 2015) using the data-set.

Results

We recorded a total abundance of 1,674 individuals inside all caves we visited, from 237 morphotypes inside ten Classes: Actinopterygii (Osteichthyes), Amphibia, Arachnida, Chilopoda, Clitellata, Diplopoda,

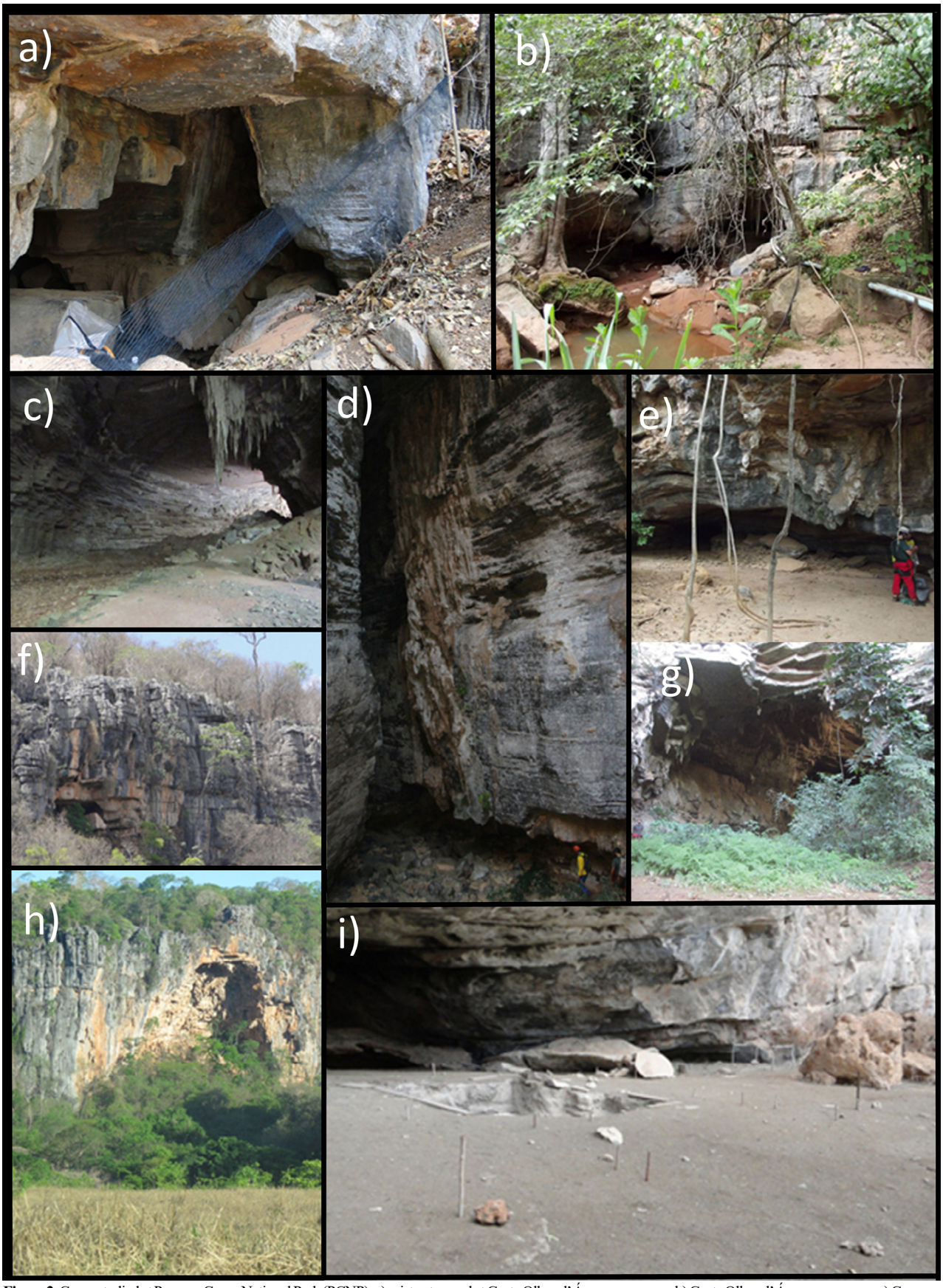


Figure 2. Caves studied at Peruaçu Caves National Park (PCNP). a) mist net armed at Gruta Olhos d' Água resurgence, b) Gruta Olhos d' Água resurgence, c) Caverna do Cascudo, d) Entrance Lapa do Cipó, e) Entrance Toca do Pedrinho, f) Entrance Gruta Bonita, g) Entrance Caverna dos Troncos, h) Entrance Gruta Janelão, i) archaeological excavations at Caverna Boquete. Photo: a, f – Arnone, I.; b, h, i – Bichuette, M. E.; c, g – Gallão, J.E.; d – Bolfarini, M.P.; e – Fonsceca-Ferreira, R.

Entognatha, Gastropoda, Insecta and Malacostraca. Both Arachnida and Insecta were richer (42.2% and 38.5%, respectively) and more abundant (46.6% and 35.9%, respectively) than the other recorded Classes.

The sole representative of Actinopterygii was the troglobitic catfish *T. itacarambiensis,* endemic from Gruta Olhos d' Água cave. Entognatha and Mammalia presented equal relative abundance of 1.06% and richness at 0.81% and 1.63%, respectively. Mammals were represented by the bats *Carollia perspicillata*, *Desmodus rotundus, Diphylla ecaudata* and an unidentified Glossophaginae, all recorded at Gruta Olhos d' *Água*. Amphibia, Clitellata and Actinopterygii, were the less abundant, with 0.22%, 0.28% and 0.67%, respectively and the less rich, with 0.81%, 0.81% and 0.4%, respectively. Diplopoda had an abundance of 1.63% and a richness of 2.04%, while Chilopoda had abundance of 1.23% and richness of 2.86%. Diplopods *Katantodesmus* showed a small abundance in several stretches of Gruta Olhos d' Água, particularly at sediment banks.

Relative abundance of Malacostraca and Gastropoda represented 8.65% and 2.58% out of the total, respectively. When considering relative richness, Gastropoda had 6.55% and Malacostraca, 3.27%. Spiders, herein including both infraorders Araneomorphae and Mygalomorphae, represented 60.7% of all arachnids recorded, with predominance of Araneomorphae. Less representative but not least important, were the arachnids of the following Orders: Opiliones (14.3%), Amblypygi (1.3%), Pseudoscorpiones (12.1%), Scorpiones (1.2%), Acari (5.4%) and Opilioacarida (0.9%) (Figure 3). Insects were represented by 13 Orders with the predominance of Coleoptera (19.3%), followed by Lepidoptera (16.6%) and Diptera (19.3%).

The PCNP has 11 troglobitic species described (Table 1), such as the amphibious isopod *Xangoniscus odara* Campos-Filho, Araujo & Taiti, 2014 (Figure 4a), found at small puddles (Campos-Filho et al. 2014) and under submerged rocks inside Lapa do Cipó cave;

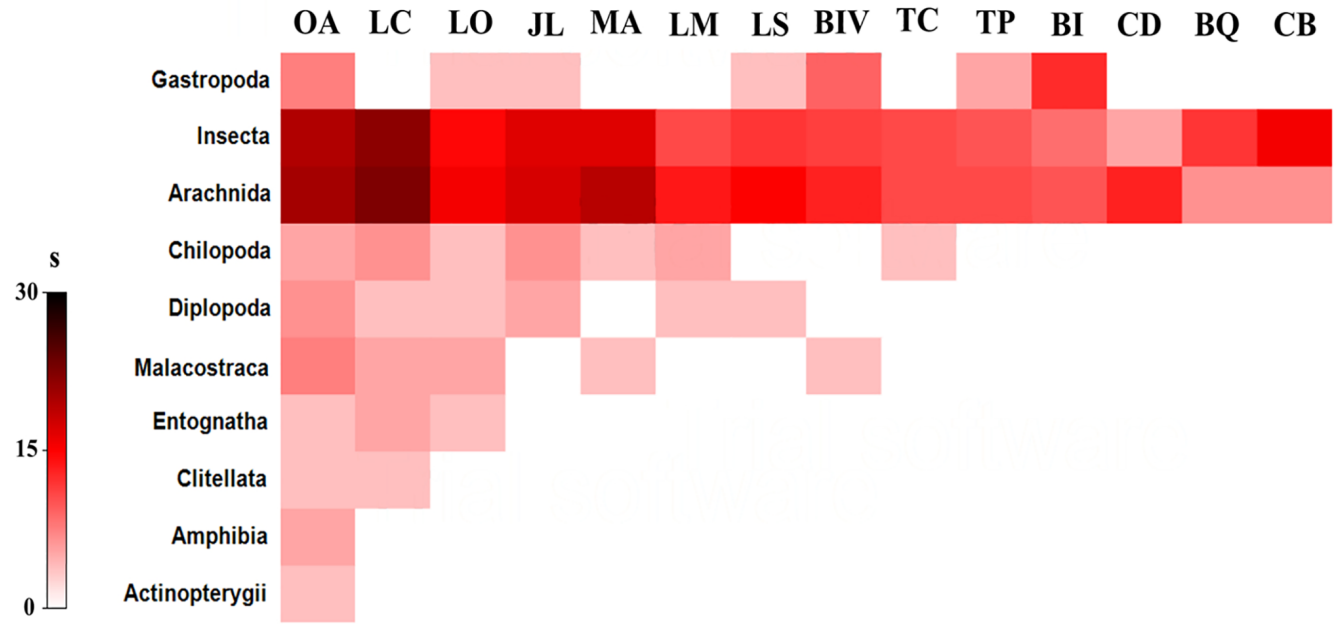


Figure 3. Species richness among Classes at 14 caves studied at Peruaçu Caves National Park (PCNP), Itacarambi municipality, state of Minas Gerais, Brazil. OA = Gruta Olhos d' Água; LC = Lapa do Cipó; MA = Gruta Mina d' Água; JL = Gruta do Janelão; LO = Lapa da Onça; CB = Caverna Bonita; BI = Lapa do Branco I; BIV = Lapa do Branco IV; LS = Lapa dos Sonhos; LM = Lapa do Mogno; BQ = Caverna Boquete; TC = Caverna Troncos; CD = Caverna Cascudo and TP = Toca do Pedrinho.

Table 1. Described troglobitic species of the PCNP.

Specie	Cave
Trichomycterus itacarambiensis Trajano & de Pinna, 1996	Gruta Olhos d' Água
Iandumoema uai Pinto-da-Rocha, 1996	Gruta Olhos d' Água and Lapa do Cipó
Pseudochthonius biseriatus Mahnert, 2001	Gruta Olhos d' Água
Charinus eleonorae Baptista & Giupponi, 2003	Gruta Olhos d' Água and Lapa do Cipó
Endecous peruassuensis Bolfarini, 2015	Gruta Olhos d' Água and Lapa do Cipó
Xangoniscus odara Campos-Filho & Taiti, 2016	Lapa do Cipó
Xangoniscus itacarambiensis Bastos- Pereira, Souza & Ferreira, 2017	Gruta Olhos d' Água
Relictopiolus galadriel Pérez-González, Monte & Bichuette, 2017	Gruta Olhos d' Água
Spelaeogammarus uai Bastos-Pereira & Ferreira, 2017	Lapa d' Água do Zezé
Spelaeometra gruta Polhemus e Ferreira, 2018	Lapa d' Água do Zezé, Lapa do Nestor, Lapa do Saco Velho and Lapa do Caboclo
Schendylops janelao Nunes, Chagas-Jr & Bichuette, 2019	Gruta do Janelão

the cricket *Endecous peruassuensis* Bolfarini & Bichuette, 2015 (Figure 4b) from Gruta Olhos d' Água and Lapa do Cipó caves (Bolfarini & Bichuette 2015), the relict Kimulidae harvestmen, *Relictopiolus galadriel* Pérez-González, Monte & Bichuette, 2017 (Pérez-González et al. 2017) (Figures 4c), the pseudoscorpion *Pseudochthonius biseriatus* Mahnert, 2001 (Figure 4d) and the recently described centipede from Gruta do Janelão cave, *Schendylops janelao* Nunes, Chagas-Jr & Bichuette, 2019 (Nunes et al. 2019) (Table 1). In addition to those described, we recorded species with conspicuous troglomorphisms such as the Diplopoda of family Oniscodesmidae (Figure 4f) and one species of Collembola (Entognatha). For troglophile category, a new spider of genus *Plato* was recorded (I. Cizauskas, pers. comm).

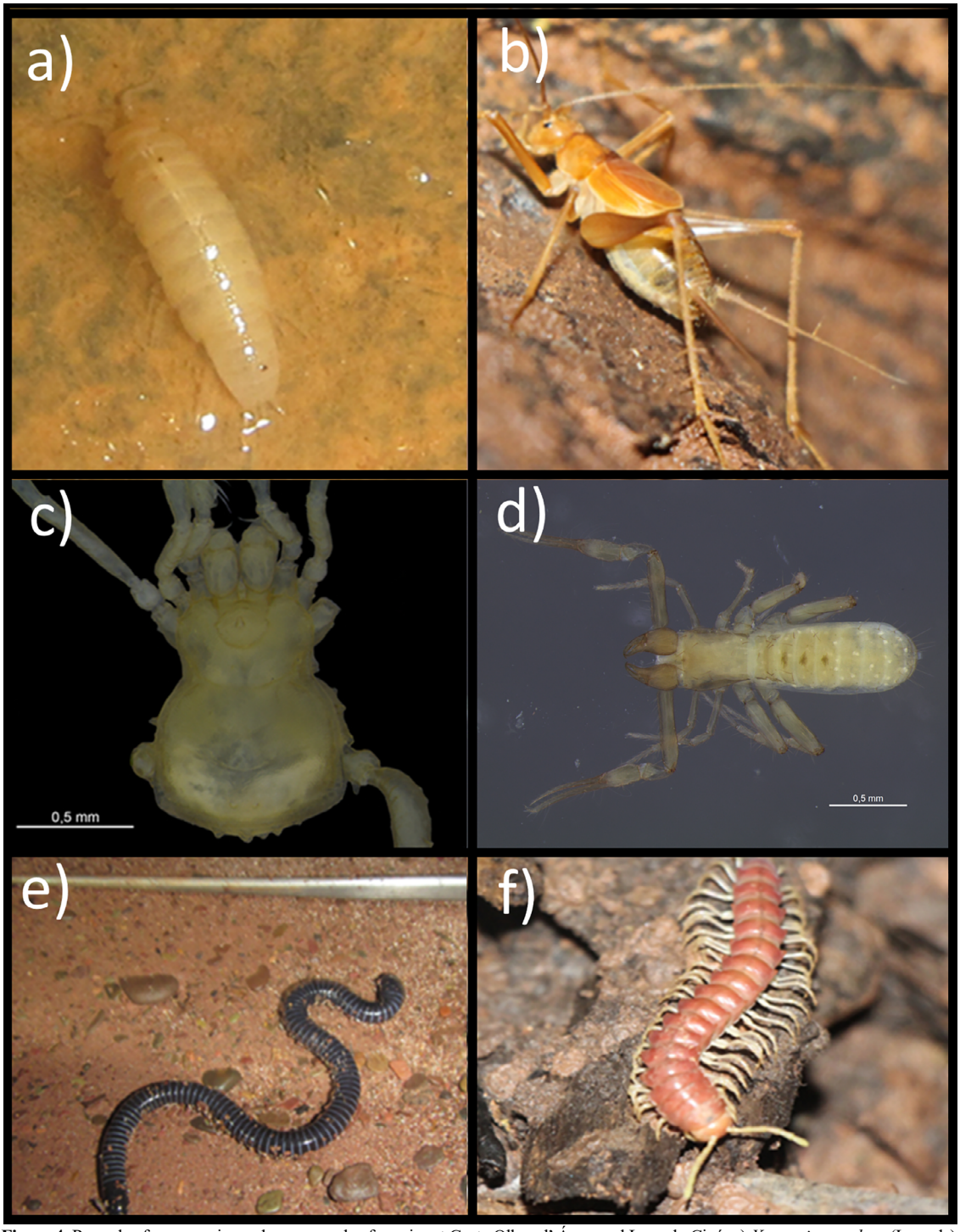


Figure 4. Records of new species and new records of species at Gruta Olhos d' Água and Lapa do Cipó. a) *Xangoniscus odara* (Isopoda) (Lapa do Cipó, troglobitic), b) *Endecous peruassuensis* (Orthoptera) (Gruta Olhos d' Água and Lapa do Cipó, troglobitic), c) *Relictopiolus galadriel* (Opiliones, Kimulidae) (Gruta Olhos d' Água, troglobitic, relict) dorsal habitus, d) *Pseudochthonius biseriatus* Mahnert, 2001 (Pseudoscorpiones) (Gruta Olhos d' Água, troglobitic), e) *Siphonops paulensis* (Gymnophiona) (Gruta Olhos d' Água, accidental), f) *Katantodesmus* n. sp. (Gruta Olhos d' Água, troglobitic). Photo: a, e - von Shimonsky, D.M.; b,d,f – Bolfarini, M.P.; c, d– Fernandes L.B.R.

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Development and extension of aphotic zones were the most contrasting physical parameters when comparing the caves (Table 2). Gruta Olhos d' Água is the longest cave with an extensive aphotic zone in the region, Gruta do Janelão presents large galleries and an extensive twilight zone with several openings to the epigean environment. The other caves show small extensions, some without aphotic zones or perennial drainages, such as Lapa do Sonho, Toca do Pedrinho and Gruta Mina d' Água. A general characterization of each cave is presented at Table 2.

Expected Taxonomic Distinctness (TD, Δ+) was 87.7. The highest value of TD (Δ+) was of Gruta Olhos d' Água (Δ+ = 90.18) (Figure 5).

Table 2. Description of the caves studied at PCNP, Itacarambi, Minas Gerais, Brazil.

Cave	Geographical coordinates	Horizontal Development (m)	Entrance	Entrance Altitude (m)	Water Stream	Zonation	Degree of preservation
Gruta Olhos d' Água	S15.1137;W44.1696	9,100	Resurgence	NI	Present	EZ/TZ/AZ	High
Lapa do Branco IV	S15.1443;W44.1930	200	Sinkhole	NI	Absent	EZ/TZ	Medium
Toca do Pedrinho	S15.1085;W44.1700	200	Sinkhole	510	Absent	EZ/TZ	Medium
Lapa da Onça	S15.1403;W44.1913	1,680	Sinkhole	501	Present	EZ/TZ/AZ	Medium
Lapa do Cipó	S15.0562;W44.1844	1,800	Sinkhole	616	Present	EZ/TZ/AZ	High
Gruta Janelão	S15.1161;W44.2416	4,740	Sinkhole	520	Present	EZ/TZ/AZ	Medium
Lapa do Mogno	S15.16231;W44.2004	230	Sinkhole	506	Present	EZ/TZ/AZ	Medium
Gruta Mina d' Água	S15.1074;W44.1694	160	Resurgence	507	Absent	EZ/TZ	Medium
Gruta Bonita	S15.1076;W44.2409	420	Sinkhole	NI	Absent	EZ/TZ/AZ	Low
Lapa do Branco I	S15.1430;W44.1926	180	Sinkhole	544	Absent	EZ/TZ	Medium
Caverna dos Troncos	S15.1004;W44.2325	220	Sinkhole	572	Present	EZ/TZ	Medium
Lapa dos Sonho	S15.0804;W44.1004	190	Sinkhole	NI	Absent	EZ/TZ	Medium
Gruta Boquete	S15.1039;W44.2374	400	Sinkhole	NI	Absent	EZ/TZ/AZ	Low
Caverna dos Cascudos	S15.0976;W44.2332	180	Sinkhole	546	Present	EZ/TZ	Medium

EZ = entrance zone; **TZ** = twilight zone; **AZ** = aphotic zone; **NI** = no information.

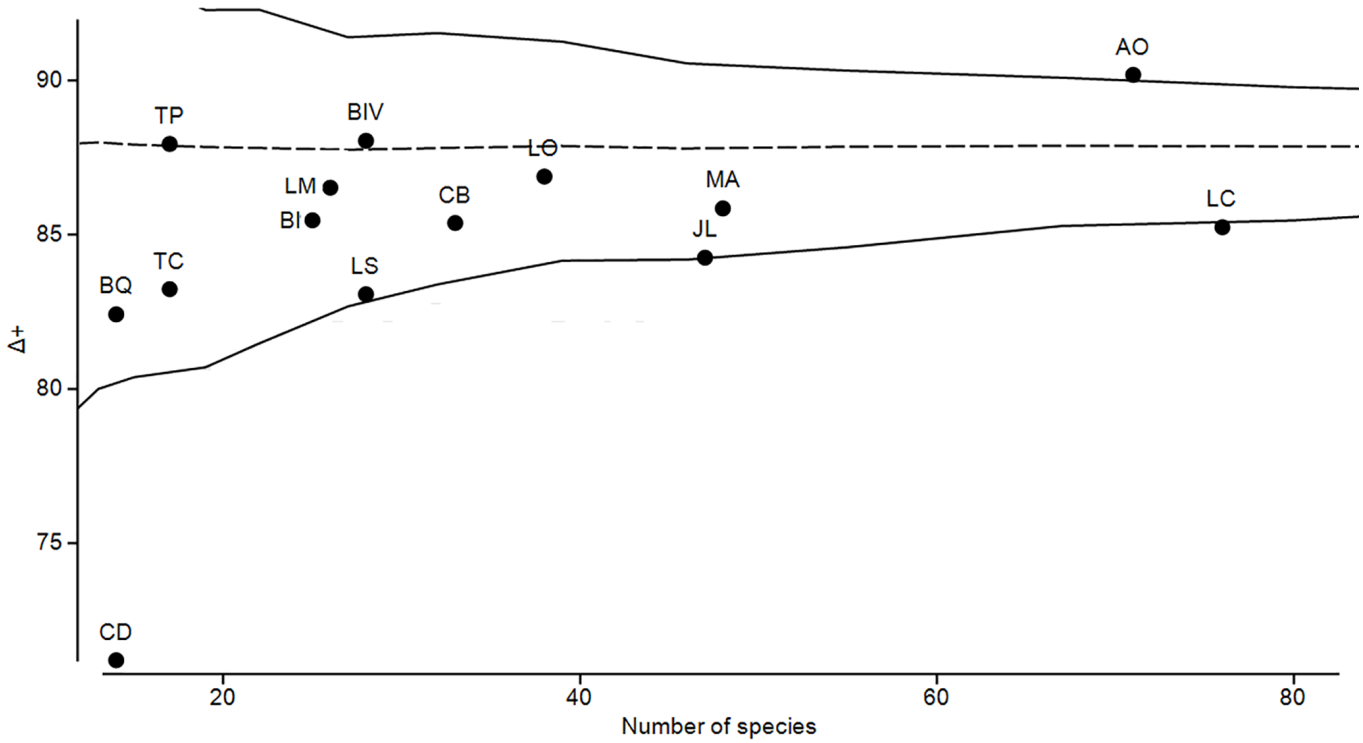


Figura 5. Values of taxonomic distinctness for the 14 caves from Cavernas do Peruaçu National Park (PNCP), Itacarambi, state of Minas Gerais, Brazil. Average Taxonomic Distinctness (Δ+, AvTD). OA = Gruta Olhos d' Água; LC = Lapa do Cipó; MA = Gruta Mina d' Água; JL = Gruta do Janelão; LO = Lapa da Onça; CB = Caverna Bonita; BI = Lapa do Branco I; BIV = Lapa do Branco IV; LS = Lapa dos Sonhos; LM = Lapa do Mogno, BQ = Caverna Boquete; TC = Caverna Troncos; CD = Caverna Cascudo and TP = Toca do Pedrinho.

Four caves presented values of TD lower than expected and outside the confidence interval: Caverna Cascudo (Δ+ = 71.21), Caverna Boquete (Δ+ = 81.54) and Lapa dos Sonhos (Δ+ = 83.07) (Figure 5, Table 3).

Discussion

Subterranean fauna of PCNP is remarkable. Our results corroborate the hypothesis that Gruta Olhos d'Água cave is a spot of subterranean biodiversity (Trajano et al. 2016) probably due the long period of environmental stability, as evidenced by its high troglobitic species richness, at least 13 so far (Perez-González et al. 2017, Gallão & Bichuette 2018). In addition, we identified another important locality of endemic and troglobitic species, the Lapa do Cipó cave (Table 4).

Besides the great number of taxa, we also recorded a significant number of troglobites at Peruaçu region. For Brazil, the highest number of troglobites is recorded at Areias System, located at the Alto Ribeira karst area, state of São Paulo, accounting for 20 species described so far, followed by Alambari de Cima cave, at the same region, with 10 troglobites (Trajano & Bichuette 2010, Trajano et al. 2016). Other spot of high subterranean diversity (Gallão & Bichuette 2015, Trajano et al. 2016) has been identified at Chapada Diamantina region, at the state of Bahia, with 23 troglobites recorded at 11 caves, 13 of them from a single cave.

The analysis of taxonomic distinction (Δ+, AvTD) takes into account that the more phylogenetically distinguishes species in a given community, the greater the diversity (Cianciaruso et al. 2009). However, when taxonomic relationships are taken into account, high TD values (Δ+, AvTD) indicate high diversity preserved spots (Clarke & Warwick 2001), as we observed for Gruta Olhos d 'Água (s = 71, Δ+ = 90.18) (Figure 5). On the other hand, despite presenting higher richness, Lapa do Cipó presented a lower than expected TD (s = 76, Δ+ = 85.24), indicating possible degradation and / or the existence of some genera with many species (Figure 5).

Among the 14 caves we studied, Gruta Olhos d' Água is remarkable by its high faunistic singularity, as shown by the high value of Taxonomic Distinctness. This value also indicates the presence of singular taxa as, for instance, troglobitic species (Cianciaruso et al. 2009, Gallão & Bichuette 2015).

A relict species (*Relictopiolus galadriel*) recorded at Gruta Olhos d'Água corroborates environmental stability, enabling survival and evolution of species whilst its populations and sister groups outside caves were extinct by several factors as, for instance, climatic changes, competitive exclusion and stochastic factors.

The Lapa do Cipó cave presented the highest species richness, among which the troglobitic populations of *I. uai*, *C. eleonorae* (Monte et al. 2015), *E. peruassuenssis* (Bolfarini & Bichuette 2015) and *X. odara* (Campos-Filho et al. 2014). Besides the importance of its fauna, species richness is also high. Even more, these three troglobitic populations occur at Lapa do Cipó and Gruta Olhos d' Água caves, suggesting that both caves are part of a complex system. However, Lapa do Cipó showed a low TD value, probably because of its faunistic similarity with other caves.

In a study conducted at Chapada Diamantina, state of Bahia, a highest value of TD was recorded for the lowest richness cave, followed by the cave with the highest number of troglobitic species (Gallão & Bichuette 2015). In the region of Presidente Olegário, state of Minas Gerais, the highest TD value among seven caves studied is related to the presence of frugivorous guano patches and the presence of some animals that have a preference for this type of substrate such as Chilopoda of the genus *Lamyctes* (Zepon 2015).

Lower values of TD may indicate severe environmental degradation and pollution (Warwick & Clarke 1998). TD values at Caverna Cascudo, Caverna Boquete, Lapa dos Sonhos and Gruta Mina d' Água caves were significantly lower than expected at least for one of these,

Table 3. Taxonomic Distinctness values of the caves studied at PCNP, Itacarambi, Minas Gerais, Brazil.

Cave	Δ+	N	s	Tgb
Gruta Olhos d' Água	90.18	330	71	10
Lapa do Branco IV	88.04	84	28	0
Toca do Pedrinho	87.94	26	17	0
Lapa da Onça	86.88	108	38	0
Lapa do Mogno	86.52	69	26	0
Gruta Mina d' Água	85.85	125	48	0
Caverna Bonita	85.56	145	32	0
Lapa do Branco I	85.47	66	25	0
Lapa do Cipó	85.24*	330	76	4
Caverna Janelão	84.62	197	47	0
Caverna dos Troncos	83.24	34	17	0
Lapa dos sonhos	83.07*	78	28	0
Caverna Boquete	81.54*	50	14	0
Caverna do Cascudo	71.21**	27	14	0

Δ+ = average Taxonomic Distinctness; **N** = number of individuals; **s** = species richness and **Tgb** = number of troglobitic species. '*' p<0,05 and '**'p< 0,001.

Table 4. Faunistic listing with the abundance of taxa for the 14 caves from Peruaçu Caves National Park (PNCP), Itacarambi, state of Minas Gerais, Brazil. **OA** = Gruta Olhos d' Água, **LC** = Lapa do Cipó, **MA** = Gruta Mina d' Água, **JL** = Gruta do Janelão, **LO** = Lapa da Onça, **CB** = Caverna Bonita, **BI** = Lapa do Branco I, **BIV** = Lapa do Branco IV, **LS** = Lapa dos Sonhos, **LM** = Lapa do Mogno, **BQ** = Caverna Boquete, **TC** = Caverna Troncos, **CD** = Caverna Cascudo, **TP** = Toca do Pedrinho, SubF = Subfilo, SubC = Subclass, O = Ordem, F = Family, SubF = Subfamily, C = Class, InfO = Infraordem and * = troglobites not yet described.

TÁXON	CB	BQ	CD	JL	OA	TC	MA	LO	BI	BIV	LC	LM	LS	TP
SubC. Lissamphibia														
O. Anura														
sp. 1					3									
O. Gymnophiona														
F. Siphonopidae														
Siphonops paulensis Boettger, 1892					1									
C. Clitellata														
sp. 1											2			
sp. 2					3									
C. Arachnida														
sp. 1					1									
sp. 2	1													
SubC. Acari														
O. Trombidiformes														
F. Erythraeidae														
sp. 1	1				4		1			6		1		
sp. 2	3				2		1					1		
sp. 3					1		1							
sp. 4					10					1	1	1		
O. Ixodida														
F. Ixodidae														
sp. 1							1		1					
sp. 2							1	1						
sp. 3							1							
O. Opilioacarida														
sp. 1				7						1				
F. Argasidae														
sp. 1					3									
O. Amblypygi														
F. Charinidae														
Charinus eleonorae Baptista & Giupponi, 2003					11						4			
F. Phrynichidae														
Trichodamon princeps Mello-Leitão, 1935							1		2	1				
O. Araneae														
InfraO. Araneomorphae														
sp. 1					1									
sp. 2								1						
sp. 3				1										

continuation Table 4

F. Araneidae														
sp. 1					1	1				8				
sp. 2											1			
Alpaida sp. 1				1			1							
F. Caponiidae														
sp. 1			1											
Nops sp. 1			2											
F. Corinnidae														
sp. 1		1	1											
sp. 2						1								
F. Ctenidae														
sp. 1			1		1	3				3		1		
sp. 2										1				
F. Deinopidae														
sp. 1												1		
F. Filistatidae														
sp. 1						1								
Misionella sp. 1		27							2		1	4		
F. Linyphiidae														
Agyneta sp. 1			1											
Sphecozone sp. 1				2										
F. Lycosidae														
sp. 1							2					2		
sp. 2				1										
F. Mysmenidae														
sp. 1	1													
F. Nesticidae														
Eidmannella pallida Emerton, 1875										7				
F. Ochyroceratidae														
Ochyrocera sp. 1			1											
F. Oonopidae														
sp. 1				1								1		
Neotrops sp. 1			1											
F. Pholcidae														
sp. 1	1		7				20		1	1	2		1	
sp. 2												3		
Ibotyporanga sp. 1						1								
Mesabolivar sp. 1		1		1		5	2	2	3	5	3	2	1	
F. Prodidomidae														
sp. 1							1			1				
F. Salticidae														
sp. 1		1			4	5				1	5	2		

continuation Table 4

F. Scytodidae														
sp. 1				2										
Scytodes sp. 1				6										
Scytodes sp. 2				4			1							
F. Segestriidae														
sp. 1				1										
Ariadna sp. 1				4										
F. Selenopidae														
Selenops sp. 1					2									
F. Sicariidae														
sp. 1		1				5	2			3				
sp. 2										1				
Loxosceles sp. 1			4		2	8	4	5	6	19	7	3	1	
Loxosceles karstica Bertani, von Schimonsky & Gallão, 2018				6										
Loxosceles ericsoni Bertani, von Schimonsky & Gallão, 2018	4	1												
F. Tetrablemmidae														
Matta sp. 1				14										
F. Tetragnathidae														
sp. 1	8		3		2	6	20		1	1	8	1	2	
sp. 2												2		
sp. 3												3		
Leucauge sp. 1							3	9	10				2	
F. Theridiidae														
sp. 1				1	2					4		6		
sp. 2										1				
sp. 3					2					1				
sp. 4										1				
sp. 5										1				
Nesticodes rufipes Lucas, 1846					14					8				
Steatoda sp. 1					1									
F. Theridiosomatidae														
sp. 1											4			
sp. 2	1													
sp. 3	1									2				
Plato sp. 1	11		1							12				
Plato sp. 2*										5				
F. Thomosidae														
sp. 1					1									
F. Trechaleidae														
sp. 1	2					3	5	4		3	3			
sp. 2					1					1				

continuation Table 4

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continuation Table 4

Tityus serrulatus Lutz & Mello, 1922			1	2	1					
O. Palpigradi										
F. Eukoeneniidae										
Eukoenenia sp. 1		1								
C. Chilopoda										
O. Geophilomorpha										
F. Geophilidae										
Hyphydrophilus sp. 1	3									
F. Schendylidae										
Schendylops sp. n. *								1		
Schendylops janelao Nunes, Chagas-Jr & Bichuette, 2019	1									
O. Scolopendromorpha										
F. Scolopendridae										
Otostigmus sp. 1							1			
Newportia Tidops balzanii Silvestri, 1895				2				2		
Otostigmus muticus Karsch, 1888					2			2		
F. Pselliodidae										
Sphendononema guildingii Newport, 1845	3		1			1	3			
C. Diplopoda										
sp. 1	2	12					1		1	
O. Polyxenida										
sp. 1					1					
O. Polydesmida										
sp. 1		7						1		
O. Spirostreptida										
sp. 1	2									
F. Oniscodesmidae										
sp. 1						1				
sp. 2		1				1				
sp. 3						1				
F. Bulimulidae										
Drymaeus sp. 1						3				
Kora corallina Simone, 2012	2					3	1		1	1
F. Epiphragmophoridae										
Epiphragmophora bernardius Pilsbry & Ihering, 1900							2			
F. Helicinidae										
Helicina brasiliensis Gray, 1824						6				
F. Odontostomidae										
Cyclodontina inflata Wagner, 1827						1				
F. Pomatiopsidae										
Idiopyrgus souleyetianus Pilsbry, 1911						5				
F. Scolodontidae										

continuation Table 4

| | | |

continuation Table 4

F. Carabidae														
Nemotarsus sp. 1	6													
sp. 1			2											
F. Curculionidae														
sp. 1	1													
F. Elateridae														
sp. 1	1													
F. Endomychidae														
sp. 1	7													
F. Ptilodactylidae														
sp. 1				12										
F. Staphylinidae														
sp. 1	1			5	1		2			2				
sp. 2	1			7		1	1			8				
sp. 3								1						
O. Diptera														
sp. 1						1				4	2	5	2	
sp. 2										1	1			
F. Cecidomyiidae														
sp. 1			1	1				12						
F. Ceratopogonidae														
sp. 1								2						
sp. 2	1													
F. Chironomidae														
sp. 1			20											
sp. 2			2											
F. Culicidae														
sp. 1										4	1	1		
sp. 2												1		
F. Dolichopodidae														
sp. 1	2	1												
F. Drosophilidae														
Drosophila sp. 1				23										
F. Keroplatidae														
sp.1				1										
Neoditomyia sp. 1						2								
F. Lauxaniidae														
sp. 1										1				
sp. 2		1												
F. Limoniidae														
sp. 1			1	3		3				1				

continuation Table 4

F. Milichiidae														
sp. 1				1	3									
F. Phoridae														
Conicera sp. 1					2									
F. Psychodidae														
sp. 1		1		1	4									
sp. 2											1			
F. Sciaridae														
sp. 1											1			
F. Sphaeroceridae														
sp. 1					1									
Ephidroidea sp. 1	1			1										
Ephidroidea sp. 2				1										
O. Hemiptera														
sp. 1					1	1	4	1			6		7	1
sp. 2													1	
F. Cixiidae														
sp. 1							1							
F. Lygaeidae														
sp. 1				1										
F. Miridae														
sp. 1	1													
F. Reduviidae														
Zelurus sp. 1	3	5		2	1		3	5			2			
Zelurus ochripennis Stal, 1854									1					
F. Gerridae														
Brachymetra albinervis Amyot & Serville, 1843						3								
O. Hymenoptera														
F. Formicidae														
sp. 1		1	1	1			1		3	3	4		2	4
sp. 2							1	1						
sp. 3								1						
sp. 4								1						
sp. 5								1						
Brachymyrmex sp. 1					5									
Brachymyrmex sp. 2					2									
Cephalotes atratus Linnaeus, 1758					1									
Hypoponera sp.1											1			
Pheidole sp. 1					1									
Sericomyrmex sp. 1				1										
Solenopsis sp. 1								2						

 http://dx.doi.org/10.1590/1676-0611-BN-2019-0810

continuation Table 4

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continuation Table 4

F. Dubinoniscidae					
sp. 1	14				
sp. 2		2	2		
sp. 3		4			
F. Scleropactidae					
sp. 1				1	
F. Stylonicidae					
Xangoniscus itacarambiensis Bastos-Pereira, Souza & Ferreira, 2017		9			
Xangoniscus odara Campos-Filho, Araujo & Taiti, 2014					20
sp. 1		1			
C. Osteichthyes					
O. Siluriformes					
F. Trichomycteridae					
Trichomycterus itacarambiensis Trajano & Pinna, 1996		12			
C. Mammalia					
O. Chiroptera					
F. Phyllostomidae					
Carollia perspicillata Linnaeus, 1758		9			
Desmodus rotundus Geoffroy, 1810		6			
Diphylla ecaudata Spix, 1823		1			
Sub. F. Golossophaginae					
sp. 1		3			

Caverna Boquete, we can state that this value may be related to anthropic impacts because of visitation. Non-significant values of TD were also found at caves from other localities. Zepon (2015), for instance, argued that the low value found at Gruta Juruva cave, Presidente Olegário, state of Minas Gerais, was due to low variety and quality of resources. In caves from Bahia, Gallão & Bichuette (2015) associated the low values of TD to extensive diamond mining in the past, which continues nowadays as a residual and clandestine activity.

Our results show that contextualized studies of diversity are indispensable to conservation policies because, more than only characterize the fauna and spots of troglobitic occurrence, they also help the identification of complex subterranean systems and expand the potential for subsequent studies. Those discoveries are fundamental to conservation of the entire subterranean systems and its area of influence, a much more efficient approach to subterranean conservation than those focusing only in a given cave.

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Author contributions

Bruno Gabriel Oliveira do Monte - Substantial contribution in the concept and design of the study, contribution to data collection, contribution to data analysis and interpretation, contribution to manuscript preparation, contribution to critical revision, adding intellectual content.

Maria Elina Bichuette - Substantial contribution in the concept and design of the study, contribution to data collection, contribution to data analysis and interpretation, contribution to manuscript preparation, contribution to critical revision, adding intellectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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Point-of-view

Increasing capacity to produce scenarios and models for biodiversity and ecosystem services

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Abstract: Extensive anthropogenic activities driven by the demand for agriculture and forestry products have led to dramatic reductions in biodiversity worldwide and significant changes in the provisioning of ecosystem services. These trends are expected to continue in the future as the world continues to develop without much consideration of the role that nature plays in sustaining human livelihoods. Scenarios and models can be important tools to help policy- and decision-makers foresee the impact of their decisions; thus, increasing capacity in creating such models and scenarios is of utmost importance. However, postgraduate training schools that focus on this topic are still rare. Here we present and reflect on the experience of the São Paulo School of Advanced Science on Scenarios and Modelling on Biodiversity and Ecosystem Services to Support Human Well-Being (SPSAS Scenarios). In addition, we introduce the Special Issue of Biota Neotropica that resulted from the activities taking place during the SPSAS Scenarios. In total, nine case studies emerged from the activities carried out during SPSAS Scenarios. These focused on a variety of ecosystems, their current drivers of change and expected trends, as well as on the development of alternative positive scenarios applying the recently developed Nature Futures Framework. We emphasize the need to increase capacity in scenario and modelling skills in order to address some of the existing gaps in producing policy-relevant scenarios and models for biodiversity and ecosystem services.
Keywords: *Scenarios; Models; Biodiversity; Ecosystem Services; Nature Futures; IPBES.*

Capacitando profissionais para o desenvolvimento de cenários e modelos em biodiversidade e serviços ecossistêmicos

Resumo: Atividades antropogênicas extensas, impulsionadas pela demanda por produtos da agricultura e da silvicultura, têm levado a reduções dramáticas na biodiversidade mundial e a mudanças significativas no provimento de serviços ecossistêmicos. Estas tendências devem continuar no futuro, pois o mundo continua a se desenvolver sem muita consideração pelo papel que a natureza desempenha em sustentar a subsistência humana. Cenários e modelos são ferramentas importantes para ajudar os tomadores de decisão a preverem o impacto de suas decisões, auxiliando na definição das melhores opções para políticas de conservação e uso sustentável; portanto o aumento da capacidade para o desenvolvimento de modelos e cenários é de suma importância. Entretanto, ainda são raros os cursos de pós-graduação que foquem na capacitação de profissionais para o desenvolvimento de modelos e cenários em biodiversidade e serviços ecossistêmicos. Neste trabalho apresentamos a experiência da Escola São Paulo de Ciências Avançadas de Cenários e Modelagem em Biodiversidade e Serviços Ecossistêmicos para Apoiar o Bem-Estar Humano (SPSAS Scenarios). Adicionalmente, apresentamos neste Número Especial da Biota Neotropica os resultados dos exercícios de modelagem e cenários desenvolvidos no decorrer da SPSAS Scenarios. No total, as atividades realizadas durante o SPSAS Scenarios resultaram em nove estudos de caso. Estes se concentraram em uma diversidade de ecossistemas, nos atuais drivers de mudança e as respectivas tendências, bem como nas

alternativas de desenvolvimento visando cenários mais positivos propostos recentemente no contexto da Framework Futuros para Natureza da Plataforma Intergovernamental de Biodiversidade e Serviços Ecossistêmicos (IPBES). Enfatizamos aqui a necessidade de acelerar a capacitação de profissionais que trabalhem com cenários e modelagem de forma a preencher algumas lacunas existentes na produção de cenários e modelos relevantes para a tomada de decisão em biodiversidade e serviços ecossistêmicos

Palavras-chave: *Cenários; Modelos; Biodiversidade; Serviços, Ecossistêmicos; Framework Futuros para Natureza; IPBES.*

Introduction

The recent publication of the Global Assessment Report on Biodiversity and Ecosystem Services by the Intergovernmental Platform for Biodiversity and Ecosystem Services (Díaz et al. 2020) has once again put the spotlight on the extensive impacts that human activities are having on our planet as a whole. Most of these changes are a response to the demand for agriculture and forestry products. For instance, it has been estimated that the world has seen a 300% increase in agricultural crop production since 1970, and about 45% increase in raw timber harvest (Díaz et al. 2020). This, however, comes at a high cost for the natural world. Alarmingly the assessment has also shown that biodiversity is declining at unprecedented rates, with an average loss of 20% of the abundance of native species since 1900 in most habitats, and nearly 1 million animal and plant species now threatened with extinction (Díaz et al. 2020). Moreover, these socio-economically driven activities have contributed to climate change. Work led by the Intergovernmental Panel for Climate Change (IPCC) has been crucial in highlighting how anthropogenic activities are impacting, and will continue to impact, the Earth's climate (IPCC 2019). It has been estimated that greenhouse gas (GHG) emissions have doubled since 1980, and the average temperature has risen by 0.7 degrees Celsius. Both the IPCC and IPBES emphasize that transformative change in the way the world is expected to develop is crucial to curb these trends and ensure we move towards a more sustainable future (Díaz et al. 2020). The recent and ongoing COVID-19 pandemic has also helped understand the potential consequences for human well-being of continuing to develop as in the past.

In this regard, scenarios and models can play an important role in supporting decision- and policy-makers in envisioning different futures under alternative pathways (or assumptions) (IPBES 2016). These have long been used at multiple scales in supporting environmental assessments (Nicholson et al. 2019), but seem to have largely failed in steering decision- and policy-makers into developing strategies and mechanisms that can lead towards sustainable futures (IPBES 2016). Developing such scenarios and models requires an interdisciplinary view and an understanding of what drives change (both directly and indirectly), the policy levers and mechanisms that might impact such change and the dimensions/aspects of biodiversity and ecosystem services that might be impacted by it (Rosa et al. 2020). Importantly, scenario exercises to date have involved limited consideration of the fundamental role that nature plays in human societies worldwide (Cardinale et al. 2016) and of the importance of adopting a pluralistic perspective on human-nature interactions (Rosa et al. 2017).

Capacity building is a crucial requirement for the development of robust scenario analysis and modelling. However, despite the growing production and use of scenarios and models by scientists, policy-makers and practitioners from across disciplines, postgraduate training courses on biodiversity and ecosystem services scenarios and models are still rare. This paper has thus two main objectives: (1) to describe and reflect on the São Paulo School of Advanced Science on Scenarios and Modelling on Biodiversity and Ecosystem Services to Support Human Well-Being (SPSAS Scenarios); and (2) introduce this Special Issue of Biota Neotropica that was an outcome of the SPSAS Scenarios with nine papers emerging from the case studies developed and elaborated by the students during this capacity-building training course.

The Summer School

The **São Paulo School of Advanced Science on Scenarios and Modelling on Biodiversity and Ecosystem Services to Support Human Well-Being** (SPSAS Scenarios) took place in the city of São Pedro (about 150 km from São Paulo, Brazil) from the 1st to 14th of July 2019. Eighty-five participants from 21 nationalities and five continents - selected after a very competitive process, 4:1 - were immersed in this residential training course which took place over approximately 90 contact hours. In accordance with the course proposal, participants and speakers were hosted in a hotel. This venue provided not only space for the meetings, but also for ice-breaker activities and extensive opportunities for interactions among participants, during meals, in the swimming pool, at the bar and in the social gatherings organized as part of the course.

Participants were predominantly female (64%). Most of them (79%) were PhD students and the remaining 21% had completed their PhD between 2017 and 2019. Among the participants, five were public servants or from multilateral organizations, and were selected with the aim of not only training them to use new tools and approaches, but also to bring to the discussion real challenges experienced by decision-makers. Participants were from a wide range of backgrounds (Figure 1).

The topics covered by SPSAS Scenarios were divided in four main modules:

1. Ecosystem Services and Nature's Contribution to People: the evolution of, and current debate around, these concepts, was presented and discussed.
2. Challenges in the Development of Scenarios and Models focusing on direct and indirect drivers in biodiversity and ecosystem services, as well as the conceptual bases of scenarios and models.
3. IPBES Assessment on Scenarios and Modeling where the main authors of this technical assessment presented and discussed their findings.
4. Scenarios and Modeling to Achieve Brazil's Nationally Determined Contribution (NDC) in which some of the experts involved in establishing the Brazilian proposal to the Paris Climate Agreement presented and discussed how those goals were established.



Figure 1. Word cloud of the diversity of professional training and background of participants, based on the frequency of the appearance of words in the item of the registration form requesting this information.

After a general introduction to biodiversity and ecosystem services (Module 1), from Module 2 onwards the students were divided into nine groups for a series of exercises entitled "real experience of modelling and scenarios". The topic of each group was suggested by the students themselves, further refined after a joint evaluation with the speakers. Each group then followed an organic process to develop their own case study alongside, and informed by, the lectures on the topics for the remainder of the SPSAS Scenarios. Their initial proposal for the case study was gradually refined in greater detail with the incorporation of new "layers" of knowledge from the speakers' presentations. First students were asked to articulate the question(s) to be addressed in the case studies, and then they started building a conceptual model that described the key components of the systems that were being studied. Second, the relationships between these key components were described and the monetary and non-monetary values of each component were discussed, first within the group, and then with all other participants for feedback. Direct and indirect drivers affecting biodiversity, ecosystem services and valuation were then addressed. Third, the students were incentivised to review existing policies that might impact their case studies, indicators they could use to track progress towards policy goals, and to use their creativity to think about alternative scenarios that could lead towards more positive futures. Finally, following this step, the students began to use existing data and tools, where possible, to model the impact of conservation policies on the drivers, and potential outcomes of their envisioned scenarios.

This organic way in which the groups developed their case studies was made possible by the availability of speakers to stay in São Pedro for a longer period than that provided exclusively for theoretical classes. In this way the speakers could follow the maturation of each case study, contributing whenever necessary to the work of the groups. The groups could schedule tutorials with the speakers in order to derive maximum benefit from their knowledge and experience. During the final presentation of the case studies the organizing committee of SPSAS Scenarios, lecturers and students decided to further develop each study and submit it for publication in this Special Issue of Biota Neotropica.

On the final day of the SPSAS Scenarios participants took some time to answer a set of questions focused on the positive and negative aspects of the School. Here are some of the comments submitted, showing that for most participants it was a valuable experience: "I found the activities really innovative and interesting. It is important to recognize that in problem-solving situations comprising different interests there will always be conflicts and it is necessary for scientists to learn how to argue and defend our position in these situations, but also take into account the demands and needs of other sectors"; "Working in a case study with an interdisciplinary group was a real challenge and opportunity at the same time. We all learned a lot from each other's background and perspective. Overall, it was a great and enriching experience to work with the development of conceptual models."; "This course was a great opportunity to see how science and policy are connected. Given this experience, now I want to adapt my research and make it more suitable for policy makers, etc."; and "The school provided an outstanding opportunity to improve my postdoctoral proposal, especially providing inputs to increase the scale and impact of my research. I believe applying the IPBES framework will be very important in the next few years and the School provided an excellent guide to do that".

The Special Issue

The study cases developed during SPSAS Scenarios became the nine papers of this Special Issue and are listed below:

1. Drivers of change in biodiversity and ecosystem services in the Cantareira System Protected Area: a prospective analysis of the implementation of public policies (Dib et al., this issue).
2. Pathways to positive scenarios for the Amazon forest in Pará state, Brazil (Siqueira-Gay et al., this issue).
3. Urban expansion in the Atlantic Forest: applying the Nature Futures Framework to develop a conceptual model and future scenarios (Lembi et al., this issue).
4. A conceptual model to understand the drivers of change in tropical wetlands: a comparative assessment in India and Brazil (Sarkar et al., this issue).
5. A conceptual model to assess the impact of anthropogenic drivers on water-related ecosystem services in the Brazilian Cerrado (Resende et al., this issue).
6. Future scenarios of land-use-cover effects on pollination supply and demand in São Paulo State, Brazil (Barbosa et al., this issue)
7. Insights for policy-based conservation strategies for the Rio de la Plata Grasslands through IPBES framework (Gorosabel et al., this issue)
8. Development of a conceptual framework for the management of biodiversity and ecosystem services in the Mexican Caribbean (Sanchez-Quinto et al., this issue)
9. Scenario-modelling for the sustainable management of non-timber forest products in tropical regions (Bondé et al., this issue).

All nine studies addressed cases where increasing human pressure affects biodiversity and some vital ecosystem services, in a variety of different ecosystems. Human pressure often results from changing land use, such as in Siqueira-Gay et al., Lembi et al. and Barbosa et al., but also from increasing direct use of species (e.g. Shea trees) or pollution (Sarkar et al.). The aims of the various case studies were in general terms similar as they all focused on understanding the drivers of changes in biodiversity or ecosystem services and on developing pathways to shift current (negative) trends.

For example: "*Thus, we aim at providing an understanding of the drivers of forest cover change in Pará state by applying the IPBES framework for proposing ways to shift current trends towards positive scenarios*" (Siqueira-Gay et al. 2020) and "*..., there is an urgent need to identify and understand the interactions between various drivers of change triggering wetland degradation and mantaining their ecological character for perpetual delivery of ecosystem services*" (Sarkar et al. 2020).

The papers emerging from this exercise at SPSAS Scenarios highlighted the breadth of topics that can be covered by scenarios and models of biodiversity and ecosystem services (Table 1). While most case studies were focused within Latin America and the Caribbean, the background and experiences of the participants resulted in one case study of sub-Saharan Africa, and one further case study involving a comparison of India and Brazil (Table 1). Moreover, case studies covered a diversity of ecosystems, including marine, aquatic, terrestrial and urban ecosystems. Within these broader categories, coastal ecosystem elements included mangroves and coral reefs, and terrestrial ecosystems including a diversity of habitats from tropical forest to savannahs, and grasslands to croplands (Table 1).

As briefly described above, once the research question was defined, the development of a model - i.e. a qualitative or quantitative description of key components of a system and of relationships between those components - began with a solid conceptual framework (Guisan & Zimmerman, 2000; IPBES, 2016) representing the understanding of that system. At first, the cases were formulated very broadly, thus the urge to formulate a conceptual model of the (eco)system central to the case studies helped the students to focus on the main issues (and the main components of the system that impact that issue), avoiding them getting lost in details. In particular, first, the key components were defined (Table 1) including the link between these key components, which was often represented visually by boxes with connecting arrows (Jackson et al., 2000). Key components varied greatly between case studies, such as water quality and quantity determining water health (Sarkar et al., 2020); forest cover change determined by urban expansion (Siqueira-Gay et al., 2020); and Shea tree cover and its harvest (Bondé et al., 2020). These key components provided the foundation on which to further build the complete conceptual model, as many influencing factors often play a role in determining changes in the key components. Challenges remained in delineating the system that is considered in the case studies, by defining boundary elements, and in keeping the conceptual model as parsimonious as possible, which required an iterative process of discussions within the modelling team (and more broadly with the other participants and teachers), consulting experts and reviewing literature (Jackson et al. 2000). In all case studies the conceptual modelling involved the formulation of a (semi-)quantitative model, enabling the evaluation of multiple scenarios.

The models represented in the nine case studies highlighted some of the most common drivers of biodiversity and ecosystem services. For instance, IPBES has identified (1) changes in land and sea use; (2) direct exploitation of organisms; (3) climate change; (4) pollution and (5) invasive alien species (Díaz et al., 2020) as the five most important direct drivers of change. These were commonly included in the case studies, such as for example in Siqueira-Gay et al. (2020), where the socio-ecological system of forest cover change in the Amazon was investigated; or in Barbosa et al. (2020) when evaluating pollination service changes in Brazil; or even in Estigarribia et al. (2020) when analysing changes in biodiversity in the grasslands of South America. Additionally, indirect drivers commonly identified independently of the geographic location of the case study were population pressure, economic growth and international demand, governance, and policy changes, such as for example in the case of Dib et al. (2020) for the Cantareira system in Brazil; or in Sarkar et al. (2020) for the wetlands of Brazil and India; or in Lembi et al. (2020) when analysing urban expansion in the Atlantic Forest; and in Bondé et al. (2020) for the shea trees in West Africa.

To monitor changes in these drivers, and their consequent impacts on the focal component of the case study, several indicators have been identified and proposed within the case studies. Some of the more commonly proposed indicators were (1) the extent of land use change (e.g. urban expansion in Lembi et al. [2020], forest cover change in Siqueira-Gay et al. [2020], or wetland extension in Sarkar et al. [2020]); (2) biodiversity change, assessed either as the number of species or local species richness (e.g., Siqueira-Gay et al. [2020]) or as the mean species abundance (e.g. Sanchez-Quinto et al. [2020]); and (3) ecosystem services change, such as was the case in Sanchez-Quinto et al. (2020) for a variety of provisioning, regulating, supporting and cultural services; and in Verde Selva et al. (2020) for water quality and quantity.

Table 1. Geographic, ecosystem and thematic focus of the papers in the Special Issue

Paper	*Country(ies)*	*Ecosystem*	*Focal point*
Sarkar et al.	India and Brazil	Wetlands	Wetland Health (water quality and quantity)
Siqueira-Gay et al.	Brazil	Amazon forest	Forest Cover Change (deforestation)
Verde Selva et al.	Brazil	Cerrado (savannah)	Water quality and quantity
Dib et al.	Brazil	Cantareira system (protected area)	Biodiversity (MSA), Sediment loss, Soil loss and Forest Cover Change
Lembi et al.	Brazil	Urban areas	Urban expansion
Barbosa et al.	Brazil	Croplands	Pollination and Crop production
Sanchez-Quinto et al.	Mexican Caribbean	Coastal and Marine	Biodiversity (Mangrove and Coral Reef MSA)
Estigarribia et al.	Rio de la Plata (Argentina, Uruguay and Brazil)	Grasslands	Biodiversity and Ecosystem function
Bondé al.	sub-Saharan Africa	Shea trees	Tree cover

Identifying the drivers and the indicators is a crucial step to then think about scenarios (and associated assumptions) creatively that can drive the system towards more positive trends. In some cases, the groups were able to use existing tools and data to derive quantitative estimates of changes in their focal components as a result of their envisioned scenarios. For instance, Sanchez-Quinto et al. (2020) used GLOBIO3 (Alkemade et al. 2009) to project changes in the mean species abundance of mangroves and proposed a modification to suit the analysis for coral reefs as well. Barbosa et al. (2020) used the OTIMIZAGRO model (Soares-Filho et al., 2013) in combination with an ecosystem services matrix approach (Burkhard et al., 2009) to estimate changes in pollination services. Dib et al. (2020) used InVEST 3.7.0 (Hamel et al. 2015) to determine changes in the Sediment Delivery Ratio (SDR).

An important advancement in global biodiversity scenarios, catalysed by the IPBES Scenarios and Models Expert Group, is the development of the Nature Futures Framework (NFF) (Pereira et al. in press). SPSAS Scenarios provided the opportunity to introduce this novel scenarios framework to the next generation of biodiversity scenario experts, and to determine if it could be applied across a diversity of case studies, primarily reflecting nature and nature's contributions to people in the global south.

The NFF emerged from a future visioning exercise with a diverse group of stakeholders from around the world, where multiple knowledge systems were brought together to imagine what the future could be for nature and nature's contributions to people (Lundquist et al., 2017; Pereira et al., in press). The NFF is underpinned by the multitude of ways that humans value, experience and perceive nature and the benefits that it provides to society (Díaz et al., 2015; O'Neill et al., 2008). The NFF can be associated with three broad suites of values which people place on nature: intrinsic, instrumental and relational (Pascual et al., 2017). In "***Nature for Nature***" people value nature for its intrinsic and existence values, and the preservation of nature's diversity and functions is of primary importance. In "***Nature for Society***" nature is viewed as a provider of direct and indirect benefits to society, where humans benefit from the instrumental values that nature provides. Finally, "***Nature as Culture***" views humans as an integral part of natural systems, where societies, cultures, traditions and faiths are intricately intertwined with nature, and relational values such as those that reflect cultural identities, mental health and ways of life are dominant (Schoolenberg et al., 2018). This concept of people living in harmony with nature is not exclusive to indigenous worldviews, for example, the wider movement to help urban and rural communities to reconnect with nature to optimize the benefits of nature for mental health and human well-being (Chan et al., 2016).

At SPSAS Scenarios, students were asked to consider how future scenarios would differ for their particular case study if the imagined future was designed to maximise a particular NFF value perspective (Nature for Nature, Nature for Society, or Nature as Culture). Students discussed how the direct and indirect drivers in their case study influenced each of the value perspectives, which policy or management interventions could be used to maximise the nature perspectives, and which biological, ecological, cultural and socioeconomic indicators could be used to assess 'success' for each nature perspective. Two of the perspectives were typically easy for students to envision: Nature for Nature, reflecting common goals of conservation movements, the use of management tools such as protected areas, and biodiversity indicators such as species richness and threatened species; and Nature for Society, with many conceptual models focussed around the production of food, wood or other natural resources, water regulation, or carbon sequestration. In contrast, the concept of Nature as Culture provided for diverse discussions; many case studies had indigenous communities as integral components of their conceptual model, allowing them to envision how indicators of success for this nature perspective were often quite different from many of the typical metrics utilised by biodiversity scenarios. Several of the papers in the Special Issue make use of the NFF, such as for example Dib et al. (2020), Lembi et al. (2020), Sarkar et al. (2020), Siqueira-Gay et al. (2020), and Verde-Selva et al. (2020), thus illustrating its flexibility to be applied to multiple ecosystems at a variety of spatial scales.

Conclusions

As the world still struggles to handle the ongoing COVID-19 pandemic, it has become ever more important to inspire transformative changes to our current lifestyles, and to steer policy- and decision-makers towards envisioning a future for our planet that can be both sustainable and economically prosperous. Current scenarios, however, still fail to do so (Rosa et al., 2020), but the emergence of the NFF (Pereira et al., in press) is a positive shift towards a more inclusive and pluralistic approach to scenario development. This is a crucial first step that can be then followed by implementation of qualitative and quantitative approaches that aim to translate such scenarios into projections of impacts on biodiversity, ecosystem services, and ultimately human well-being. With the experience of SPSAS Scenarios and the variety of case studies addressed in the resulting Special Issue, we have shown the potential of increasing capacity in scenario and modeling training, and the flexibility that the NFF offers to address quite distinct case studies. It is our hope that with this kind of training activity, and the widespread adoption of the NFF, the knowledge and critical thinking of positive scenario development can be spread across institutions. This can, in turn, lead to innovative modeling approaches, thereby collectively helping to deliver transformative changes and more evidence-based policy- and decision-making.

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Authors' Contributions

Isabel M.D. Rosa: contribution to the concept and design of the SPSAS Scenarios; substantial contribution to manuscript preparation adding intellectual content; contribution to critical revision

Carolyn J. Lundquist: contribution to the concept and design of the SPSAS Scenarios; contribution to critical revision, adding intellectual content; contribution to critical revision

Simon Ferrier: contribution to the concept and design of the SPSAS Scenarios; contribution to critical revision, adding intellectual content; contribution to critical revision

Rob Alkemade: contribution to the concept and design of the SPSAS Scenarios; contribution to critical revision, adding intellectual content; contribution to critical revision

Paula F. Drummond de Castro: substantial contribution to the concept, organization and design of the SPSAS Scenarios; contribution to manuscript preparation adding intellectual content; contribution to critical revision

Carlos A. Joly: substantial contribution to the concept, organization and design of the SPSAS Scenarios; contribution to manuscript preparation adding intellectual content; contribution to critical revision

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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Inventory

Checklist of the fishes from Jamari River basin, in areas under influence of dams, Rondônia, Brazil

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Abstract: The Madeira River is the most extensive tributary of the Amazon River and has the largest diversity of fishes in the world. On its right bank, the Madeira River receives the Jamari River, in which the first hydroelectric power plant (HPP) in State of Rondônia, Samuel HPP, was built. Besides this, other dams were built in the Jamari River and its tributaries, however, the available information in the scientific literature about the ichthyofaunistic diversity of this basin is rare. This work aims to provide an ichthyofaunistic inventory in a region of the Jamari river basin, in the State of Rondônia, where three small hydropower plants (SHPs) were implemented. The ichthyofauna was sampled in 16 expeditions between August 2015 and December 2018. Gill nets and seine nets were used with different meshes, as well as longlines and cast nets at different times of the day. Additionally, 81 INPA lots of species from the Samuel HPP area of influence were reanalyzed. Fish were identified according to the specialized literature, as well as in consultations with experts of various taxonomic groups. Voucher specimens of the species were cataloged and deposited in the ichthyological collection of the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia) of the Universidade Estadual de Maringá. A total of 230 species were recorded, of which 22 were putative new species, 117 were added to the Jamari River basin and 28 to the Madeira River basin. The continuation of the studies in this section of the Jamari river basin is fundamental for analysis of local impact due to the presence of dams. Moreover, the addition of putative new species to the Madeira River basin indicates gaps in the knowledge of Neotropical ichthyofauna.
Keywords: *Diversity, species list, Madeira River, Amazon basin, freshwater fish.*

Lista das espécies de peixes da bacia do rio Jamari, em áreas sob influência de reservatórios, Rondônia, Brasil

Resumo: O rio Madeira é o mais extenso afluente do rio Amazonas e possui a maior biodiversidade de peixes do mundo. Em sua margem direita, o rio Madeira recebe o rio Jamari, no qual foi construída a primeira usina hidrelétrica (UHE) do estado de Rondônia, a UHE Samuel. Além desta, outros barramentos foram construídos no rio Jamari e em seus afluentes, contudo são raras as informações disponíveis na literatura científica sobre a diversidade ictiofaunística desta bacia. O objetivo deste trabalho foi providenciar um inventário ictiofaunístico na região da bacia do rio Jamari, no estado de Rondônia, onde foram implantadas três pequenas centrais hidrelétricas (PCHs). A ictiofauna foi amostrada em 16 expedições entre os meses de agosto de 2015 e dezembro de 2018. Foram utilizadas redes de espera e arrasto com malhas de diversos tamanhos, além de espinhéis e tarrafas em diferentes períodos do dia. Adicionalmente, 81 lotes de espécies do INPA da área de influência da UHE Samuel foram reanalisados. Os peixes foram identificados de acordo com a literatura especializada, bem como em consultas com especialistas de diversos grupos taxonômicos. Exemplares testemunho das espécies foram catalogados e depositados na coleção ictiológica do Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura da Universidade Estadual de Maringá. Foram registradas 230 espécies, destas, 22 são possíveis espécies novas, 117 são acrescentadas à bacia do rio Jamari e 28 à bacia do rio Madeira. A continuação dos estudos neste trecho da bacia do rio Jamari é fundamental para análises de impacto local devido à presença de barramentos. Além disso, a adição de possíveis novas espécies à bacia do rio Madeira aponta lacunas no conhecimento da ictiofauna Neotropical.
Palavras-chave: *Diversidade, lista de espécies, rio Madeira, bacia Amazônica, peixe de água doce.*

Introduction

The Amazon basin is recognized for its high number of fish species, and the rate of endemism reaches large values, representing almost half of the recorded species (Reis *et al*. 2016). This ecosystem is mainly affected by the pollution from the use of mercury by mining, construction of dams, deforestation and overexploitation of several natural resources (Castello *et al*. 2013). Amazonian rivers have a lowly exploited hydroelectric potential in comparison to other Neotropical basins (Lima *et al*. 2017). Meanwhile, in this region, some 175 large hydroelectric plants are already in operation or under construction and 277 are planned for the coming years (Castello & Macedo 2016).

Among the tributaries of the Amazon River, the Madeira River is the most extensive and one of the main rivers in South America, draining an area of approximately 984,000 km^2 (Fearnside 2014). Its biodiversity is one of the largest in the world and recent studies have reported the existence of approximately 1,000 fish species (Ohara *et al*. 2015), of a total of 3,000 species estimated for the entire Amazon basin (Queiroz *et al*. 2013a).

The Jamari River is one of the main tributaries of the Madeira River, draining approximately 29,067 km^2 (IBGE 2018). It is economically important for the State of Rondônia, especially since it was dammed to install the Samuel Hydroelectric Power Plant (HPP) in 1989, the first of the state (IBGE 2018). The single available inventory of the Jamari river ichthyofauna, reporting 122 species, focused the area around the Samuel dam, and was included in a study of the impacts caused by the power plant (Santos 1996).

Species richness estimates in Brazilian freshwater ecosystems are scarce and imprecise. Few basins have been inventoried, due to the lack of funding and poor gathering infrastructure (Agostinho *et al*. 2005). Inventories are important for recording species distributions, discovering new species, and comparing changes in richness and abundance over time due to environmental changes (Baird 2010).

Because (1) there is only data from an environmental impact study of Samuel HPP (Santos 1996); (2) the knowledge of ichthyofauna is limited to the studies carried out for the three other small hydropower plants (SHPs), so it is gray literature and it is not easily accessible; we do not know the approximate data of richness of fish species in the area. Thus, this study aimed to provide an ichthyofaunistic inventory of Jamari River basin, Rondônia, Brazil. In order to do this, we used collection data from fishes sampled around Samuel HPP and other three SHPs currently installed.

Material and Methods

1. Study area

The Jamari River is 563 km long and drains an area of 29,067 km². It is one of the eight sub-basins of the Madeira River. Its headwaters are near of Campo Novo de Rondônia town, northwest of Serra dos Pacaás Novos, and flows into the right bank of the Madeira River in the State of Rondônia (IBGE 2018). Its main right-bank tributaries are Branco, Preto do Crespo, Canaã and Quatro Cachoeiras Rivers, and the left-bank ones are Maçangana and Candeias Rivers. The ichthyofauna was sampled in the Jamari River basin, in the area occupied by the Canaã, Santa Cruz de Monte Negro and Jamari SHPs, all in the State of Rondônia (Figure 1, Table 1).

The Canaã SHP is located in the Canaã River, near the municipality of Ariquemes. The Canaã River presents upstream preserved riparian vegetation, with low flow velocity and shallow depth. The other SHPs were installed in the main course of Jamari River. The Santa Cruz de Monte Negro SHP is located near the municipality of Monte Negro. Its upstream section presents preserved riparian vegetation, low hydrometric level (average 1 meter) and, in narrower areas, waterfalls with formation of waterholes are observed. The Jamari SHP is located downstream of the Santa Cruz de Monte Negro SHP. Its upstream section presents low water level (average 1 m), moderate flow, numerous rock outcrops and punctual rapids. Downstream, the Jamari River is wider (mean of 35 m), it has a strong flow, but with backwater areas.

2. Sampling

The specimens were collected with authorizations 01/2015, 02/2015 and 03/2015 sent by the Secretaria de Estado do Desenvolvimento Ambiental (SEDAM) provided to JCBS. A total of 16 expeditions were carried out between August 2015 and December 2018 with the use of four different capture devices. Gillnets (2.4; 3; 4; 5; 6; 7; 8; 10; 12; 14 and 16 cm between opposite knots) were operated in the marginal region and remained exposed from 16h to 8h on the following day, with a search at 22h. At the reservoir areas, gill nets were installed simultaneously in the marginal region, in the sub-surface of the open areas (pelagic region; surface) and deep areas (bathypelagic region; modified from Smith & Petrere Junior, 2008).

Seine nets (10 m in length and 0.5 cm mesh) were operated once per turn at the littoral zone, during the nocturnal and diurnal period. Longlines (20 hooks, 10 units of 4/0 interposed by 10 units of 7/0) were operated in all environments. Hooks were baited at sunset and searched at night and in the morning of the following day. Cast nets (2.4, 4 and 6 cm between opposite knots) were operated in the lotic environments, each sample including five throws, with sampling at nocturnal and diurnal periods.

3. Fish identification

The captured fish were anesthetized in clove oil, fixed in formalin and sent to the Biologic Consultoria Ambiental laboratory. Subsequently, they were kept in 70% alcohol solution and sent for identification in the laboratory of the ichthyology collection of the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia) of the Universidade Estadual de Maringá. The classification by family and higher taxonomic levels followed Betancur-R *et al*. (2017) for bony fishes and McEachran & Aschliman (2004) for Myliobatiformes. The classification of Characiformes followed Betancur-R *et al*. (2019). The classification of Loricariidae followed Lujan *et al*. (2015). The identification of the species was based on specialized papers (species descriptions, taxonomic revisions, etc.), on the keys present in Queiroz *et al*. (2013a), as well as on consultation with specialists in each taxonomic group. Individuals of the putative new species were photographed (Figure 3). Vouchers were deposited in the ichthyology collection of the Nupélia and they are available at http://splink.cria.org.br/. Uncatalogued specimens were in poor condition.

Because there are several differences between the list of the species sampled by us and that of Santos (1996), we decided to reanalyze lots collected by him and deposited at the Instituto Nacional de Pesquisas da Amazônia (INPA) collection. This reanalysis had two goals: (1) find

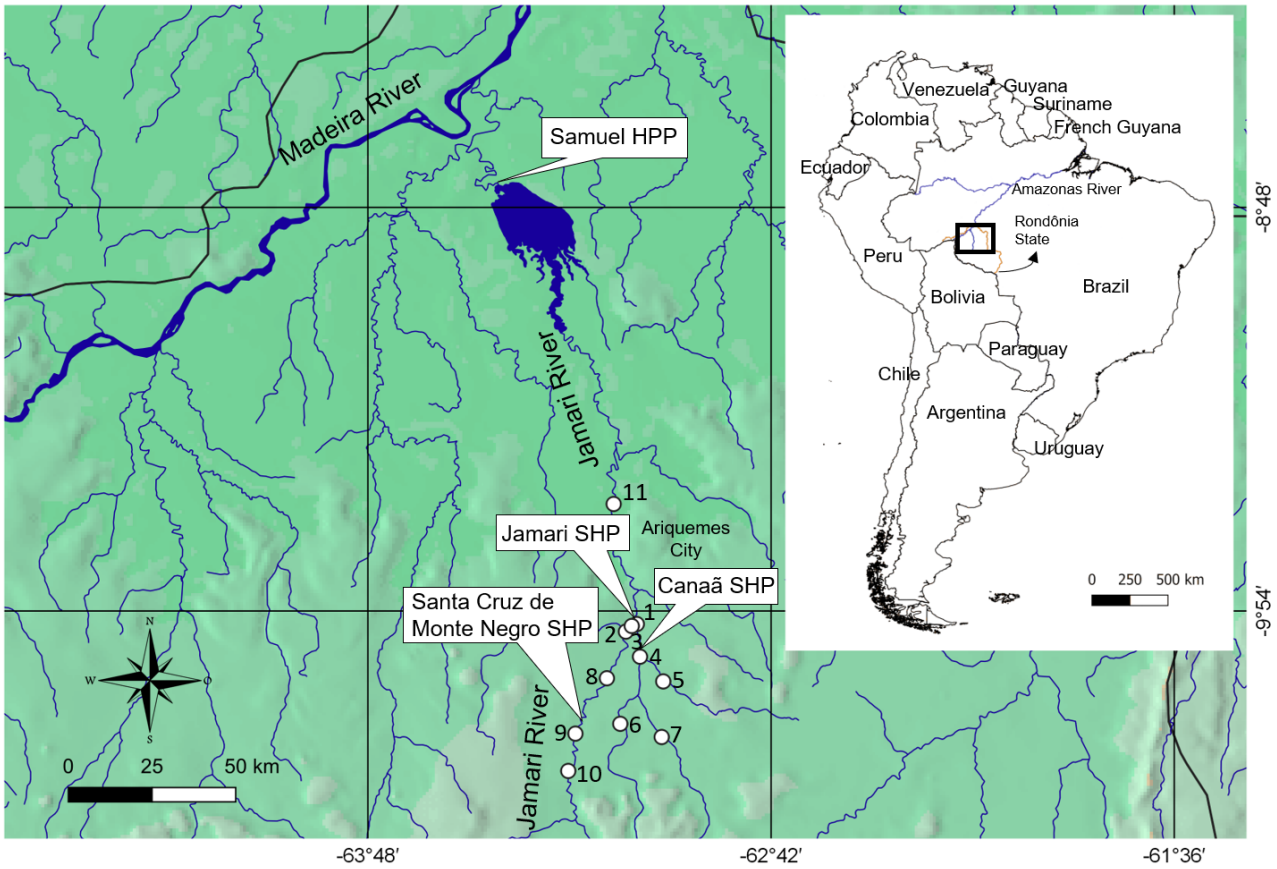


Figure 1. Sampling stations in the Jamari River: Canaã, Jamari and Santa Cruz de Monte Negro SHPs, with their approximate geographical coordinates: 1 - Downstream of Jamari and Canaã SHPs; 2 - Itapoana River; 3 - Jamari SHP reservoir; 4 - Canaã SHP reservoir; 5 - Quatro Cachoeiras River; 6 - Upstream of the Canaã SHP; 7 - Pardo River; 8 - Downstream of Santa Cruz de Monte Negro SHP and Upstream of Jamari SHP; 9 - Santa Cruz de Monte Negro SHP reservoir; 10 - Upstream of Santa Cruz de Monte Negro SHP; 11 - Downstream of Jamari SHP.

species from the Jamari River which were not collected by us, in order to increase the number of species included in our list; (2) verify the taxonomic identity of the specimens collected by Geraldo Santos and included in Santos (1996), given that many species have been described or revised since 1996. Whenever we felt certain that a given species in our list could not have been presented in the list by Santos (1996) under a misidentified name, we considered it to be a new record for the Jamari River basin, unless the species has been recorded in a revisionary study or species description.

Queiroz *et al*. (2013a) did not record for the Madeira River basin some of the species recorded herein in the Jamari River basin. This is partially explained by the presence of putatively new species so far known only from the Jamari River basin, although some of the possible new species listed herein are probably more widespread in the Madeira River basin. Other species, which are already described, have been reported from the Madeira River basin in other papers, dealing with taxonomic revisions or species descriptions: *Leporinus bleheri* Géry (1999), *Petulanos intermedius* (Winterbottom 1980) (see Sidlauskas & Santos 2005), *Myloplus zorroi* Andrade, Jégu & Giarrizzo (2016), *Mylossoma albiscopum* (Cope 1872) (see Mateussi *et al*. 2018), *Charax pauciradiatus* (Günther 1864) (see Menezes & Lucena 2014), *Leporacanthicus galaxias* Isbrücker & Nijssen (1989), *Pimelodus albofasciatus* Mees 1974 (see Santos 1996), *Satanoperca curupira* Ota, Kullander, Deprá, da Graça & Pavanelli (2018). All of the species above have been reported in Brazilian territory, except *L. bleheri*, which was sampled in the Verde River, on the border between Brazil and Bolivia.

Other species were identified in Queiroz *et al*. (2013a) with a different name: *Leporinus desmotes* = *L. jatuncochi* (see Burns *et al*. 2017), *L. cylindriformes* = *L. niceforoi* (this paper), *Moenkhausia* sp. "virgulata" = *Astyanax guaporensis* (see Marinho & Ohara 2013), *Moenkhausia* sp. "collettii alta" = *Astyanax guianensis* (see Marinho *et al*. 2015), *Moenkhausia* cf. *megalops* = *M. abyss* Oliveira & Marinho (2016), *Moenkhausia* sp. "lepidura longa" = *M. hasemani* (see Marinho & Langeani 2016), *Ancistrus* sp. 2 "Sotério" = *Ancistrus* cf. *dolichopterus* (this paper), *Acistrus* sp. 1 "Baixinho" = *Ancistrus* sp. (this paper), *Hemiancistrus* sp. "Bamburro" = *Peckoltia* cf. *ephippiata* Armbruster, Werneke & Tan (2015), *Pterygoplichthys pardalis* = *P. disjunctivus* Weber (1991), *Hemidoras morrisi* = *Opsodoras morrisi* (see DoNascimiento *et al*. 2017), *Opsodoras ternetzi* = *Tenellus ternetzi* (see Birindelli 2014), *Rhamdia quelen* = *Rhamdia* sp. (this paper), *Hypophthalmus edentatus* = *Hypophthalmus oremaculatus* (see Littmann *et al*. 2015), "*Pseudopimelodus*" *pulcher* = *Rhyacoglanis* sp. (see Shibatta & Vari 2017).

Table 1. Location of sampling stations in the Jamari River during the expeditions between August 2015 and December 2018.

Number	Sampling stations	Geographic coordinates
1	Downstream of Jamari and Canaã SHPs	9°56'20.73" S, 63°4'8.10" W
2	Itapoana River	9°57'22.83" S, 63°5'45.79" W
3	Jamari SHP reservoir	9°56'27.63" S, 63°4'47.87" W
4	Canaã SHP reservoir	10°1'28.93" S, 63°3'26.96" W
5	Quatro Cachoeiras River	10°14'37.06" S, 62°59'53.70" W
6	Upstream of the Canaã SHP	10°12'27.50" S, 63°6'40.57" W
7	Pardo River	10°5'31.45" S, 62°59'38.49" W
8	Downstream of Santa Cruz de Monte Negro SHP and Upstream of Jamari SHP	10°5'0.56" S, 63°8'52.10" W
9	Santa Cruz de Monte Negro SHP reservoir	10°14'3.79" S, 63°14'1.34" W
10	Upstream of Santa Cruz de Monte Negro SHP	10°20'10.13" S, 63°15'11.71" W
11	Downstream of Jamari SHP	9°36'30.61" S, 63°7'45.49" W

Results

The 49,947 specimens captured and those belonging to the 81 INPA lots are distributed in 230 species belonging to 42 families and ten orders (Table 2). Just the 81 INPA lots reanalyzed by us yielded an additional 55 species (Table 2). A total of 117 species were added to the Jamari River basin and 28 species to the Madeira River basin (Table 2).

The richest order was Characiformes, with 18 families and 121 species (52.6%), followed by Siluriformes with ten families and 63 species, (27.4%) and Cichliformes with one family and 21 species (9.1%) (Figure 2). Gymnotiformes presented five families with 14 species (6.1%), Clupeiformes presented two families and four species (1.7%) and Myliobatiformes presented one family and two species (0.9%) (Figure 2). Synbranchiformes, Pleuronectiformes, Beloniformes, Tetraodontiformes presented just one species, 0.4% each. Sciaenidae, which is *incertae sedis* in Eupercaria, was represented by a single species too (0.4%) (Figure 2).

The richest family was Characidae with 45 species (19.6%), followed by Cichlidae with 21 species (9.1%) and Anostomidae with 20 species (8.7%) (Figure 2). Loricariidae and Pimelodidae presented 14 species each (6.1% each); Serrasalmidae 13 (5.7%); Curimatidae and Doradidae 10 each (4.3% each) (Figure 2). The other families summed 83 species (total of 36.1%) (Figure 2). Among the latter, 13 families (Parodontidae, Prochilodontidae, Chalceidae, Lebiasinidae, Aspredinidae, Cetopsidae, Hypopomidae, Engraulidae, Synbranchidae, Achiridae, Belonidae, Tetraodontidae and Sciaenidae) presented only one species (total of 5.7%) (Figure 2).

Among captured and reexamined specimens, 22 putatively new species were found, representing approximately 9.6% of all species: *Leporinus* sp., *Apareiodon* sp., *Astyanax* sp., *Hyphessobrycon* sp., *Moenkhausia* sp., *Thayeria* sp. "hemiodus", *Creagrutus* sp., *Gymnotus* sp., *Corydoras* sp., *Ancistrus* sp., *Hypostomus* sp., *Typhlobelus* sp., *Ceptosidium* sp., *Phenacorhamdia* sp., *Rhamdia* sp., *Megalonema* sp., *Pimelodus* sp., *Batrochoglanis* sp. "aff. B. *villosus*", *Rhyacoglanis* sp., *Synbranchus* sp., *Geophagus* sp. 1 and *Geophagus* sp. 2 (Figure 3).

Discussion

Our study added 117 species to the 122 listed by Santos (1996) from the Jamari River basin, and 28 species to the 820 listed by Queiroz *et al*. (2013a) from the Madeira River basin in Brazilian territory. From those INPA lots reanalyzed, several species collected by Geraldo Santos were not included in Santos (1996), not even under a different name. However, we were not able to verify all the identifications by Santos (1996), once the author did not provide the catalog numbers of the lots analyzed by him, and we failed to find in the INPA collection several lots collected in the Jamari River basin. The record of 22 putatively new species and the scarce information on the threat status of most species recorded in the present study are examples of gaps still existing in the knowledge of Neotropical ichthyofauna.

The results followed the known patterns for Neotropical ichthyofauna (Lowe-McConnell 1999), showing the highest percentage of Characiformes species, followed by Siluriformes and Cichliformes. The same proportion at the order level was found for other sites in the Madeira River basin (Camargo & Giarrizzo 2007, Perin *et al*. 2007, Casatti *et al*. 2013). Regarding families with greater species richness, our work presented greater richness in Characidae, followed by Cichlidae and Anostomidae. However, other authors obtained different relative amounts: Characidae>Cichlidae>Loricariidae (Camargo & Giarrizzo 2007); Characidae>Loricariidae>Cichlidae (Casatti *et al*. 2013); Loricariidae>Characidae>Cichlidae (Perin *et al*. 2007); Curimatidae> Characidae>Loricariidae (Araújo *et al*. 2009). Although this difference suggests the high variability of species distribution in the different tributaries of the Madeira River basin, and probably a high percentage of species to be discovered (Casatti *et al*. 2013), those works were conducted in distinct environments (*e.g*. streams, Araújo *et al*. 2009, Casatti *et al*. 2013 and Perin *et al*. 2007; river, Camargo & Giarizzo). Also, those studies employed different fishing gears, which tend to capture different species, as shown by Oliveira *et al*. (2014).

Jamari River has Samuel HPP, which was installed in 1989, and three other SHPs which were installed after 2015. We did not analyze the effects from those dams installed in the Jamari River basin, but literature shows that tropical rivers are the main targets for dam construction due to their high hydroelectric potential (ANA 2019), which also affects aquatic ecosystems (Fearnside 2014). In Brazil, the Amazon basin is already considered the final energy frontier, since the other basins of the country have their hydroelectric potential almost exhausted (Doria *et al*. 2018, ANEEL 2019). If, on the one hand, hydroelectric plants generate more energy, on the other they cause both environmental and socio-economic impacts. The most evident issue of dam construction is the habitat fragmentation with blocking of access between the spawning and initial development sites of the migratory species (Agostinho *et al*. 2002), which makes the development of new populations unfeasible.

Table 2. List of fish species from areas altered by the Canaã, Santa Cruz de Monte Negro and Jamari SHPs, and by the Samuel HPP, all in the Jamari River basin, Rondônia, Brazil. The presence in each sampling site is represented by an "x". Species which are new records for the Jamari and/or Madeira river basins are indicated by an "*". Species we were not capable to notify if they are new records are indicated by "?". The threat categories for species are in accordance with the IUCN (2019) Red List (Data Deficient = DD; Least Concern = LC). Species which do not have information in the IUCN (2019) are indicated by "-". In the Madeira River column, "a" represents species which were reported from the Madeira River basin in other papers, but not in Queiroz *et al*. (2013a); "b" represents those species which have been identified in Queiroz *et al*. with a different name (see Material and Methods to more information). The numbers in the header represent the sample stations (see Figure 1). *Characidium* aff. *zebra* was collected in our work, but it was not deposited at NUP. References for classification are in Material and Methods.

Classification	Sampling sites											New records		IUCN	Voucher
	1	2	3	4	5	6	7	8	9	10	11	Jamari River	Madeira River		
CHONDRICHTHYES															
MYLIOBATIFORMES															
Potamotrygonidae															
Potamotrygon falkneri Castex & Maciel 1963	x											*		DD	NUP 19827
Potamotrygon orbignyi (Castelnau 1855)		x						x				*		LC	NUP 19376
OSTEICHTHYES															
CLUPEIFORMES															
Engraulidae															
Lycengraulis batesii (Günther 1868)														LC	INPA 10401, INPA 12092
Pristigasteridae															
Ilisha amazonica (Miranda Ribeiro 1920)												*		LC	INPA 7451, INPA 16249
Pellona castelnaeana Valenciennes 1847														LC	INPA 15154
Pellona flavipinnis (Valenciennes 1837)														LC	INPA 7450
CHARACIFORMES															
Crenuchidae															
Characidiinae															
Characidium aff. *zebra* Eigenmann 1909					x		x			x		*		-	INPA 14143
Characidium etheostoma Cope 1872					x					x		*		-	NUP 19333
Erythrinidae															
Hoplerythrinus unitaeniatus (Spix & Agassiz 1829)		x										*		-	NUP 19389
Hoplias gr. *malabaricus* (Bloch 1794)	x	x	x	x	x	x	x	x	x	x	x			-	NUP 19747
Anostomidae															
Anostomoides atrianalis Pellegrin 1909												*		-	INPA 10621, INPA 15182, INPA 15185, INPA 15193
Gnathodolus bidens Myers 1927												*		-	INPA 48820
Hypomasticus pachycheilus (Britski 1976)	x											*		-	NUP2 1266, INPA 1371
Laemolyta proxima (Garman 1890)	x	x	x	x		x		x		x	x			-	NUP 19352
Laemolyta taeniata (Kner 1858)	x	x		x				x			x			-	NUP 19526
Leporellus vittatus (Kner 1858)	x							x				*		-	NUP 19320
Leporinus bleheri Géry 1999								x				*	a	-	NUP 19446
Leporinus brunneus Myers 1950												*		-	INPA 15403, INPA 15411
Leporinus fasciatus (Bloch 1794)	x		x	x	x	x	x	x	x	x	x			-	NUP 19531
Leporinus friderici (Bloch 1794)	x	x	x	x	x	x	x	x	x	x	x			-	NUP 19353
Leporinus jamesi Garman 1929												*		-	INPA 52170
Leporinus jatuncochi Ovchynnyk 1971	x				x	x	x	x			x	*	b	-	NUP 19381
Leporinus niceforoi Fowler 1943	x	x	x	x	x	x	x	x	x	x			b	LC	NUP 19375
Leporinus sp.		x		x	x	x	x	x	x	x		*	*	-	NUP 19345
Megaleporinus trifasciatus (Steindachner 1876)								x				*		-	NUP 19745
Petulanos intermedius (Winterbottom 1980)													a	-	INPA 15183

Continuation Table 2.

Classification	Sampling sites											New records		IUCN	Voucher
	1	2	3	4	5	6	7	8	9	10	11	Jamari River	Madeira River		
Pseudanos gracilis (Kner 1858)											x	*		-	NUP 20794
Pseudanos trimaculatus (Kner 1858)					x		x	x	x	x	x			-	NUP 19318
Rhytiodus argenteofuscus Kner 1858														-	INPA 10638
Schizodon fasciatus Spix & Agassiz 1829	x	x	x	x	x	x	x	x	x	x	x			-	NUP 19332
Chilodontidae															
Caenotropus labyrinthicus (Kner 1858)	x		x					x	x	x	x			-	NUP 19439
Caenotropus schizodon Scharcansky & Lucena 2007	x		x	x			x	x	x	x	x	*		-	NUP 19361
Curimatidae															
Curimata cyprinoides (Linnaeus 1766)								x		x		*	*	-	NUP 19341
Curimatella meyeri (Steindachner 1882)								x		x	x			-	NUP 20754
Cyphocharax leucostictus (Eigenmann & Eigenmann 1889)	x	x				x		x	x	x	x	?		-	NUP 19553
Cyphocharax notatus (Steindachner 1908)	x	x		x	x	x	x	x	x	x	x	*		-	NUP 19480
Cyphocharax spiluropsis (Eigenmann & Eigenmann 1889)	x	x	x	x	x	x	x	x	x	x	x	?		-	NUP 19479
Potamorhina altamazonica (Cope 1878)	x			x		x	x	x			x			-	NUP 19542
Potamorhina latior (Spix & Agassiz 1829)	x						x				x			-	NUP 21267
Psectrogaster amazonica Eigenmann & Eigenmann 1889	x											*		-	NUP 19541
Psectrogaster essequibensis (Günther 1864)	x	x	x	x		x	x	x	x	x	x			-	NUP 19362
Steindachnerina guentheri (Eigenmann & Eigenmann 1889)	x	x			x	x	x	x	x	x		*		-	NUP 19400
Cynodontidae															
Cynodon gibbus (Spix & Agassiz 1829)														-	INPA 16341
Hydrolycus armatus (Jardine 1841)	x											*		-	Uncatalogued
Hydrolycus scomberoides (Cuvier 1819)														-	INPA 13291
Hydrolycus tatauaia Toledo-Piza, Menezes & Santos 1999														-	INPA 13281
Rhaphiodon vulpinus Spix & Agassiz 1829	x		x			x		x			x			-	NUP 19356
Hemiodontidae															
Hemiodus gracilis Günther 1864		x	x	x	x		x	x	x	x		?		-	NUP 19336
Hemiodus unimaculatus (Bloch 1794)	x	x	x	x	x	x	x	x	x	x	x			-	NUP 19548
Parodontidae															
Apareiodon sp.	x	x		x	x	x		x	x	x		*		-	NUP 19455
Prochilodontidae															
Prochilodus nigricans Spix & Agassiz 1829	x	x	x	x	x	x	x	x	x	x	x			-	NUP 19321
Serrasalmidae															
Colossoma macropomum (Cuvier 1816)			x	x	x			x				*		-	NUP 20797
Metynnis lippincottianus (Cope 1870)	x	x	x	x	x				x	x	x	*		-	NUP 19493
Metynnis maculatus (Kner 1858)		x			x							*		-	NUP 19383
Myleus setiger Müller & Troschel 1844		x				x	x		x			?		-	NUP 19576
Myloplus asterias (Müller & Troschel 1844)	x	x	x	x	x	x	x	x		x		?		-	NUP 19515
Myloplus rubripinnis (Müller & Troschel 1844)	x	x	x	x	x	x	x	x	x	x		?		-	NUP 19842
Myloplus zorroi Andrade, Jégu & Giarrizzo 2016	x	x	x		x	x	x	x	x	x	x	?	a	-	NUP 19843
Mylossoma albiscopum (Cope 1872)											x		a	-	NUP 21268
Serrasalmus compressus Jégu, Leão & Santos 1991	x	x	x	x	x	x	x	x	x	x	x	?		-	NUP 19834
Serrasalmus eigenmanni Norman 1929		x	x	x	x	x	x	x	x	x	x			-	NUP 19330
Serrasalmus maculatus Kner 1858	x						x		x	x		?		-	NUP 19837
Serrasalmus rhombeus (Linnaeus 1766)	x	x	x	x	x	x	x	x	x	x	x			-	NUP 19818

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Continuation Table 2.

Classification	Sampling sites											New records		IUCN	Voucher
	1	2	3	4	5	6	7	8	9	10	11	Jamari River	Madeira River		
Serrasalmus spilopleura Kner 1858	x	x	x		x		x	x	x	x		?		-	NUP 19436
Acestrorhynchidae															
Acestrorhynchinae															
Acestrorhynchus falcatus (Bloch 1794)		x			x	x								-	NUP 19388
Acestrorhynchus falcirostris (Cuvier 1819)														-	INPA 15260
Acestrorhynchus heterolepis (Cope 1878)	x	x	x	x	x	x	x	x	x	x	x	*		-	NUP19354
Acestrorhynchus microlepis (Jardine 1841)	x	x	x	x	x	x	x	x	x	x	x			-	NUP19366
Bryconidae															
Brycon amazonicus (Agassiz 1829)														LC	INPA 16383
Brycon falcatus Müller & Troschel 1844	x	x	x			x		x		x				-	NUP 19386
Brycon melanopterus (Cope 1872)														-	INPA 16446
Brycon pesu Müller & Troschel 1845	x			x			x		x	x				-	NUP 19348
Chalceidae															
Chalceus epakros Zanata & Toledo-Piza 2004	x		x	x			x	x	x			?		-	NUP 19441
Characidae															
Stethaprioninae															
Astyanax anterior Eigenmann 1908		x			x							?		-	NUP 19549
Astyanax gr. *bimaculatus* (Linnaeus 1758)			x				x		x			?		-	NUP 19413
Astyanax guaporensis Eigenmann 1911	x							x				?	b	LC	NUP 20714
Astyanax guianensis Eigenmann 1909	x					x					x	?	b	-	NUP 20790
Astyanax cf. *maximus* (Steindachner 1876)		x			x	x						?		-	NUP 19442
Astyanax multidens Eigenmann 1908	x										x	?	*	-	NUP 19422
Astyanax sp.	x	x	x		x	x	x	x		x	x	?	*	-	NUP 19560
Ctenobrycon spilurus (Valenciennes 1850)	x	x	x	x	x	x	x	x	x		x	*		-	NUP 19404
Hemigrammus geisleri Zarske & Géry 2007	x	x		x	x	x	x	x	x	x	x	*		-	NUP 19406
Hemigrammus ocellifer (Steindachner 1882)												*		-	INPA 20838
Hemigrammus vorderwinkleri Géry 1963						x						*		-	NUP 19410
Hyphessobrycon diancistrus Weitzman 1977											x	*		-	NUP 20779
Hyphessobrycon sweglesi (Géry 1961)						x						*		-	NUP 19409
Hyphessobrycon sp.						x						?	*	-	NUP 21269
Jupiaba acanthogaster (Eigenmann 1911)		x			x	x	x	x	x	x		*		-	NUP 19419
Jupiaba anteroides (Géry 1965)												?		-	INPA 16535
Jupiaba cf. *scologaster* (Weitzman & Vari 1986)	x	x	x		x		x	x		x	x	?	*	-	NUP 19425
Jupiaba zonata (Eigenmann 1908)	x	x			x	x	x	x		x		?		-	NUP 19418
Microschemobrycon callops Böhlke 1953		x		x	x	x	x	x	x	x		*		-	NUP 19417
Microschemobrycon guaporensis Eigenmann 1915	x	x			x	x	x	x	x	x	x	*		-	NUP 19459
Microschemobrycon melanotus (Eigenmann 1912)		x			x	x		x			x	*		-	NUP 19496
Moenkhausia abyss Oliveira & Marinho 2016	x							x			x	?	b	-	NUP 19568
Moenkhausia ceros Eigenmann 1908												*		-	INPA 10767, INPA 11116, INPA 20891
Moenkhausia collettii (Steindachner 1882)	x	x	x		x	x	x	x		x	x	*		-	NUP 19719
Moenkhausia cotinho Eigenmann 1908												*		-	INPA 20921
Moenkhausia gr. *dichroura* (Kner 1858)					x							?	?	-	NUP 19506
Moenkhausia gracilima Eigenmann 1908	x	x		x	x	x	x	x	x	x	x	?		-	NUP 19570
Moenkhausia grandisquamis (Müller & Troschel 1845)	x				x						x	*		-	NUP 19347
Moenkhausia hasemani Eigenmann 1917	x	x		x	x	x	x	x		x	x	?	b	-	NUP 19469
Moenkhausia mikia Marinho & Langeani 2010	x	x			x	x	x	x		x	x	?	*	-	NUP 19449

Continuation Table 2.

Classification	Sampling sites											New records		IUCN	Voucher
	1	2	3	4	5	6	7	8	9	10	11	Jamari River	Madeira River		
Moenkhausia oligolepis (Günther 1864)		x			x	x	x	x		x		*		-	NUP 19370
Moenkhausia pankilopteryx Bertaco & Lucinda 2006	x	x	x	x	x	x	x	x		x	x	*		-	NUP 19408
Moenkhausia sp.		x			x	x		x		x	x	*	*	-	NUP 19720
Poptella compressa (Günther 1864)	x	x	x	x	x	x	x	x	x	x	x			-	NUP 21270
Thayeria sp. "hemiodus"	x							x			x	*		-	NUP 19483
Stevardiinae															
Creagrutus cf. *beni* Eigenmann 1911		x										*		-	NUP 20733
Creagrutus sp.	x	x	x		x	x	x	x	x	x	x	*	*	-	NUP 19579
Knodus heteresthes (Eigenmann 1908)	x	x		x	x	x	x	x	x	x	x	*		-	NUP 19384
Xenurobrycon cf. *pteropus* Weitzman & Fink 1985		x				x						*	*	-	NUP 19520
Tetragonopterinae															
Tetragonopterus chalceus Spix & Agassiz 1829	x	x	x		x	x	x	x	x	x	x	?		-	NUP 19475
Characinae															
Charax pauciradiatus (Günther 1864)		x			x	x	x			x	x	*	a	-	NUP 19561
Phenacogaster retropinnus Lucena & Malabarba 2010	x	x	x		x	x	x	x	x	x	x	*		-	NUP 19416
Roeboides affinis (Günther 1868)	x	x	x	x	x	x	x	x	x	x	x			LC	NUP 19349
Cheirodontinae															
Serrapinnus microdon (Eigenmann 1915)						x	x					*		-	NUP 19528
Serrapinnus notomelas (Eigenmann 1915)		x					x	x	x	x		*		-	NUP 19405
Ctenoluciidae															
Boulengerella cuvieri (Spix & Agassiz 1829)	x	x	x	x	x	x	x	x	x	x	x			-	NUP 19444
Boulengerella maculata (Valenciennes 1850)														-	INPA 7335, INPA 7336
Iguanodectidae															
Bryconops aff. *caudomaculatus* (Günther 1864)	x	x	x	x	x	x	x	x	x	x	x	?		-	NUP 19317
Bryconops gracilis (Eigenmann 1908)	x	x	x	x	x	x	x	x	x	x	x	*	*	LC	NUP 20708
Bryconops cf. *melanurus* (Bloch 1794)	x	x	x	x	x	x	x	x	x	x	x	*	*	-	NUP 21272
Iguanodectes variatus Géry 1993												*		-	INPA 16406
Lebiasinidae															
Pyrrhulininae															
Nannostomus digrammus (Fowler 1913)												*		-	INPA 44369
Triportheidae															
Agoniatinae															
Agoniates halecinus Müller & Troschel 1845	x	x	x	x				x	x	x	x	?		-	NUP 19492
Triportheinae															
Triportheus angulatus (Spix & Agassiz 1829)	x							x			x			-	NUP 19421
GYMNOTIFORMES															
Gymnotidae															
Electrophorus electricus (Linnaeus 1766)					x	x		x		x				LC	NUP 19828
Gymnotus carapo madeirensis Craig, Crampton & Albert 2017		x	x		x			x	x			*		-	NUP 19535
Gymnotus aff. *javari* Albert, Crampton & Hagedorn 2003												*	*	-	INPA 9841
Gymnotus gr. *pantherinus* (Steindachner 1908)												*	*	-	INPA 9838
Gymnotus sp.									x			*	?	-	NUP 21273
Apteronotidae															
Apteronotus albifrons (Linnaeus 1766)			x									*		-	NUP 19574
Apteronotus cf. *caudimaculosus* de Santana 2003									x			*	*	-	Uncatalogued

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Continuation Table 2.

Classification	Sampling sites											New records		IUCN	Voucher
	1	2	3	4	5	6	7	8	9	10	11	Jamari River	Madeira River		
Hypopomidae															
Brachyhypopomus beebei (Schultz 1944)												*		-	INPA 19947
Rhamphichthyidae															
Gymnorhamphichthys rondoni (Miranda Ribeiro 1920)						x	x					*		-	NUP 20738
Rhamphichthys rostratus (Linnaeus 1766)		x			x	x		x	x	x	x	?		-	NUP 19836
Sternopygidae															
Eigenmannia limbata (Schreiner & Miranda Ribeiro 1903)			x									*		-	NUP 21274
Eigenmannia gr. *trilineata* López & Castello 1966	x	x	x	x	x	x	x	x	x	x	x	?	*	-	NUP 19575
Rhabdolichops caviceps (Fernández-Yépez 1968)												*	*	-	INPA 27966
Sternopygus macrurus (Bloch & Schneider 1801)		x			x	x	x	x		x		*		-	NUP 19371
SILURIFORMES															
Callichthyidae															
Callichthys callichthys (Linnaeus 1758)												*		-	INPA 48761
Corydoras similis Hieronimus 1991		x				x		x				*		-	NUP 20709
Corydoras sp.					x							*	?	-	NUP 21275
Hoplosternum littorale (Hancock 1828)												*		-	INPA 11169
Megalechis picta (Müller & Troschel 1849)												*		-	INPA 11176
Loricariidae															
Rhinelepinae															
Pseudorinelepis genibarbis (Valenciennes 1840)														-	INPA 7340
Loricariinae															
Farlowella smithi Fowler 1913							x					*		-	NUP 19556
Loricaria cataphracta Linnaeus 1758	x	x	x	x	x	x	x	x	x	x	x			-	NUP 19585
Rineloricaria castroi Isbrücker & Nijssen 1984						x						?		-	NUP 19597
Hypoptopomatinae															
Otocinclus mangaba Lehmann A., Mayer & Reis 2010							x					*		-	NUP 20775
Hypostominae															
Ancistrus cf. *dolichopterus* Kner 1854	x	x			x	x	x	x				?	b	LC	NUP 19322
Ancistrus sp.					x	x	x	x	x	x		?	b	-	NUP 19337
Hypostomus cf. *hemicochliodon* Armbruster 2003	x	x	x	x	x	x	x	x	x	x	x	?	*	-	NUP 19603
Hypostomus sp.	x	x	x		x		x	x	x	x	x	?		-	NUP 19587
Lasiancistrus schomburgkii (Günther 1864)	x	x	x		x	x	x	x	x	x	x	*		LC	NUP 19338
Leporacanthicus galaxias Isbrücker & Nijssen 1989	x										x		a	-	NUP 19423
Peckoltia brevis (La Monte 1935)	x		x					x	x	x	x	?	*	-	NUP 19343
Peckoltia cf. *ephippiata* Armbruster, Werneke & Tan 2015	x	x	x		x	x	x	x	x	x	x	?	b	-	NUP 19346
Pterygoplichthys disjunctivus (Weber 1991)								x				?	b	-	NUP 19323
Trichomycteridae															
Henonemus punctatus (Boulenger 1887)	x											*		-	NUP 20704
Typhlobelus sp.										x		*	?	-	NUP 20722
Vandellia beccarii Di Caporiacco 1935	x											*	*	-	NUP 21276
Aspredinidae															
Pterobunocephalus depressus (Haseman 1911)						x	x					*		-	NUP 19378
Auchenipteridae															
Ageneiosus inermis (Linnaeus 1766)	x	x	x	x	x	x	x	x	x	x	x			-	NUP 19753
Auchenipterichthys coracoideus (Eigenmann & Allen 1942)		x	x	x		x		x			x	?		LC	NUP 19364

Continuation Table 2.

Classification	Sampling sites											New records		IUCN	Voucher
	1	2	3	4	5	6	7	8	9	10	11	Jamari River	Madeira River		
Auchenipterichthys cf. *punctatus* (Valenciennes 1840)												*	*	-	INPA 22669
Auchenipterus nuchalis (Spix & Agassiz 1829)	x		x	x	x	x		x	x	x	x			LC	NUP 19367
Centromochlus heckelii (De Filippi 1853)														-	INPA 10904, INPA 10944, INPA 10959
Duringlanis altae (Fowler 1945)								x				*		DD	NUP 20784
Parauchenipterus porosus (Eigenmann & Eigenmann 1888)		x	x	x	x	x	x	x	x	x	x	?		-	NUP 19365
Tatia orca (Sarmento-Soares, Lazzarotto, Rapp Py-Daniel & Leitão 2017)			x			x			x	x	x	*	*	-	NUP 19327
Tympanopleura brevis (Steindachner 1881)			x					x		x		*		-	Uncatalogued
Cetopsidae															
Cetopsidium sp.												*	*	-	INPA 6503
Doradidae															
Acanthodoras cf. *cataphractus* (Linnaeus 1758)						x						*		-	NUP 20746
Acanthodoras spinosissimus (Eigenmann & Eigenmann 1888)												*		-	INPA 12151
Leptodoras praelongus (Myers & Weitzman 1956)												*		-	INPA 26730
Nemadoras humeralis (Kner 1855)												*		-	INPA 21427
Opsodoras morrisi (Eigenmann 1925)												*	b	-	INPA 12178, INPA 22970
Ossancora fimbriata (Kner 1855)												*		LC	INPA 12155
Oxydoras niger (Valenciennes 1821)	x		x	x	x		x	x	x					-	NUP 19355
Platydoras armatulus (Valenciennes 1840)	x	x	x	x	x	x	x	x	x			*		-	NUP 19350
Tenellus leporhinus (Eigenmann 1912)												*	*	-	INPA 22005, INPA 49999
Tenellus ternetzi (Eigenmann 1925)	x					x	x	x		x	x	*	b	-	NUP 19569
Heptapteridae															
Phenacorhamdia sp.												*	?	-	INPA 8003
Pimelodella serrata Eigenmann 1917	x	x	x	x	x	x	x	x	x	x	x	?		-	NUP 19326
Rhamdia sp.		x				x						*	b	-	Uncatalogued
Pimelodidae															
Brachyplatystoma vaillantii (Valenciennes 1840)												*		-	INPA 14439
Calophysus macropterus (Lichtenstein 1819)														-	INPA 5981, INPA 22883
Hemisorubim platyrhynchos (Valenciennes 1840)	x	x	x	x	x	x	x	x	x	x				-	NUP 19750
Hypophthalmus oremaculatus Nani & Fuster 1947	x		x	x				x	x	x	x		b	-	NUP 19465
Leiarius pictus (Müller & Troschel 1849)						x					x	*		-	NUP 20806
Megalonema sp.	x	x			x	x	x	x		x		*	?	-	NUP 19372
Pimelodus albofasciatus Mees 1974	x	x	x	x	x	x	x	x	x	x	x		a	-	NUP 19358
Pimelodus blochii Valenciennes 1840	x		x	x			x	x	x	x	x			-	NUP 19357
Pimelodus ornatus Kner 1858	x	x			x	x	x	x	x	x	x	*		-	NUP 19756
Pimelodus sp.	x		x	x	x		x	x	x	x		*	*	-	NUP 19486
Pinirampus pirinampu (Spix & Agassiz 1829)	x		x					x	x		x			-	NUP 21277
Pseudoplatystoma punctifer (Castelnau 1855)	x	x	x	x	x	x	x	x	x	x	x			-	NUP 19373
Pseudoplatystoma tigrinum (Valenciennes 1840)	x			x										-	NUP 19360
Sorubim elongatus Littmann, Burr, Schmidt & Isern 2001	x		x					x		x	x	?		-	NUP 19527
Pseudopimelodidae															
Batrochoglanis sp. "aff. *B. villosus*"						x						*		-	NUP 20681, INPA 9518

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Continuation Table 2.

Classification	Sampling sites											New records		IUCN	Voucher
	1	2	3	4	5	6	7	8	9	10	11	Jamari River	Madeira River		
Rhyacoglanis sp.												*	b	-	INPA 9517
Pseudopimelodus bufonius (Valenciennes 1840)							x					*		-	NUP 19407
SYNBRANCHIFORMES															
Synbranchidae															
Synbranchus sp.												*	?	-	INPA 11065
PLEURONECTIFORMES															
Achiridae															
Hypoclinemus mentalis (Günther 1862)												*		-	INPA 11014
CICHLIFORMES															
Cichlidae															
Acaronia nassa (Heckel 1840)														-	INPA 7611, INPA 7612, INPA 12093
Aequidens tetramerus (Heckel, 1840)				x		x	x			x		*		-	NUP 19382
Apistogramma pulchra Kullander 1980												*		-	INPA 7663, INPA 11877
Apistogramma resticulosa Kullander 1980			x									*		-	NUP 19514
Biotodoma cupido (Heckel 1840)												*		-	INPA 11652
Chaetobranchus flavescens Heckel 1840		x										*		-	NUP 19387
Cichla pinima Kullander & Ferreira 2006	x	x	x	x	x			x	x	x		?		-	NUP 19315
Cichla pleiozona Kullander & Ferreira 2006	x	x	x	x	x	x	x	x	x	x	x	?		-	NUP 19313
Cichlasoma boliviense Kullander 1983					x	x	x					*		-	NUP 19334
Crenicichla johanna Heckel 1840	x		x	x	x		x	x	x	x				-	NUP 19335
Crenicichla marmorata Pellegrin 1904												?		-	INPA 1505, INPA 1506, INPA 1799, INPA 2101, INPA 2102, INPA 2950
Crenicichla semicincta Steindachner 1892			x									?		-	NUP 19512
Geophagus cf. *neambi* Lucinda, Lucena & Assis 2010	x											?	*	-	NUP 19463
Geophagus sp. 1	x	x	x	x	x	x	x	x	x	x	x	?	*	-	NUP 19504
Geophagus sp. 2			x					x	x	x		?	*	-	NUP 19507
Heros spurius Heckel 1840														-	INPA 7672
Hypselecara temporalis (Günther 1862)						x								-	NUP 19325, INPA 7568
Mesonauta festivus (Heckel 1840)														-	INPA 7774
Pterophyllum scalare (Schultze 1823)												*		-	INPA 10491
Satanoperca curupira Ota, Kullander, Deprá, da Graça & Pavanelli 2018		x	x	x		x	x	x	x	x			a	-	NUP 19328
Satanoperca jurupari (Heckel 1840)		x	x	x	x	x	x	x						-	NUP 19402
BELONIFORMES															
Belonidae															
Potamorrhaphis guianensis (Jardine 1843)											x	*		-	NUP 20773
TETRAODONTIFORMES															
Tetraodontidae															
Colomesus cf. *asellus* (Müller & Troschel 1849)												*		-	INPA 9255, INPA 9258
INCERTAE SEDIS															
Sciaenidae															
Pachypops fourcroi (Lacepède 1802)	x		x					x			x	*		-	NUP 19543

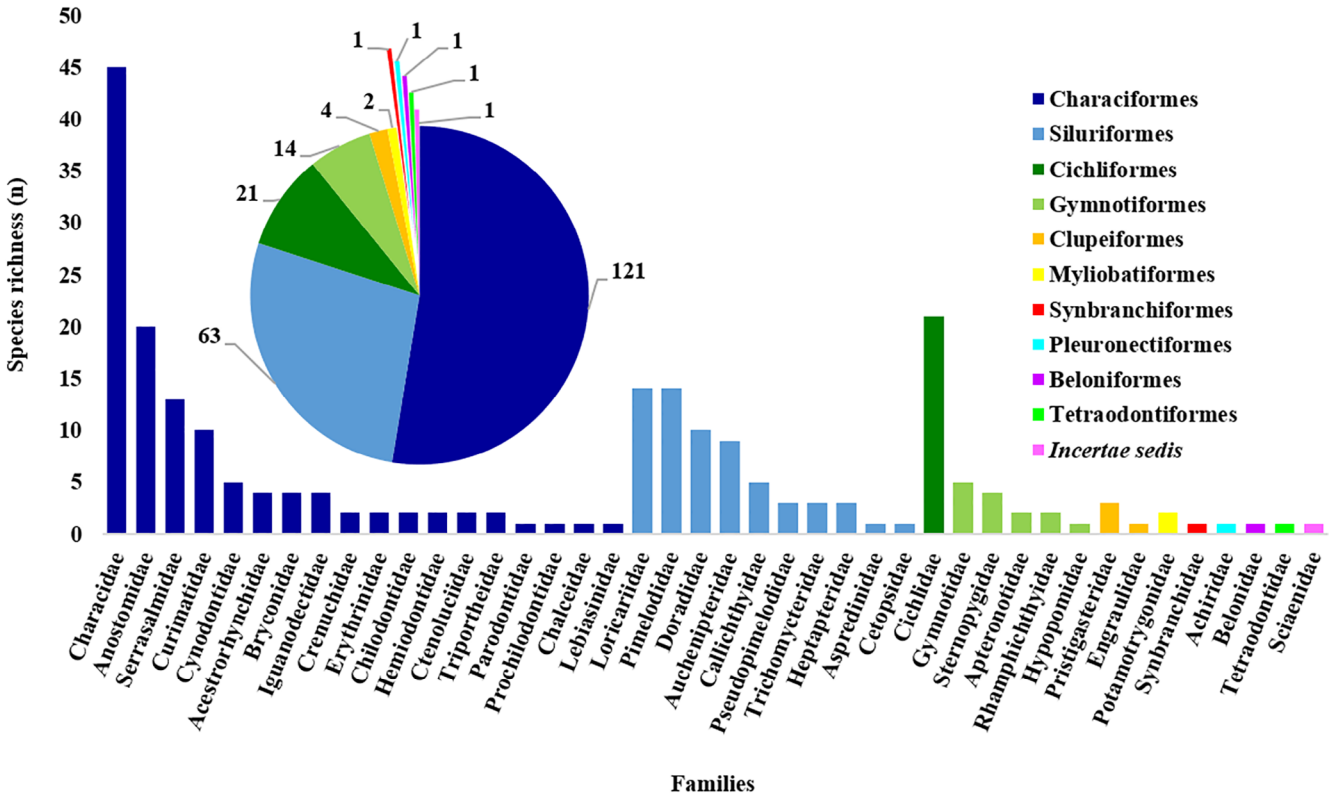


Figure 2. Distribution of number of species by families and orders.

Many migratory fish species have commercial importance for the State of Rondônia, for example, branquinha-cascuda (*Psectrogaster amazonica*), curimatã (*Prochilodus nigricans*), cuiu-cuiu (*Oxydoras niger*), barba-chata (*Pinirampus pirinampu*), among others (Doria *et al*. 2012). However, it is common for anglers to be excluded from plans for the construction of hydroelectric dams, mitigation and compensation of social and ecological impacts (Doria *et al*. 2018).

The Jamari River presented high species richness (230) compared to the other tributaries of Madeira River in which studies were carried out. Among them, 48 in streams of the urban region of Rondônia (Perin 2007), 133 in the preservation area of Marmelos River (Camargo & Giarrizzo 2007), 448 in Aripuanã River and in the middle Madeira River (Rapp Py-Daniel *et al*. 2007), 74 in Belmont Stream (Araújo *et al*. 2009), 174 in the middle Madeira River (Torrente-Vilara *et al*. 2011), 160 in Guariba and Roosevelt Rivers (Pedroza *et al*. 2012), 189 in Cuniã Lake (Queiroz *et al*. 2013b), 40 in streams of the Machado River basin (Casatti *et al*. 2013) and 74 species in Tarumã River, also belonging to the Machado River basin (Costa *et al*. 2017). Richness varies depending on the size and age of the reservoir and on the sampled basin, where the river basins of the Amazon region are richer when compared to others in the Neotropical region (Agostinho *et al*. 2016). Even though species richness increases in the initial years of the reservoir (heterotrophic phase) (Agostinho *et al*. 2007), it is only a reflection of the connection of different biotopes previously isolated (Agostinho *et al*. 2007, Agostinho *et al*. 2016), occurring the inverse later, whereas only tolerant species survive in the new environment (Agostinho *et al*. 2016). Due to the high species richness and the presence of migratory fish, it is essential to carry out continuous monitoring of the Jamari River ichthyofauna, in order to detect potential impacts generated by SHPs in the subsequent years. Also, the enhanced knowledge that would be obtained through continuous sampling would result in better decisions regarding environmental management of the basin, avoiding negative impacts on the diversity and distribution of the fish assemblage.

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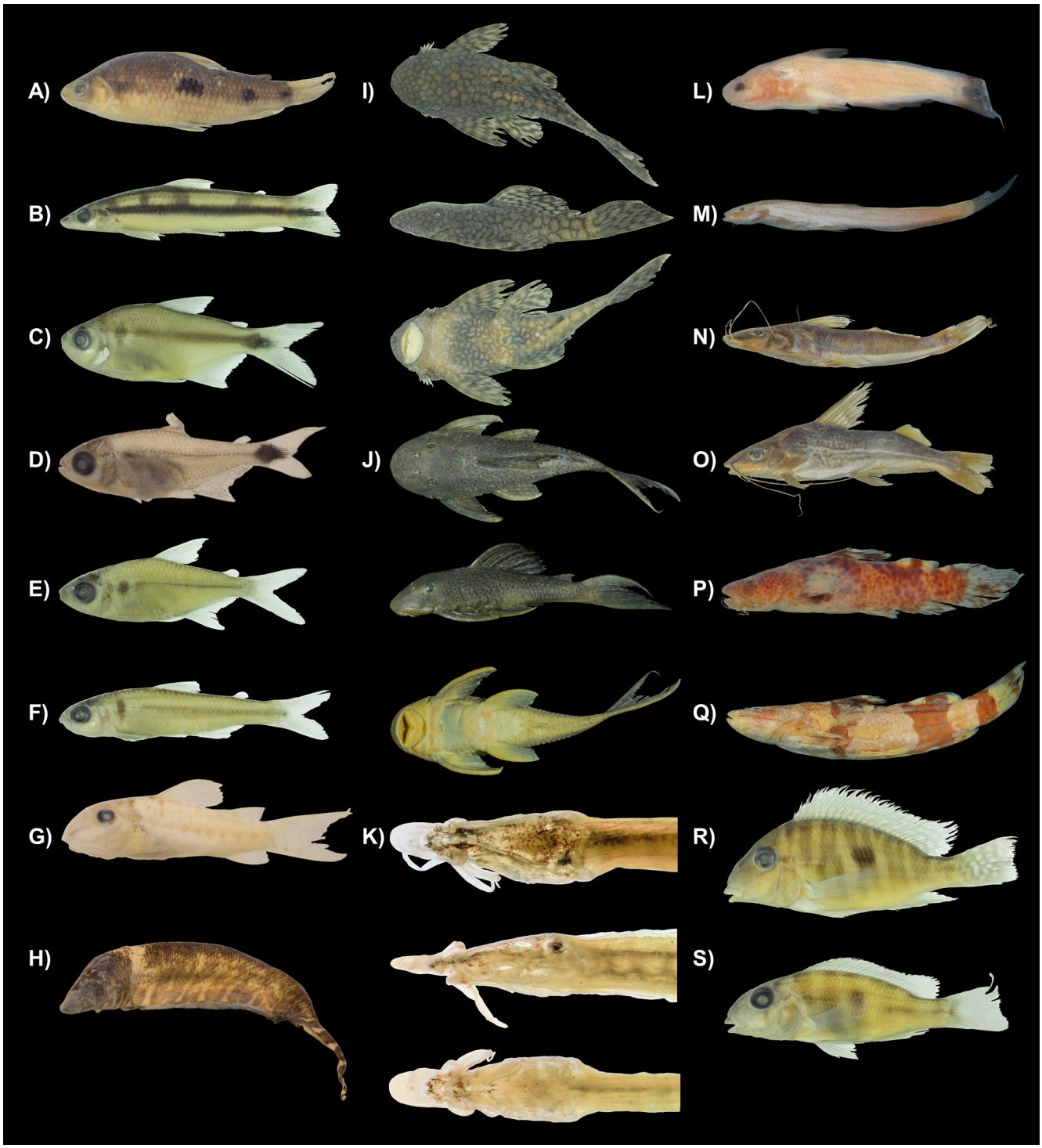


Figure 3. Putatively new species of Jamari River basin. A) *Leporinus* sp., NUP19345, 154.0 mm SL; B) *Apareiodon* sp., NUP9455, 65.4 mm SL; C) *Astyanax* sp., NUP19560, 50.0 mm SL; D) *Hyphessobrycon* sp., NUP21269, 14.0 mm SL; E) *Moenkhausia* sp., NUP19720, 24.0 mm SL; F) *Creagrutus* sp. 1, NUP19579, 33.0 mm SL; G) *Corydoras* sp., NUP21275, 19.0 mm SL; H) *Gymnotus* sp., NUP21273, 160.0 mm SL; I) *Ancistrus* sp. 1, NUP19337, 60.0 mm SL; J) *Hypostomus* sp., NUP19587, 107.0 mm SL; K) *Typhlobelus* sp., NUP20722, 28.0 mm SL; L) *Cetopsidium* sp., INPA6503, 22.3 mm SL; M) *Phenacorhamdia* sp., INPA8003 55.0 mm SL; N) *Megalonema* sp., NUP19372, 161.0 mm SL; O) sp., NUP19486, 152.0 mm SL; P) *Batrochoglanis* sp. "aff. B. villosus", INPA9518, 44.2 mm SL; Q) *Rhyachoglanis* sp., INPA9517, 58.5 mm SL; R) *Geophagus* sp. 1, NUP19504, 89.8 mm SL; S) *Geophagus* sp. 2, NUP19507, 29.6 mm SL.

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Author contributions

Rianne Caroline de Oliveira: Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Gabriel de Carvalho Deprá: Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Cláudio Henrique Zawadzki: Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

João Carlos Barbosa da Silva: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Weferson Júnio da Graça: Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

The specimens were collected with authorizations 01/2015, 02/2015 and 03/2015 sent by the Secretaria de Estado do Desenvolvimento Ambiental (SEDAM) provided to João Carlos Barbosa da Silva from Biologic Consultoria Ambiental.

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Inventory

Stream fish from recently deforested basins in the Meridional Amazon, Mato Grosso, Brazil

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Abstract: The replacement of tropical forests to production systems is one of the leading causes of riverine ecosystem alterations. However, current assemblages' composition may also result from the time since these transformations have begun. Therefore, the knowledge of diversified historical scenarios can facilitate the accomplishment of actions that involve the aquatic environments recovery. In this study, an inventory of stream fish was carried out in basins whose deforestation was intensified in the last 20 years, to compose a baseline for ecological and taxonomic studies. The habitat, physical and chemical variables, and the fish assemblages from 60 streams in the northwest region of the state of Mato Grosso, in the Aripuanã and Juruena river basins, were sampled with standardized procedures. For a total of 130 species, a numerical predominance of small-sized Characidae and great rarity were registered, with 50 species represented by less than ten individuals and 19 singletons. Approximately 15% of the sampled taxa were identified only at the generic level, and for several taxa, more detailed taxonomic and molecular studies are required in order to achieve satisfactory identifications. None threatened species were so far reported. On the other hand, two specimens of non-native species were sampled. Although habitat quality is higher in forested streams, no differences in the species richness were registered when compared to the pasture with riparian forest streams or to more deforested streams. However, abundance was greater in these last two streams groups as a result of small-sized characins dominance.
Keywords: *inventory, neotropical ichthyofauna, deforestation, baseline, Characidae.*

Peixes de riachos de bacias recentemente desmatadas na Amazônia Meridional, Mato Grosso, Brasil

Resumo: A substituição de florestas tropicais por sistemas de produção representa uma das principais fontes de alteração nos ecossistemas de riachos. Contudo, a composição atual das assembleias também depende do tempo decorrente desde o início dessas transformações e, desta forma, o conhecimento de cenários históricos variados pode facilitar a realização de ações que envolvam a recuperação de ambientes aquáticos. Neste estudo, foi realizado o inventário dos peixes de riachos em bacias cujo desmatamento foi intensificado nos últimos 20 anos, para compor uma linha de base que possa ser usada em estudos ecológicos e taxonômicos. Foram amostradas as variáveis do hábitat, físicas e químicas e os peixes de 60 riachos da região noroeste do estado de Mato Grosso, nas bacias dos rios Aripuanã e Juruena. No total, 130 espécies foram registradas, com predominância numérica de pequenos caracídeos e grande número de espécies raras, sendo 50 espécies representadas por menos que dez indivíduos e

19 por apenas um indivíduo. Aproximadamente 15% dos táxons amostrados foram identificados somente no nível genérico e vários precisam de estudos taxonômicos e moleculares mais detalhados para alcançar identificações satisfatórias. As espécies não-nativas foram representadas por dois exemplares e nenhuma espécie sabidamente ameaçada foi registrada. Embora a qualidade do hábitat seja superior nos riachos florestados, não houve diferenças na riqueza das assembleias quando comparada aos riachos de microbacias de pastagem, porém com faixa ripária florestada, ou com maior desmatamento. Contudo, a abundância foi maior nesses dois grupos de riachos, como resultado da dominância de caracídeos de pequeno porte.

Palavras-chave: *inventário, ictiofauna neotropical, desmatamento, linha de base, Characidae.*

Introduction

The land use in the watershed can alter environmental characteristics that influence the populations' performance (Jonsson et al. 2011) and the fish assemblages' composition (Roth et al. 1996, Stauffer et al. 2000). Nearby to the water bodies, the riparian buffer integrity shows great influence on the aquatic environment and its components (see Pusey & Arthington 2003, Quinn 2005, Teels et al. 2006, Lorion & Kennedy 2009, Luke et al. 2019 and authors therein). Although several studies explore watershed and riparian scales, little is known about how the history of land use changes affects current communities and ecosystems (but see Maloney & Weller 2011, Aguirre-Gutierrez et al. 2015, Östlund et al. 2015). Harding et al. (1998) were the first ones to highlight the importance of land use history on the current fish fauna composition in North American streams. Indeed, historical data may show that two distinct areas can present similar land coverage, but with different trajectories through time (Ferraz et al. 2009); that is, deforestation may have occurred at the beginning of human occupation or later, or have been abrupt or gradual. These differences may explain to a great extent the composition and diversity patterns of current assemblages (Maloney & Weller 2011, Brejão et al. 2018).

One way to investigate community modifications over time is by obtaining baselines in areas that were modified at different times along history. Recently, the Southern Amazon, in the state of Mato Grosso, has been a target of an intense deforestation (Valdiones et al. 2018). Despite this, in this region there are a significant number of protected areas as indigenous lands, sustainable use units, and legal reserves. This landscape configuration represents a very diversified environmental gradient, allowing us to understand how deforestation under different historical land use changes affects fish fauna. Thus, our aim was to carry out an inventory of stream fish assemblages in watersheds whose deforestation has been intensified for the last 20 years to compose a baseline that can be used in future ecological and taxonomic studies, as well as to subsidize basin management and restoration actions.

Materials and Methods

1. Study area and site selection

The study area was located in the northwest portion of the Mato Grosso State, in the Cotriguaçu, Juína, and Aripuanã municipalities (Figure 1, Table 1). The Mato Grosso State has an area of 903,357 km^2 and it is the third largest state of Brazil, including portions of the Amazon, Cerrado, and Pantanal biomes (Picoli et al. 2018). The Amazonian biome in Mato Grosso includes the Amazon Forest and the Seasonal Forest, which together occupy about 53% of the territory of the state (Picoli et al. 2018). This study was developed in areas of Amazon Forest, in the middle portion of the Aripuanã and Juruena (left bank) rivers, which are included in the *Madeira Brazilian Shield* and *Tapajós-Juruena* ecoregions (Abell et al. 2008, WWF & TNC 2015). These drainages were chosen due to the recent deforestation, with higher intensity occurring after 2000 (Figure 1) and because the primary land use conversion was from forest to pasture (Figure 2).

Using Geographic Information Systems (GIS) tools, 30 independent watersheds were selected in each river basin, which resulted in 60 stream reaches to be sampled. Samples were carried out at the beginning of the dry season (between May and July) in 2017 and 2018 to avoid possible changes related to seasonality. Stream reaches were from first to third order (according to Strahler 1957) and 80 m long. Three scenarios were sampled (Figure 3, Table 1): 16 streams with more than 50% native forests covering the watershed and the riparian buffer (FOR); 15 streams with pasture predominance in the watershed, but with more than 50% the riparian buffer covered by forests (PAS+RIP); and 29 streams with less than 50% of forests in the watershed and in the riparian buffer (DEF).

2. Data collection

Before the fish sampling, the stream habitat was quantified with a standardized protocol that evaluates the physical structure in the instream and riparian area, by calculating the Physical Habitat Index (PHI) based on Barbour et al. (1999), Kazyak (2001) and modified by Casatti et al. (2006). PHI varies from 0 to 180: from 0 to 45, conditions indicate strong deviation from the minimally disturbed references; from 46 to 90, there is significant deviation from the references; from 91 to 135, conditions indicate that some aspects of physical habitat may not resemble those found in references; from 136 to 180, streams are comparable to minimally disturbed references (Roth et al. 1996).

Fish sampling was conducted under ICMBio ("Instituto Chico Mendes de Conservação da Biodiversidade") permits (8894-1/2017, 11435-1/2018). Upstream and downstream reaches were blocked using block nets (5 mm mesh) and, during one hour, two collectors sampled fish with a seine (1.5 × 2 m, 2 mm mesh) and a dip net (0.5 × 0.8 m, 2 mm mesh). Soon after the collection, fishes were euthanized in clove oil solution (Lucena et al. 2013). Fish identification was conducted by specialists, and all specimens are deposited in the Fish Collection of the Zoology and Botany Department (DZSJRP, vouchers 21469-22629), in the São Paulo State University "Júlio de Mesquita Filho", São José do Rio Preto, São Paulo State, Brazil.

3. Data analysis

The inventory representativeness was evaluated by the Coleman rarefaction (Colwell et al. 2004), which was compared to other two non-parametric richness estimators, the ICE (Incidence Coverage Estimator,

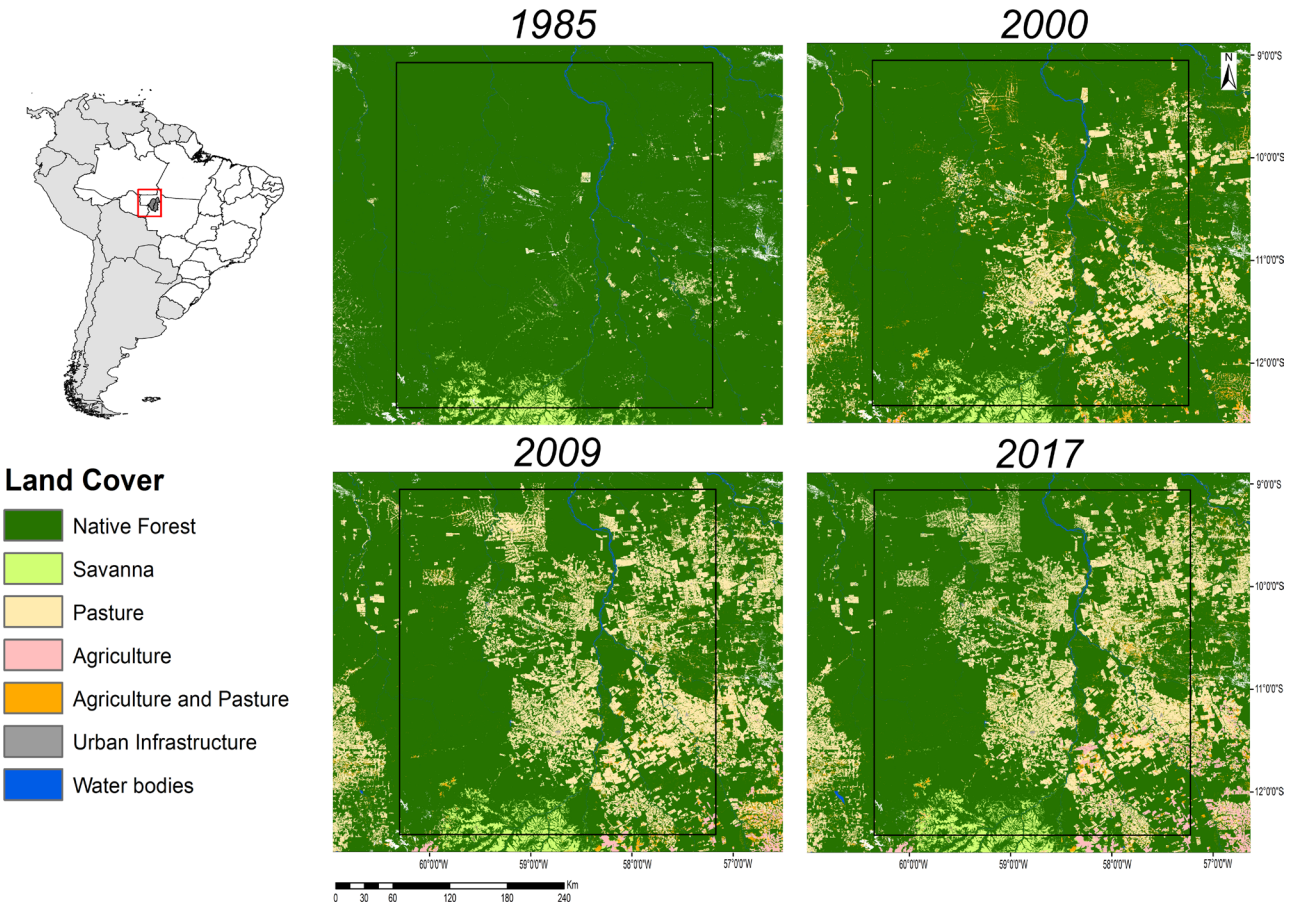


Figure 1. Land cover in the northwest Mato Grosso State from 1985 to 2017 (MAPBIOMAS, 2019). The red square in the country map indicates the studied region.

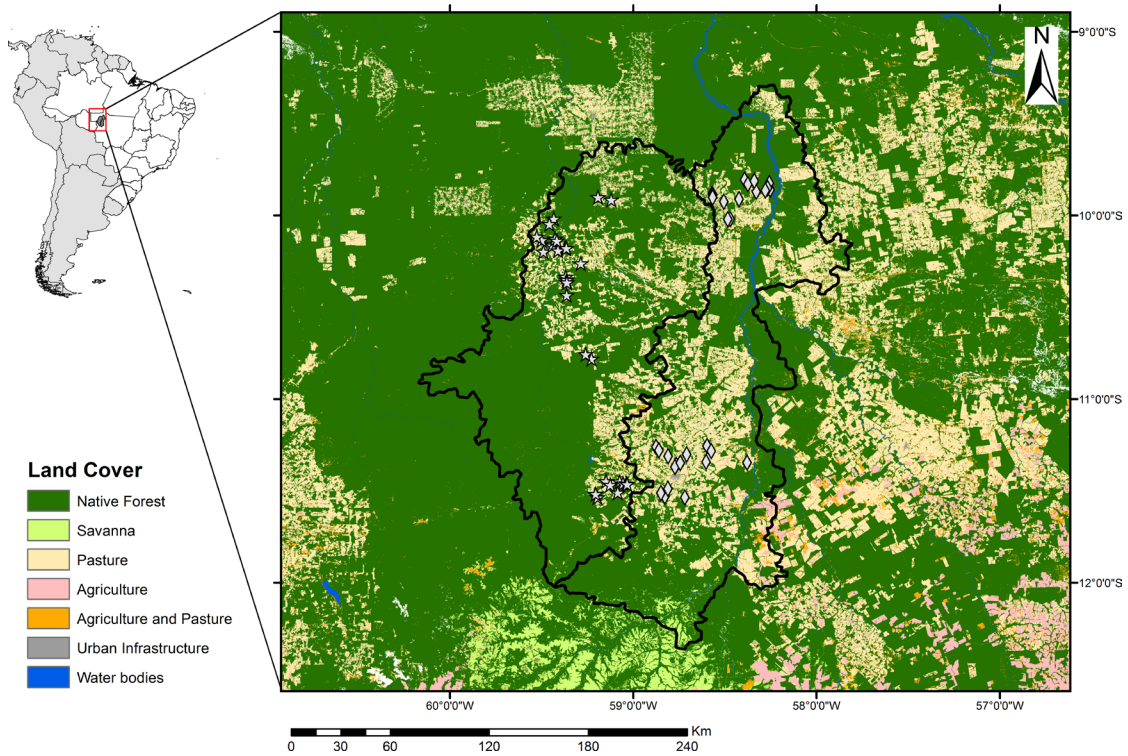


Figure 2. Location of the Aripuanã (stars) and Juruena (diamonds) sampled reaches in the Mato Grosso State, Brazil. The red square in the country map indicates the studied region. Land cover was based on MAPBIOMAS (2019).

Table 1. Geographical coordinates (X, Y, UTM zone 21L, datum WGS84) and municipalities of the 60 streams sampled in the Aripuanã (A) and Juruena (J) river basins, Mato Grosso State, Brazil, according to their groups (FOR, forested; PAS+RIP, pasture with riparian forests, DEF, deforested).

ID	X	Y	Municipalities	Groups
A7	233378	8891583	Aripuanã	FOR
A8	230757	8888490	Aripuanã	FOR
A9	259716	8904825	Aripuanã	FOR
A10	267681	8903390	Aripuanã	FOR
A13	226347	8878700	Aripuanã	FOR
A17	241349	8854972	Aripuanã	FOR
A19	241488	8845724	Aripuanã	FOR
A20	256488	8807420	Aripuanã	FOR
A21	253042	8810164	Aripuanã	FOR
A26	272791	8726933	Juína	FOR
A28	260704	8723926	Juína	FOR
J18	0362236	8913869	Cotriguaçu	FOR
J21	0361200	8910845	Cotriguaçu	FOR
J22	0359823	8909364	Cotriguaçu	FOR
J26	0347332	8915782	Cotriguaçu	FOR
J27	0349420	8913214	Cotriguaçu	FOR
A1	227350	8871821	Aripuanã	PAS+RIP
A3	232603	8875583	Aripuanã	PAS+RIP
A5	234184	8879533	Aripuanã	PAS+RIP
A11	235275	8878407	Aripuanã	PAS+RIP
A12	241074	8874028	Aripuanã	PAS+RIP
A14	223304	8880776	Aripuanã	PAS+RIP
A15	249723	8864879	Aripuanã	PAS+RIP
A25	278336	8731978	Juína	PAS+RIP
A29	259643	8725961	Juína	PAS+RIP
A30	268210	8731484	Juína	PAS+RIP
J4	0312725	8724285	Juína	PAS+RIP
J19	0335065	8902505	Cotriguaçu	PAS+RIP
J25	0328326	8905007	Cotriguaçu	PAS+RIP
J28	0353157	8915101	Cotriguaçu	PAS+RIP
J29	0338827	8892060	Cotriguaçu	PAS+RIP
A2	233183	8876438	Aripuanã	DEF
A4	240342	8873978	Aripuanã	DEF
A6	236024	8872545	Aripuanã	DEF
A16	240805	8856783	Aripuanã	DEF
A18	241512	8853320	Aripuanã	DEF
A22	273929	8733554	Juína	DEF
A23	275946	8732520	Juína	DEF
A24	277753	8732329	Juína	DEF
A27	265777	8733720	Juína	DEF
J1	0300866	8724744	Juína	DEF
J2	0298447	8726758	Juína	DEF
J3	0302592	8729477	Juína	DEF
J5	0307532	8743830	Juína	DEF
J6	0306712	8742555	Juína	DEF
J7	0313600	8750169	Juína	DEF
J8	0325761	8755312	Juína	DEF
J9	0328313	8752288	Juína	DEF
J10	0325269	8745762	Juína	DEF
J11	0349605	8745429	Juína	DEF
J12	0295350	8754632	Juína	DEF
J13	0297087	8752553	Juína	DEF
J14	0302552	8749054	Juína	DEF
J15	0309902	8745005	Juína	DEF
J16	0362678	8909927	Cotriguaçu	DEF
J17	0354388	8908701	Cotriguaçu	DEF
J20	0344172	8904108	Cotriguaçu	DEF
J23	0328127	8907223	Cotriguaçu	DEF
J24	0328417	8906436	Cotriguaçu	DEF
J30	0337440	8891940	Cotriguaçu	DEF

Lee & Chao 1994) and the ACE (Abundance Coverage Estimator, Lee & Chao 1994), using the software EstimateS 9.10 (Colwell 2013). Species with only one specimen were considered singletons and those that occurred only in one stream reach were considered as uniques (Colwell 2013). The Kruskal-Wallis test was used to compare PHI, species richness, and abundance between stream groups (significance level $\alpha = 0.05$), since the normal distribution was rejected according to the previously Shapiro-Wilk test applied to these variables. The Dunn's post hoc test was carried out after obtaining a significant result in a Kruskal-Wallis test. These analyses were conducted in the PAST 3.25 software (Hammer et al. 2001). Whittaker plots (relative abundance in the y-axis and abundance rank in the x-axis) were constructed to describe the species abundance patterns in each stream group (Matthews & Whittaker 2015).

Results

A total of 18,504 specimens belonging to 130 species, 73 genera, 27 families, and six orders were collected (Table 2). Seven species of small characins (*Knodus* sp. 1, *Hemigrammus* cf. *rodwayi*, *Jupiaba acanthogaster*, *Moenkhausia levidorsa*, *Inpaichthys kerri*, *Moenkhausia oligolepis*, and *Hyphessobrycon* aff. *agulha*) accounted for more than 50% of the total abundance in the streams from Aripuanã and Juruena river basins (Table 2, Figure 4). On the other hand, 50 species were represented by less than ten individuals and 19 were singletons. Regarding occurrence, eight species were present in at least 50% of the sites (*Knodus* sp. 1, *Characidium* aff. *zebra*, *Moenkhausia oligolepis*, *Rineloricaria* sp., *Ituglanis* cf. *amazonicus*, *Aequidens gerciliae*, *Hoplias* cf. *malabaricus*, and *Eigenmannia macrops*, Figure 4) whereas 39 species were uniques (Table 2). Two specimens of the non-native



Figure 3. General view of a forested stream (A), a stream in a pasture microbasin, but with forested riparian buffer (B), and a deforested stream (C). In order, streams are J18, J19, and J15. Photos: María Angélica Pérez-Mayorga.

Oreochromis niloticus and no endangered or threatened species were recorded. ACE and ICE indicated that the set of species in this area could reach 147 and 171 species, respectively (Figure 5).

Forested streams showed the highest physical habitat quality (Chi-square = 14.14, $P = 0.0008$, Figure 6). Although the differences in terms of the physical habitat quality, species richness did not differ significantly among groups (Chi-square = 4.31, $P = 0.1145$, Figure 7A). However, species abundance was significantly lower in forested streams when compared to the others (Chi-square = 15.76, $P = 0.0004$, Figure 7B, Figure 8).

Discussion

In terms of orders or families' composition, the present inventory is in agreement with several studies conducted in the Neotropical streams since Lowe-McConnell (1999), where Characiformes and Siluriformes species represent the classical fish composition (cf. also Reis et al. 2003, Barros et al. 2011, Buckup et al. 2011, Queiroz et al. 2013, Ohara et al. 2017). Indeed, any deviation from Characiformes and Siluriformes prevalence can be expected in degraded conditions, where non-native opportunist species of the Cichliformes and Cyprinodontiformes may prevail (Ferreira et al. 2018, Ruaro et al. 2018). Since Aripuanã and Juruena river basins are under relatively recent occupation, this is not the case until now. Whereas the major families and orders are well known, the same is not true at the species level. Almost 15% of the sampled taxa were identified only to genus level, and several of them require more detailed taxonomic and molecular studies (e.g., *Astyanax* aff. *bimaculatus*, *Characidium* aff. *zebra*, *Rhamdia* aff. *quelen*). *Ancistrus* and *Hypostomus* members deserve special attention because of their great diversity inter and intrabasins, probably with undescribed species. *Hemiodus bimaculatus* was recently described by Nogueira et al. (2019) and two other putative new species of *Astyanax* and *Hyphessobrycon* are being analyzed by our team (Carvalho et al. 2019).

One of the first studies in this region was developed by Soares (1979), in one stream from the Aripuanã river basin. Of 20 fish species recorded by her, seven were unidentified at species level. This clearly demonstrates that, even 40 years later, the taxonomic resolution of Amazonian fishes still demands for more detailed studies and the overall fish diversity of this biome is far from being properly known.

Table 2. Overall abundance and frequency of occurrence (FO, in %) of each fish species sampled in the stream reaches of the Aripuanã (A) and Juruena (J) river basins. Relative abundance (in %) of each species is presented according to the stream condition (FOR, forested; PAS+RIP, pasture with riparian forests, DEF, deforested). Classification follows Frick et al. (2019). Asterisk indicate non-native species.

TAXON	A	J	FO	FOR	PAS+RIP	DEF
CHARACIFORMES						
Parodontidae						
Parodon cf. *buckleyi* Boulenger, 1887	0	3	3	0	0	0.03
Curimatidae						
Cyphocharax gangamon Vari, 1992	0	49	20	0.66	0.25	0.19
Cyphocharax notatus (Steindachner, 1908)	1	0	2	0.00	0.02	0.00
Cyphocharax spiluropsis (Eigenmann & Eigenmann, 1889)	47	0	10	0.40	0.31	0.20
Steindachnerina fasciata (Vari & Géry, 1985)	8	6	15			
Prochilodontidae						
Prochilodus nigricans Spix & Agassiz, 1829	27	1	8	0.04	0.47	0.01
Anostomidae						
Anostomus ternetzi Fernández-Yépez, 1949	1	0	2	0	0.02	0
Leporinus cf. *britskii* Feitosa, Santos & Birindelli, 2011	0	7	3	0	0	0.07
Leporinus friderici (Bloch, 1794)	8	31	23	0.09	0.07	0.31
Leporinus gomesi Garavello & Santos, 1981	25	0	13	0.31	0.13	0.10
Leporinus reticulatus Britski & Garavello, 1993	0	4	2	0	0.07	0
Leporinus cf. *santosi* Britski & Birindelli, 2013	0	48	15	0	0.24	0.33
Crenuchidae						
Elachocharax pulcher Myers, 1927	0	12	2	0	0.22	0
Characidium aff. *zebra* Eigenmann, 1909	122	180	77	0.79	2.16	1.54
Characidium sp.	0	2	2	0	0.04	0
Melanocharacidium cf. *auroradiatum* Costa & Vicente, 1994	0	8	2	0	0.15	0
Hemiodontidae						
Hemiodus bimaculatus Nogueira, Langeani & Netto-Ferreira, 2019	0	3	2	0	0.05	0
Hemiodus sterni (Géry, 1964)	0	1	2	0	0	0.01
Bryconidae						
Brycon falcatus Müller & Troschel, 1844	0	1	2	0	0	0.01
Iguanodectidae						
Bryconops cf. *caudomaculatus* (Günther, 1864)	260	23	48	2.85	2.30	0.85
Bryconops cf. *giacopinii* (Fernández-Yépez, 1950)	0	40	15	0.26	0.02	0.31
Characidae						
Aphyocharax sp.	1	0	2	0	0.02	0
Astyanax cf. *anterior* Eigenmann, 1908	256	0	12	2.81	1.65	0.94
Astyanax aff. *bimaculatus* (Linnaeus, 1758)	17	44	23	0.09	0.22	0.44
Astyanax cf. *maximus* (Steindachner, 1876)	215	22	32	2.90	0.67	1.25
Astyanax sp.	81	49	33	1.27	0.33	0.77
Creagrutus ignotus Vari & Harold, 2001	0	228	28	0.09	1.36	1.41
Creagrutus petilus Vari & Harold, 2001	30	0	3	0	0.54	0
Hemigrammus cf. *geisleri* Zarske & Géry, 2007	1	0	2	0	0.02	0
Hemigrammus cf. *lunatus* Durbin, 1918	87	0	2	0	1.58	0
Hemigrammus microstomus Durbin, 1918	0	1	2			
Hemigrammus aff. *ocellifer* (Steindachner, 1882)	0	1	2	0.04	0	0
Hemigrammus cf. *parana* Marinho, Carvalho, Langeani & Tatsumi, 2008	0	31	5	0.70	0	0.14

 http://dx.doi.org/10.1590/1676-0611-BN-2019-0744

Continuation Table 2.

TAXON	A	J	FO	FOR	PAS+RIP	DEF
Hemigrammus cf. *rodwayi* Durbin, 1909	0	2112	35	4.22	15.82	10.68
Hemigrammus silimoni Britski & Lima, 2008	217	0	12	0.66	3.36	0.16
Hemigrammus sp.	89	0	3	0	1.61	0
Hyphessobrycon aff. *agulha* Fowler, 1913	241	202	43	7.99	2.85	0.97
Hyphessobrycon peugeoti Ingenito, Lima & Buckup, 2013	0	12	3	0.26	0	0.06
Hyphessobrycon vilmae Géry, 1966	179	4	23	1.45	0.96	0.91
Hyphessobrycon sp.	36	0	25	0	0.65	0
Inpaichthys kerri Géry & Junk, 1977	495	0	18	2.59	6.13	0.91
Jupiaba acanthogaster (Eigenmann, 1911)	0	1310	37	0.26	7.53	8.30
Jupiaba anteroides (Géry, 1965)	21	1	8	0.70	0.11	0
Jupiaba cf. *apenima* Zanata, 1997	110	0	13	4.22	0.07	0.09
Jupiaba meunieri (Géry, Planquette & Le Bail, 1996)	0	2	2	0	0	0
Jupiaba pirana Zanata, 1997	0	10	5	0	0.11	0.04
Knodus sp. 1	820	4380	95	21.83	12.43	37.50
Knodus sp. 2	2	0	2	0	0.04	0
Moenkhausia cf. *collettii* (Steindachner, 1882)	38	30	13	0.31	1.00	0.06
Moenkhausia cotinho Eigenmann, 1908	10	0	5	0.04	0.16	0
Moenkhausia gr. *lepidura* (Kner, 1858)	0	31	10	0.04	0.09	0.23
Moenkhausia levidorsa Benine, 2002	157	446	35	0.88	1.18	4.83
Moenkhausia mikia Marinho & Langeani, 2010	31	0	5	0.70	0.11	0.08
Moenkhausia oligolepis (Günther, 1864)	352	136	75	6.46	3.12	1.58
Moenkhausia pankilopteryx Bertaco & Lucinda, 2006	7	0	2	0.31	0	0
Moenkhausia cf. *pirauba* Zanata, Birindelli & Moreira, 2010	0	202	33	0.26	1.43	1.09
Phenacogaster retropinnus Lucena & Malabarba, 2010	122	92	23	0.13	2.61	0.63
Poptella compressa (Günther, 1864)	83	0	10	0.88	1.14	0
Serrapinnus cf. *microdon* (Eigenmann, 1915)	23	108	10	0	0	1.22
Serrapinnus cf. *micropterus* (Eigenmann, 1907)	0	483	25	1.45	2.89	2.72
Serrapinnus aff. *notomelas* (Eigenmann, 1915)	2	0	3	0	0.02	0.01
Tetragonopterus argenteus Cuvier, 1816	1	0	2	0	0.02	0
Tetragonopterus chalceus Spix & Agassiz, 1829	0	2	3	0	0.02	0.01
Thayeria cf. *obliqua* Eigenmann, 1908	9	0	2	0.	0.16	0
Serrasalmidae						
Myloplus asterias (Müller & Troschel, 1844)	0	14	12	0	0.04	0.11
Utiaritichthys longidorsalis Jégu, Tito de Morais & Santos, 1992	11	0	7	0.31	0.05	0.01
Acestrorhynchidae						
Acestrorhynchus falcatus (Bloch, 1794)	0	4	7	0.09	0	0.02
Erythrinidae						
Erythrinus erythrinus (Bloch & Schneider, 1801)	14	7	20	0.31	0.07	0.09
Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)	1	1	3	0	0	0.02
Hoplias cf. *malabaricus* (Bloch, 1794)	26	45	53	0.35	0.29	0.44
Ctenoluciidae						
Boulengerella maculata (Valenciennes, 1849)	1	0	2	0	0.02	0
SILURIFORMES						
Cetopsidae						
Cetopsis sandrae Vari, Ferraris & de Pinna, 2005	0	7	8	0.22	0	0.02

Continuation Table 2.

TAXON	A	J	FO	FOR	PAS+RIP	DEF
Trichomycteridae						
Ituglanis cf. *amazonicus* (Steindachner, 1882)	107	60	55	0.70	0.64	1.08
Ituglanis sp.	0	1	2	0.04	0	0
Stegophilus panzeri (Ahl, 1931)	0	1	2	0	0.02	0
Callichthyidae						
Callichthys callichthys (Linnaeus, 1758)	3	2	8	0.04	0.02	0.03
Corydoras cf. *bondi* Gosline, 1940	1	0	2	0.04	0.00	0.00
Corydoras cf. *polystictus* Regan, 1912	0	9	7	0.00	0.05	0.06
Corydoras sp.	15	65	28	0.66	0.34	0.43
Megalechis thoracata (Valenciennes, 1840)	0	7	2	0	0	0.07
Loricariidae						
Ancistrus sp. 1	5	85	30	0.61	0.34	0.53
Ancistrus sp. 2	2	8	12	0.04	0.05	0.06
Ancistrus sp. 3	197	226	45	4.83	1.42	2.19
Ancistrus sp. 4	137	0	17	2.15	1.23	0.19
Ancistrus sp. 5	73	0	3	0.00	1.29	0.02
Curculionichthys itaim Roxo, Dias, Silva & Oliveira, 2017	0	710	47	3.16	3.16	4.33
Farlowella smithi Fowler, 1913	13	7	8	0.53	0.15	0
Hypostomus sp. 1	69	0	25	0.53	0.44	0.31
Hypostomus sp. 2	10	0	2	0.00	0.18	0.00
Hypostomus sp. 3	2	0	2	0.00	0.04	0.00
Hypostomus sp. 4	0	180	37	0.48	0.09	1.53
Hypostomus sp. 5	0	2	3	0.00	0.00	0.02
Hypostomus sp. 6	0	1	2	0.00	0.00	0.01
Lasiancistrus schomburgkii (Günther, 1864)	40	0	2	0	0.73	0
Loricaria sp.	4	0	7	0.09	0.02	0.01
Parotocinclus aripuanensis Garavello, 1988	21	0	3	0	0.38	0
Rineloricaria lanceolata (Günther, 1868)	8	0	8	0.04	0.11	0.01
Rineloricaria sp.	351	192	72	5.05	4.12	1.88
Spatuloricaria evansii (Boulenger, 1892)	1	0	2			
Pseudopimelodidae						
Microglanis poecilus Eigenmann, 1912	0	11	7	0	0.04	0.08
Heptapteridae						
Cetopsorhamdia sp. 1	125	35	43	2.99	0.67	0.51
Imparfinis sp. 1	10	0	12	0.18	0.04	0.04
Imparfinis sp. 2	15	0	10	0.40	0.11	0.00
Imparfinis sp. 3	0	5	5	0.00	0.05	0.02
Mastiglanis cf. *asopos* Bockmann, 1994	3	0	2	0	0.05	0
Myoglanis sp.	20	3	18	0.31	0.09	0.10
Imparfinis stictonotus (Fowler, 1940)	0	310	17	1.49	2.00	1.55
Phenacorhamdia sp.	5	70	43	0.26	0.44	0.42
Pimelodella cf. *howesi* Fowler, 1940	3	98	27	0.75	0.51	0.52
Rhamdia aff. *quelen* (Quoy & Gaimard, 1824)	22	7	25	0.26	0.16	0.13
Auchenipteridae						
Parauchenipterus porosus (Eigenmann & Eigenmann, 1888)	26	0	18	0.31	0.20	0.07

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Continuation Table 2.

TAXON	A	J	FO	FOR	PAS+RIP	DEF
Tatia aulopygia (Kner, 1858)	16	1	10	0.44	0.09	0.02
GYMNOTIFORMES						
Gymnotidae						
Gymnotus cf. *carapo* Linnaeus, 1758	16	17	32	0.35	0.11	0.18
Sternopygidae						
Eigenmannia macrops (Boulenger, 1897)	32	105	52	0.79	0.27	0.97
Sternopygus macrurus (Bloch & Schneider, 1801)	3	1	7	0	0.07	0
Rhamphichthyidae						
Gymnorhamphichthys rondoni (Miranda Ribeiro, 1920)	0	1	2	0	0.02	0
Hypopomidae						
Brachyhypopomus cf. *sullivani* Crampton, de Santana, Waddell & Lovejoy, 2017	1	11	13	0.09	0.05	0.07
CYPRINODONTIFORMES						
Poeciliidae						
Pamphorichthys cf. *scalpridens* (Garman, 1895)	0	3	2	0	0	0.03
SYNBRANCHIFORMES						
Synbranchidae						
Synbranchus cf. *madeirae* Rosen & Rumney, 1972	6	0	8	0.09	0.05	0.01
CICHLIFORMES						
Cichlidae						
Aequidens gerciliae Kullander, 1995	47	63	53	1.14	0.24	0.66
Caquetaia spectabilis Steindachner, 1875	5	0	2	0	0.09	0
Cichla mirianae Kullander & Ferreira, 2006	0	1	2	0.04	0	0
Crenicichla aff. *acutirostris* Günther, 1862	0	10	12	0.00	0.05	0.07
Crenicichla cf. *hemera* Kullander, 1990	34	0	20	0.53	0.31	0.05
Crenicichla aff. *isbrueckeri* Ploeg, 1991	1	0	2	0.04	0.00	0.00
Crenicichla aff. *semicincta* Steindachner, 1892	0	3	5	0.04	0.02	0.01
Geophagus cf. *altifrons* Heckel, 1840	16	0	2	0	0.29	0
Geophagus mirabilis Deprá, Kullander, Pavanelli & Graça, 2014	1	0	2	0	0.02	0
Heros spurius Heckel, 1840	4	0	2	0	0.07	0
Oreochromis niloticus (Linnaeus, 1758)*	0	2	3	0	0	0.02
TOTAL	**5,755**	**12,749**	**-**	**100**	**100**	**100**

The predominance of small-sized characins is another common pattern observed in Amazonian streams (Barros et al. 2011, Brejão et al. 2013, Casatti et al. 2013, Montag et al. 2018). In general, these species are considered opportunistic regarding their feeding strategies, which show high trophic plasticity, being recognized as generalist feeders (Ferreira et al. 2012, Manna et al. 2012, Barros et al. 2017). Despite being commonly classified as opportunistic, these small characins occupy the habitat by using different strategies (see Ceneviva-Bastos & Casatti 2007, Brejão et al. 2013). There are species with fusiform bodies, forming numerous shoals and more specialized in the capture of items dragged by the current on the water surface, close to the stream bed (e.g., *Knodus* sp. 1) or in the marginal habitats (e.g. *Hemigrammus* cf. *rodwayi*, *Inpaichthys kerri*, *Hyphessobrycon* aff. *agulha*). Other species have relatively higher bodies, forming small groups with different food tactics that forage in different microhabitats (e.g., *Jupiaba acanthogaster*, *Moenkhausia levidorsa*, *Moenkhausia oligolepis*). Therefore, naturalistic studies are encouraged in the Amazonian streams to describe these behavioral differences and give subsidies for more complex ecological approaches.

Considering the overall assemblage, widespread species (those present in at least 50% of the streams) belong to more diversified groups in terms of their biology (see Van Der Sleen & Albert 2018). Among them, there are the nektonic drift-feeding tetras (*Knodus* sp. 1, *Moenkhausia oligolepis*), the bottom-dwelling insectivores known as South American darters (*Characidium* aff. *zebra*) and catfishes (*Ituglanis* cf. *amazonicus*), the bentonic periphytivores armoured catfishes (*Rineloricaria* sp.), the nektobenthic sit-and-wait carnivores trahiras (*Hoplias* cf. *malabaricus*), the riverbank invertivores knifefishes (*Eigenmannia macrops*), and the nektobenthic omnivores cichlids (*Aequidens gerciliae*).

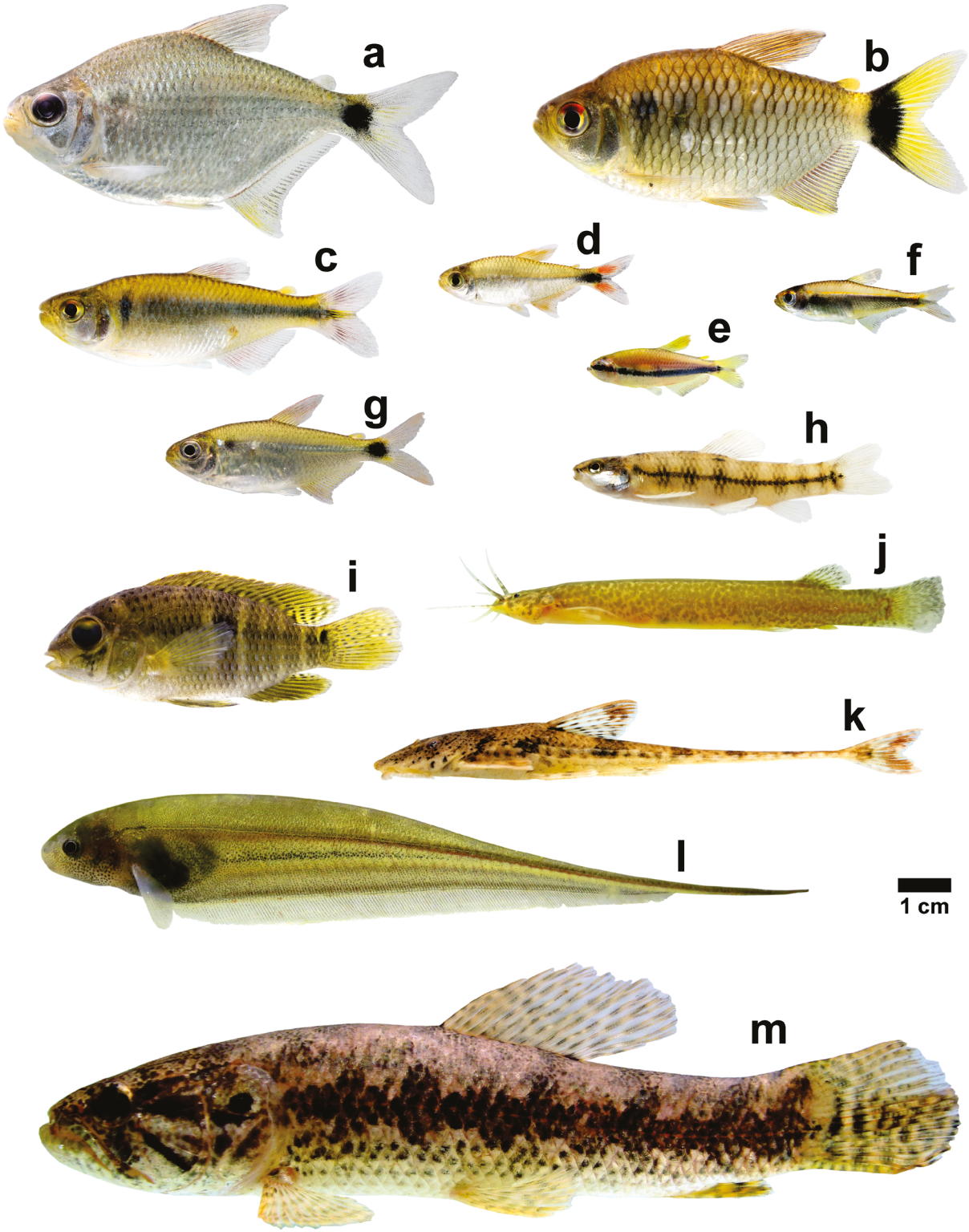


Figure 4. Species that contributed the most for total abundance and occurrence in the *Aripuanã* and *Juruena* river basins. a. *Moenkhausia levidorsa*; b. *Moenkhausia oligolepis*; c. *Knodus* sp. 1; d. *Hemigrammus* cf. *rodwayi*; e. *Inpaichthys kerri*; f. *Hyphessobrycon* aff. *agulha*; g. *Jupiaba acanthogaster*; h. *Characidium* aff. *zebra*; i. *Aequidens gerciliae*; *j*. *Ituglanis* cf. *amazonicus*; *k*. *Rineloricaria* sp.; l. *Eigenmannia macrops*; m. *Hoplias* cf. *malabaricus*. Photos: Angelo Rodrigo Manzotti.

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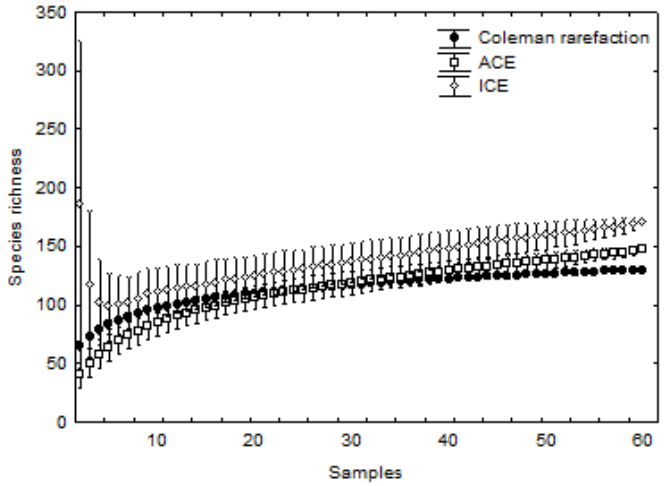


Figure 5. Observed richness (obtained by the Coleman rarefaction curve) and the curves of estimated number of species derived from ACE (Abundance Coverage Estimator) and ICE (Incidence Coverage Estimator) by 999 randomizations against cumulative samples.

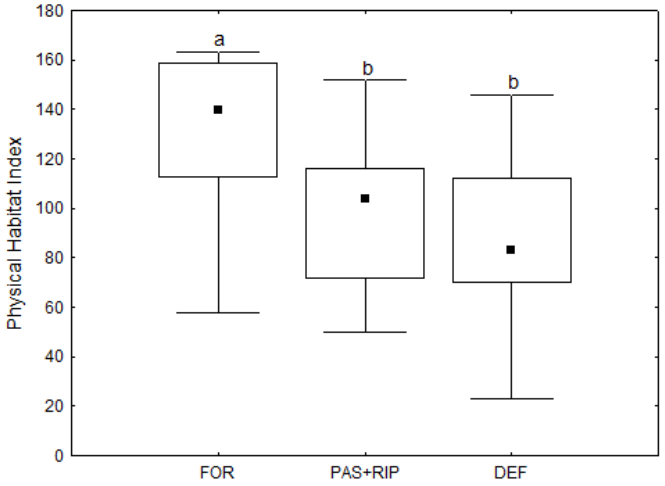


Figure 6. Physical Habitat Index for forested (FOR), pasture with riparian forests (PAS+RIP), and deforested streams (DEF). Squares represent median, boxes represent 25th and 75th percentiles, and lines represent the minimum and maximum values. Different letters indicate significant differences according to the Dunn´s post-hoc test ($P < 0.05$).

Rarity is another pattern observed from these assemblages since 15% of the species were singletons and 30% were uniques. This high occurrence of rare species mirrors another pattern for Amazonian streams, as indicated by several studies (e.g., Barros et al. 2011, Carvalho et al. 2011, Casatti et al. 2013, Ohara & Loeb 2016, Montag et al. 2018). However, the set of rare species was not the same in Aripuanã River and in Juruena River. For instance, *Geophagus mirabilis* were rare in Aripuanã River, whereas *Hemiodus bimaculatus* and *H. sterni* were in Juruena River. According to Fernandes et al. (2013), differences in species composition between regions can be attributed to the success of each species in the colonization of distinct watersheds (local scale) or due to evolutionary events (regional scale). Considering that Aripuanã and river Juruena belong to different ecoregions, it is likely to presume that events at regional scale can be the primary driver for the differences observed in this study. Indeed, a recent study has revealed that the

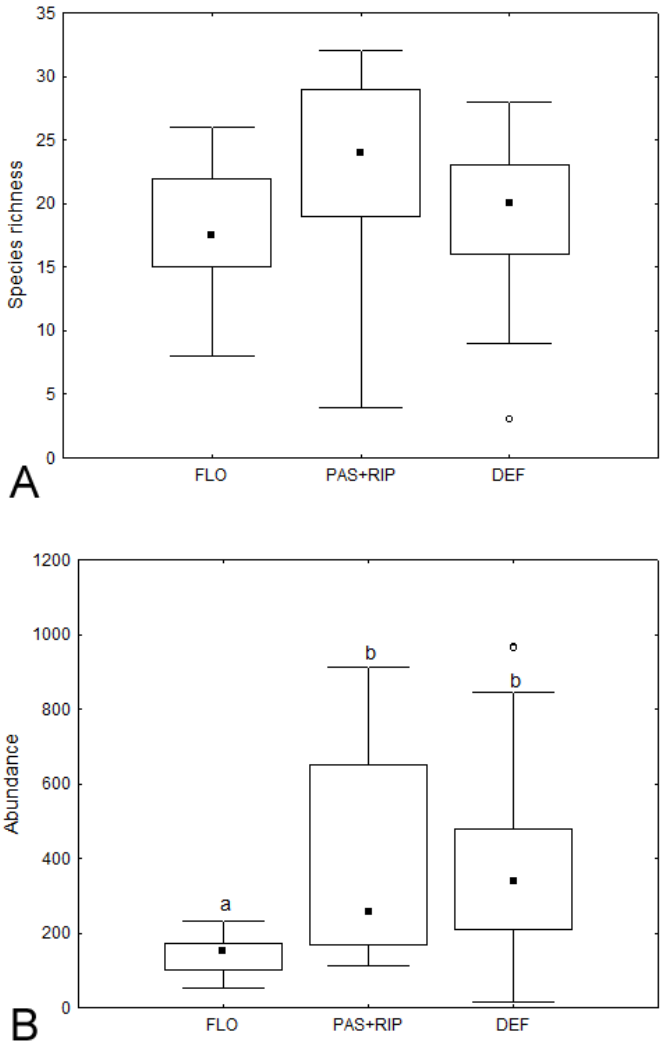


Figure 7. Species richness (A) and abundance (B) for forested (FOR), pasture with riparian forests (PAS+RIP), and deforested streams (DEF). Squares represent median, boxes represent 25th and 75th percentiles, lines represent the minimum and maximum values, and open circle represents outliers. Different letters indicate significant differences according to the Dunn´s post-hoc test ($P < 0.05$).

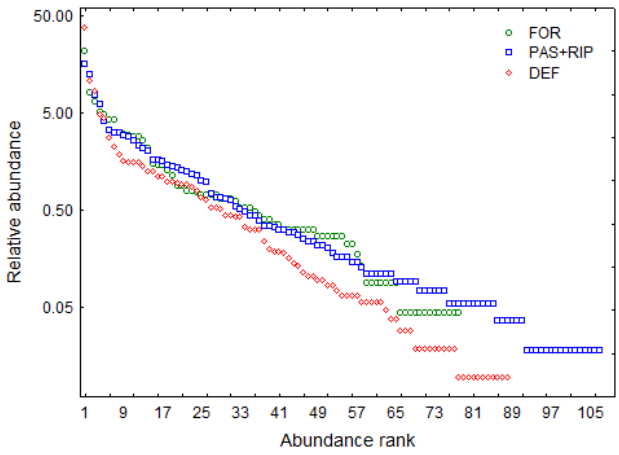


Figure 8. Rank-abundance distribution of fish fauna sampled in the forested (FOR), pasture with riparian forests (PAS+RIP), and deforested streams (DEF). Y axis shows species abundance; X axis ranks each species in order from most to least abundant. Each symbol represents one species.

Dardanelos and Andorinhas waterfall complex is an important barrier for the fish fauna in the Aripuanã river basin (Silva et al. 2019).

Although streams from the forested group presented better physical habitat conditions than streams from the other groups, the species richness was similar among groups, which indicates that changes in the physical habitat have not already reached the threshold to affect fish richness. Based on our knowledge from a neighbor basin (Machado River, in Rondônia state), progression of the impacts over time may deteriorate physical habitat quality above this threshold leading to the replacement of sensitive species by more resistant ones, which affects the fish assemblage structure (Brejão et al. 2018). Unlike the species richness, the fish abundance was greater in the pasture with riparian forest and in the deforested streams than in the forested streams. Fish that contributed the most for the higher abundance in these two groups were the small characins that are, as previously discussed, opportunistic-feeders. In addition, their reproductive strategy can also be viewed as opportunistic, since they are able to grow fast, mature early, and spawn more than once annually (Winemiller 1989, Carvalho et al. 2007). These characteristics let them to successfully proliferate even in degraded conditions (Brejão et al. 2018). Indeed, Whittaker plots revealed that relative abundances are unevenly spread amongst the species from each stream group and, therefore, the abundance variation seems to be an important sentinel to signal early assemblages' responses to disturbance.

The high fish diversity in the Meridional Amazon showed a high proportion of rare, endemic and undescribed species. According to MMA (2019), these areas encompass high biological importance and should be a priority target for Brazilian biodiversity conservation actions. Unfortunately, uncontrolled land use changes are a reality in this region located on the boundaries of the Amazonian deforestation arc, which will continue to advance, notably if no effective measures would be taken to regulate deforestation.

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Author Contribution

Lilian Casatti contributed to the concept and design of the study, data analysis, data interpretation, and manuscript preparation.

Gabriel Lourenço Brejão, Hugmar Pains da Silva, María Angélica Pérez-Mayorga, Angelo Rodrigo Manzotti, Jaquelini Oliveira Zeni, and Bruno Martins Santos Ramires contributed to field data collection, digitalization, analysis, interpretation, and critical revision, adding intellectual content.

Fernando Rogério Carvalho and Francisco Langeani contributed to fish identification, data interpretation and critical revision, adding intellectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

The study conforms to the legal Brazilian requirements regarding animal welfare, including those relating to fish euthanasia.

Data availability

Fish collection is available in the Species Link system (http://splink.cria.org.br/).

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Thematic Review

A conceptual model to understand the drivers of change in tropical wetlands: a comparative assessment in India and Brazil

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Abstract: Tropical wetlands are amongst the most biodiverse ecosystems on Earth and have immense socio-ecological value. However, tropical wetlands are considered exploitable resources and continue to be drained and converted to other "productive" uses. It is therefore urgent to identify and understand the interactions between various drivers of change triggering degradation of such wetlands. In the present study, we systematically reviewed and analyzed the existing literature on wetlands in two tropical countries namely India and Brazil with special reference to inland wetlands, and proposed a conceptual model illustrating the intricate linkages of such wetlands with different drivers of change. We also developed the Nature Futures' Framework to depict the diverse values of inland wetlands contributing to human wellbeing in the two tropical countries. Findings revealed similar drivers of change triggering the degradation of Indian and Brazilian wetlands. These include changes in climate & land use, population growth, poor land governance due to weak policies, besides other anthropogenic activities such as deforestation, and overexploitation of wetland resources. Among these, land-use change such as agriculture intensification and infrastructure development were the major direct drivers; whereas, institutional and governance factors such as the absence of concrete policy measures were the major indirect drivers threatening the inland wetlands in India and Brazil. Results also revealed some contrasting drivers of change such as illegal human settlements, and land grabbing by the brick industry for Indian wetlands; while, gold mining and intensification of bovine systems for Brazilian wetlands. Our paper also provides an insight into the status of wetland conservation in India and Brazil. We recommend the promotion of community-based conservation practices while adopting sustainable livelihood strategies by the local people for the conservation and wise use of inland wetlands in India and Brazil. The arguments raised in the paper have the potential to assist the stakeholders and/or decision-makers towards implementing sustainable management strategies for inland wetlands in the two countries, and tropical wetlands in general.

Keywords: *Conceptual model; ecosystem services; sustainable management; wetland conservation; inland wetlands; nature futures' framework; nature's contribution to people.*

Un modelo conceptual para comprender los impulsores del cambio en los humedales tropicales: una evaluación comparativa en India y Brasil

Resumen: Los humedales tropicales se encuentran entre los ecosistemas con mayor biodiversidad en la Tierra y tienen un inmenso valor socioecológico. Sin embargo, los humedales tropicales se consideran recursos exploTables y continúan siendo drenados y convertidos a otros usos "productivos". Por lo tanto, es urgente identificar y comprender las interacciones entre varios impulsores del cambio que desencadenan la degradación de dichos humedales. En el presente estudio, revisamos y analizamos sistemáticamente la literatura existente sobre humedales en dos países tropicales, a saber, India y Brasil, con especial referencia a los humedales continentales, y propusimos un modelo conceptual que ilustra el intrincado vínculo de dichos humedales con diferentes impulsores del cambio. También desarrollamos el Marco de Nature Futures para resaltar los diversos valores de los humedales continentales de India y Brasil que contribuyen al bienestar humano en los dos países tropicales. Los resultados revelaron impulsores similares de los cambios que desencadenan la degradación de los humedales de la India y Brasil, incluidos los cambios en el clima y el uso de la tierra, el crecimiento de la población, las políticas débiles y la mala gobernanza de la tierra, además de otras actividades antropogénicas como la deforestación y la sobreexplotación de recursos. Entre estos, el cambio en el uso de la tierra, como la intensificación de la agricultura y el desarrollo de infraestructura, fueron los principales impulsores directos, mientras que los factores institucionales y de gobernanza, como la ausencia de medidas políticas concretas, fueron el principal impulsor indirecto que amenazó los humedales continentales de India y Brasil. Los resultados también revelaron algunos factores de cambio contrastantes, como los asentamientos humanos ilegales y el acaparamiento de tierras por parte de la industria del ladrillo para los humedales indios; mientras que la extracción de oro y la intensificación de los sistemas bovinos para los humedales brasileños. Nuestro documento también proporciona una visión sobre el estado de la conservación de humedales en India y Brasil. Recomendamos la promoción de prácticas de conservación basadas en la comunidad al adoptar estrategias de medios de vida sostenibles por parte de la población local para la conservación y el uso racional de los humedales continentales en India y Brasil. Los argumentos planteados en el artículo tienen el potencial de ayudar a las partes interesadas y / o los tomadores de decisiones para implementar estrategias de gestión sostenible para los humedales continentales en los dos países, y para los humedales tropicales en general.

Palabras clave: *Modelo conceptual; servicios ecosistémicos; gestión sostenible; conservación de humedales; humedales del interior; marco de futuros de la naturaleza; contribución de la naturaleza a las personas.*

Introduction

Wetlands refer to the land saturated with water, either seasonally or permanently. Cowardin (1991) defined wetlands as the transitional lands between the terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water. According to the Ramsar Convention (1971), wetlands are the *"areas of marsh, fen, peatland or water, whether natural or artificial permanent or temporary, with water that is static or flowing; fresh, brackish, or salty, including areas of marine water the depth of which at low tide does not exceed six meters"*. Categorized as coastal (also termed as tidal, saltwater or estuarine wetlands), and inland (also termed as non-tidal, freshwater wetlands) (Barbier et al. 1997), wetlands are amongst the most productive ecosystems on Earth (Ghermandi et al. 2008). They exist in every climatic zone, from dry regions to high altitudes, from the tropics to the polar regions and include deltas, floodplains, flooded forests, lakes, mangroves, marshes, peatlands, rice-fields, rivers, and swamps (Wetlands International, https://www.wetlands.org). Covering only 7% of Earth's surface, wetlands deliver ecosystem services worth of at least US$ 47 trillion per year, which accounts for 43% of the value of all ecosystems on Earth (Davidson et al. 2019). Thus, wetlands make a vital contribution towards the social, cultural and economic well-being (Emerton & Bos 2004, Turner et al. 2008), given their intricate relationship with the socio-economic system (Figure 1). According to Ramsar (2018), wetlands are known to significantly contribute to the Sustainable Development Goals, either directly or indirectly, and hence, conservation and wise use of wetlands are regarded as the cost-effective investments for the governments.

Tropical wetlands are considered as one of the most biodiverse ecosystems in the world (Junk 2002). In every continent, tropical wetlands significantly contribute to the regional and national economy and support a large number of local communities (Junk et al. 2002, Gopal 2013, Roggeri 2013, Junk et al. 2014). However, wetlands in the tropics are degrading at an alarming rate due to the rapid population growth and economic development during the last century, and consequently their conversion into different land-use types for the production of food and other commercial goods (Junk et al. 2002, Murdiyarso et al. 2010, Koh et al. 2011, Gopal 2013, Roggeri 2013). In addition, changes in seasonal hydrology due to extreme weather events as a result of climate change have further threatened the tropical wetlands (Junk et al. 2002, Gopal 2013, Roggeri 2013, Middleton & Souter 2016). Moreover, weak- policy and management strategies that do not consider long-term conservation strategies comprise the most important factors affecting the natural integrity of tropical wetlands (Gopal 2013, Bassi et al. 2014). Such negative impacts are expected to become more intense in the near future despite the economically valuable ecosystem services provided by tropical wetlands (Decleer et al. 2016, Osland & Middleton 2018). Consequently, the health and well-being

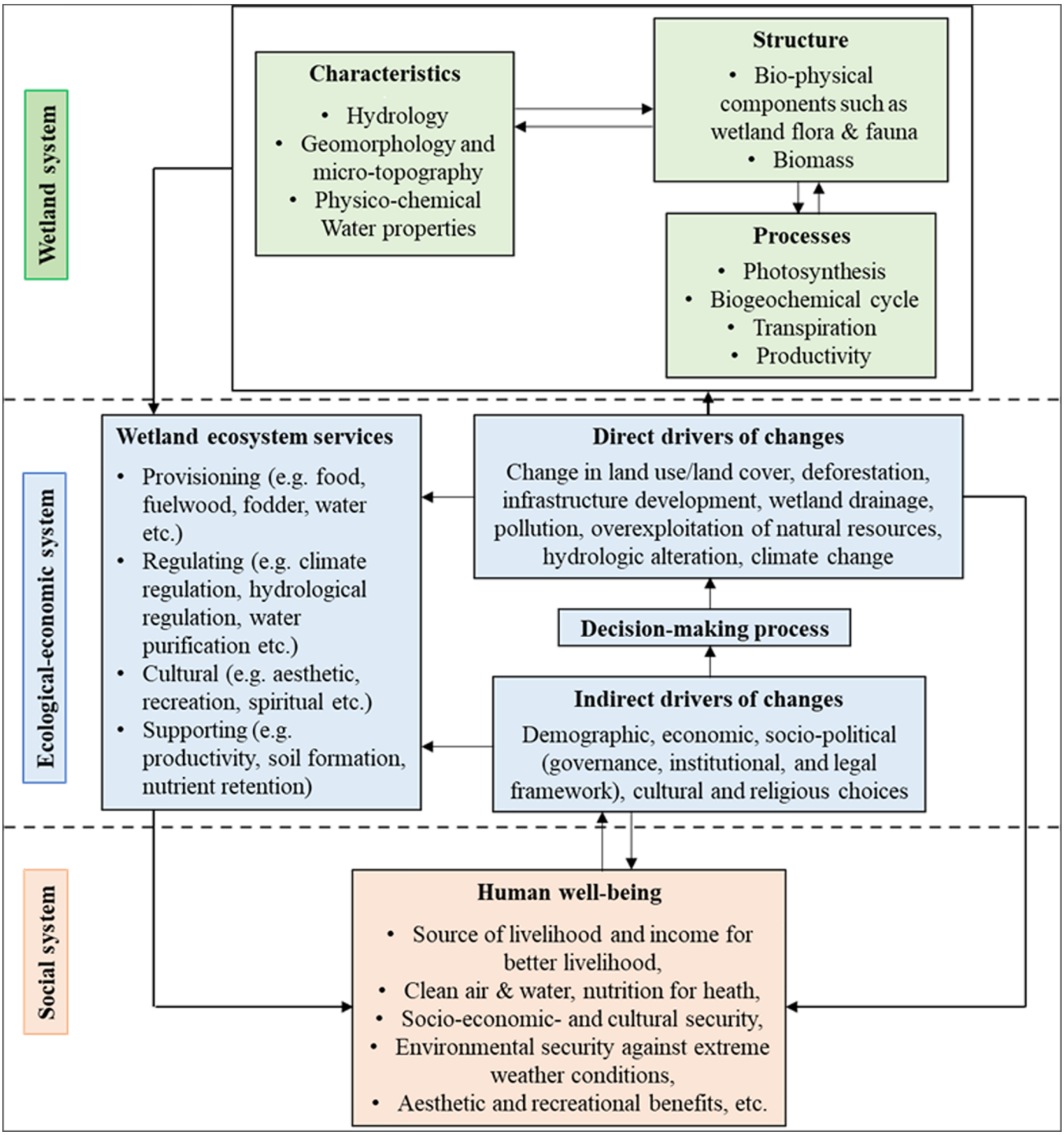


Figure 1. The linkage between wetlands with socio-economic systems and human well-being (adapted from Millennium Ecosystem Assessment 2003).

of dependent communities would be severely affected, further pushing them towards socio-economic bankruptcy (Millennium Ecosystem Assessment 2005). Literature suggests that poor understanding of the impact of developmental activities and other drivers on the ecology and functioning of wetlands is one of the potential causes for conversion and/or reclamation of tropical wetlands (Roggeri 2013).

Hence, there is an urgent need to identify and understand the interactions between various drivers of change triggering wetland degradation and maintain their ecological character for perpetual delivery of ecosystem services. In this regard, conceptual models could play a vital role in the formulation and implementation of evidence-informed policy measures towards conservation and wise use of wetlands at various spatiotemporal scales (Palmeri et al. 2000). Conceptual models are valuable communication tools that provide a simplified representation of the current knowledge of a system by portraying the complex interactions of ecosystem processes with

the various drivers of change (Gross 2003, Imgraben et al. 2014, Wiebkin 2014). Drivers of change refer to all factors that directly or indirectly change the ecological systems, anthropogenic assets, nature's contributions to people, and good quality of life (IPBES, https://ipbes.net/glossary/driver). Direct drivers of change (both natural and anthropogenic) such as climate change, pollution, land-use change, invasive alien species, over-exploitation of natural resources, etc., have a direct influence on biodiversity and ecosystem processes. Conversely, indirect drivers including socio-economic and demographic trends, socio-cultural factors, governance, technological innovation, etc. do not directly affect nature, rather affect the direction, level, or rate of direct drivers (Ferrier et al. 2016).

Considering the above, we systematically reviewed the existing literature on wetlands to collect information on the different drivers of change for wetlands in two tropical countries namely India and Brazil with special reference to inland wetlands. India and Brazil comprise some of the most important tropical wetlands distributed in the dry-wet climates (Osland and Middleton 2018), which sustains the livelihood of a significant portion of the human population (Wantzen et al. 2008, Junk et al. 2014, Kumar et al. 2017).

The specific objectives of the study were to (i) develop a conceptual model to identify and understand the interactions between various direct and indirect drivers triggering the degradation of inland wetlands in India and Brazil; and, (ii) develop the Nature Futures' Framework illustrating the diverse values of inland wetlands of India and Brazil contributing to human wellbeing; besides, identifying the indicators to measure and monitor changes in wetland values. The proposed conceptual model could support in understanding the intricate relationship of the various factors affecting the integrity of tropical inland wetlands. The arguments raised in the paper have the potential to assist the stakeholders and/or decision-makers towards implementing sustainable management strategies for inland wetlands in India and Brazil, and tropical wetlands in general.

Materials and Methods

1. Study area

The present study focused on the tropical inland wetlands in India and Brazil. Inland/non-tidal wetlands are located in floodplains along rivers and streams (riparian wetlands); isolated depressions along the margins of lakes and ponds; marshes, swamps, wet meadows and other low-lying areas where the soil surface is intercepted by groundwater or precipitation; and dominated by herbaceous plants, shrubs, and trees (US Environmental Protection Agency, https://www.epa.gov/wetlands/what-wetland). India is endowed with 19 different types of wetlands comprising both inland (lakes/ponds, high-altitude wetlands, riverine wetlands), and coastal (lagoons, intertidal/salt marsh, mangroves, coral reefs) wetlands (Panigrahy et al. 2012). In India, wetlands cover 28,205,200 ha (8.99%) of the total 315,274,196 ha area of the country (Figures 2a and 2c), 43.4% of which is accounted for natural inland wetlands (Panigrahy et al. 2012). Whereas, Brazil harbors diverse wetlands including the 'Pantanal Matogrossense' (Mato Grosso Floodplains), river floodplains, Amazonian wetlands (igapos, igarapes, etc), and coastal ecosystems (mangroves, beaches, lagoons) (Diegues 1994). , Brazilian wetlands cover 88,113,898 ha (10.40%) of the total 847,307,527 ha area of the country (Figures 2b, and 2c). The Pantanal of Brazil is the largest inland wetland on Earth (Junk et al., 2014, Cunha et al. 2015), covering an area of 140,000 sq. km which accounts for ~ 1.65% of the total geographical area of the country. In addition to the natural wetlands, man-made wetlands such as dams, reservoirs, salt pans, tanks also exist in both the countries stretching around thousands of kilometers (Diegues 1994, Panigrahy et al. 2012).

Wetlands in India provide a wide range of ecosystem services towards sustenance of local livelihood through the provision of agriculture, fishery, irrigation, jute-retting, fuelwood, raw materials for house construction and small-scale industries like pottery and handicrafts, fodder for livestock, and ecotourism (Das et al. 2000, Sarkar et al. 2019a). Palanisami et al. (2010) reported that 60% of India's tank-irrigated area is provided by wetlands in the states of Andhra Pradesh, Karnataka, and Tamil Nadu. Indian wetlands also play a significant role in carbon stocking due to their high biodiversity (Pal et al. 2017, Sarkar et al. 2019b), although agricultural activities have shown wetlands as net emitters, rather than net sinks of carbon (Kathiresan & Thakur 2008). In addition, wetlands in India have also been shown to be important refuges for ~ 1200 and 1300 species of migratory birds from Europe during the winter months (Agarwall 2011). Similarly, the Pantanal ecosystem in Brazil has a great contribution towards livelihood sustenance of the local communities through the provision of various ecosystem services such as agriculture, fish, wild edible plants, ecotourism, medicinal plants, pasture for cattle grazing, etc. (Serrati 2018). In addition, Pantanal provides raw materials for house construction, making of boats, fuelwood, etc. (Chiaravalloti 2016), thus supporting the economic and cultural activities of the traditional communities (Reis et al. 2006). Pantanal also provides refuge to a wide variety of flora and fauna, including many endangered species such as jaguar (*Panthera onca*) and Brazilian giant otter (*Pteronura brasiliensis*) (Alho & Sabino 2011). Despite the provision of various ecosystem services, both Indian and Brazilian wetlands are being lost at an alarming rate due to increasing anthropogenic pressures (Bassi et al. 2014, Junk et al. 2014). Consequently, loss of these wetlands would severely affect the health and well-being of the dependent communities (Millennium Ecosystem Assessment 2005); besides, disrupting the continuous flow of ecosystem services indispensable for sustaining the biosphere (Tolessa et al. 2017).

Methods

1. Development of the conceptual model

The development of the conceptual model comprised of three steps as follows:

Step 1 comprised a systematic review of existing literature on wetlands to gather information on the different drivers of change for inland wetlands in India and Brazil. We included both scientific and grey literature in the English language, published until December 2019 (with an open initial date). Since much expert knowledge is informal and undocumented (Drescher et al. 2013), inclusion of grey literature (or non-commercially published literature such as technical reports, thesis, government documents, etc.) may ensure the inclusion of comprehensive and representative sample of available research (Haddaway & Bayliss 2015). For literature review, we used the ISI Web of Science platform using the combination of keywords: "wetland" AND "drivers";

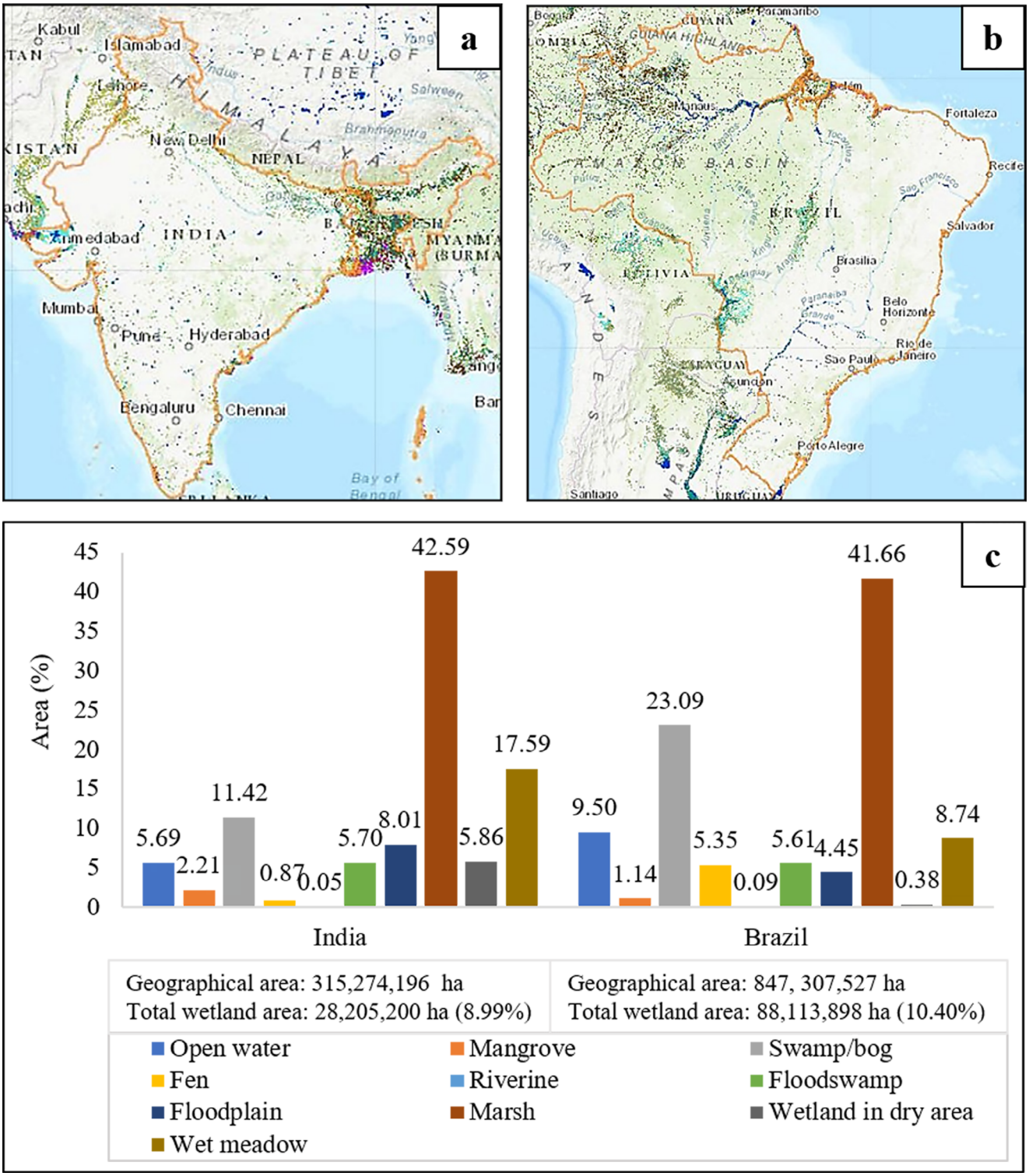


Figure 2. Distribution of wetlands in India (a), and Brazil (b), the area covered under different wetland types in India and Brazil (c). (Source: Global Wetlands, https://www.cifor.org/global-wetlands/).

"wetland" AND "conservation*"; "wetland" AND "ecosystem services*". For each combination, we added the countries such as Brazil* OR India*. The asterisk (*) symbol was used with keywords that might be referred to with alternate endings. To avoid information loss, we did not include the keyword "inland" with "wetlands" because of the reason that the definition of wetlands in India and Brazil is still ongoing (Bassi et al. 2014, Gomes & Magalhães 2017).

In *step 2*, all the literature returns were filtered through quickly scanning the title and abstracts of published articles. Literature describing new techniques, new species or occurrence of species, coastal

wetlands, wetlands from other countries, etc. not directly related to our study were excluded. The filtered documents thus obtained were later analyzed in detail to extract information on the direct and indirect drivers of inland wetlands in India and Brazil.

The final step: *step 3*, comprised the development of the conceptual model following the 'Expert-based models' approach (Ferrier et al. 2016). An expert is someone who knows the subject of interest gained through life experience, education or training and thus possesses both scientific and non-scientific knowledge (Drescher et al. 2013). It is important to mention that the present study was developed under the close supervision of experts from Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), and Brazilian Platform on Biodiversity and Ecosystem Services (BPBES) during the 'São Paulo School of Advanced Science (SPSAS) on Scenarios and Modelling on Biodiversity and Ecosystem Services to Support Human Well-Being' held in Sao Pedro, Brazil during July 1-14, 2019. During the two-week course, we were engaged in rigorous brainstorming, besides regular discussion with the experts to develop the conceptual model.

The Nature Futures' Framework was developed following Rosa et al. (2017). We also identified the indicators to measure and monitor changes in the diverse values of inland wetlands in India and Brazil. Information on indicators was obtained again through brainstorming during the process of model development at the school mentioned above. In addition, we also reviewed the literature on indicators developed by well-known classification systems namely The Economics of Ecosystems and Biodiversity (TEEB 2010, Berghoffer and Schneider 2015), and the Common International Classification of Ecosystem Services (CICES, Haines-Young and Potschin 2013). During the entire process of model development, authors' practical experiences and in-depth understanding of the hydrology, geology, ecology of inland wetlands, their ecological and socio-cultural values, and associated socio-economic responses was constructive.

Results

1. Drivers of change of inland wetlands in India and Brazil

The literature search revealed 685 articles, of which, 377 articles were on inland wetlands of Brazil, and 308 articles were on inland wetlands of India (Appendix 1). Of the 377 articles, only 92 articles (24.40%) from Brazil were relevant to our study which were later analyzed to collect required information. Whereas, only 104 (33.77%) relevant articles out of 308 articles from India were analyzed to collect required information. Of the total 196 selected articles from both countries, 162 (82.65%) studies addressed direct drivers of change for inland wetlands; while, some studies simultaneously studied both direct and indirect drivers. Results

Table 1. Direct and indirect drivers prevailing in inland wetlands of India and Brazil revealed through literature review.

Types of drivers	Drivers of change	Drivers common to		
		India	Brazil	Both
Direct drivers	Population growth			×
	Over-exploitation of fish and other wetland resources			×
	Habitat degradation through agriculture intensification, deforestation			×
	Infrastructure development such as the building of roads and dikes, construction for human settlement			×
	Climate change			×
	Introduction of exotic/invasive species (plants and animals)			×
	Siltation due to deforestation			×
	Pollution from industrial effluents and agricultural run-offs, waste disposal			×
	Hunting, and poaching			×
	Illegal settlements in wetland catchment	×		
	land grabbing by brick industry	×		
	Mining of mineral reserves like gold		×	
	Blooming of traditional bovine systems		×	
Indirect drivers	Economic and demographic factors such as unplanned tourism			×
	Technological factors such as the construction of dams and hydropower plants			×
	Institutional and governance factors such as inadequate policies, lack of land use planning or loophole in management actions			×

'×' represents the presence of drivers of change in the respective countries

revealed both similar and contrasting drivers of changes triggering the degradation of inland wetlands in India and Brazil. A list of the drivers of change affecting the inland wetlands in India and Brazil as identified from the literature survey is presented in Table 1.

Some of the major direct drivers of change common to inland wetlands in India and Brazil includes overexploitation of fish and other wetland resources like fuelwood, fodder, timber; global climate change; infrastructure development such as building of roads and dikes; agriculture intensification; habitat degradation and siltation intensified by soil erosion due to deforestation in the highlands and catchment areas; pollution from industrial effluents and agricultural run-offs, etc. (Table 1). Whereas, major indirect drivers of change common to both countries include technological factors such as the construction of dams and hydropower plants; institutional and governance factors such as loophole in management actions due to inadequate policy actions, or lack of land use planning (Table 1). Results revealed that in both countries, land-use change was the major direct driver; whereas, institutional and governance factors such as the absence of concrete policy measures, or loophole in management actions were major indirect drivers threatening the inland wetlands in India and Brazil (Table 2). Results also revealed some contrasting drivers of change for both countries, including illegal human settlements in catchment areas, and land grabbing by brick producing industry in Indian wetlands. And, mining of mineral reserves like gold, and intensification of traditional bovine systems in Brazilian wetlands (Table 1).

2. *Development of the conceptual model and Nature Futures' Framework*

Based on the results obtained above, we developed a conceptual model comprising of four components namely drivers, ecological processes, socio-economic processes, and the focal component – wetland health (Figure 3). The conceptual model depicts how the identified drivers of changes, both direct and indirect, interact with one another and with ecological processes, and finally influence the focal component of the model i.e., wetland health. We identified four ecological processes such as hydrology, water quality and quantity, soil quality and quantity, and habitat availability for biodiversity that determines the health of a wetland ecosystem (Figure 3). In the model, we represented the ways how the drivers of change, coupled with socio-economic processes (which capture the indirect drivers of change such as policies and socio-cultural factors) impact on the ecological processes, responsible for maintaining wetland health. The relationship between the components of the model is depicted by the arrows, which shows the direction of the impact of each process. We also highlighted how the identified drivers impact on the ecological and social processes as well as on each other (Figure 3). For example, climate change affects wetland hydrology, and soil quality and quantity through changes in flooding cycles, particularly in seasonal wetlands. Climate change also acts on land use through changes in vegetation cover due to the anomalies in precipitation and temperature. While, feedback can exist between climate change and land-use change through micro-climatic changes caused by the changes in land use/land cover. Social processes such as policy and legislation also influence the drivers such as population growth and land-use change, for e.g., by restricting the types of land use that can be allowed in a particular area of wetland.

The Nature Futures' Framework developed in the present study depicts the diverse values obtained from inland wetlands of India and Brazil which contribute to human wellbeing (Figure 4). We identified a total of twenty values contributed by the inland wetlands in India and Brazil towards human well-being (Figure 4, Table 3). These values can be broadly grouped as 'Nature for Nature', 'Nature for Society', and 'Nature as Culture', all of which are interrelated. Of these identified values, a majority (15) of the values overlapped between three categories namely, Nature for Nature, Nature for society, and Nature as culture due to the inter-dependence of human and ecological processes in inland wetlands (Figure 4). The unique indicators that can be used to measure each wetland value as identified under the Nature Futures' Framework are presented in Table 3.

Discussion and Conclusions

Wetlands are complex ecosystems characterized by an intricate relationship with the climatic, hydrological, biochemical, geomorphological, and pedological variables, necessary for maintaining its ecological character. Such complexity makes it difficult for the

Table 2. Number of studies that identified direct and indirect drivers of change in inland wetlands of India and Brazil.

Driver	Type (Direct or Indirect)	Number of studies (India)	Number of studies (Brazil)
Land-use/ land-cover change	Direct	41	39
Pollution		11	3
Climate change		8	6
Natural resource use and exploitation		7	8
Invasive species		2	6
Natural drivers (e.g. monsoon*, wildfire)		5	6
Governance and/or institutional	Indirect	17	25
Socio-cultural factors		6	16
Technological factors		2	1
Economic factors		3	11
Demographic factors		2	1

*Not covered by the IPBES categories but included in our work to account for studies that identify impacts of natural drivers such as seasonal rainfal on wetlands.

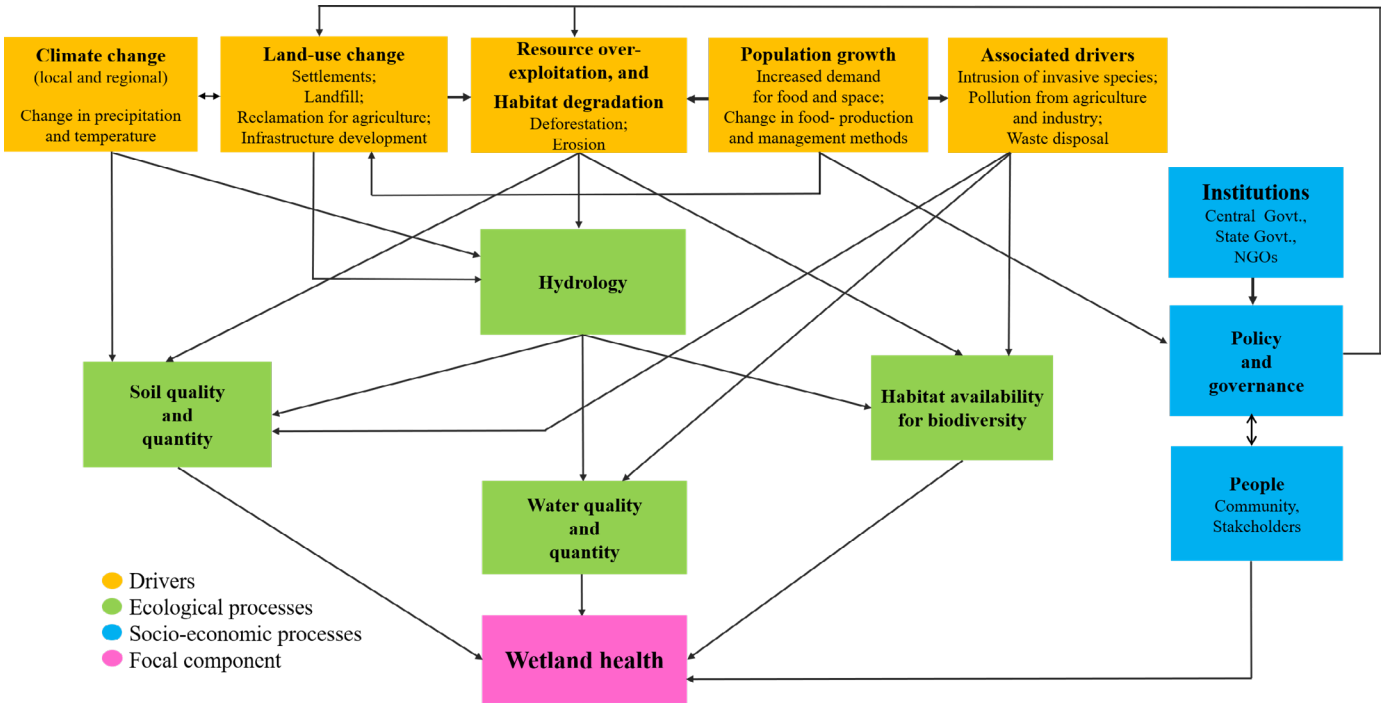


Figure 3. Conceptual model depicting the intricate relationship of wetland health with the different drivers of change. The arrows indicate the relationship and feedbacks between the different drivers, processes, and focal component of the model.

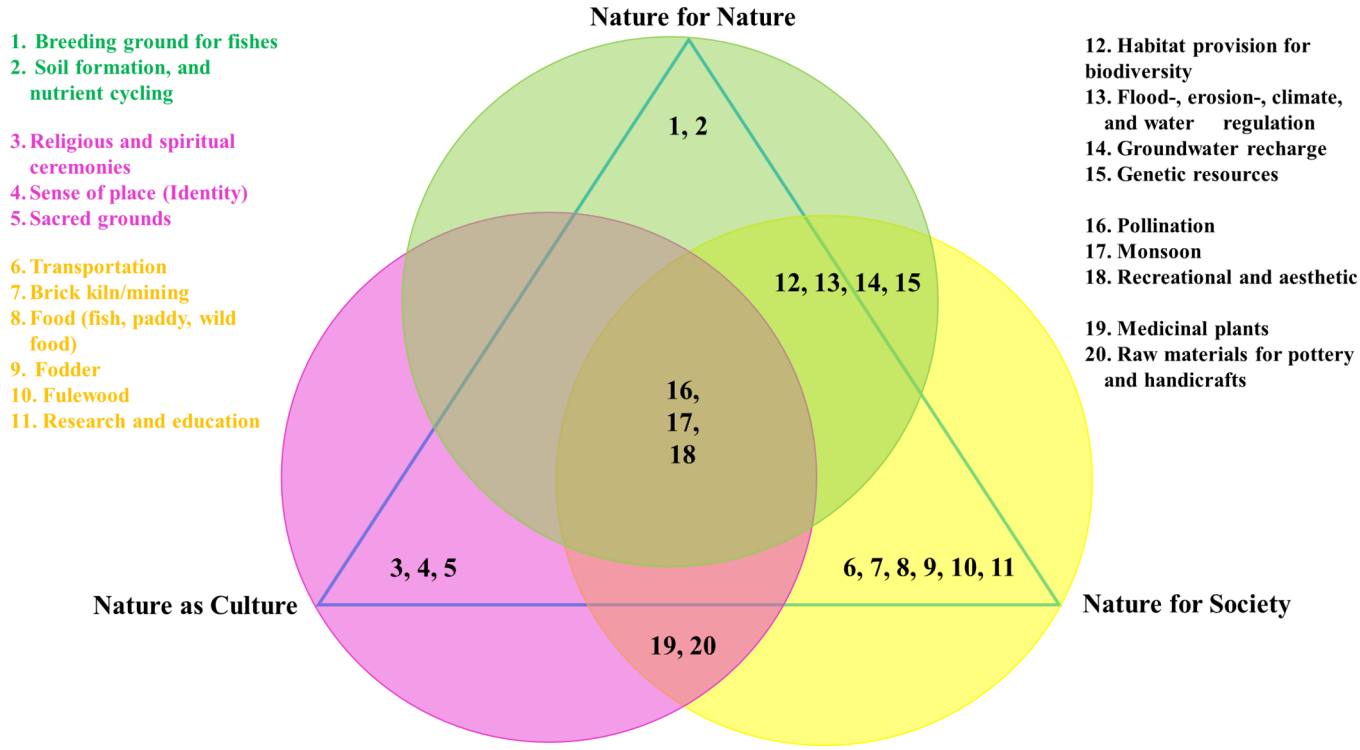


Figure 4. Nature Futures' Framework illustrating the diverse values of inland wetlands of India and Brazil contributing to human wellbeing.

Table 3. Indicators to measure the different values of inland wetlands in India and Brazil under the Nature Futures' Framework.

Wetland value	Indicator
Habitat for biodiversity	Number of species and abundance [2]
Breeding grounds for fishes	The population growth rate of fishes (%)
Soil formation	Rate of sediment deposition (kg m^{-2})
Religious and spiritual ceremonies	Number of cultural events
Sense of place/identity	Perception
Sacred ground	Number of sacred grounds
Transportation	Number of routes, passengers and boats
Brick production/mining	Quantity of bricks produced/ mining products (year $^{-1}$)
Food (fish, paddy and wild food)	Yield/amount harvested (kg ha $^{-1}$ year $^{-1}$) [1, 2]
Fodder for animals	Number of species of fodder grasses and other plants [2]
Fuelwood	Quantity of fuelwood harvested (tonnes year $^{-1}$) [1]
Research and education	Number of research groups/ studies in the wetland
Flood control, climate regulation	Total flooded area (ha) and volume of water stored (m^3); deforested area (ha), carbon- stock (tonnes C ha^{-1}), and sequestration (tonnes C ha^{-1} $year^{-1}$) in wetland components
Groundwater recharge	The volume of groundwater in wells (m^3)
Genetic resources	Number of wild species of economically useful plants
Pollination	Number of species (pollinators) and productivity of plants (kg ha^{-1} year $^{-1}$) [2]
Monsoon	Amount of rainfall (mm), length of the monsoon (days year $^{-1}$)
Medicinal plants	The trade volume of medicinal species ($ ha $^{-1}$) [1]
Pottery and handicrafts	Income from pottery and handicrafts ($ year $^{-1}$), the quantity of raw materials harvested (kg ha $^{-1}$ year $^{-1}$), and products prepared (quantity year $^{-1}$)
Recreational and aesthetic	Income from recreation and tourism ($ year $^{-1}$)

[1,2] represents the source classification system for respective indicators proposed by TEEB and CICES, respectively.

implementation of proper legislation measures for the conservation and protection of wetlands (Gomes & Magalhães 2017). In this regard, conceptual models can portray the complex interactions of ecosystem processes with their various drivers in a simpler way, thus, assisting in the formulation of informed policy measures (Gross 2003, Imgraben et al. 2014, Wiebkin 2014, Gomes & Magalhães 2017, Serrati 2018).

Our conceptual model for inland wetlands of India and Brazil explicitly represents the interconnected nature of the various drivers of change and ecosystem processes with wetland health and the feedbacks amongst them. As shown in the model, drivers like climate change, land-use changes, overexploitation of fish and other wetland resources, habitat degradation, population growth, and other associated drivers such as pollution from industry and agricultural run-offs, invasive species, and disposal of municipal wastes were the common drivers of change for inland wetlands both in India and Brazil (Alho & Vieira 1997, Das et al. 2000, Prasad et al. 2002, Vila da Silva et al. 2003, Junk et al. 2005, Ministry of Environment & Forests 2007, Central Pollution Control Board 2008, Wantzen et al. 2008, Dandekar et al. 2011, Junk et al. 2014, Mozumder et al. 2014, Roque et al. 2016, Gomes & Magalhães 2017, Padmavathi et al. 2017, Ghosh et al. 2018, Serrati 2018, Schulz et al. 2019). Among these, the major common land-use changes in and around inland wetlands include encroachment through draining and landfill, intensive agricultural activities, infrastructure development, technological interventions such as the adoption of new and improved food production methods, construction of dams and hydropower plants, etc. Of these, agricultural intensification is a potential driver causing the shrinkage in the areal extent of inland wetlands in both the countries, thus degrading their various socio-ecological services (Mato Grosso do Sul 1989, Bassi et al. 2014). In addition, intensification of agricultural activities in India has caused increased consumption of fertilizers from about 2.8 million tonne (1973-1974) to 28.3 million tonne (2010-2011) (Bassi et al. 2014), leading to eutrophication in wetlands, which further declines fish stock, and cultural values (Verhoeven et al. 2006). Similarly, intensive agricultural activities in and around the Pantanal floodplain in Brazil have severely altered the natural landscapes of the region over the last two decades (Mato Grosso Do Sul 1989). In addition, booming of the soy industry is also threatening the Pantanal ecosystem, one of the richest wildlife havens on the planet (Londoño 2017). Moreover, changing economic and political requirements, and unplanned tourism has been negatively impacting the wetland ecosystems in both the countries (Junk & Cunha 2005, Bassi et al. 2014, Schulz et al. 2019). Furthermore, erratic rainfall patterns and elevated temperature as a result of climate change have further imposed a direct threat to the extent of tropical wetlands by altering the hydrological regimes (Gopal 2013, Schulz et al. 2019). Climate change processes are known to have intensified effects on the hydrological cycle which further intensify various climatologic events (Ching et al. 2015). Such effects of climate change are also expected to magnify the impacts of freshwater demand on freshwater ecosystems (MEA 2005), and has already been influencing the hydrological regime of inland wetlands in India and Brazil (Patel et al. 2009, Roggeri 2013). In addition, climate change is likely to impact on the soil health through physical, chemical and biological properties of soil (Patil & Lamnganbi 2018).

In terms of the contrasting drivers of changes, illegal settlements in the catchment area, and land grabbing by brick kiln industry comprised the specific drivers for the inland wetlands in India. Urban expansion

and population growth have increased the demand for the supply of bricks for construction leading to the proliferation of brick industries in India (Sharma et al. 2019). Such industries established near the wetland periphery uses rich topsoil from low-lying wetland areas, which along with releasing highly intensive heat destroys the soil quality and its productivity, degrading the overall quality of the environment (Gupta 2006, Noll 2015, Sharma et al. 2019). In addition, inland wetlands in India are also threatened by illegal human settlements (Mozumder et al. 2014). Whereas, excessive gold mining and intensification of traditional bovine systems (Hylander et al. 2000, Roggeri 2013, Londoño 2017, Bergier 2019, Schulz et al. 2019) were the specific drivers of change threatening the inland wetlands of Brazil. All these pressure pose a major threat to the continued existence, size, as well as wetland integrity, creating a high level of uncertainty about the future of inland wetland in India and Brazil (Ioris 2013, Bassi et al. 2014), and for the tropical wetlands in general (Gopal 2013).

With a population of 1.27 billion and a population growth rate of 1.17%, India is the world's second-most populous country (FAO 2019). While, with a population of 209 million and a population growth rate of 0.73% (World Bank 2017), Brazil is the fifth most populous nation in the world. These radical population growth rates are a pointer to the pressure on the available natural resources in Brazil and India, wetlands inclusive (Guerra et al. 2020a). Increased population also comes with the challenge of higher demand for food, infrastructure and increased waste generation all of which cause both direct and indirect pressure on the inland wetlands in both the nations as represented in the conceptual model. For instance, the hydrology of the wetlands is being affected by the changes in local climate, land use as well as other human activities like landfilling, infrastructure development such as the construction of dikes & dams, deforestation, and overexploitation. In the same vein, as shown in the model, wetland hydrology is a major determinant of the quality and quantity of soil and water as well as habitat availability for biodiversity (Guerra et al. 2020b). Our model also highlights how the soil- quality, and quality is affected by changes in local climate, land-use, and other anthropogenic activities. In addition, the conceptual model also identified the potential role of the NGOs and Institutions in maintaining the natural integrity of tropical wetlands (Gopal 2013). Therefore, there is a need to put in place the public-private partnerships at community and regional levels for conservation and sustainable management of such wetlands.

India and Brazil have been the signatories of the Ramsar Convention since 1982 and 1993 respectively, with currently 37 Ramsar sites in India covering a total area of 1,067,939 hectares, and 27 Ramsar sites in Brazil covering a total area of 26,794,455 hectares (Ramsar, https://www.ramsar.org). The Ramsar sites thus account for 3.79% and 30.41% of the overall area covered by wetlands in India and Brazil, respectively. However, there is no concrete national policy for the sustainable management and protection of wetlands in India and Brazil (Junk et al. 2014, Bassi et al. 2014, Gomes & Magalhães 2017). In India, the judicious use of wetlands in the country still needs to gain momentum. Previously, wetlands were governed indirectly through other legal instruments including the Indian Forest Act 1927, Wildlife (Protection) Act 1972, Water (Prevention and Control of Pollution) Act 1974, Environmental (Protection) Act 1986, and Biodiversity Act 2002 of India. Provisions under these acts govern pollution of water bodies, identification of ecologically sensitive areas and conservation of aquatic biodiversity in the country which could be applied to wetlands, but without an explicit mention of the term 'wetland' (Bassi 2015). Limited understanding of wetlands as unique ecosystems and their key functions amongst the policy-makers might be the reason for the absence of proper legal instruments on wetland conservation in India (Bassi 2015). The National Environmental Policy of India (2006) recognized no national system of managing wetlands despite the international commitments made under the Ramsar Convention. Later, this recognition led to the enactment of the Wetlands (Conservation and Management) Rules, 2010. The rules vest the governance of wetlands under the Central Wetlands Regulatory Authority, and places restrictions on activities such as land reclamation within the wetland. However, the rules have been criticized as being restrictive on the types of wetlands that are regulated, restricting them to several categories. This include the Ramsar sites, UNESCO world heritage sites, wetlands in ecologically important areas, high altitude wetlands of an area of 5 ha or more, and low altitude wetlands of an area of 500 ha or more (Bassi 2015). Consequently, a large number of smaller wetlands, particularly the ones at low altitudes are overlooked and/or ignored, making them vulnerable to the impacts of drivers such as reclamation and land-filling (Dandekar et al. 2011). For instance, India has 757.06 thousand wetlands (Space Applications Centre 2011); however, only 37 of these have been identified as Ramsar sites as of the beginning of 2020. And, only 115 wetlands have garnered attention under the wetland conservation programs like National Wetland Conservation Program so far (Ministry of Environment, Forest and Climate Change, Govt. of India, http://www.moef.nic.in). While the remaining ones are highly neglected due to limited financial and technical support provided from central government (Bassi et al. 2014). Similarly, there is little progress to advance studies on Brazilian wetlands which led to marginalization in the conceptual and legal protection aspects for the wetlands. Although Brazil is endowed with several large wetlands, e.g., the floodplains of the Amazon River and several of its tributaries, Paraná and Paraguay Rivers, Pantanal Matogrossense; wetlands in Brazil are rarely mentioned in federal legislation, state constitutions, or environmental legislation (Junk et al. 2014). Literature revealed that the term 'wetland' is only used in the Native Vegetation Protection Law (Grasel et al. 2019), and most of the wetland terms in Brazil only had a regional application with weak conceptualization (Maltchik et al. 2018). Although ~11% of Brazilian territory is covered by wetlands (Global wetlands, https://www.cifor.org/global-wetlands/), wetland inventories in Brazil are still incomplete (Junk et al. 2014). Discussion on the Brazilian Forest Code suggests very little protection for the country's wetlands (Piedade et al. 2012), and the governmental policy instruments focus more on enforcing the existing environmental legislation, rather than forming a new policy instrument specifically for the wetlands (Junk et al. 2014). The 1988 Brazilian constitution only distinguished the Pantanal as a National Heritage site (Junk et al. 2014), and so far, only 27 wetlands as mentioned before are protected under the Ramsar Convention. Thus, the status of wetland conservation is very much similar between India and Brazil, revealing inappropriate policy measures and the absence of concrete governing policies specifically dedicated to the conservation of wetlands in both the countries.

Considering the above, our study, therefore recommends that all-inclusive policies routed from the local communities whose livelihood depends on these wetlands be put in place. We argue that adoption

of initiatives to change the attitudes of local people as well as the government authorities is vital towards conservation of wetlands because, the wetland-dependent communities and local stakeholders could play an instrumental role in better implementation of government policies, and might act as effective care-takers of wetlands (IUCN, https://www.iucn.org/content/working-wetlands-landowners-and-local-stakeholders-life-return-rural-wetlands). There are many success stories on the proper management of wetland resources through community engagement (AWS 2001). For instance, wetlands have been effectively managed by the local people in Nepal (Shrestha 2011). While, the Life+ Return of Rural Wetlands project aiming at the restoration, management, and establishment of wetland habitats in Finland, works on a local level by encouraging and involving the local communities and stakeholders. By 2016, the project has already delivered meaningful outcomes in terms of supporting wetland biodiversity on a landscape level, thereby safeguarding the wetland habitats and the associated services. Hence, if informed properly, the local people could play an effective role in implementing concrete actions and positive changes in formulating long term policy and management practices; thus, yielding best conservation results (Kibwage et al. 2008). Moreover, we also recommend the adoption of some policy measures to create zonation within the wetland ecosystems and its catchment areas. Furthermore, conservation policies should also include (i) controlled mesh size for fishing activities (ICES 2004), (ii) regulation of fishing activities during the breeding seasons (Sadovy and Domeier 2005), (iii) restriction of brick kilns/mining activities in the core zone of wetlands, (iv) regulation of infrastructural development along the wetland catchments (Bassi et al. 2014), (v) mass awareness on wetland conservation (Paul et al. 2011, Lamsal et al. 2015), (vi) training in wetland science and management (Gopal 2013), (vii) stakeholder engagement at the local level to develop appropriate policy measures for wetland management (Kibwage et al. 2008, Lamsal et al. 2015). Such practices could restrict the destructive anthropogenic practices within the wetland core zone thus, maintaining the natural integrity of wetlands to underpin the continuous delivery of ecosystem services. Consequently, these policies will ensure protection of the diverse wetland values identified under the Natures Futures' Framework by safeguarding Nature for Nature (natural biological processes and habitats), Nature for Society (wetland resources such as food, fodder, and fuelwood), and ultimately delivering Nature as Culture services (conserving cultural practices, sacred grounds and a sense of identity for the local people). Further studies could focus on developing different scenarios to explore the effectiveness of the different policy recommendations and project their impacts on the indicators under the Nature Futures' Framework identified in the present study. While developing the conceptual model and potential policies for improved wetland conservation, integration of perspective of the local stakeholders in important, and should be discussed with the local people who directly interact with these ecosystems, which is a limitation of the present study.

Studies also suggest the promotion of sustainable livelihood options as a vital way to check further degradation of wetlands due to overexploitation (Lamsal et al. 2015). In this regard, the promotion of alternate livelihoods such as (i) ecotourism, (ii) entrepreneurial activities such as preparing handicraft items using aquatic macrophytes and other wetland resources could ensure livelihood security of the dependent communities (Lamsal et al. 2015). Although tourism has great potential for regional socio-economic development, a healthy and clean wetland is important to attract tourists (TEEB, http://www.teebweb.org/wetlands-as-a-sustainable-tourism-destination/). Therefore, it is important to preserve or restore the ecological integrity of wetlands and maintain the aesthetic beauty of the same. With this in mind, tourism activities in wetlands must include adoption of sound planning and management practices, for e.g., limiting the number of visitors based on the seasons, zoning of wetland areas to restrict the access and transportation of the tourists to core zone/sensitive areas, and restriction on any tourism-related constructions within the core zone (TEEB, http://www.teebweb.org/wetlands-as-a-sustainable-tourism-destination/). However, the lack of skills and financial support could be an obstacle to adopting alternative livelihood options by the local communities. In this regard, proper training and financial incentives at the initial stage, and creation of markets for the handicraft products by the local agencies would facilitate the local people in adopting alternate livelihood options (Lamsal et al. 2015).

Tropical wetlands are continuing to be regarded as resources that can be exploited, at least at a local level (Gopal 2013). Although a few tropical wetlands have received international recognition under the Ramsar Convention, national policies aiming at wetland conservation are either non-existent or very weak in both India and Brazil. Our study revealed massive anthropogenic interventions such as encroachment, changes in land use, habitat degradation, agricultural intensification, hydrological alterations through channelization & construction of dams, dumping of industrial-, and municipal wastes, and agriculture and urban runoffs have serious impacts on inland wetlands in India and Brazil. Such anthropogenic interventions are common to other tropical wetlands as well, especially in the developing countries. Although both India and Brazil harbor a diverse wetland ecosystem, there is no policy instruments that explicitly defines the term 'wetland'. Wetlands are being given very little protection under the existing environmental legislations, with no implementation of new policies focusing solely on wetlands. However, considering the inter-dependence of human and wetland ecosystems as identified by the Nature Futures' Framework in the present study, it is indispensable to maintain the hydrological regimes and natural integrity of tropical wetlands to support human well-being and the overall biosphere. In this regard, our proposed conceptual model could help in understanding the intricate association of various drivers of change on the ecological processes and overall wetland-health; thus, assisting in the implementation of appropriate management actions at the local or regional level for inland wetlands in the two countries, and tropical wetlands in general.

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Author Contributions

Priyanka Sarkar: has substantial contribution in the concept and design of the study, manuscript preparation, critical revision and addition of intellectual content of the manuscript.

Mercy Salami: has substantial contribution in the concept and design of the study, manuscript preparation, critical revision and addition of intellectual content of the manuscript.

Yvonne Githiora: has substantial contribution in the concept and design of the study, manuscript preparation, critical revision and addition of intellectual content of the manuscript.

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Alma Navarro: has substantial contribution in the concept and design of the study, and

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Diana Clavijo: has substantial contribution in the concept and design of the study.

Maíra Padgurschi: has substantial contribution in the concept and design of the study, manuscript preparation, critical revision and addition of intellectual content of the manuscript.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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Editorial

Fostering capacity building on Scenarios and Modelling on Biodiversity and Ecosystem Services to Support Human Well-Being

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Predictive models have become important tools for examining the way that systems are likely to react to environmental and policy changes while exploring uncertainties. Even considering the limits of their predictability (mostly because of data availability, and incapacity of anticipating unforeseeable events), foresight approaches became a very useful tool to increase the knowledge, engage stakeholders and create anticipatory intelligence. Therefore, they are increasingly being used to study the possible effects of human actions on Earth, its biodiversity and associated ecosystem services. Such models are typically based on a set of assumptions, so-called scenarios, which provide an approach for exploring how plausible alternative futures may unfold and comparing the potential consequences of different decisions in different future contexts.

Scenarios and models allow the exploration and communication of the results of different narratives ("futures") for social, economic and environmental development. Scenarios are indispensable for supporting science-based policy formulation and implementation (Pereira et al, 2010).

In order to capture the consequences of the growing threats to biodiversity and ecosystem services, scenarios have become timely a key component in decision-making (IPBES 2016a). There are various advantages in adopting this approach, such as: 1) the capacity to foresee future changes in biodiversity and ecosystem services as a result of fluctuations in various ecological and socioeconomic drivers, and 2) the usability at multiple spatial scales – from local to global levels – which allows to understand, for example, impacts of climate change on forests and protected areas, or on management of fishing grounds. There are, however, certain constrains to this approach, for instance, the limited coverage and range of sectors and cases, and the availability of data. This shed light on a very wide range of enhancements that can be made in scenarios that would improve their use in decision-making.

The need for a step change in the capacity to foresee credible future changes was lead the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) that organized a working group with over 80 experts from all regions of the world, to produce a report. The Methodological Assessment report on scenarios and models of biodiversity and ecosystem services, published in 2016, become a milestone as it reviewed the state-of-the-art and highlighted the existing gaps in scenarios and models for biodiversity and ecosystem services change. One of the key messages of the report points out that an appropriate planning, investment and capacity-building, among other efforts, could overcome significant remaining challenges in developing and applying scenarios and models (IPBES 2016b).

In this respect, and aligning with the ambition of organizations such as IPBES, the São Paulo School of Advanced Science on Scenarios and Modelling on Biodiversity and Ecosystem Services to Support Human Well-Being Scenarios (SPSAS Scenarios) addressed the relationship of dependence, particularly between ecosystem services sustained by biodiversity, and human well-being. Human well-being depends directly on ecosystem services (Pascual et al 2017) such as pollination associated with food production, protection of water resources associated with water for consumption and for energy production, mitigation of climate change impacts and intangible services fundamental to emotional and often spiritual balance. Scenarios and models that are able to capture these dependencies can become essential tools for sustainable management and development in the long-term.

Decision makers in governments, private sector and civil society want more robust information regarding plausible futures of biodiversity and ecosystem services. They want to understand how the drivers impacting biodiversity and ecosystem services might evolve in the future, and what the consequences might be for biodiversity, ecosystem services and nature's contributions to people. They also want to understand the implications of different policy choices on biodiversity and ecosystem services, and how to achieve policy targets (IPBES 2016b)

The idea was that by providing expert advice on models and scenarios that are currently available, and by explaining how to use them and in what context, the SPSAS Scenarios would make it possible to enhance the use of these tools in biodiversity and ecosystem services governance. Aiming to spread the knowledge assembled by IPBES in its assessment, and to help the biodiversity community to make a step change in its capacity to foresee plausible future changes as a result of various socioeconomic drivers, the BIOTA/FAPESP Research Program, the Brazilian Platform on Biodiversity and Ecosystem Services/BPBES and the Inter-American Institute for Global Change Research/IAI organized the São Paulo School of Advanced Science on Scenarios and Modelling on Biodiversity and Ecosystem Services to Support Human Well-Being Scenarios (SPSAS Scenarios).

In this context SPSAS Scenarios contributed to the training of students, future researchers and professionals in the area of biodiversity and ecosystem services modelling and scenarios, who will eventually become leading academics in research centres, government agencies, companies and industries, international organizations and several other sectors and institutions.

By bringing together the team of experts that led the IPBES Methodological Assessment (IPBES 2016a, b), it was possible also to update all SPSAS Scenarios with the vision and concept of the Nature Futures Framework (Lundquist et al. 2017, Pereira et al. in press) that integrates both qualitative narratives and quantitative model output (Figure 1).

"The Nature Futures Framework (NFF) forms the foundation for developing scenarios of positive futures for nature, to help inform assessments of policy options across multiple scales. The NFF places relationships between people and nature at its core. Because people relate to nature in multiple ways, there are a wide variety of desirable nature futures, with different goals and visions which can be synergistic or in conflict with one another" (https://ipbes.net/scenarios-models).

The nine papers presented in this Special Issue of Biota Neotropica are the result of the work developed by the 90 participants of the SPSAS Scenarios - 46 Brazilian, 23 from Latin America Countries, 9 from Europe, 6 from North America, 4 Africa and 2 from Asia/Oceania.

Each group chose a topic related to environmental change and during the school worked on incorporating layers of complexity, as the theoretical background was being presented and discussed by several experts. So, this Special Issue is the result of a collective effort on disseminating IPBES principles, tools and methodologies to train professionals to use the best available knowledge to bridge the gap between science and police, generating much better polices for biodiversity and ecosystem services conservation, restauration and sustainable use.

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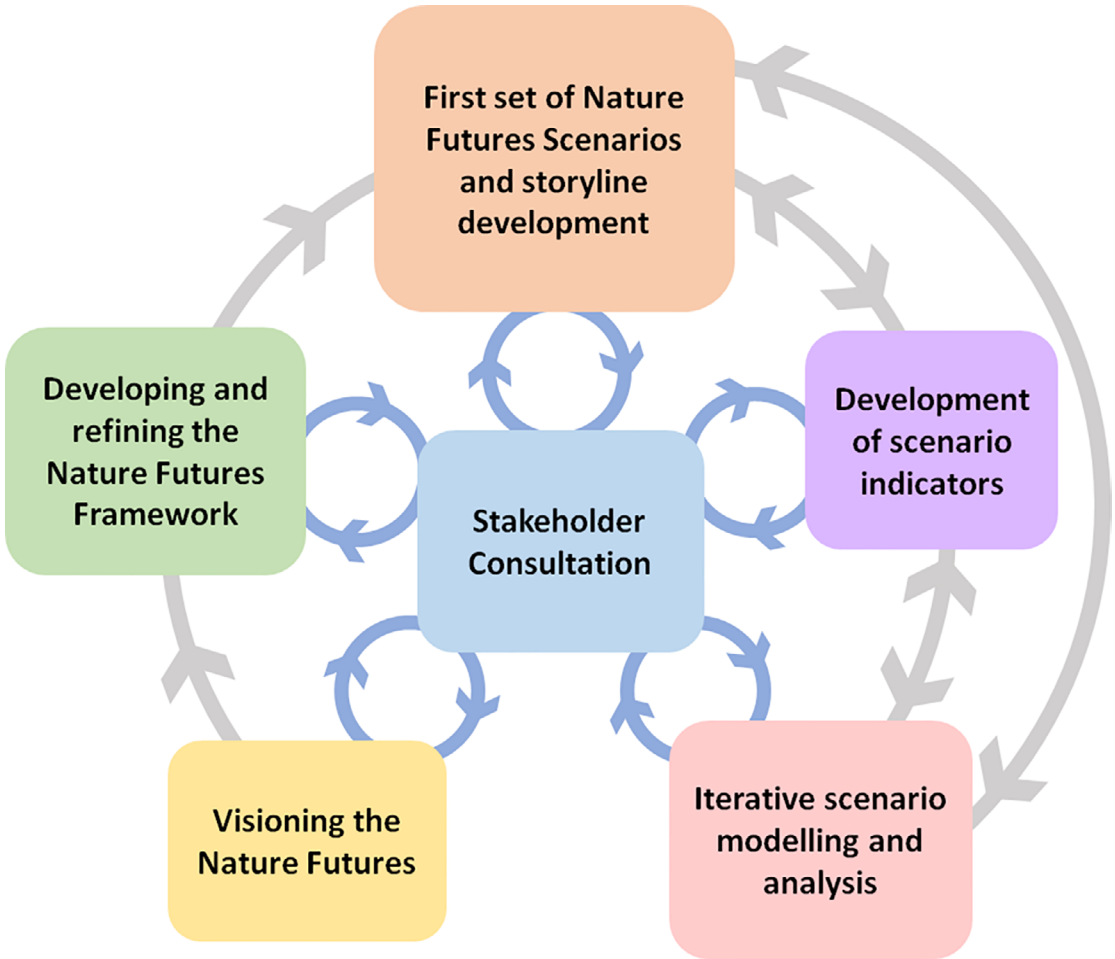


Figure 1. Iterative process for Nature Futures Scenarios development (adapted from https://ipbes.net/scenarios-models).

Author Contributions

Carlos A. Joly, Paula Drummond de Castro and Simone A. Vieira contributed equally to manuscript preparation.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript

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Article

Accessing the subterranean ant fauna (Hymenoptera: Formicidae) in native and modified subtropical landscapes in the Neotropics

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Abstract: Several studies have characterized and delimited subterranean ant assemblages. Soil extraction, one of the methods employed to access this fauna, employs the removal of monoliths. One of the most widely used methods for the extraction of soil sampling is called TSBF (developed by the Tropical Soil Biology and Fertility Programme). This method provides relevant data about the species associated with the soil. In the present study we characterized assemblages of subterranean ants using the TSBF method in different subtropical areas of the Neotropics. We considered two sampling designs in different localities. The first design resulted in 315 TSBF samples obtained from layers at distinct depths. The second design resulted in 270 TSBF samples and 270 epigaeic pitfall trap samples. This material was used to delimit the species that occur exclusively in the subterranean stratum (TSBF) and that are not found on the soil surface. A total of 281 species were recorded. Of these, 57 can be considered subterranean, based on their occurrence in subterranean strata. We also verified that the highest occurrence of ants was in the first 10 cm of soil depth. Due to the importance of using methods that efficiently extract the subterranean ant fauna in studies, we suggest the TSBF method should be used to sample ants or to associate this method with epigaeic pitfall traps to delimit strictly subterranean assemblages in specific community stratification studies.
Keywords: *Soil, hypogaeic, Brazil, monoliths, pitfall.*

Avaliação da mirmecofauna subterrânea (Hymenoptera: Formicidae) em paisagens nativas e modificadas na região subtropical do Neotrópico

Resumo: Vários estudos têm caracterizado e delimitado assembleias de formigas subterrâneas. A extração de solo, um dos métodos utilizados para amostragem dessa fala, implica na remoção de monólitos. Um dos métodos mais utilizados na extração de monólitos é chamado TSBF (desenvolvido pelo Programa *Tropical Soil Biology and Fertility*). Esse método fornece dados extremamente relevantes sobre as espécies associadas ao solo. No presente estudo, nós caracterizamos as assembleias de formigas subterrâneas usando o método TSBF em diferentes áreas subtropicais do Neotrópico. Utilizamos dois delineamentos amostrais distintos. O primeiro delineamento resultou em 315 amostras de TSBF obtidas a partir da estratificação do solo. O segundo resultou em 270 amostras de TSBF mais 270 provenientes de armadilhas pitfall epigeicas. Esse material foi utilizado para delimitar espécies que ocorrem exclusivamente no estrato subterrâneo (TSBF) e não são encontradas na superfície do solo. Registramos um total de 281 espécies. Destas, 57 podem ser consideradas subterrâneas (baseado na ocorrência no respectivo estrato). Também verificamos que a maior ocorrência de formigas se deu nos primeiros 10 cm de profundidade. Devido à importância do uso de métodos que coletem eficientemente formigas subterrâneas, sugerimos o uso do método TSBF em estudos de estratificação de comunidades ou sua associação a armadilhas do tipo pitfall epigeica para delimitar assembleias estritamente subterrâneas.
Palavras-chave: *Solo, hipogeicas, Brasil, monólitos, pitfall.*

Introduction

Ants are conspicuous organisms present in most terrestrial environments (Folgarait 1998), from the arboreal to the subterranean strata (Lucky *et al.* 2013, Jacquemin *et al*. 2016). However, little is known about underground ant assemblages (Ryder Wilkie *et al*. 2007, Andersen & Brault 2010, Jacquemin *et al.* 2012), mainly because there are few efficient and specific methods for collecting this important fauna (Wong & Guénard 2017). Underground ants are the last biodiversity frontier to be explored in Formicidae (Rider Wilkie *et al*. 2007, Andersen & Brault 2010), and are also important for the understanding of the origin and evolution of Formicidae (Lucky *et al*. 2013). In addition, subterranean ants are considered bioturbators *sensu strictu* (Bottinelli *et al*. 2015), and because they respond to drastically changes in soil density, they can serve as bioindicators (Schmidt *et al*. 2013).

Aiming to develop an efficient sampling method for subterranean ants, researchers have been testing useful sampling techniques that can be replicated. Wong & Guénard (2017) compiled the published research on the collecting methods of subterranean ants and classified them into three types: (1) subterranean baits, (2) soil sampling, and (3) direct sampling. Most of those publications (65%) described the use of baits or other attractive items (Wong & Guénard 2017), which favor the capture of predatory, generalist and mass-recruiting species (Longino 2000, Bestelmeyer *et al*. 2000, Schmidt & Solar 2010, Wong & Guénard 2017).

Amongst the methods classified as "soil sampling" is the extraction of monoliths (Delabie & Fowler 1995, Fowler *et al*. 2000, Andersen & Brault 2010, Wong & Guénard 2017). The use of monoliths is promising because it enables us to determine the vertical stratification of species in the soil, among other advantages (see: Jacquemin *et al*. 2012, Jacquemin *et al.* 2016, Wong & Guénard 2017). A widely used technique of monolith extraction in soil macrofauna studies was proposed by the Tropical Soil Biology and Fertility Program (TSBF) (Anderson & Ingram 1993) and was standardized by the International Organization for Standardization (ISO) in the ISO norm 23611-5:2011. This technique, known as TSBF method, generates a substantial volume of ant specimens. It consists of the removal of soil monoliths that are 25 x 25 cm and are taken 20 or 30 cm deep in the soil, followed by hand sorting extraction of the associated fauna (Bartz *et al*. 2014a, Rosa *et al*. 2015, ISO 2018).

Despite the massive volume of material that has been sampled using the TSBF method, published information on the ecological dynamics of the ants collected using it is insufficient. This is a function of the fact that Pedobiology studies (which employ the TSBF method with high frequencies) traditionally identify the collected material at high taxonomic levels (like Order, Family and Genera) and therefore do not give information on community composition and species ecology (see: Lourente *et al*. 2007, Klenk *et al*. 2009, Correia 2010, Lima *et al*. 2010, Rousseau *et al* 2010, Zagatto 2014, Benazzi *et al*. 2013, Pereira *et al*. 2012, Gutiérrez *et al.* 2017).

The present work characterizes subterranean ant assemblages in three subtropical regions of the Neotropics using two sampling methods: TSBF and epigaeic pitfall traps. *In situ* extraction methods, like monoliths, can help to detect ecological, behavioral and morphological patterns, since the specimens collected using these methods are not attracted from other strata (from the surface, for example). Furthermore, TSBF is widely disseminated in studies that evaluate the impact of land use systems on the underground soil (micro, meso and macro fauna) (Lavelle *et a*l 1997, Bartz *et al* 2014a, Rosa *et al*. 2015). In order to improve the scientific contribution of this study, we characterize the ant assemblages and compare the communities at the species level.

Material and Methods

1. Study area

The specimens came from three localities in the Southern Region of Brazil: (1) Ponta Grossa, *Campos Gerais* region, state of Paraná; (2) Western and (3) Plateau, regions of the state of Santa Catarina. In each region of Santa Catarina, the samples were collected from three municipalities: Xanxerê, Chapecó and São Miguel do Oeste in the West and Lages, Otacílio Costa and Campo Belo do Sul in the Plateau (Figure 1).

Ponta Grossa is in the Second Plateau of Paraná, about 120 kilometers from the state capital, Curitiba. According to Maack (2012), the region is characterized by open grasslands with *Araucaria angustifolia* (Bertol.) Kuntze 1898 patches, within the Atlantic Forest domain. Climate is type Cfb (climatic classification of Köppen-Geiger) -subtropical humid, without defined dry periods throughout the year and with the average temperature of the warmest month lower than 22 °C. The sampled areas have mean elevation of 875 m and total annual rainfall between 1.300 and 1.800 mm throughout the year (IAPAR, 1978). Seven land use systems (LUSs) were sampled: (1) Integrated Crop-livestock (ICL); (2) Integrated Crop-livestock-forestry (ICLF); (3) Grazed native field (GN); (4) *Eucalyptus* sp. plantation (EP); (5) no-tillage (NT); (6) *Campos Gerais* (CG), and (7) Mixed Ombrophilous forest (F). The native areas, CG and F, were at Vila Velha State Park (25°14'17" S 50°0'39" W). The land use systems ICL, ICLF, and GN were in the Model Farm of the *Instituto Agronômico do Paraná* (IAPAR) (25° 5' 11" S 50° 9' 38" W) and the EU and NT systems were at the Experimental Field of the *Empresa Brasileira de Pesquisas Agropecuárias* (Embrapa) (25°08'17" S 50°04'47" W).

The western region of Santa Catarina is characterized by humid subtropical Cfa climate, with no defined dry season, and the average temperature during the warmest month is above 22 °C (Bartz *et al*. 2014a). The native forest in the Western region of the state is a transition between mixed ombrophilous and semi-deciduous forest (Bartz *et al*. 2014b). In the Plateau region the climate is classified as Cfb (as described for Ponta Grossa), and native grasslands with mixed ombrophilous forest patches predominate (Rosa 2013). The municipalities of each region of Santa Catarina were chosen based on their geographic characteristics, soil type, LUSs, and management history. Five LUSs were sampled in each of the three municipalities: (1) Native forest (FN); (2) *Eucalyptus* sp. plantation (EP); (3) Pasture (PA); (4) No-tillage (NT) and (5) Integrated Crop-livestock integration (ICL) (for details on the location and characterization of the areas see: Rosa 2013, Bartz *et al*. 2014a, b, Rosa *et al*. 2015).

All areas were part of a study of soil quality in different land use systems developed by the Embrapa Forestry (Colombo, PR), and Santa Catarina SisBiota Project, led by the *Universidade Estadual de Santa Catarina* (UDESC) at Chapecó. In these projects, soil fauna was evaluated as an indicator of soil quality in different LUS.

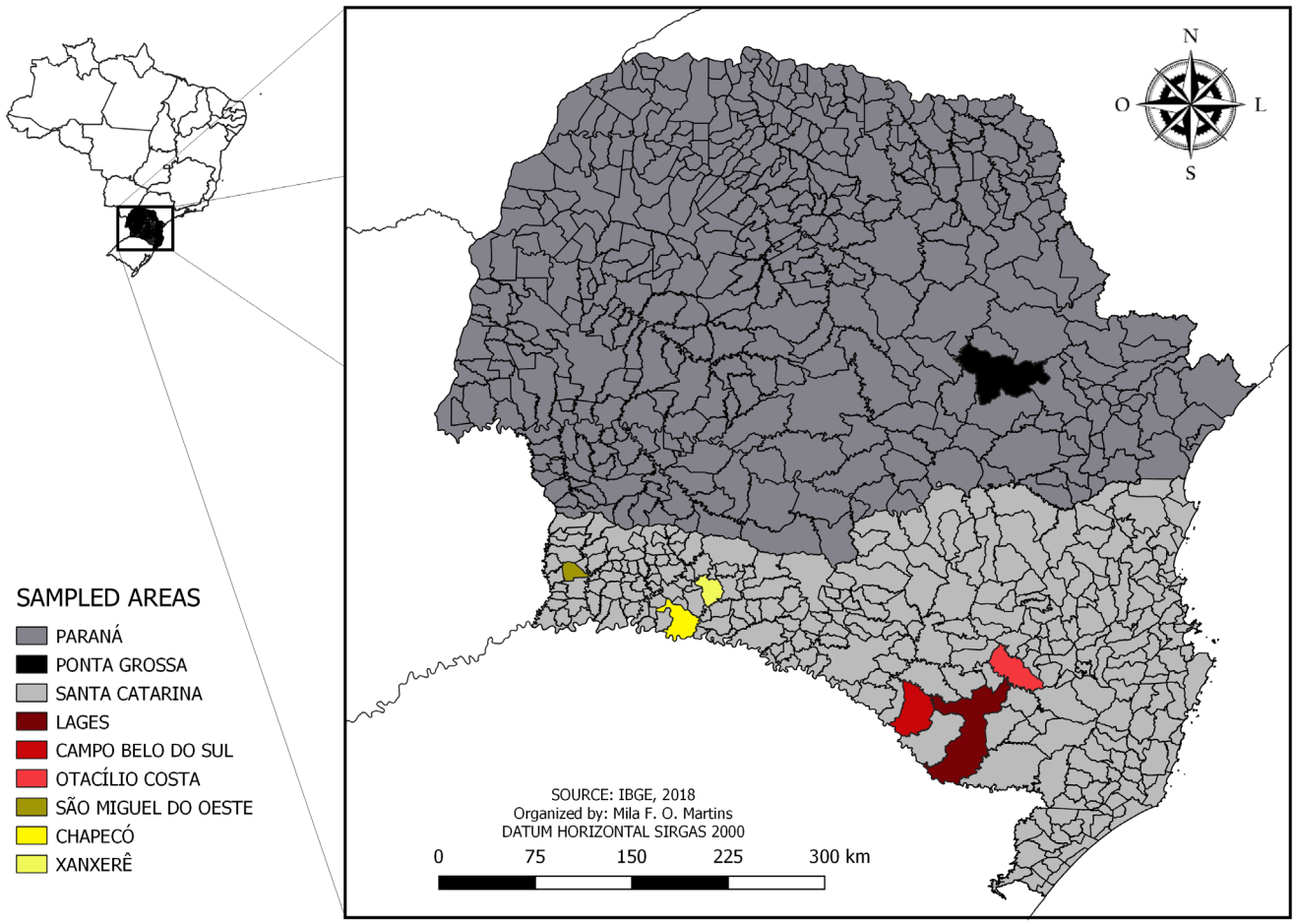


Figure 1. Map of the sampled areas.

2. *Sampling design*

The Tropical Soil Biology and Fertility Program organizes measures to monitor soil quality through the removal of monoliths in places where financial and technological resources are limited. The soil monoliths were 25 x 25 cm, and the depth at which they were collected was variable according to the extent of horizon A of the soil (Anderson & Ingram 1993, ISO 2018). This method can be applied to any soil type. The area for the removal of monoliths is delimited by a metallic quadrangular structure, followed by the excavation and removal of soil layers. Each layer is packed separately, and the associated fauna can be extracted either in the field or in the laboratory, with or whitout assistance of a stereomicroscope (Anderson & Ingram 1993). In the present study, all extractions were performed in the laboratory, without stereomicroscope. Our extractions, in Ponta Grossa, were made in layers up to 20 cm, delimited in three strata: 0 - litter; I – 0 to 10 cm and II – 10 to 20 cm. In Santa Catarina, extractions were not stratified.

We used material from two different sample designs, according to the research group involved in the sampling. In Paraná, samples were collected on four different dates. In the areas of ICLF, ICL, NF, NT, and EU, samples were taken in October and November 2012 and in April and May 2013. In the Vila Velha State Park, samples were taken in September 2013 and in January 2014. All areas of Santa Catarina (West and Plateau) were sampled in the course of two seasons: winter (July and August 2011) and summer (December 2011 and January 2012).

In Paraná, for each area (seven LUSs) three plots of 50 x 100 m (0.5 hectares) were delimited per LUS, within which five monoliths were extracted, separated by at least 200 m. These samples were distributed in a central transect, 20 meters from the edge of the plot. A zigzag pattern was drawn with samples always at least 20 m apart and following the slope of the plot (Zagatto, 2014) (Figure 2). A total of 105 monoliths (seven LUSs x three plots x five monoliths) were collected, divided into the depth layers mentioned above (0, I and II), totalling 315 sample units per season of the year (630 total samples).

In Santa Catarina, one area of each LUS (NF, EU, PA, ICL, and NT) was evaluated in each of the three municipalities per region (West and Plateau). Sampling grids, with nine points mounted in three lines of three points each, were sampled 20 m from the border and 30 m apart in each LUS, totaling one hectare. At each point a monolith was extracted and an epigaeic pitfall trap was installed (one meter distant from the monolith) (Figure 3). Each pitfall trap consisted of a 200 ml capacity recipient, half filled with water and detergent, buried with the opening at ground level and left in the field for 72 hours. A total of 270 samples of TSBF and 270 of epigaeic pitfalls (three municipalities x five LUSs x nine monoliths x two regions) were obtained per season (1080 total samples).

The ants from all areas were conditioned in 80% alcohol and sent to the *Laboratório de Sistemática e Biologia de Formigas* of the *Universidade Federal do Paraná* (UFPR). The material was processed

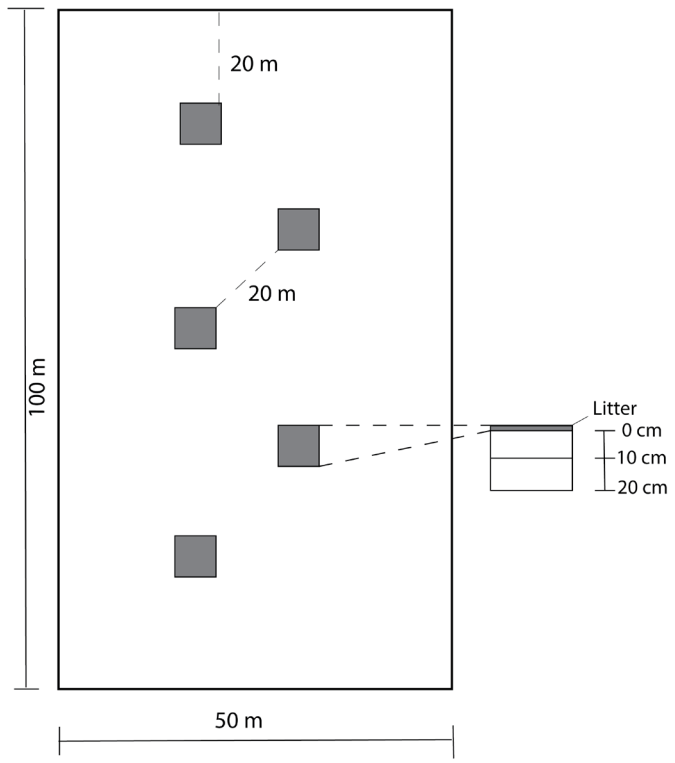


Figure 2. Schematic drawing of the sampling design in the state of Paraná. Adapted from Zagatto (2014).

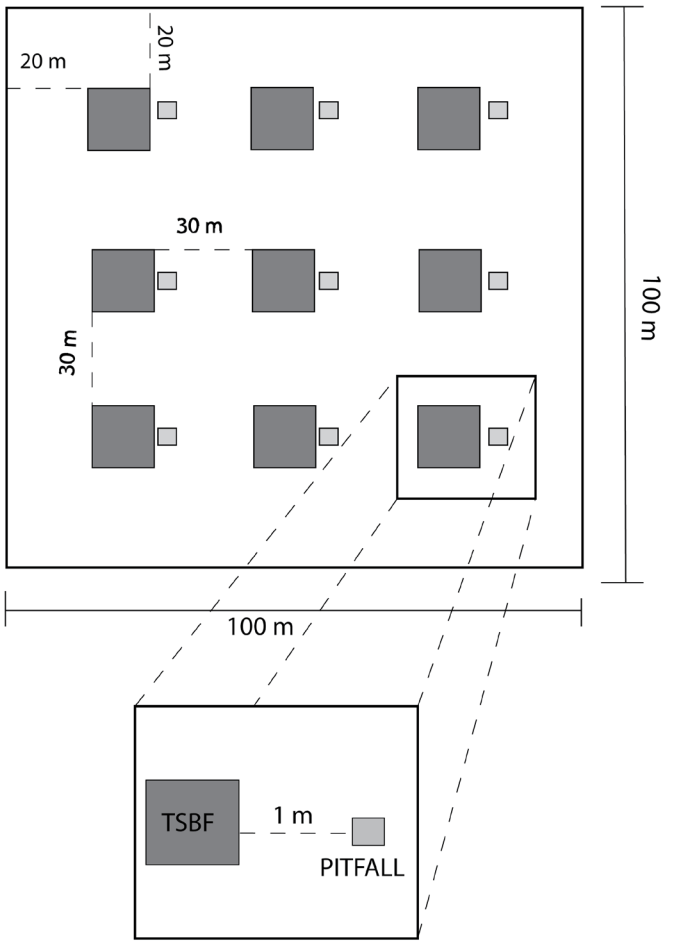


Figure 3. Schematic drawing of the sampling design in the state of Santa Catarina. Adapted from Bartz *et al.* (2014), and Rosa *et al.* (2015).

and identified to the specific level whenever possible. The identifications were generally based on the Guide for the Ant Genera of Brazil (Baccaro *et al.*, 2015). In addition, UFPR specialists (Alexandre C. Ferreira, Gabriela P. Camacho, John E. Latke, Mayron Escárraga, Rodrigo M. Feitosa, and Thiago S. R. da Silva) were consulted to confirm species identifications. Finally, whenever necessary, we performed comparisons with the material deposited in the *Coleção Entomológica Padre Jesus Santiago Moure* at UFPR (DZUP), where voucher material was deposited. The species that were not possible to name were identified as morphospecies.

3. *Data analysis*

Due to differences in the sampling design, the data were organized in two separate matrices that indicate presence and absence: one matrix with data from Paraná and the other with data from Santa Catarina. Since samples were taken at different seasons to increase the likelihood of finding different species, each species in a sampling unit was considered only once, regardless of the season when it was collected, as suggested by Brandão *et al* (2011). The observed richness (Sobs) obtained by each method and stratum were compared with the richness estimated by Jackniffe1 and Bootstrap. These estimators were chosen because they provide a satisfactory balance in the analyses, since they separately consider the effect of species occurring in a single sample (Jackniffe1) and of all species in the samples, without overweighting the presence of rare species (Bootstrap). To determine whether a species is epigaeic or hypogaeic, we used the exclusivity criterion: species collected only by the TSBF method or those present only in strata I and II were considered subterranean; conversely, the species collected only by pitfall traps or those present only in stratum 0 of the TSBF method were considered epigaeic. We used the samples from Paraná to evaluate the sampling efficiency of the TSBF method, since only these samples were stratified (layer separation by depth). The stratification allowed us to evaluate the presence of ants in the different strata, providing data not only on ant richness but also on aspects related to their biology (stratum of occurrence).

A generalized linear mixed model (GLMM) was used to verify if the presence of ants in strata was homogeneous (providing an equal probability of collection success between the layers). The model was elaborated from the proportion of ant occurrence in the plots (ranging from 0 to 5, in a half-hectare), with the strata as fixed variables and the LUSs as random variables. The model was compared by maximum likelihood and the data were evaluated for overdispersion, assuming a binomial distribution.

The analyses and graphs were performed in the R environment (version 3.1.3, R-CORE-TEAM 2016) with the *vegan*, *car*, *MASS*, *iNEXT* and *lme4* packages. The map of the localities was generated using Program QGis v. 2.16.3 and the coordinates provided in Zagatto (2014) and Rosa (2013) and the shape files obtained from the Brazilian Institute of Geography and Statistics data base - IBGE (2016). The figures were drawn in Adobe Illustrator (version CC 2018).

Results

1. *Richness and species frequency*

In total, 281 ant species were collected (considering all counties sampled and the different methods – epigaeic pitfall trap and TSBF). These species were distributed in 49 genera and 10 subfamilies (Table 1). The subfamilies with the greatest number of species were Myrmicinae, with 175 (61.4% of the species collected); Formicinae, 39 (13.7%); and Ponerinae, with 32 species (11.2%). The richest genera were *Pheidole*, with 98 species (34%), *Solenopsis* and *Hypoponera* with 22 species (7.7%) each.

In Santa Catarina, 238 species were collected by both methods (epigaeic pitfall and TSBF). Pitfalls collected 202 species and generated 1,585 records of occurrence, while the TSBF collected 149 species, generating 769 records (Table 2). From the total, 89 species were collected only in pitfall (51.7% of them composed by the genus *Pheidole*) and 36 only in the TSBF (Table 1). The three most frequent species in the pitfalls were *Pachycondyla striata* Smith, 1858, *Pheidole subarmata* Mayr, 1884 and *Linepithema micans* (Forel, 1908), with 109, 97 and 71 occurrences, respectively. In TSBF the species with the greatest number of records were *Hypoponera* sp. 1, *Hypoponera* sp. 8 and *Pheidole subarmata,* with 60, 57 and 42 records, respectively.

Table 1. Species list by region (Campos Gerais, West and Plateau) and municipality. PG - Ponta Grossa, SMO - São Miguel do Oeste, CHP - Chapecó, XAN - Xanxerê, LGS - Lages, OTC - Otacílio Costa, and CBS - Campo Belo do Sul). The species sampled exclusively by a method (in Santa Catarina) are indicated by symbols: ♦ - TSBF, ♣ - Pitfall; and the exclusive species per stratum are indicated with superscript numbers: ^{0} - litter, ^{I} - stratum I (0-10 cm), and ^{II} - stratum II (10-20 cm).

Species	Paraná		Santa Catarina				
	Campos Gerais		West			Plateau	
	PG	SMO	CHP	XAN	LGS	OTC	CBS
Amblyoponinae							
Fulakora armigera (Mayr, 1887)♦						X	
Fulakora elongata (Santschi, 1912)♦^{I}	X	X			X	X	X
Dolichoderinae							
Dorymyrmex brunneus Forel, 1908	X	X		X			
Dorymyrmex sp. 1♣			X				X
Dorymyrmex sp. 2♣							X
Linepithema gallardoi (Brèthes, 1914)♣		X					X
Linepithema humile (Mayr, 1868)♣	X					X	
Linepithema iniquum (Mayr, 1870)		X				X	
Linepithema leucomelas (Emery, 1894)♣					X		
Linepithema micans (Forel, 1908)	X	X	X	X	X	X	X
Linepithema pulex Wild, 2007^{I}	X						
Dorylinae							
Labidus coecus (Latreille, 1802)		X				X	
Labidus praedator (Smith, 1858)♣						X	X
Neivamyrmex sp. 1♦^{II}	X	X	X				
Neocerapachys splendens (Borgmeier, 1957)♦	X					X	
Sphinctomyrmex stali Mayr, 1866♦		X					
Ectatomminae							
Ectatomma edentatum Roger, 1863♣			X		X		
Ectatomma permagnum Forel, 1908^{I}	X						
Gnamptogenys rastrata (Mayr, 1866)♣					X		
Gnamptogenys regularis Mayr, 1870	X						
Gnamptogenys nr. *striatula*	X		X	X	X		X
Gnamptogenys sp. n. A♦						X	
Gnamptogenys striatula Mayr, 1884^{I}	X		X	X	X	X	X
Gnamptogenys sulcata (Smith, 1858)♣					X		
Typhlomyrmex major Santschi, 1923♦	X	X	X	X	X	X	X
Typhlomyrmex pusillus Emery, 1894^{I}	X		X		X	X	X

Continuation Table 1.

Species	Paraná		Santa Catarina				
	Campos Gerais		West		Plateau		
	PG	SMO	CHP	XAN	LGS	OTC	CBS
Formicinae							
Acropyga decedens (Mayr, 1887)♦					X		
Acropyga goeldii Forel, 1893	X			X	X	X	
Brachymyrmex coactus Mayr, 1887[I]	X						
Brachymyrmex pilipes Mayr, 1887♣	X		X				
Brachymyrmex pilipes gr. sp. 1♦		X					
Brachymyrmex sp. 1	X	X	X	X	X	X	
Brachymyrmex sp. 2	X	X	X	X	X	X	X
Brachymyrmex sp. 3	X	X	X	X	X	X	X
Brachymyrmex sp. 4	X						
Brachymyrmex sp. 5	X	X	X	X		X	
Brachymyrmex sp. 6	X	X		X		X	
Brachymyrmex sp. 7	X		X	X	X	X	X
Brachymyrmex sp. 8♣					X		
Brachymyrmex sp. 9		X				X	
Brachymyrmex sp. 10♣		X		X		X	
Camponotus balzani Emery, 1894					X	X	X
Camponotus blandus (Smith, 1858)					X	X	X
Camponotus brasiliensis Mayr, 1862[I]	X						
Camponotus crassus Mayr, 1862	X	X	X			X	X
Camponotus melanoticus Emery, 1894♣[I]	X	X	X		X		X
Camponotus novogranadensis Mayr, 1870	X		X	X			
Camponotus nr. *cingulatus*♣					X		X
Camponotus punctulatus Mayr, 1868					X	X	X
Camponotus renggeri Emery, 1894[II]	X		X	X			X
Camponotus rufipes (Fabricius, 1775)		X	X	X		X	X
Camponotus sexguttatus (Fabricius, 1793)[II]	X						
Camponotus zenon Forel, 1912♣			X	X			X
Camponotus sp. 1[I]	X						
Camponotus sp. 2	X						
Camponotus sp. 4♣							X
Camponotus sp. 5♣							X
Camponotus sp. 6♣				X			
Myrmelachista catharinae Mayr, 1887♣				X			
Myrmelachista nodigera Mayr, 1887♣						X	
Myrmelachista gallicola Mayr, 1887[I]	X						
Nylanderia fulva (Mayr, 1862)[I]	X	X	X	X			
Nylanderia sp. 1	X	X	X	X		X	
Nylanderia sp. 2			X	X	X		
Nylanderia sp. 3♦		X					

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Continuation Table 1.

Species	Paraná		Santa Catarina				
	Campos Gerais		West		Plateau		
	PG	SMO	CHP	XAN	LGS	OTC	CBS
Heteroponerinae							
Heteroponera dentinodis (Mayr, 1887)					X	X	X
Heteroponera mayri Kempf, 1962		X		X			X
Heteroponera microps Borgmeier, 1957♣		X					
Myrmicinae							
Acanthognathus ocellatus Mayr, 1887♦			X				
Acromyrmex aspersus (Smith, 1858)♣			X				
Acromyrmex crassispinus (Forel, 1909)[I]	X	X	X	X	X		X
Acromyrmex landolti (Forel, 1885)♣					X		
Acromyrmex lundii (Guérin-Méneville, 1838)♣					X		X
Acromyrmex subterraneus (Forel, 1893)♣			X	X			X
Apterostigma sp. 1			X				
Apterostigma sp. 2♣			X	X			
Atta sexdens (Linnaeus, 1758)		X	X	X	X	X	
Carebara sp. 1♦			X				
Carebara sp. 2♣						X	X
Carebara brasiliana Fernández, 2004♣			X				
Crematogaster ampla Forel, 1912♣						X	X
Crematogaster bruchi Forel, 1912	X		X				
Crematogaster corticicola Mayr, 1887♣	X			X			
Crematogaster quadriformis Roger, 1863			X		X		
Crematogaster sp. 1				X			
Crematogaster sp. 2					X		X
Cyphomyrmex rimosus (Spinola, 1851)		X	X		X	X	X
Cyphomyrmex sp. 1	X						
Cyphomyrmex sp. 2		X	X			X	X
Cyphomyrmex sp. 3♣						X	
Hylomyrma balzani (Emery, 1894)		X	X		X	X	X
Hylomyrma reitteri (Mayr, 1887)[I]	X	X	X				
Megalomyrmex pusillus Forel, 1912							X
Mycetophylax asper (Mayr, 1887)♣				X			
Mycetophylax lectus (Forel, 1911)		X	X	X			X
Mycetophylax olitor Forel, 1893		X					X
Mycetophylax plaumanni Kempf, 1962		X		X			
Mycocepurus goeldii (Forel, 1893)	X		X	X			
Mycocepurus smithii (Forel, 1893)		X	X				
Ochetomyrmex semipolitus Mayr, 1878♣					X		
Octostruma rugifera (Mayr, 1887)			X		X	X	X
Octostruma stenognatha (Brown & Kempf, 1960)♣		X				X	X
Oxyepoecus plaumanni Kempf, 1974[I]	X						
Oxyepoecus reticulatus Kempf, 1974	X	X	X		X	X	
Oxyepoecus rosai Albuquerque & Brandão, 2009		X	X			X	

Continuation Table 1.

Species	Paraná		Santa Catarina				
	Campos Gerais		West		Plateau		
	PG	SMO	CHP	XAN	LGS	OTC	CBS
Pheidole aberrans Mayr, 1868	X	X	X	X	X	X	X
Pheidole acutidens (Santschi, 1922)♣						X	
Pheidole breviseta Santschi, 1919		X	X	X	X	X	X
Pheidole cavifrons Emery, 1906	X				X	X	X
Pheidole fallax gr. sp. 1[0]	X						
Pheidole gertrudae Forel, 1886[0]	X	X	X	X			
Pheidole heyeri Forel, 1899		X	X	X	X	X	X
Pheidole oxyops Forel, 1908	x						
Pheidole nr. *rosula*					X	X	X
Pheidole radoszkowskii Mayr, 1884[I]	X						
Pheidole rosae Forel, 1901	X						
Pheidole subarmata Mayr, 1884	X	X	X	X	X	X	X
Pheidole transversostriata Mayr, 1887		X					
Pheidole triconstricta Forel, 1886		X	X	X			
Pheidole vafra Santschi, 1923	X						
Pheidole sp. n. A	X						
Pheidole sp. n. I[I]	X						
Pheidole sp. n. N[I]	X						
Pheidole sp. 1	X						
Pheidole sp. 2♦[I]	X		X				
Pheidole sp. 3[I]	X						
Pheidole sp. 4	X						
Pheidole sp. 5[I]	X						
Pheidole sp. 6	X						
Pheidole sp. 7	X						
Pheidole sp. 8	X						
Pheidole sp. 9	X						
Pheidole sp. 10	X						
Pheidole sp. 11		X			X	X	X
Pheidole sp. 12		X					X
Pheidole sp. 13					X	X	
Pheidole sp. 14♣		X			X	X	X
Pheidole sp. 15♣		X	X		X		X
Pheidole sp. 16♣		X	X	X		X	X
Pheidole sp. 17♣		X		X	X		
Pheidole sp. 18					X	X	
Pheidole sp. 19		X	X	X	X	X	X
Pheidole sp. 20			X	X	X	X	X
Pheidole sp. 21		X			X	X	
Pheidole sp. 22♦						X	
Pheidole sp. 23♣					X		
Pheidole sp. 24♣		X		X		X	
Pheidole sp. 25♣		X					

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Continuation Table 1.

Species	Paraná		Santa Catarina				
	Campos Gerais		West		Plateau		
	PG	SMO	CHP	XAN	LGS	OTC	CBS
Pheidole sp. 26		X	X		X		X
Pheidole sp. 27		X					
Pheidole sp. 28♣				X			
Pheidole sp. 29♣		X	X			X	X
Pheidole sp. 30			X	X	X		X
Pheidole sp. 31		X	X	X			
Pheidole sp. 32♦					X		
Pheidole sp. 33				X		X	
Pheidole sp. 34			X		X	X	
Pheidole sp. 35♣					X	X	X
Pheidole sp. 36♣			X				
Pheidole sp. 37♣				X	X		X
Pheidole sp. 38♣			X	X			
Pheidole sp. 39♣		X					
Pheidole sp. 40♣		X	X	X	X		
Pheidole sp. 41			X	X	X		X
Pheidole sp. 42♣		X	X				
Pheidole sp. 43♣					X	X	X
Pheidole sp. 44♣		X	X				
Pheidole sp. 45♣		X	X	X	X	X	X
Pheidole sp. 46♣			X	X	X		X
Pheidole sp. 47♣		X	X	X			
Pheidole sp. 48♣			X	X	X		
Pheidole sp. 49♣		X	X	X			
Pheidole sp. 50			X			X	
Pheidole sp. 51			X			X	
Pheidole sp. 52						X	X
Pheidole sp. 53♣				X			
Pheidole sp. 54♣		X					
Pheidole sp. 55♣		X	X				
Pheidole sp. 56♣				X		X	X
Pheidole sp. 57					X		X
Pheidole sp. 58♦					X		
Pheidole sp. 59♣					X		
Pheidole sp. 60♣					X		
Pheidole sp. 61					X	X	
Pheidole sp. 62		X	X	X			
Pheidole sp. 63♣				X			
Pheidole sp. 64♣				X			
Pheidole sp. 65♣				X			
Pheidole sp. 66♣							X
Pheidole sp. 67♣		X					
Pheidole sp. 68				X	X		X

Continuation Table 1.

Species	Paraná		Santa Catarina				
	Campos Gerais		West		Plateau		
	PG	SMO	CHP	XAN	LGS	OTC	CBS
Pheidole sp. 69♦						X	
Pheidole sp. 70♣					X		
Pheidole sp. 71♣		X					
Pheidole sp. 72♣					X	X	X
Pheidole sp. 73♣					X		X
Pheidole sp. 74♣						X	
Pheidole sp. 75♣					X		X
Pheidole sp. 76♣				X		X	X
Pheidole sp. 77♣				X	X	X	
Pheidole sp. 78♣							X
Pheidole sp. 79♣				X			
Pheidole sp. 80♣		X					
Pogonomyrmex naegelli Emery, 1878	X		X		X	X	
Rogeria bruchi Santschi, 1922♦					X		
Solenopsis gr. *geminata* sp. 1[I]	X						
Solenopsis gr. *geminata* sp. 2		X	X	X	X	X	X
Solenopsis gr. *geminata* sp. 3♣			X	X			
Solenopsis invicta Buren, 1972	X	X	X	X	X	X	X
Solenopsis sp. 1♣	X	X		X			
Solenopsis sp. 2	X	X				X	
Solenopsis sp. 3[I]	X			X		X	X
Solenopsis sp. 4	X						
Solenopsis sp. 5	X						
Solenopsis sp. 6[II]	X						
Solenopsis sp. 7♣	X					X	
Solenopsis sp. 8[I]	X						
Solenopsis sp. 9	X	X	X	X	X	X	X
Solenopsis sp. 10		X	X	X	X	X	X
Solenopsis sp. 11			X	X	X		X
Solenopsis sp. 12		X	X	X	X	X	X
Solenopsis sp. 13		X	X	X	X	X	X
Solenopsis sp. 14♣		X	X		X	X	
Solenopsis sp. 15		X	X	X	X	X	X
Solenopsis sp. 16		X					X
Solenopsis sp. 17					X	X	
Solenopsis sp. 18♦				X			
Strumigenys appretiata (Borgmeier, 1954)					X		X
Strumigenys denticulata Mayr, 1887♦			X				
Strumigenys eggersi Emery, 1890		X	X				
Strumigenys louisianae Roger, 1863[I]	X						
Strumigenys oglobini Santschi, 1936♣		X					
Strumigenys nr. *epinotalis*[I]	X						

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Continuation Table 1.

Species	Paraná		Santa Catarina				
	Campos Gerais		West		Plateau		
	PG	SMO	CHP	XAN	LGS	OTC	CBS
Strumigenys nr. *louisianae* sp. 1♣					X		
Strumigenys nr. *louisianae* sp. 2			X	X	X	X	
Strumigenys nr. *louisianae* sp. 3♣					X		
Mycetomoellerius holmgreni Wheeler, 1925					X	X	X
Mycetomoellerius sp. 1					X	X	X
Mycetomoellerius sp. 2♣					X		
Tranopelta gilva Mayr, 1866	X				X		
Wasmannia affinis Santschi, 1929	X	X	X		X	X	
Wasmannia auropunctata (Roger, 1863)		X	X	X	X	X	X
Wasmannia sulcaticeps Emery, 1894		X	X		X	X	
Ponerinae							
Centromyrmex brachycola (Roger, 1861)	X						
Hypoponera foreli (Mayr, 1887)	X	X	X	X	X	X	X
Hypoponera opaciceps (Mayr, 1887)		X	X	X	X	X	X
Hypoponera sp. 1	X	X	X	X	X	X	X
Hypoponera sp. 2	X	X	X	X			X
Hypoponera sp. 3	X						
Hypoponera sp. 4	X						
Hypoponera sp. 5♦	X		X		X	X	
Hypoponera sp. 6 I	X	X		X	X	X	X
Hypoponera sp. 7	X						
Hypoponera sp. 8	X	X	X	X	X	X	X
Hypoponera sp. 9^{0}	X						
Hypoponera sp. 10^{I}	X				X	X	X
Hypoponera sp. 11	X		X	X	X	X	X
Hypoponera sp. 12^{II}	X						
Hypoponera sp. 13		X			X	X	X
Hypoponera sp. 14			X			X	
Hypoponera sp. 15						X	X
Hypoponera sp. 16♦		X	X		X	X	X
Hypoponera sp. 17♦			X	X			
Hypoponera sp. 18♦					X		
Hypoponera sp. 19♦						X	
Hypoponera sp. 21♦						X	
Hypoponera sp. 22♦				X			
Hypoponera sp. 23♦	X	X					
Neoponera bucki (Borgmeier, 1927)♣					X		X
Odontomachus chelifer (Latreille, 1802)		X	X	X			
Pachycondyla harpax (Fabricius, 1804)		X	X	X			X
Pachycondyla striata Smith, 1858		X	X	X	X	X	X
Rasopone ferruginea (Smith, 1858)♦				X			
Simopelta curvata (Mayr, 1887)♦		X	X				

Continuation Table 1.

Species	Paraná		Santa Catarina				
	Campos Gerais		West			Plateau	
	PG	SMO	CHP	XAN	LGS	OTC	CBS
Proceratiinae							
Discothyrea sexarticulata Borgmeier, 1954[0]	X						
Proceratium brasiliense Borgmeier, 1959♦						X	
Pseudomyrmecinae							
Pseudomyrmex flavidulus (Smith, 1858)♦	X	X					
Pseudomyrmex gracilis (Fabricius, 1804)[I]	X						
Pseudomyrmex longus (Forel, 1912)[I]	X						
Pseudomyrmex termitarius (Smith, 1877)♦			X				
Pseudomyrmex sp. 1	X		X				
Pseudomyrmex sp. 2♣							X
Total number of species	**101**	**103**	**108**	**94**	**111**	**109**	**101**

Table 2. Observed (Sobs) and estimated (estimators: Jackknife 1 – Jack1 and Bootstrap - Boot) richness and number of exclusive species by method (Pitfall and TSBF) in Santa Catarina.

Methods	Sobs	Jack1	Boot	Exclusive
Pitfall	202	260	227	89
TSBF	149	213	176	36
Total	238	294	323	-

In Paraná, the TSBF method collected 101 species (Table 1), with 44, 88 and 52 species at strata 0, I and II (Table 3), and 97, 301 and 121 occurrence records, respectively. Four out of the 101 species were collected exclusively in stratum 0, 30 only in stratum I and five in stratum II (Table 1). The most frequent species were *Hypoponera* sp. 1, *Brachymyrmex* sp. 5 and *Pheidole cavifrons* Emery, 1906, with 53, 25 and 16 occurrence records. Species occurrences in strata were as follows: in litter (stratum 0), the three most frequent species were *Hypoponera* sp. 1, with 12 records; *Brachymyrmex* sp. 1, and *Brachymyrmex* sp. 5, with seven records each. In stratum I (0-10 cm), the most frequent species were *Hypoponera* sp. 1, *Hypoponera* sp. 3 and *Brachymyrmex* sp. 3, with 29, 17 and 14 records, respectively. In stratum II (10-20 cm), the highest frequency was recorded for *Hypoponera* sp. 1, *Brachymyrmex* sp. 5 and *Pheidole cavifrons*, with 12, 8 and 7 records.

Table 3. Observed richness (Sobs) and estimated (estimators: Jackknife 1 – Jack1 E Bootstrap - Boot) and number of exclusive species by strata (0 - litter, I - 0-10 cm, and II- 10-20 cm).

Strata	Sobs	Jack1	Boot	Exclusive
0	44	66	54	4
I	88	125	106	30
II	53	77	64	5
Total	101	129	114	-

The collector curves constructed for each method demonstrate that a greater effort would be required to reach the asymptote (although this is apparently close), and that the number of accumulated species per sample unit was greater in pitfall than in TSBF (Figure 4a). Epigaeic pitfall collected 77% and TSBF 70% of the numbers estimated by Jackknife 1 and 89% and 84% of the numbers estimated by Bootstrap (Table 2).

The collector curves for strata performed with data from Paraná show that under the same sampling effort there is a greater addition of species in stratum I, in relation to the others (Figure 4b). The numbers of species observed approximate the Bootstrap estimated values (Table 3). The species collected in each stratum correspond to 66%, 70% and 69% of the species estimated by Jackknife 1 (for strata 0, I and II respectively) and 81%, 83% and 83% of the species estimated by Bootstrap. The total number of species corresponds to 78% and 88% of the estimate by Jackknife 1 and Bootstrap, respectively.

2. Subterranean ant assembly characterization

In the regions of Santa Catarina, we obtained 89 species exclusively in the epigaeic stratum and 36 species in the subterranean stratum. Seven species were recorded for the first time in the Plateau region of Santa Catarina and were collected only by TSBF: *Acropyga decedens* (Mayr, 1887), *Fulakora armigera* (Mayr, 1887), *Gnamptogenys reichenspergeri* (Santschi, 1929), *Neocerapachys splendens* (Borgmeier, 1957), *Proceratium brasiliense* Borgmeier, 1959, *Sphinctomyrmex stali* Mayr, 1866 and *Typhlomyrmex major* Santschi, 1923. No new records were found for the western region. Fifty-eight species were collected in Pitfall traps only once, while single species occurrences in TSBF samples totalled 64. These numbers correspond to different proportions ($\chi^2 = 7.05$, p = 0.007, gl = 1), with 28.7% and 42.9%, respectively, of the total species collected by each method.

In Paraná, where the method utilised was exclusively TSBF, seven species were present only in stratum I: *Fulakora elongata* (Santschi, 1912), *Gnamptogenys reichenspergeri*, *Oxyepoecus plaumanni* Kempf 1974, *Pheidole radozskowskii* Mayr, 1884, *Pseudomyrmex gracilis*

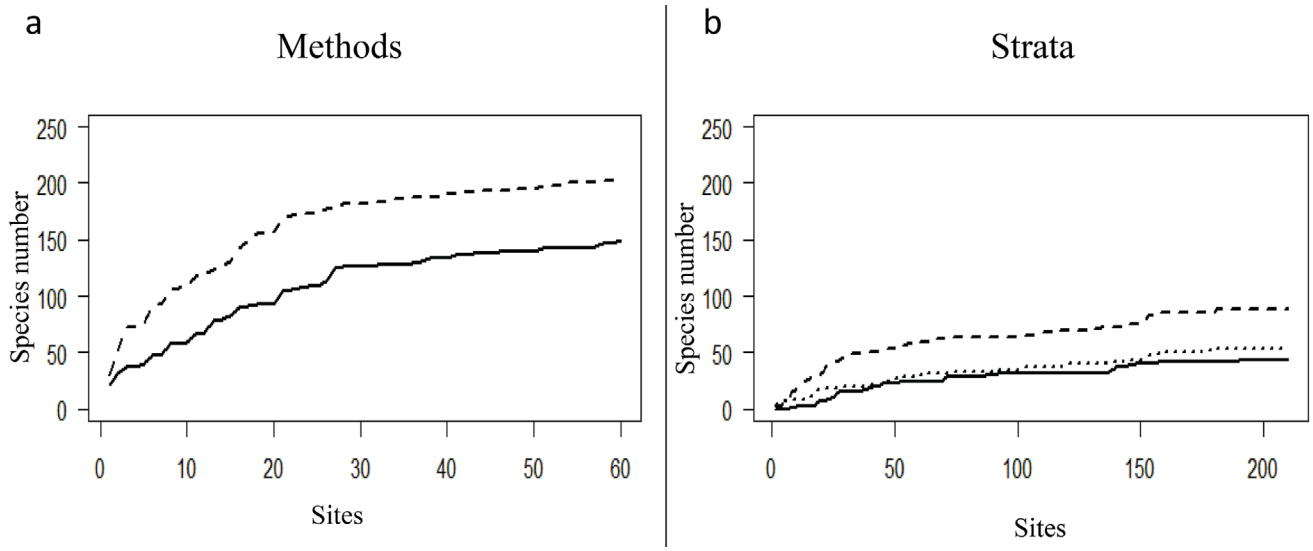


Figure 4. a - Collector's curves for both methods (Pitfall and TSBF). Dashed line: Pitfall; and continuous line: TSBF. b - Collector's curve for the strata. Continuous line: stratum 0; dashed line: stratum I; and dotted line: stratum II.

(Fabricius, 1804), *P. longus* (Forel, 1912) and *Tranopelta gilva* Mayr, 1866. In stratum II, *Neivamyrmex* sp.1 was the only species (with only one occurrence).

The number of species with only one record of occurrence in strata was 22 for stratum 0, 37 for stratum I and 24 for stratum II (Figure 5a, b, and c). These species correspond to 50%, 42.1% and 46.1% of the total species collected in each stratum. The graph of observed richness (Sobs) and frequency of occurrence per stratum (Figure 5d) shows that in stratum I there is a great number of species that occur more frequently. Stratum I had the highest number of occurrence frequencies, once this is the stratum with the highest number of occurrences of ants (GLMM, Binomial, $z = 5{,}239$, $df = 4$, $p < 0.05$), with a probability of occurrence of 86.10 % in the sampled areas.

Discussion

The present study delimited and characterized subterranean ant assemblages in the subtropical regions of the Neotropics. In these regions, only two previous studies collected subterranean ants: (1) Silva & Silvestre (2004) in Western Santa Catarina, and (2) Schmidt & Diehl (2008) in Rio Grande do Sul. This is the first survey that evaluates subterranean ant assemblages in Paraná and the Plateau region of Santa Catarina. Despite the different sampling efforts, the aforementioned publications presented 32 and seven species belonging to the subterranean stratum, representing only 28% and 20% of the total species observed by those authors, respectively. Considering the number of species with restricted occurrence in the subterranean stratum in all sampled localities, our results were similar (in percentage): 57 species, or 20.2% of the total collected (Table 1).

The biology of most subterranean species is unknown. TSBF samples provide data of occurrence and preference among strata, nesting, and species composition in the different soil layers. The manual extraction of ants in the stratified monoliths, characteristic of this method, provides the opportunity for *in loco* observation of the collected organisms. Wong & Guénard (2017) emphasized the importance of the "observer bias" (represented by different levels of experience in active collections), in which a collector may underestimate the presence of subterranean ants (especially the small ones) in samples or even in the field. This error can be reduced if sorting is performed under a stereomicroscope.

The total number of species observed in each municipality of Santa Catarina is extremely close to that observed in other studies already conducted in those regions (see Silva & Silvestre 2004, Ulysséa *et al.* 2011, Lutinski & Morais 2013). However, the number of species collected in Paraná is considerably high when compared with the richness found by other studies employing different methods for sampling subterranean ants (see Table 1 and Wong & Guénard 2017). This could indicate a higher efficiency of TSBF in sampling subterranean ants in these areas. However, additional studies comparing methods for collecting hypogaeic ants are indispensable to confirm this tendency. These comparisons should especially consider the most practical and widely employed method currently, the hypogaeic pitfall traps (Schmidt & Solar, 2010).

When epigaeic pitfall traps and TSBF are compared, it becomes clear that pitfall traps capture a greater number of species that have a high frequency of occurrence. However, when evaluating the number of infrequent species, TSBF is superior (42.7% of the species sampled). This may be explained by the fact that pitfall traps remained in the field for 72 hours, increasing the likelihood of species occurring more than once and increasing the number of species captured (see Lasmar *et al* 2017). Another factor that can explain this difference is the higher ant activity in the ground surface due to nesting and foraging than in the hypogaeic stratum (Jacquemin *et al.* 2016). In addition, in Santa Catarina, 36 species were collected exclusively by TSBF. This means that 15% of the species sampled there in this study would not have been registered without an association between the pitfall and a specific sampling method for the subterranean stratum.

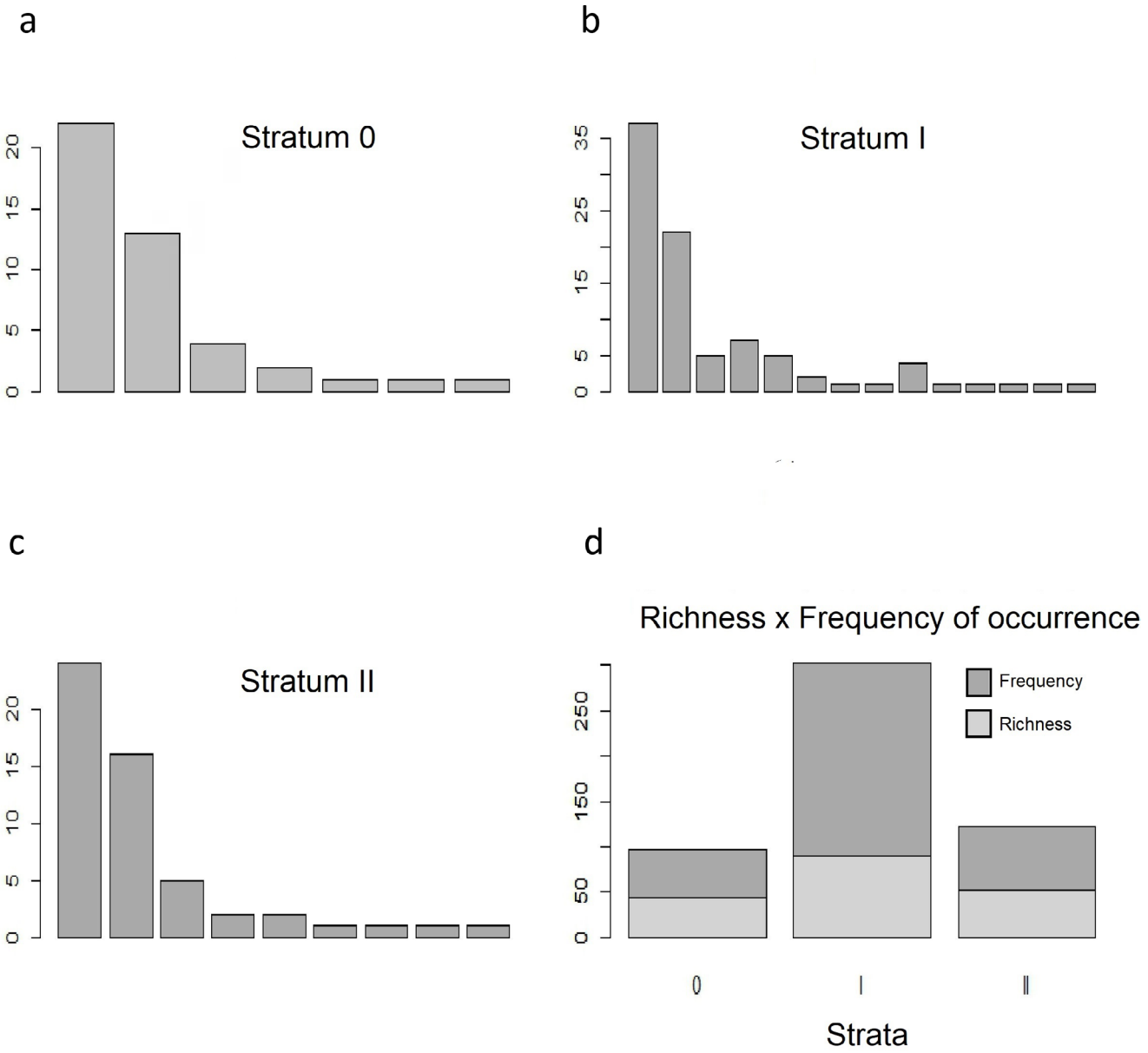


Figure 5. a to c - Fisher graphs for each stratum sampled in Paraná; d - Comparative graph of observed richness (Sobs) and frequency of occurrence between the strata.

The results obtained by the GLMM analysis of the Paraná data show that stratum I has more species than the other strata. A similar result was found by Andersen & Brault (2010) and Rider Wilkie *et al.* (2007), who also obtained a greater number of species in the topsoil and a great number of exclusive species (19 species) in this layer (up to 12,5 cm). These results indicate a tendency for greater richness and frequency of occurrence in this stratum, which consequently must be considered during the sampling design of projects focusing on subterranean ants or even in comprehensive inventories of the ant fauna.

Sampling methods that record assemblages in different vertical strata allow for a more efficient evaluation of the association between ants and micro habitats. This association was effective for the delimitation of species that occur in different strata also in Jacquemin *et al.* (2016) and in the present work. The criterion of exclusive delimitation of occurrence used here proved to be efficient, as observed by Fowler *et al.* (2000). Most species identified by these authors belonged to a unique stratum (collected only in epigaeic traps or only in hypogaeic traps). Considering the exclusivity of occurrence in the strata, and collection methods (pitfall and TSBF), 33% of the total species are epigaeic and 20% are hypogaeic.

More than a quarter (28.5%) of the species identified in this study are subterranean and most can be considered infrequent. We thus consider the criterion "exclusivity" (stratum and/or method) a good approach for delimiting the subterranean habit, as already mentioned in literature (e.g. Fowler *et al.* 2000). However, the delimitation of subterranean ant species was possible only with the association of epigaeic and hypogaeic sampling methods. In addition, we found that in stratified TSBF samples the 0-10 cm stratum has the greatest number of species

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and highest frequency of occurrence. This fact, allied to the number of species obtained through sampling by the TSBF method, indicates that this is a useful method for sampling subterranean ants.

The localities sampled in this study are under intense pressure for urbanization and agricultural production. Thus, TSBF is a promising tool in diversity assessments (because it is a widely used method in soil quality studies, facilitating the acceptance by producers for the development of research in their areas), especially to access the impact of human activities on subterranean species. In addition, it was demonstrated that the TSBF captures rarely sampled species or species that are still undiscovered.

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Author Contributions

Mila Ferraz de Oliveira Martins: contributed substantially in the concept of the study, in data collection, data analysis and interpretation, and to prepare the manuscript.

Marcílio José Thomazini: contributed in the concept and design of the study; data collection, and to critical revision, adding intellectual content.

Dilmar Baretta: did a substantial contribution in the concept and design of the study, data collection, contributed to data analysis and interpretation and did a critical revision, adding intellectual content

Marcio Gonçalves da Rosa: contributed in the concept and design of the study, data collection, data analysis and interpretation, and did a critical revision, adding intellectual content

Maurício Rumenos Zagatto: contributed in the concept and design of the study, and data collection.

Alessandra Santos: contributed in the concept and design of the study, and data collection.

Herlon S. Nadolny: contributed in data collection

Guilherme B. X. Cardoso: contributed in data collection

Cintia C. Niva: contributed in data collection

Marie L. C. Bartz: contributed in the concept and design of the study, and data collection.

Rodrigo M. Feitosa: contributed substantially in the concept of the study, in data collection, data interpretation, and to prepare the manuscript.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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Article

Pathways to positive scenarios for the Amazon forest in Pará state, Brazil

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SIQUEIRA-GAY, J., YANAI, A. M., LESSMANN, J., PESSÔA, A. C. M., BORJA, D., CANOVA, M., BORGES, R. C. **Pathways to positive scenarios for the Amazon forest in Pará state, Brazil.** Biota Neotropica. 20(suppl. 1): e20190905. https://doi.org/10.1590/1676-0611-BN-2019-0905

Abstract: Infrastructure projects and agriculture expansion are increasingly threatening forest conservation in Pará state (Brazil). It becomes necessary to address the implications of these activities on the Amazon complex socio-ecological system, considering both material and non-material aspects of Nature´s Contributions to People (NCP). Multiple studies developed future scenarios for the Amazon, but only a few have focused on discussing positive futures derived from policies and interventions based on conservation and human well-being. Here, we aim at understanding the drivers of forest cover change to produce positive scenarios for the future of the Amazon forest in Pará state. By using the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) conceptual framework, we identified as direct drivers of forest cover change: (i) roads construction; (ii) forest degradation; (iii) hydropower projects; (iv) urban expansion; (v) agriculture and pasture expansion; (vi) rural land occupation; (vii) mining; (viii) climate change. As indirect drivers we identified: (i) energy demand; (ii) population growth; (iii) land prices; (iv) commodity demand; (v) consumption behavior. The development of conservation strategies in the borders of deforested areas is needed given the high demand for Nature´s Contributions to People supply. We also propose policies to address the main drivers of forest cover change, influencing land management and consumption behavior in the state. At last, we envision future positive scenarios that would emerge from policy applications and sustainable actions. Based on our study, we discuss the importance of social learning for developing pathways leading to positive futures that consider the integrity and development of both ecological and social systems.

Keywords: Deforestation, Biodiversity, Ecosystem services, Forest degradation, Conceptual framework, IPBES.

Caminhos de cenários positivos para a floresta Amazônica no estado do Pará, Brasil.

Resumo: Projetos de infraestrutura e expansão agrícola estão cada vez mais ameaçando a conservação florestal no estado do Pará (Brasil). Assim, torna-se necessário abordar as implicações dessas atividades no complexo sistema sócio ecológico da Amazônia, considerando aspectos materiais e não materiais das Contribuições da Natureza para as Pessoas (NCP).Vários estudos desenvolveram cenários para o futuro da floresta Amazônica, porém poucos foram aqueles focados em discutir futuros positivos, derivados da aplicação de políticas e de intervenções baseadas em estratégias de conservação e de sustentabilidade. Neste trabalho buscamos entender os principais fatores determinantes da mudança na cobertura florestal no estado do Pará, de forma a produzir cenários positivos para o futuro da floresta amazônica nesse estado. A partir da estrutura conceitual proposta pela Plataforma Intergovernamental sobre Biodiversidade e Serviços Ecossistêmicos (IPBES) identificamos as principais pressões diretas e indiretas que influenciam na perda de floresta no estado, e os articulamos em um modelo conceitual. As pressões diretas identificadas foram: (i) construção de estradas; (ii) degradação florestal; (iii) projetos para construção de hidrelétricas; (iv) expansão urbana; (v) expansão da agricultura e da pecuária; (vi) ocupação de terras rurais; (vii) mineração; (viii) mudanças climáticas. As pressões indiretas identificadas foram: (i) demanda por energia; (ii) crescimento populacional; (iii) preços da terra; (iv) demanda por commodities; (v) hábitos de consumo. Assim, evidenciamos a importância do desenvolvimento de estratégias de conservação nas áreas de fronteiras de desmatamento devido à alta demanda e oferta por Contribuições da Natureza para as Pessoas (NCPs). Foram propostas políticas para influenciar mudança no gerenciamento da terra e nos hábitos de consumo de forma a abordar os principais fatores de mudança da cobertura florestal no estado. Por fim, nós construímos cenários futuros positivos que emergiriam da aplicação de políticas e ações voltadas para sustentabilidade da natureza e dos serviços ecossistêmicos. Com base em nossa avaliação, enfatizamos a importância do aprendizado social para que possam ser discutidos os caminhos que levam a futuros positivos, que consideram a integridade e o desenvolvimento tanto dos sistemas sociais quanto dos sistemas ecológicos.

Palavras-chave: Desmatamento, Biodiversidade, Serviços ecossistêmicos, Degradação florestal, Modelo conceitual, IPBES.

Introduction

The Amazon rainforest is one of the most biodiverse regions on Earth (Laurance et al. 2002). This region is key to sustain life, mitigating climate change by sinking and stocking carbon (Pütz et al. 2014). Its ecological processes and systems also represent a major element to sustain the production of goods relevant to human wellbeing, such as food, minerals, and timber (Strand et al. 2018). Furthermore, it is a culturally rich region, home to traditional and indigenous communities. These communities maintain a unique knowledge, that is instrumental for forest conservation (Agrawal 1995).

Drivers of forest cover change, such as infrastructure projects and agriculture expansion, largely affect the provision of ecological processes and functions, ultimately hindering the maintenance of Amazonian ecosystem integrity, at local, regional, and global scales. The Pará state (Brazilian Eastern Amazon) presented the highest forest loss of the Brazilian Amazon states in 2019 (3,862 km²), with an increasing rate of 41% when compared to 2018 (Brazil, INPE, 2019). This rate followed a history of anthropogenic occupancy (last 50 years) mainly caused by anthropogenic actions such as road building (Fearsnide 2008, Soares-Filho et al. 2004), hydropower projects (Athayde et al. 2019), mining (Lobo et al. 2018, Sonter et al. 2017, Souza-Filho et al. 2016) and agriculture expansion (Brown et al. 2016, Simmons et al. 2007, Simon & Garagorry 2005), which challenges forest conservation within the state.

In response to these pressures, the Brazilian government has proposed a series of policies, such as PPCDAm (Portuguese acronym for: Action Plan for the Prevention and Control of Deforestation in the Legal Amazon), that includes the creation of new protected areas (Herrera et al. 2019), and the soy and beef moratorium (Gibbs et al. 2015, Boucher et al. 2013). However, the clash between multiple worldviews and understandings of environmental governance and global change has challenged the implementation of these socio-environmental policies (Rodrigues-Filho et al. 2015, Carvalho et al. 2019) and the current trends of increasing deforestation, mainly in response to political actions, suggests further degradation of the Amazon forest (West et al. 2019, Armenteras et al. 2019).

The Brazilian Amazon, a very complex socio-ecological system, represents an arena for the interplay between scientific and local representations (e.g., oral accounts, metaphors, symbols, and values) (Rajão 2013). Although multiple factors are often neglected by studies of forest governance, including the cultural and relational values that forest have to local people, these aspects are of primary importance for the development of protection, conservation and sustainability policies (Chan et al. 2018). Therefore, the region needs a shift from traditional ways of building scenarios and policies towards a more integrative and nature-centered pathway for building a sustainable future for the Amazon forest.

The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) proposed a novel conceptual framework that gauge the multiple factors influencing and controlling environmental change (Díaz et al. 2015). One of the key elements of this framework is the notion of Nature´s Contributions to People (NCP).

As presented (Díaz et al. 2018, p. 270), the NCP concept has two main features: "first, the NCP approach recognizes the central and pervasive role that culture plays in defining all links between people and nature". "Second, the use of NCP elevates, emphasizes, and operationalizes the role of indigenous and local knowledge in understanding nature's contribution to people."

As such, IPBES contribution to environmental governance is twofold. Firstly, the NCP framework builds on a participatory process through reviews and workshops conducted with stakeholders across the globe. Secondly, the framework not only draws on scientific knowledge from various streams (e.g. natural, economic, social and engineering) but also developed by integrating knowledge produced by a broad spectrum of stakeholders, such as indigenous and local people, nongovernmental organizations (NGOs), and governments (Díaz et al. 2015). The IPBES new understanding of human-nature relationships has motivated the production of the Nature Futures Framework (NFF), which allows multiple actors to create policies and practices considering different views on nature and values. This framework also represents a tool to develop positive narratives to push forward pro-environment behavior and to discuss potential actions towards meeting global environmental goals (Rosa et al. 2017, Lundquist et al. 2017).

Previous studies conducted in the Amazon have proposed future projections considering new infrastructure construction involving different approaches to model forest cover change close to roads, infrastructure projects and protected areas (Laurance et al., 2001; Rosa et al., 2013; Soares-Filho et al., 2006). However, few of them provide an integrative positive future with different views and values of Amazon and propose policies targeting reducing forest cover change. Thus, we aim at providing an understanding of the drivers of forest cover change in Pará state by applying the IPBES framework for proposing ways to shift current trends towards positive scenarios. We identified the main drivers causing forest loss to propose policies that tackle it in Pará state. We seek mainstreaming knowledge and values in the decision-making of tropical forest conservation, grasping the environmental change caused by socio-environment relationships.

Materials and Methods

This work started with a series of exercises facilitated by researchers, scholars, and experts who work with policy-science interface and have extensive knowledge about the IPBES framework (Díaz et al. 2015). These exercises took place at the São Paulo School of Advanced Science on Scenarios and Modelling on Biodiversity and Ecosystem Services to Support Human Well-Being from July 1 to 15, 2019.

The main steps to develop positive scenarios included (Figure 1): (i) identifying main drivers (direct and indirect) of forest cover change; (ii) building a conceptual model that links drivers to forest cover change and their interrelationships; (iii) assessing NCPs by considering their local supply and demand; (iv) analyzing the NFF; (v) proposing policies to reduce regional forest loss; (vi) discussing implications for positive scenarios.

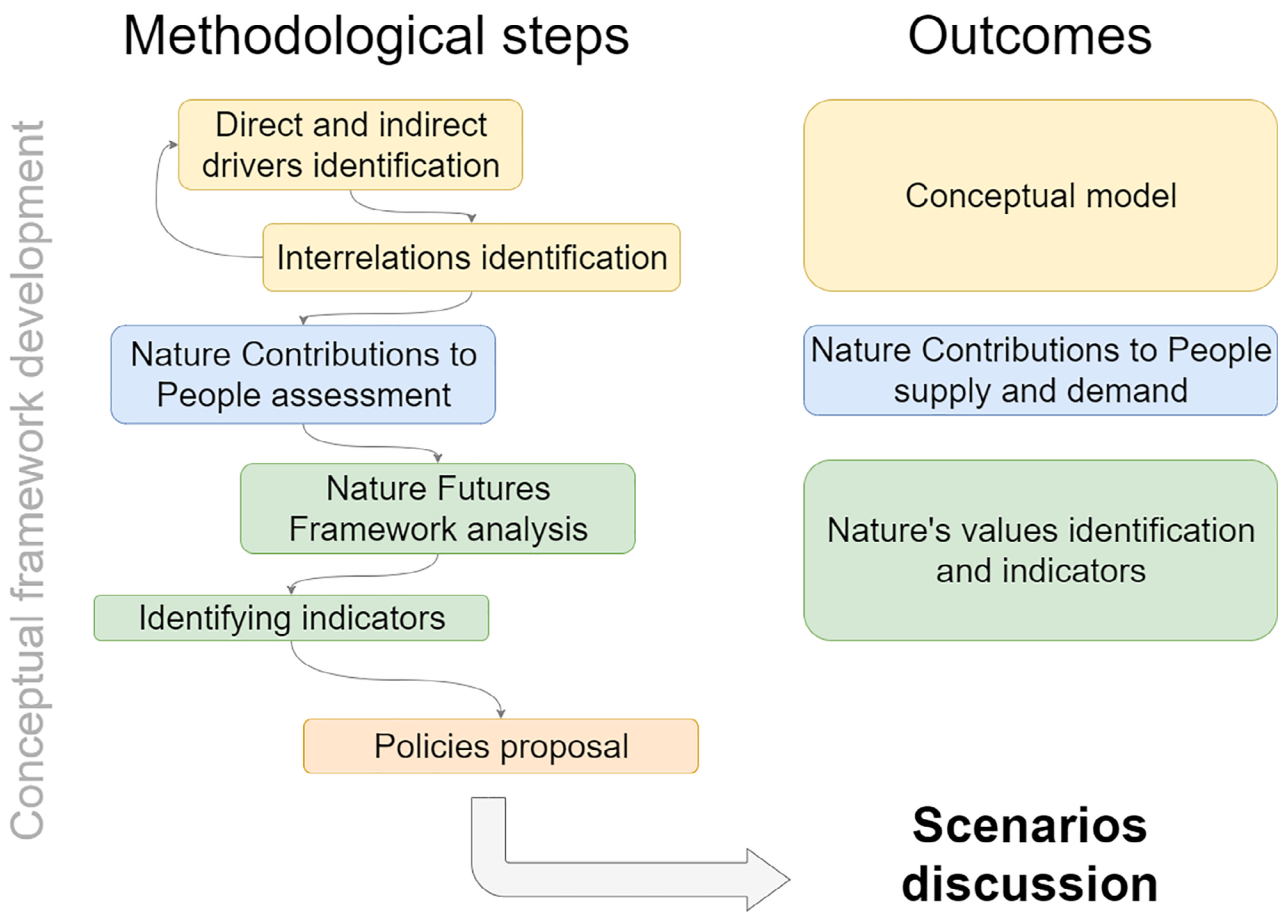


Figure 1. Flowchart with the steps from the conceptual framework development to policies and scenarios proposals.

Our study object is the forest cover change in Pará state, Brazil (Figure 2). The increased deforestation allied with action of multiples drivers of forest cover change evidence the importance of sustainability policy development in Pará (Figure 2C). The second largest state in Brazil, Pará plays an important role in the socio-economic dynamic in the Brazilian Amazon, sheltering large dams, mining areas and highways projects.

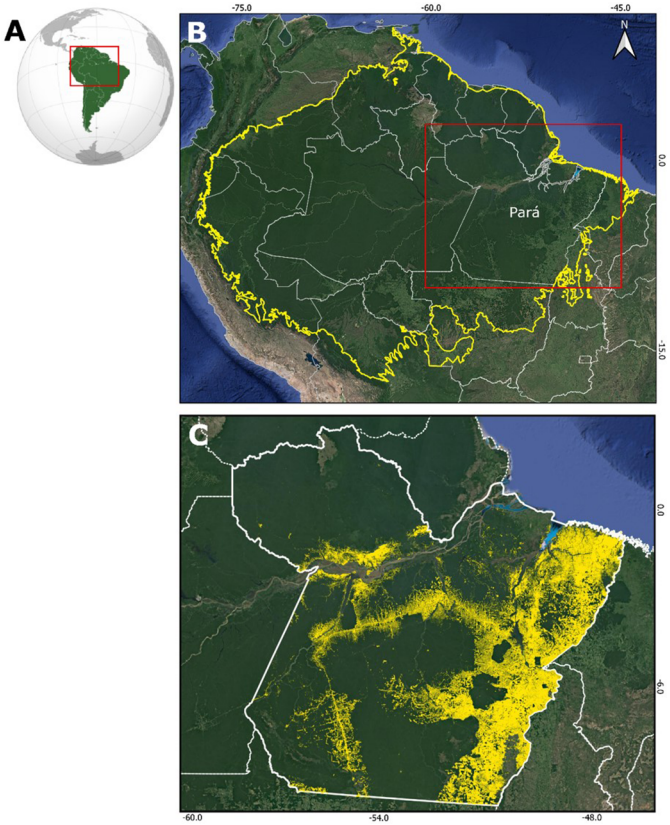


Figure 2. Pará state location. Location of the Amazon basin in South America (A), location of Pará in the Amazon (B), accumulated deforestation in Pará state until 2016 in yellow, eastern portion corresponding to the Brazilian Arc of deforestation within Pará (C).

1. *Identifying the drivers and building the conceptual model*

Forest cover change in Pará state represents our focal component; therefore, our conceptual model grasps this issue by identifying the main drivers, which were used to build policies and envision future scenarios. Direct drivers are those directly affecting forest cover change, while indirect drivers are those altering the level or rate of impact of one or multiple direct drivers (Diaz et al. 2015, Metzger et al. 2017). From drivers' identification, we seek to answer: which are the main anthropogenic activities causing forest loss and decreasing its quality in Pará state during recent years, and how are these activities interconnected? Firstly, we gathered our perceptions regarding the most prominent drivers of forest cover change in Pará, then used a literature review to support our understanding. Using the keywords "deforestation" and "amazon" accompanied by "agriculture", or "mining", or "urban expansion", or "roads", or "climate change", or "logging", or "fires", or "energy demand", or "occupation", we searched in Scopus search on 11 July 2019. Finally, we scoped in works related to Pará state or Eastern Amazon, including those related to indirect drivers, their interplay with multiple drivers and their level of effect on direct drivers.

The drivers and their interconnections were identified through a series of interactions with focus groups and oral presentations, when the most important issues were reviewed before updating the conceptual framework. The exercises were guided by IPBES experts and we used the multiple views of the graduate students who attended the course, but no traditional knowledge or public consultation was taken as reference.

2. *Identifying NCP demand and supply*

Previous studies emphasize the importance of analyzing the dynamics of land-use change and the flow of ecosystem services to inform decision-making (Burkhard et al. 2014). Land-cover refers to the biophysical features of the Earth's land surface (e.g., forest, mangrove, and water). Land-use refers to the use given by humans to exploit available lands (e.g., mining, crops, and pasture) aiming at obtaining specific products or benefits from this use (Turner et al. 1993). Some natural land-covers play important roles in providing different NCPs, while most anthropogenic land-uses represent, by featuring the beneficiaries, the demand. To identify the most critical NCPs, as a requirement to design tailor-made conservation policies, we used a matrix based on Burkhard et al. (2014) to discuss past changes affecting the provision and demand of NCPs (Figure 3).

As a reference, we used the land use and cover classes (Figure 3) from MapBiomas (MapBiomas Project, 2019). With the classes available, we built a matrix to evaluate the relative importance of each land use and cover providing and supplying NCPs. Based on the knowledge of all authors (n=7), we evaluated the importance of each NCP in the context of Pará state. The average of the grades provided by the group members was calculated to produce one matrix with the importance of each land use and cover types for supplying NCPs and another for demanding NCPs (Figure 3). The supply matrix assessed the capacity of different land use and land cover classes to support NCP's integrity and their provision with the values ranged between 0 (no relevant capacity) and 5 (very high relevant capacity). The demand matrix was also evaluated with values from 0 (no relevant demand) to 5 (very high relevant demand).

Given the importance and consequently, the high score of the regulation of climate NCP, we created the supply/demand budget maps for this NCP (Figure 3). We identified the main processes of land use and cover change using change matrix and transition maps from DINAMICA EGO software (Soares-Filho et al. 2002). The maps used had a spatial resolution of 30 m, and they were downloaded in raster format from https://mapbiomas.org.

3. *Connecting to the Nature Futures Framework – NFF*

NFF is based on a holistic triangular conceptual framework that seeks to maximize the nature benefits for three core human-nature relationships: nature for nature (intrinsic value and function of nature), nature for people (diverse use of nature for interest of people), and nature as culture (human as part of nature) (Rosa et al. 2017, Lundquist et al. 2017). Using this conceptual framework, we seek to identify trajectories leading to positive futures, including not only the protection of ecosystems, but also the conservation of nature's values related to key NCPs.

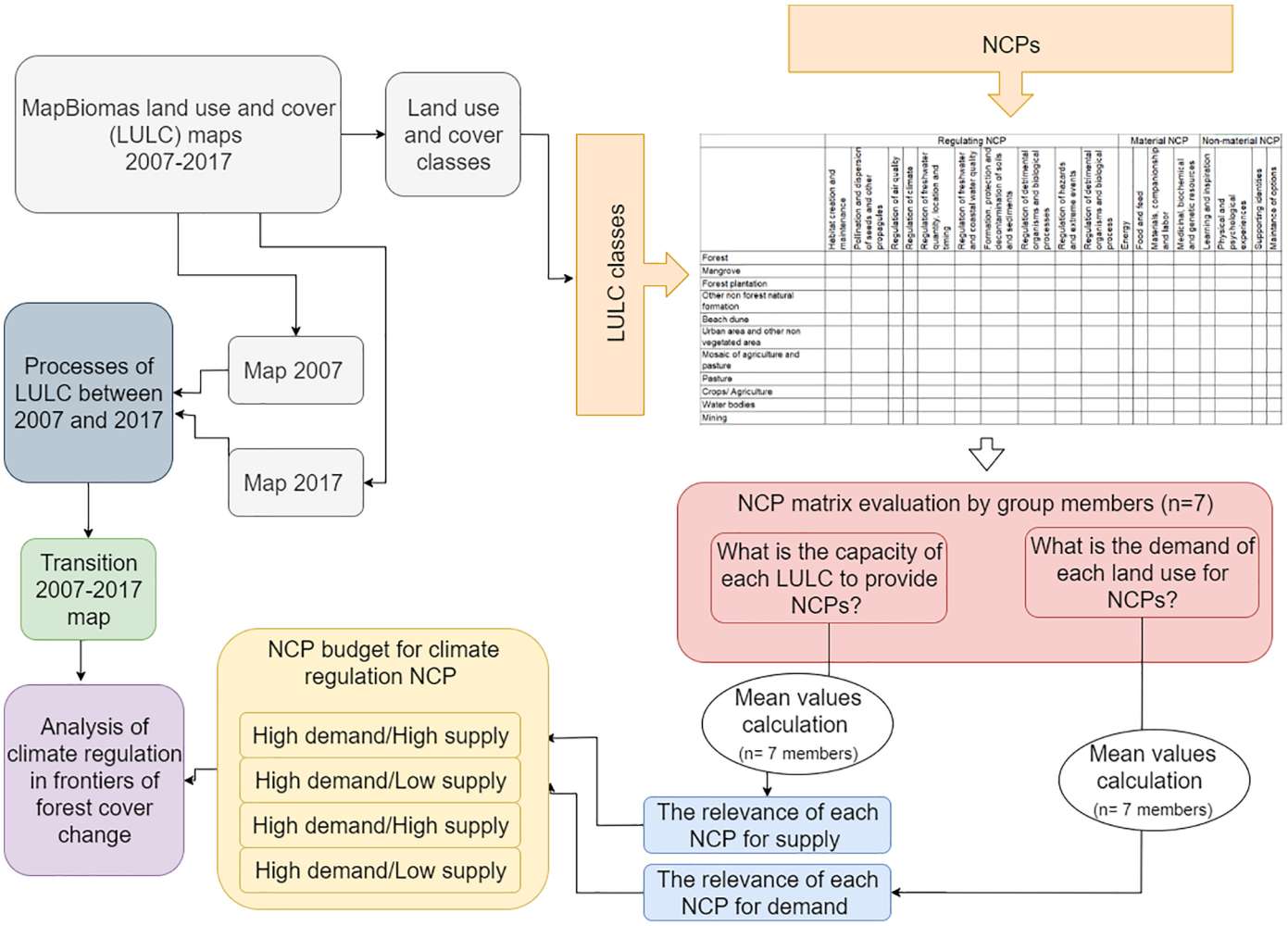


Figure 3. The main steps for NCP matrix calculation and analysis

We started by developing three perspectives on how the main NCPs selected can be valued in Pará state: as nature for nature, as nature for people and nature as culture. Based on the literature, we simulated the integration of different perspectives that several stakeholders may have, including those from indigenous people and local communities. We discussed among the group and with other course participants how values and tradeoffs could be addressed regarding potential futures for Pará state. For example, *Freshwater quality and quantity* in the Amazon forests could be intrinsically valued as important for nature because it creates habitats for a large range of freshwater biodiversity as well as sustaining the water cycle (Collen et al. 2014). Likewise, this NCP is important for the wellbeing of Amazon people since it supports transportation, fishing and agriculture activities (Junk et al. 2007, Foley et al. 2007). Moreover, this NCP sustains the identity of many local communities whose spiritual practices and knowledge are tied to water bodies (Anderson & Veilleux 2016). Finally, we proposed indicators to measure and monitor the policy's effectiveness in delivering the nature future envisioned for each NCP. These indicators can be integrated into modeling trajectories and scenarios of nature futures for Pará state (Schoolenberg et al. 2018). For selecting the indicators, we focused on answering three main questions concerning the NCPs and their associated nature perspective (e.g., Regulation of Climate for Nature as Society): what should we measure here? How do we measure this? How feasible is to collect data needed for measuring this? Based on these questions, we included and adapted indicators proposed by IPBES (2018) to evaluate the NCPs. However, there was a need for a broader range of indicators to express the various values and the social and environmental contexts of the Brazilian Amazon region. Thus, as suggested by Schoolenberg et al. (2018), we added indicators based on a literature review and proposed new ones, especially for nature's values related to culture and society.

4. *Proposing policies and discussing potential scenarios*

The policies were designed to tackle the main direct drivers of forest cover change presented in our conceptual model (Lundquist et al. 2017), including mainly targeting consumption behavior and product supply. The policies were firstly built based on the authors' knowledge of the local political context. Then, a literature review was conducted to support and improve the policies, considering public policies previously implemented in the Brazilian Amazon. We intended to propose behavioral change through education for sustainable development, as well as the advance of technology to regulate and monitor land cover changes. We present future positive scenarios that would emerge from the application of our proposed policies, considering societal tendencies, land-use changes, climate changes, and natural resources sustainability.

Results

1. Conceptual model for forest cover change in Pará state

Based on the literature review and group discussions, we identified eight direct drivers and five indirect drivers (Table 1) leading to forest cover change in Pará state (Figure 4). Forest degradation is defined as a state of anthropogenically induced succession, where ecological processes that underlie forest dynamics are diminished (Ghazoul et al. 2015). Among anthropogenic activities that cause degradation, fire and logging are significantly present in the Amazonian landscape and are extensively studied (Nepstad et al. 1999, Gerwing 2002, Cochrane 2003, Aragão et al. 2007, Silva Junior et al. 2018, Brando et al. 2020). Here, we considered forest degradation caused by fires and logging a direct driver of forest cover change. Land occupation was set as the mean of human occupation with small properties and urban settlements, which differs from agriculture and pasture expansion that represents the advancing of large rural crop production and livestock areas. We do not consider regeneration as one type of forest cover change, focusing only on potential negative drivers.

Table 1. Direct and indirect drivers of deforestation in Pará state and the reference papers supporting drivers impact.

Direct drivers of deforestation:	**References**
Roads	Soares-Filho et al. (2006); Barber et al. (2014)
Degradation by fire and logging	Barlow et al. (2012); Anderson et al. (2015); Pinheiro et al. (2016)
Hydropower projects	Athayde et al. (2019); Chen et al. (2015); Fearnside (2006, 2015)
Urban expansion	Tritsch & Le Tourneau (2016)
Agriculture and pasture expansion	Cabral et al. (2018); Simon & Garagorry (2005)
Land occupation	Brown et al. (2016); Fearsnide (2008)
Climate change	Anderson et al. (2015); Aragão et al. (2018)
Mining	Sonter et al. (2017); Souza-Filho et al. (2016)
Indirect drivers of deforestation:	**References**
Energy demand	Fearnside (2006); Latrubesse et al. (2017)
Population growth	Perz (2002)
Land price	Mahar (1989)
Commodity demand	Gibbs et al. (2015); Soterroni et al. (2019)

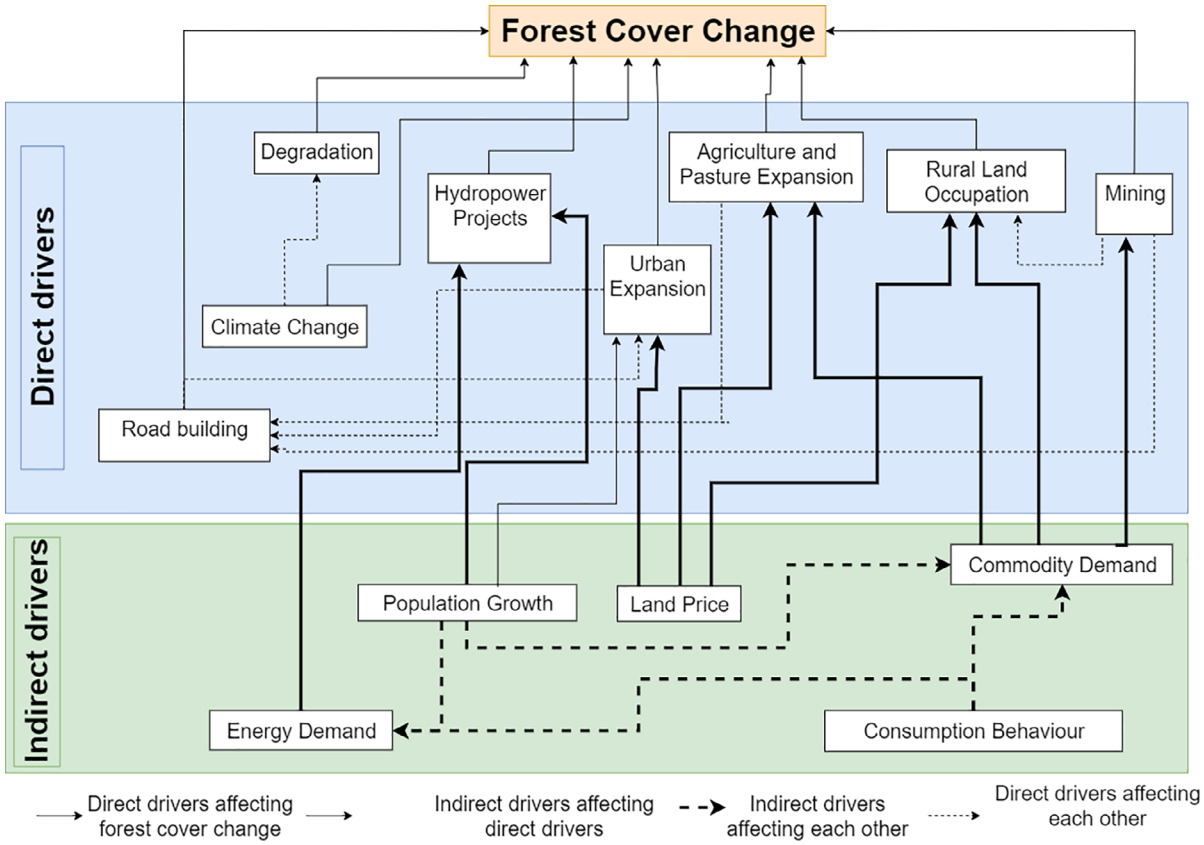


Figure 4. Conceptual framework for assessing deforestation in Pará state, based on IPBES conceptual framework (Diaz et al. 2015). Upper blue zone: direct drivers. Lower green zone: indirect drivers.

Roads provide access to intact forested areas, resulting in a significant impact on landscape (Soares-Filho et al. 2006). In the Brazilian Amazon nearly 95% of total deforestation spots are located within 5.5 km of road networks (Barber et al. 2014). Figure 5A shows an example in the Novo Repartimento municipality, where clearing along roads was caused by land occupation, agriculture expansion and cattle ranching (Tritsch and Le Tourneau, 2016). Besides that, the creation of settlement projects (Yanai et al. 2017) and illegal occupation of undesignated public lands, indigenous lands and conservation units (Fearnside, 2008) influenced deforestation rates in Pará and in other Brazilian Amazon states.

By clearing the remaining forest in the city's outskirts and within the built-up areas, urban expansion plays an important role as a driver of forest cover change in Pará (Tritsch and Le Tourneau, 2016). For example, at Belém metropolitan area, known as "*grande Belém*", the capital of Pará state, the remaining forest has decreased 64% due to urban expansion (from 588 km^2 to 377 km^2), between 1986 to 2006 (Leão et al. 2008). In addition, an intense urban growth in Altamira, the largest Brazilian municipality, was triggered by the construction of Belo Monte dam (Figure 5B) (Feng et al., 2017). Although the growth in job opportunities attracts people to these areas, more than 16,000 people have been displaced to urban resettlements as a result of the flooding areas (Feng et al. 2017).

Thus, population growth is an indirect contribution to forest-cover change, as it influences urban expansion and rural land occupation, while triggering infrastructure construction (e.g., dams) and increasing energy and commodities demand. The demand for food also increases with the increasing population, which in turn requires more land for food production (e.g. crops and livestock) (Li et al. 2019). In Pará, two areas faced a significant population growth resulting in intense deforestation during the 1970s and 1980s: Altamira, in the Transamazon Highway corridor; and São Felix do Xingu, in the southeastern frontier of Pará. In Altamira municipality, population growth was caused by colonization projects (settlement project) in the early 1970s, while in São Felix do Xingu migrant farmers and ranchers cleared large areas for pasture (Perz 2002).

Hydropower projects in the Brazilian Amazon produce a great environmental and social impact. Large areas are cleared for the reservoir construction and large indigenous lands and conservation units are flooded, causing displacement and threatening local livelihoods (e.g.

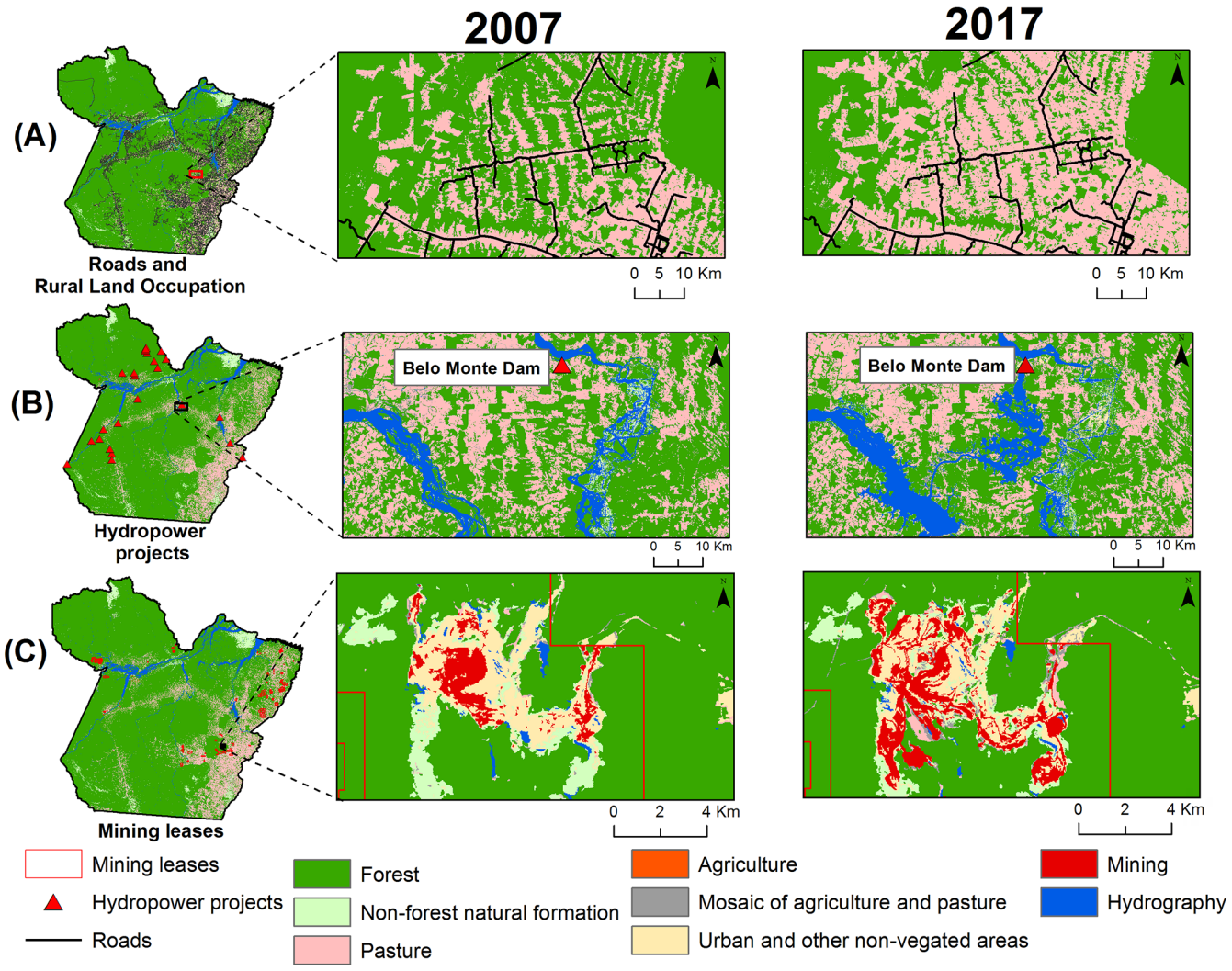


Figure 5. Land cover in 2007 and 2017. (A) Surrounding road building and rural land occupation in Novo Repartimento municipality. (B) Surrounding hydropower projects at the Belo Monte dam. (C) Surrounding mining leases at the Carajás National Forest.

fisheries and hunting) (Athayde et al. 2019). In addition, reservoirs emit methane, which contributes to climate change (Fearnside 2006, 2015). Figure 5B shows the distribution of dam projects in Pará state, and the zoomed area shows the Belo Monte dam before (2007) and after the flooding (2017). Most of the demand for energy in the Brazilian Amazon comes from the aluminum export industry. In fact, the Brazilian Amazon is home to aluminum smelting companies that are expected to cover most of the international market demand (Fearnside 2006).

Fires make the forest more vulnerable as a way to cause degradation, especially during long periods of dry season (Foley et al. 2007, Silva Junior et al. 2018). Besides that, episodes of severe droughts (e.g. El Niño) tend to become more frequent over the years due to climate change, increasing tree mortality and, consequently, the vulnerability to fires (Nepstad et al. 2007, Brando et al. 2014, Brando et al. 2020). Such processes, as forest degradation and climate change, set up a positive feedback, where degraded forests are increasingly under threat (Rosa et al. 2013). The land price is related to the "improvements" (in Portuguese: *benfeitoria*) made by the landowner or the state. For instance, *benfeitoria* considers the presence of pasture or agricultural areas in the farm; the larger the pasture, the higher the land price. In addition, cleared parts of the landholding have the purpose of ensuring land tenure rights, as they show that the land is occupied (Mahar 1989).

Mining activities cause forest cover change within and beyond boundaries of their operation (e.g. infrastructure development, urban expansion, livelihood demands) (Sonter et al., 2017; Siqueira-Gay & Sánchez 2019). Several mining projects operate in Pará (Lobo et al. 2018) for various metals exploitation (e.g. iron, bauxite, clay, aluminum, tin, limestone, nickel, and silica). Their impact can extend for 70 km radius from mining leases (Sonter et al. 2017). Figure 5C shows the expansion of iron ore mining activities in Carajás from 2007 to 2017.

Forest cover change drivers in Pará state and their interrelations represent a very complex system. A simplified description of our conceptual model is shown in Figure 4. We chose to maintain the links of major importance only, in order to keep a simplified feasible version of our conceptual framework. However, the model considers that policy-relevant factors, such as commodity price, access to credits for cattle ranching, Forest Code enforcement level, and shifts in policy paradigms caused by changes in the government will also affect the dynamics of forest cover change (Rodrigues-Filho et al. 2015).

2. *Forest cover change influences on key NCPs*

In the ten years' period under analysis (i.e. 2007 to 2017), forest cover in Pará state showed a reduction of 1.6%, representing a mean loss of 1,592 km^2 per year. In the same time, agriculture and pasture indicated an increased by 7.9%. From the total forest area cleared (15,921 km^2) during this period, 82.7% (13,170 km^2) was converted into pasture and agriculture. Forest plantations and mining were the classes with the highest percentage of increase in ten years, with 922.8% (166.7 km^2) increase for forest plantation and 168.8% (71.7 km^2) for mining activities. Urban and other non-vegetated areas also had an important increment; this class showed an increase of 41.8% (710.0 km^2) and could be associated with urban expansion in the Pará state.

We evaluated the NCP supply and demand of each land use and land cover considering the Pará state study area. The three NCPs with higher supply capacity are *materials and assistance*, *energy*, *food & feed* (Table 2). Forest and mangroves areas are the most important land-cover classes for providing NCPs (Figure 6). The NCP demand analysis revealed the *regulation of freshwater quantity*, *regulation of climate* and *formation, protection,* and *decontamination of soils and sediments* as the most relevant (Table 3). The urban areas and mosaic of agriculture and pasture represent the land-uses with the highest NCPs demand.

We also evaluated the balance between supply and demand (i.e., budget of NCP) of the regulation of climate NCP (Figure 7). Thus, natural formations and hydrography are areas with high supply and low/intermediate demand of NCP. Agriculture, pasture and urban areas had high demand and low supply. Forest and mangroves present low demand and high supply. The frontiers of forest cover changes, such as roads, are regions of special attention for conservation due to the high demand and supply of natural resources. Rivers and pasture have an intermediate level of importance in providing and demanding NCPs, while beach dunes have the lowest levels of supply as well as demand.

3. *Connecting to the Nature Futures Framework*

Each key NCPs can be valued differently according to perspectives on how people relate to nature. For example, we found that *food & feed, energy,* and *materials and assistance* can be more related to values of "nature for people" and "nature as culture" than to "nature as nature". This is because these NCPs are focused on human wellbeing and, specifically, on the elements from nature that directly sustain people's physical existence and material assets (known as "Material NCPs", Díaz et al. 2018). By contrast, *freshwater regulation, climate regulation,* and *soil protection* can be highly valued according to all perspectives because these "Regulating NCPs" are key for sustaining functional and structural aspects of organisms and ecosystems and, indirectly, the quality of human life (Díaz et al. 2018). We also identified a set of indicators for each NCP and different values (Table 4) to reflect the plurality of human-nature relationships. For the NCP of *regulation of water quality and quantity* we presented cultural, such as maintenance of water bodies important for cultural practices and recreation, socioeconomic, such as navigability index, as well as other usual indicators such as parameters for aquatic habitat quality.

4. *Policies proposal*

The first legal environmental regulation device was the Forest Code of 1934 (replaced in 1965), updated in 2012 as the "New Forest Code" (Soares-Filho et al. 2014), which establishes usage limits and protection of native vegetation within private properties. In 2004, the federal government implemented the Action Plan to Prevention and Control of Deforestation in the Legal Amazon (PPCDAm), aiming to gradually and continuously reduce deforestation in the Legal Amazon, as well as to provide subsidies to a more sustainable regional development (Maia et al. 2011). The plan considered a chain of deforestation causes to organize its four thematic axes, which are i) Land and territorial planning, ii) Environmental monitoring and control, iii) Promotion of sustainable production activities, and iv) Economic and regulatory instruments, and each axis was integrated during a phase of the plan. The PPCDAm, which is now in its fourth phase, contributed to the reduction of deforestation in the region through reinforcement of monitoring and surveillance actions and by expanding the conservation unit's system (Arima et al. 2014, Ministério do Meio Ambiente 2016). Also, some international instruments, such as the Amazon Fund and

Table 2. Assessment of the NCP supply matrix of different land-use and land-cover classes. Color gradient indicates supply values. High values of supply tend to be red, low values tend to be green. Adapted from Burkhard et al. (2014).

	Habitat creation and maintenance	Pollination and dispersion of seeds and other propagules	Regulation of air quality	Regulation of climate	Regulation of freshwater quantity, location and timing	Regulation of freshwater and coastal water quality	Formation, protection and decontamination of soils and sediments	Regulation of detrimental organisms and biological processes	Regulation of hazards and extreme events	Regulation of detrimental organisms and biological process	Energy	Food and feed	Materials and assistance	Medicinal, biochemical and genetic resources	Learning and inspiration	Physical and psychological experiences	Supporting identities	Maintenance of options
Forest	5	5	5	5	5	5	4	5	5	4	4	5	5	5	5	5	5	4
Mangrove	5	4	5	5	5	5	5	5	5	4	3	5	5	4	5	4	5	4
Forest plantation (e.g., eucalyptus)	2	1	2	2	1	1	2	2	2	2	3	0	3	2	1	1	1	1
Other non-forest natural formation (e.g., savanna, campinarana, grassland)	4	4	4	4	4	3	4	4	4	4	3	4	3	4	4	4	4	4
Beach dune	3	1	1	1	2	2	3	2	2	2	2	0	2	2	4	4	3	3
Urban area and other non-vegetated area (e.g., roads, constructions)	0	0	0	0	0	0	0	0	0	0	1	0	2	0	2	2	1	1
Mosaic of agriculture and pasture (area where pasture and agriculture could not be separated in different classes	1	2	1	1	1	1	1	1	1	1	2	4	2	1	2	1	1	1
Pasture	0	1	1	1	0	0	0	0	1	1	1	3	2	1	1	1	1	2
Crops/ Agriculture	2	2	1	1	1	0	1	1	1	1	3	4	2	2	2	1	1	1
Water bodies	5	4	4	4	5	5	4	5	5	4	4	5	4	4	5	5	5	4
Mining	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	1	0	1

the Reducing Emissions from Deforestation and Forest Degradation (REDD) program were created to support activities and policies to reduce deforestation at local scale (Correa et al. 2019; Pinsky et al. 2019). In accordance to national initiatives, Pará state has created the Green County program, to tackle forest loss in the municipalities with higher deforestation rates and implemented the Rural Environmental Registry (Cadastro Ambiental Rural – CAR) which forced landowners to submit their land boundaries, therefore supporting the monitoring of legal reserves (Nepstad et al. 2014). Another environmental program in action in Pará is the Ecological ICMS, which refers to an ecological fiscal transfer, from the state to municipalities committed to environmental actions. However, the application of this program remains controversial (Tupiassu et al. 2019).

The policies we propose represent a response to address the drivers of forest cover change, their interconnections (Figure 4), and the NCP demand analysis (Section 2 of results). The policies intend to reduce forest cover change mainly by tackling two key drivers: consumption behavior and product supply.

Pará minus: Land management to tackle illegal deforestation

This policy intends to reduce mainly the illegal deforestation in Pará state, one important pathway of forest cover change. By proposing this policy, we aim to address the drivers of rural land occupation, agriculture and pasture expansion, unofficial road building and forest degradation. A similar action plan has been applied in Pará by the Federal Prosecutors' Office (Ministério Público, MPF-PA) during the second phase of the Action Plan to Prevention and Control of Deforestation in the Legal Amazon (PPCDAm-II, 2008-2011), resulting in a reduction of deforestation in the state. The actions focused on regulating the complete supply chain, including the production, distribution and the buyers´ responsibility as well as regulation of legal reserves inside agricultural properties. With the implementation of these actions, supermarkets started to require an origin label for the meat they purchase (Arima et al. 2014).

Pará minus draws on the notions of co-management and decentralized environmental governance, where the knowledge of direct resource users is prioritized to build adaptive forest governance (Ostrom, 2015). Here, users coordinate actions to manage in a sustainable way, guaranteeing access and control, to natural resources (Ribot & Peluso 2009).

This policy proposes the decentralization of governance systems by conceding power to local communities to manage their forest with the assistance of multiple institutions (e.g., NGOs) and implement monitoring efforts to avoid new areas of illegal deforestation. The core

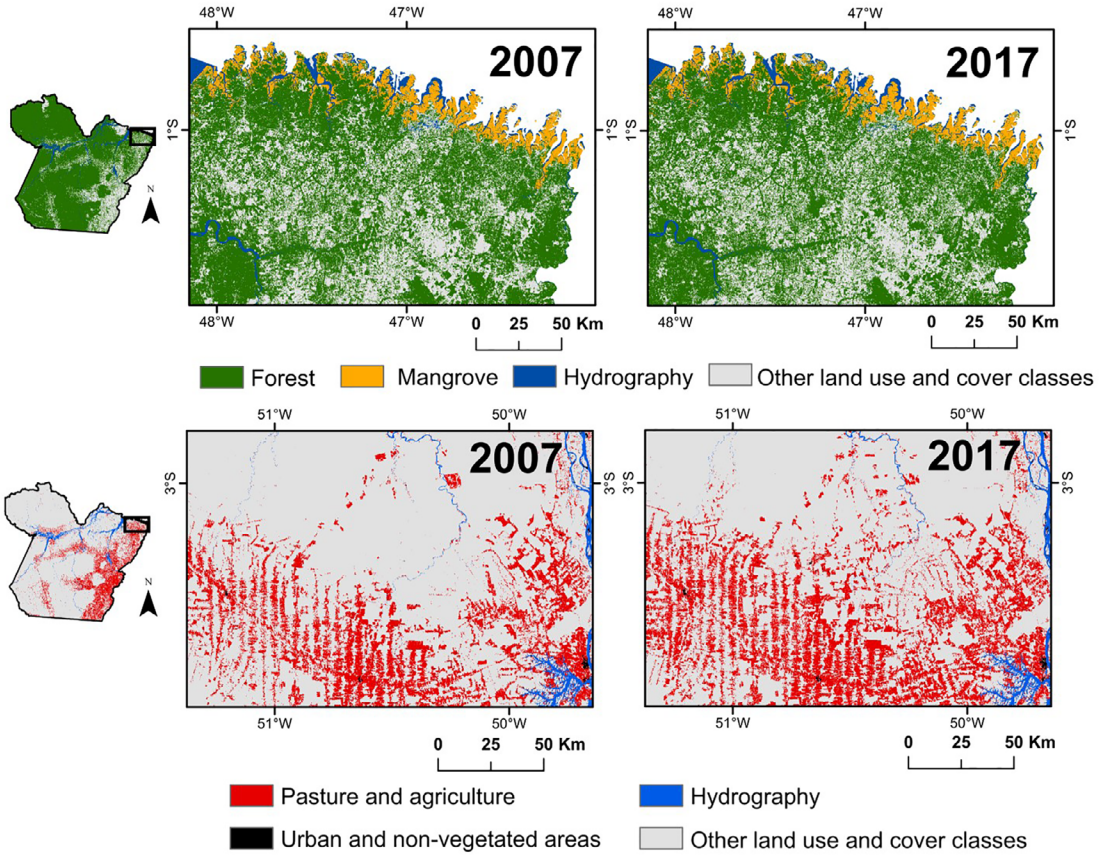


Figure 6. Land cover in 2007 and 2017 showing the relevant areas of NCPs supply in Pará state.

actions to be performed as part of this policy include: i) Enforce forest decentralization efforts to allow small governance units taking decisions about their resources in a sustainable way; ii) Provide technological tools and training to communities to facilitate sustainable development and monitoring efforts; iii) Enforce the protection of indigenous territories and protected areas, by creating an inheritance tax scheme and fines to illegally cleared forest areas; iv) Perform a land reform to distribute underused or abandoned land to individuals or organizations committed to sustainability and conservation efforts or return the land to indigenous or traditional communities; v) Regulate for the mandatory sustainable use of undesignated public lands, and prohibit (with fines applicable) clearing of pristine forest areas; vi) Create alliances and strengthen existing ones to make the forest monitoring and controlling efforts more effective, while facilitating social learning process in the local communities. Social learning is a key element to ensure participatory and adaptive resource governance. It is defined as "collective action and reflection that occurs among different individuals and groups as they work to improve the management of human and environmental interrelations" (Keen et al. 2012).

Pará Consumo: Change consumption behavior

In Portuguese, Pará Consumo is a pun with the name of the state, which means "stop". This way, the name of the policy means to stop consuming. Consumption behavior is a key indirect driver of forest loss and climate change (Figure 4). For instance, excessive meat consumption and soy plantation to produce animal food are relevant contributors to agriculture and pasture expansion. Thus, we suggest that environmental education can change the current population consumption behavior and thus, reduce the demand for meat and, consequently, the pressure for clearing new areas to agriculture and pasture. Although few investigations were found about the effectiveness of policies to tackled consumption behavior in the Amazon, Assunção et al. (2015) demonstrated that the lower the price of agricultural outputs, the lower are the deforestation rates. Therefore, a behavioral change towards consumption reduction will also produce deforestation decreases.

The following actions would be undertaken under this policy: i) Create an educational program to promote awareness on NCP provision, the value of forest conservation and damage caused by cattle ranching. This program would be within the whole educational system by restructuring the curriculum; ii) Promote other options for protein consumption instead of beef; iii) Create a tax incentive for large companies that join the beef moratorium (an agreement of not buying meat from newly deforested areas) or that support the educational program of awareness on NCP provision (action i).

5. *Positive scenarios*

We propose positive scenarios for Pará state, considering the trends of the main drivers of forest cover change identified and the suggested policies (Figure 8). We envision three future scenarios following the two proposed policies. The first scenario considers that only Pará minus was properly implemented, the second scenario considers that only Pará consumo was properly implemented, and the third scenario involves the trends in drivers following the proper implementation of both policies in Pará state.

Table 3. Assessment of the NCP demand matrix. Color gradient indicates demand values. High values of demand tend to be red, low values tend to be green. Adapted from Burkhard et al. (2014).

	Habitat creation and maintenance	Pollination and dispersion of seeds and other propagules	Regulation of air quality	Regulation of climate	Regulation of freshwater quantity, location and timing	Regulation of freshwater and coastal water quality	Formation, protection and decontamination of soils and sediments	Regulation of detrimental organisms and biological processes	Regulation of hazards and extreme events	Energy	Food and feed	Materials and assistance	Medicinal, biochemical and genetic resources	Learning and inspiration	Physical and psychological experiences	Supporting identities	Maintenance of options
Forest	2	2	1	1	2	1	0	2	1	1	1	1	1	0	1	1	1
Mangrove	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0
Forest plantation (e.g., eucalyptus)	1	1	0	1	2	2	2	1	2	1	1	2	1	0	0	0	1
Other non forest natural formation (e.g., savanna, campinarana, grassland)	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Beach dune	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Urban area and other non vegetated area (e.g., roads, constructions)	2	2	4	4	4	4	3	3	4	4	4	4	3	4	4	3	4
Mosaic of agriculture and pasture (area whre pasture and agriculture could not be separeted in different classes	2	4	2	4	4	3	4	3	3	3	2	3	2	1	1	1	1
Pasture	2	2	2	4	4	3	3	3	3	2	2	3	2	1	1	1	1
Crops/ Agriculture	2	4	2	4	4	2	4	4	4	2	2	2	2	1	1	1	1
Water bodies	1	0	0	2	2	2	1	1	0	1	1	1	1	1	1	1	1
Mining	2	1	2	1	2	2	3	2	2	5	1	3	1	1	1	1	1

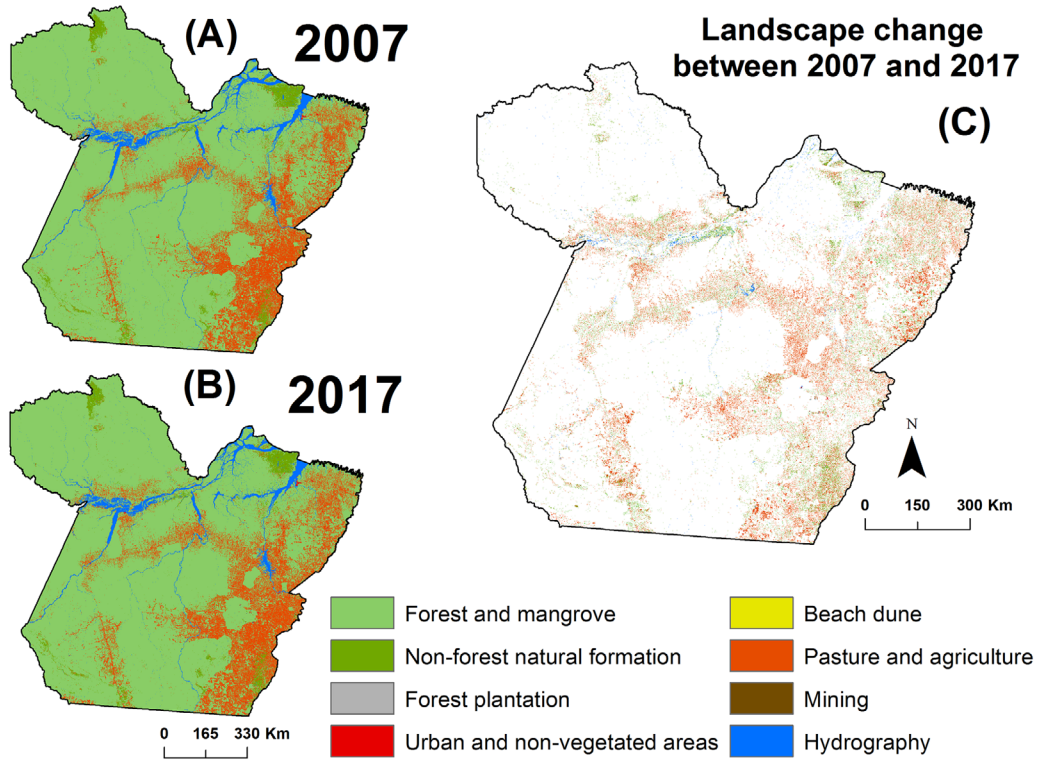


Figure 7. Balance for budget of supply and demand for the regulation of climate in (A) 2007 and (B) 2017 and (C) the change between 2007 and 2007 in the Pará state.

Table 4. Valuation of key NCPs for Pará state into Nature's values, their related variables and proposed indicators for monitoring.

NCPs	Nature's values	Variable	Indicators	Source of the indicators
Regulation of freshwater quality and quantity	Nature for nature	Aquatic habitat	Physical, chemical and biological parameters of freshwater systems	IPBES (2018)
		Microclimate regulation	Soil moisture, precipitation, evapotranspiration, temperature flow rate, and runoff	IPBES (2018)
	Nature for society	Fishing	Amount of wild capture fisheries for domestic consumption	IPBES (2018)
		Transportation	Channel connectivity index, navigability index	Zhang et al. (2009)
		Water supply for human consumption	Volume of water available per capita, time needed to fetch water, distance to water source	The Sphere Project (2011)
		Water quality for human consumption	Proportion of population using safely drinking water	IPBES (2018)
	Nature as culture	Identity of traditional communities	Maintenance and protection of lakes and rivers that support cultural practices and recreational activities of local communities	Proposed by this study
Regulation of climate	Nature for nature	Regulate climate, hydrological and bio-chemical cycles	Monitoring radiation, temperature, rainfall, volume of rivers, ground water flows patterns	De Groot et al. (2002); Millenium Ecosystem Assessment (2003)
	Nature for society	Protection against global warming, protection against extreme events	Monitoring temperature, floods, droughts events (e.g., El Niño, La Niña)	De Groot et al. (2002)
	Nature as culture	Maintenance a climate favorable for human well-being	Improvement in the quality of human health, recreation and cultural activity	De Groot et al. (2002)
Formation, protection and decontamination of soils	Nature for nature	Carbon storage and nutrient regulation	Average carbon content above and below soil	IPBES (2018)
		Soil biodiversity	Species richness, functional diversity, food web structure, nitrogen fixation	IPBES (2018)
	Nature for society	Quality of soil, crops/food	Nutrient content in crops and gathered food, erosion and sedimentation reduction	IPBES (2018)
	Nature as culture	Traditional agricultural systems	Land area dedicated to this type of production	Proposed by this study
Food & feed	Nature for society	Food security/sovereignty	Amount of wild game consumption, diversity of edible plant species	IPBES (2018)
		Small scale agriculture	Total yield per unit area by each crop	IPBES (2018)
	Nature as culture	Traditional ways of life	Frequency of food-related activities (e.g. management, hunting, fishing) within a community	Proposed by this study
Energy	Nature for society	Energy consumption for the population	Amount of increase in energy consumption in the urban and rural areas	Proposed by this study
	Nature as culture	Improve the wellbeing in isolated areas	Amount of traditional communities located in isolated areas that have the quality of life improved through the access of energy (electricity)	Proposed by this study
Materials and assistance	Nature for society	Diversity of forest materials	Number of raw forest materials in the production-to-consumption system of local communities (e.g. wood, fibers, waxes, paper, resins, dyes)	Proposed by this study
		Trend in income from forest material production and trade	Average household income (cash, subsistence, barter) of producer households from raw materials.	Ruiz Perez et al. (2004)
	Nature as culture	Diversity of forest material uses	Number of uses of raw forest material in local communities (e.g. construction, clothing, printing, ornamental, decoration, company)	Proposed by this study

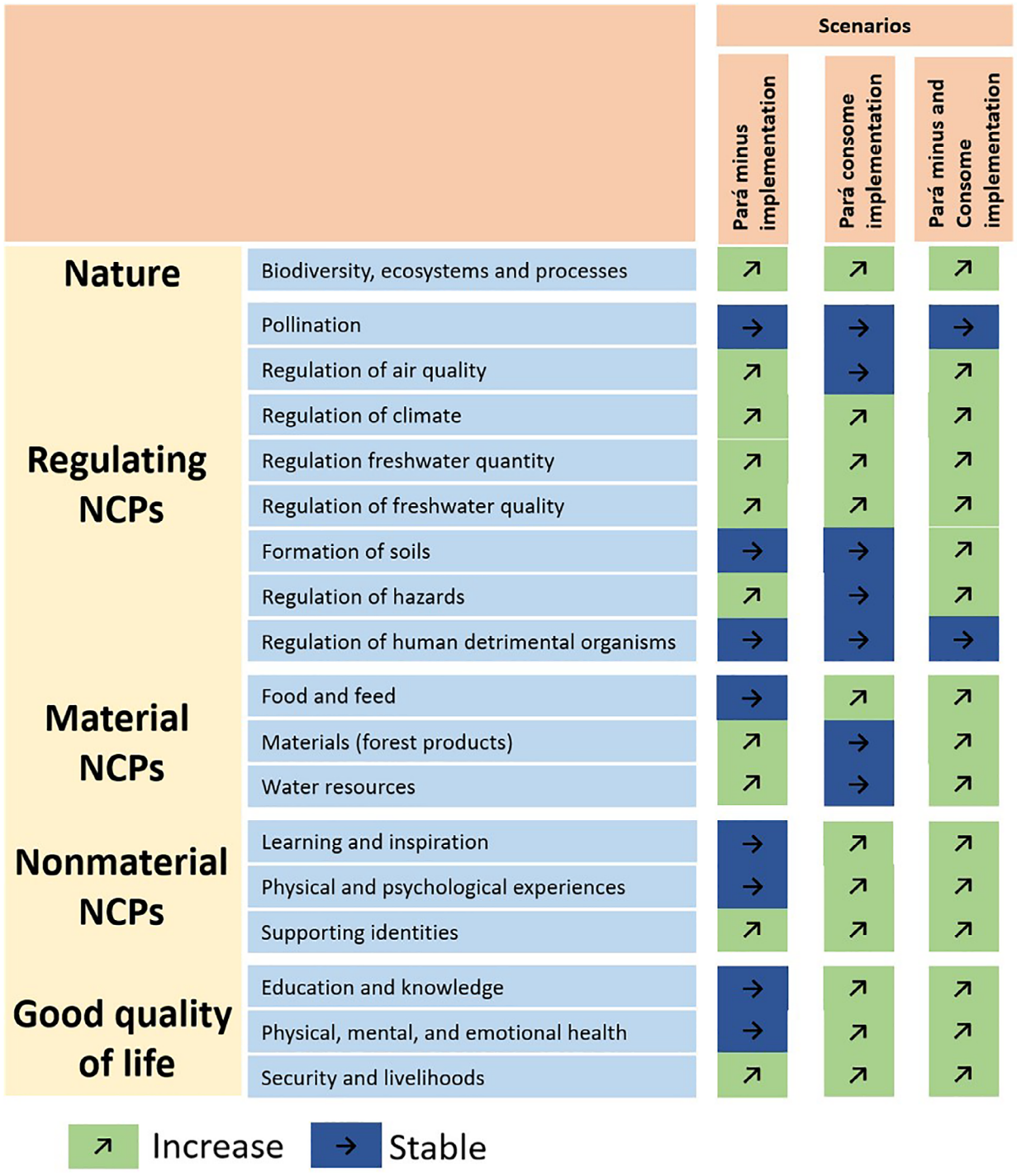


Figure 8. Envisioned impacts on nature, Nature Contributions to People and good quality of life according to the three proposed future positive scenarios for Pará state.

Scenario 1 – positive outcomes from the application of Pará minus

We have the maintenance of the forest cover area in Pará state through regional development and sustainability, conservation and sustainable development actions. Decentralization actions would focus on local development and welfare, controlling and preventing the occurrence of new deforestation through degradation, road building, mining, land occupation, agriculture, and pasture expansion. Technological input would change the "business as usual" in the region, reducing deforestation and ensuring local production.

A land reform and the regulation of undesignated public lands would also strengthen conservation value through sustainable use, production, and a conservation budget from local government. Social learning development is a fundamental tool for ensuring participatory and adaptive resource governance; in the long term, it would work to ensure that conservation and development (through sustainability) can work together in the same stage by promoting the interaction

of stakeholders to reflect on the problems they face and integrate their knowledge (Schmidt 2017, Pahl-Wostl et al. 2007). Economic development would be based on the non-extractives' use of deforested areas (e.g. eco-tourism and payment for ecosystem services projects), which would prevent deforestation. Traditional extractive activities from the region (e.g. açaí and Brazil nuts extraction) would adopt sustainable practices and respect product seasonality, integrating the traditional way of extraction with technology and sustainability. Thus, the enacted laws might ensure land-use change control, regulating climate change and the sustainable use of natural resources.

Scenario 2 - positive outcomes from the application of Pará Consumo

The positive outcomes of this scenario include: conservation and sustainability through education to shift consumption behavior; an enhanced awareness of the value of the NCPs and the damage caused by cattle ranching; an increment in social welfare by promoting life quality supported by NCPs (nature and society development) and economic development (e.g. jobs, local income flow). This scenario envisions changes in other types of social behavior through the application of innovative strategies for fostering sustainability. Among these strategies is the creation of a food market that motivates the production and consumption of local products. This would not only have positive gains in fighting climate change due to the reduction of carbon emissions from transportation, but it may create nature recreational opportunities for people. In large urban centers, this would also promote the establishment of urban farms, committed to low emissions and sustainable production. Besides that, the institutions would gain legitimacy to stop land-use change and replace it through sustainable use (through tax incentive), which in turn would tackle climate change and environmental sustainability by creating a new economy that does not depend on extractive industries while ensuring the provision of natural resources for future generations. Aligned with the shift in consumption behavior and the increased awareness of NCPs value, there would emerge an increased awareness to waste destination and recycling.

Scenario 3 – Positive outcomes from the application of both policies

This scenario envisions regional sustainable development together with environmental awareness and behavioral change. This scenario considers the outcomes from successfully applying policies one and two: forest management decentralization, technology for sustainability, reinforcement of protected areas, a substantial reduction in deforestation rate, conservation and sustainable use of undesignated public lands, and an educational behavioral change towards sustainable consumption. Other positive outcomes include sustainable economic development, based on green solutions, controlling or reducing drivers of forest cover change; increased social development; employment generation based on NCPs provision and maintenance; cultural empowerment through social learning; land-use and climate change control through sustainable use of natural resources.

Discussion

The IPBES framework allowed us to discuss the main drivers and their implications considering diverse socio-cultural aspects and biodiversity conservation and human well-being. We argue that the proposed policies would support positive scenarios by addressing the main drivers and promoting positive changes in the region.

Roughly 65% of Brazilian timber extraction takes place in Pará state (Verissimo 1998, Pinheiro et al. 2016). The construction of roads (1970s) has provided access to previously remote forest areas, connecting the Brazilian Amazon to central and northeast Brazil. This new connection has contributed to the migration in the region, fostering access to natural resources and facilitating trading of forest resources, while producing economic development in the region. Also, these policies led to a regional transformation of smallholder subsistence farming into extensive large-scale farming (Müller-Hansen et al. 2019).

Unlike the Brazilian Cerrado, fires are not part of the natural cycles in the Amazon. Instead, a close link between fires and anthropogenic material actions s (e.g., deforestation and climate change) and development models that intensify resource extraction and violation of indigenous rights can be outlined for the Amazon region (Aragão et al. 2018), considerably increasing carbon emissions and reducing NCP supplies (Anderson et al. 2015). Although hydropower projects are defended as clean and renewable energy source, studies have shown the high impact of damming Amazon rivers to local biodiversity (aquatic and terrestrial) (Latrubesse et al. 2017) and human livelihoods, including local traditional and indigenous people (e.g. loss of local food sources and population displacement) (Athayde et al., 2019; Fearnside 2015).

Given this background, this study proposes a positive vision (i.e. "what we want?") for the Amazon forest in Pará state, and the policies and scenarios ("how to get there?") to support this vision. The IPBES and Nature Futures Framework (Lundquist et al. 2017, Díaz et al. 2018) encouraged us to develop a more holistic future for the Amazon forest in Pará, where not only intrinsic values of forests for biodiversity are considered but also their values for human wellbeing and cultural maintenance. We also proposed a set of indicators to track how we approximate these positive visions. We note that some indicators would have compatible desired trajectories. Taking water as an example, Funder the nature for nature perspective, we envision a future where Amazonian freshwater bodies provide a healthy aquatic habitat according to physical, chemical and biological parameters. This trend would be compatible with improving the provision of drinking water to the local population, an indicator for nature for people. Besides that, there are trade-offs between the trends of some indicators and different nature's perspectives. Fishing by local communities and the maintenance of their traditional ways of life are indicators for nature for people and nature as culture, respectively (Table 4). But if not sustainable, the increases of fishing to an industrial level could modify the natural ecological communities of freshwater systems, negatively affecting aquatic habitat and, therefore, the nature as nature indicators.

It is instrumental to understand how the indicators are connected to integrate them into the models and future scenarios, as well as provide and historical and consistent data time series. The latter represents a challenge for the new proposed indicators, especially those related to "nature as culture" value, such as an in-depth anthropological assessment of traditional knowledge and food-related practices in local communities. Likewise, it is necessary to work with local traditional and indigenous communities for obtaining the required data using both qualitative and quantitative methods.

The policies focused on the drivers of land management and consumption behavior, revealing the reflection on interventions that can be explored to produce positive futures for the region. We emphasize that policies that former governments have implemented, including the PPCDAm (Herrera et al. 2019, Gibbs et al. 2015) should be strengthened instead of weakened as indicated trend of Brazilian government.

Given the importance of creating scenarios based on biodiversity conservation and human wellbeing (Rosa et al. 2017), we extrapolate the implications of the successful implementation of our proposed policies. A way to create hurdles for illegal deforestation could be by fomenting land control in protected areas and regulating the use of undesignated public lands, allied to empower local communities. Moreover, we evidence the importance of consumption behavioral change in order to address the decreasing demand for unsustainable commodities and, consequently, avoiding forest cover change. Therefore, we emphasize the prominent role played by education as the most important way to address consumption behavior by creating awareness of interrelations between people´s everyday choices of transportation, food and clothing, for example, with climate change. The educational curricula should be revisited having a pluricultural worldview, similar to what Ecuador and Bolivia have intended through their Constitutions under the notions of Sumak Kawsay and Sumak Qamaña, respectively (Acosta, 2010). Such a worldview represents an avenue to legitimize indigenous knowledge and practices. For example, to raise awareness within the young generations, the curricula can include reading indigenous stories that show the close link between indigenous people and nature, which can ultimately influence societal behavior.

Conclusions

There is a lack of integrative view on how forest cover change affects the ecosystem and human wellbeing. In order to provide a broader picture of environmental change, we firstly identified drivers of deforestation and potential links between them to illustrate how they are affecting forest cover change in Pará state. We identified as direct drivers: (i) roads construction; (ii) forest degradation; (iii) hydropower projects; (iv) urban expansion; (v) agriculture and pasture expansion; (vi) rural land occupation; and (vii) mining; (viii) climate change; and as indirect drivers: (i) energy demand; (ii) population growth; (iii) land prices; (iv) commodity demand; (v) consumption behavior. In Pará state, regulation of freshwater quantity, regulation of climate and formation, protection, and decontamination of soils and sediments are the most relevant NCP for demand and the materials and assistance, food & feed and energy are critical for supply. Considering the NCP climate regulation, the frontiers of deforestation (e.g. roads) are regions of special attention due to the high demand and supply of natural resources. Rivers and pasture play an intermediate role providing and demanding NCPs, while beach dunes present the lowest level of supply as well as demand.

Our proposed policies aimed at addressing the main drivers and discuss positive scenarios to conserve material and immaterial aspects of the pluralist environment of Pará state. We found that it is essential to expand the data available on indicators to track possible changes in the values of each NCPs, especially for those values related to societies and cultures. It is necessary to move beyond existing metrics for depicting an aspirational future for the Amazonian forest and the sustainability of NCPs in Pará state.

Although we advanced in terms of understanding current drivers of change and how they are interconnected, our conceptual model certainly has some limitations. Our results did not capture the entire socio-ecological reality behind forest cover change in Pará since our conceptual model did not include the knowledge of local forest users and indigenous people. It could be refined by adding the knowledge of other stakeholders (e.g., indigenous people, local population and governments) because we have not been able to include fundamental knowledge coming from resource users.

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Author contributions

Juliana Siqueira-Gay: substantial contribution in the concept and design of the study, to data collection and to data analysis and interpretation; wrote, added intellectual content and review the final version of the manuscript; provided significant contribution to manuscript preparation

Aurora Miho Yanai: substantial contribution in the concept and design of the study, to data collection and to data analysis and interpretation; wrote, added intellectual content and review the final version of the manuscript.

Janeth Lessmann: substantial contribution in the concept and design of the study, to data collection and to data analysis and interpretation; wrote, added intellectual content and review the final version of the manuscript.

Ana Carolina M. Pessôa: substantial contribution in the concept and design of the study, to data collection and to data analysis and interpretation; wrote, added intellectual content and review the final version of the manuscript.

Danilo Borja: substantial contribution in the concept and design of the study, to data collection and to data analysis and interpretation; wrote, added intellectual content and review the final version of the manuscript.

Moara Canova: substantial contribution in the concept and design of the study, to data collection and to data analysis and interpretation; wrote, added intellectual content and review the final version of the manuscript.

Rafael Borges: substantial contribution in the concept and design of the study, to data collection and to data analysis and interpretation;

wrote, added intellectual content and review the final version of the manuscript.

Conflicts of interest

All authors declare that to have no conflict of interest related to the publication of this manuscript.

Ethics

All authors declare to be in compliance with all ethical stablished guidelines. No human subject was used in this study.

Data availability

All data used for the development of this study is already made available in methods section.

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Article

A conceptual model to assess the impact of anthropogenic drivers on water-related ecosystem services in the Brazilian Cerrado

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Abstract: The development of strategies that conciliate anthropogenic activities with nature conservation is becoming increasingly urgent, particularly in regions facing rapid conversion of native vegetation to agriculture. Conceptual modelling enables assessment of how anthropogenic drivers (e.g. land use/land cover change and climate change) modify natural processes, being a useful tool to support strategic decision-making. The present work describes a conceptual model to evaluate water-related ecosystem service provision under different land use scenarios in the Matopiba region of the Brazilian Cerrado, the world's most biodiverse savanna and an agricultural frontier. Model variables were determined (direct drivers, indirect drivers, focal components and responses) and the Nature Futures Framework was consulted to incorporate socio-ecological components and feedbacks. Future scenarios were developed considering potential trajectories of drivers and governance responses that may impact land use in the region, including the possibility of full compliance with Forest Code and implementation of the Soy Moratorium in the region. The conceptual model and scenarios developed in the present study may be useful to improve understanding of the complex interactions among anthropogenic drivers, water-related ecosystem services and their potential repercussions for natural and social systems of the region. Governance decisions will be critical to maintaining the ecosystems of the region, the services it provides and the culture and tradition of the people historically embedded in the landscape. In acknowledgment of humanity's dependence on nature, the importance of inverting the way scenarios are used is highlighted. Rather than using scenarios to measure the impacts of different policy options on nature, scenarios representing the desired outcomes for biodiversity and ecosystem services can be used to inform how policies can guarantee ecosystem integrity into the future.

Keywords: *Nature's contributions to people; alternative scenarios; Nature Futures Framework; science-based policy; neotropical savanna; Forest Code; Soy Moratorium; Matopiba region.*

Um modelo conceitual para avaliar o impacto de fatores antropogênicos nos serviços ecossistêmicos relacionados à água no Cerrado

Resumo: O desenvolvimento de estratégias que conciliem atividades antropogênicas com a conservação da natureza tem se tornado cada vez mais urgente, principalmente em regiões que enfrentam uma rápida conversão da vegetação nativa em agricultura. Modelos conceituais permitem avaliar como fatores antropogênicos (por exemplo, mudança de uso e cobertura do solo e mudanças climáticas) modificam os processos naturais, sendo uma ferramenta útil para apoiar a tomada de decisões estratégicas. O presente trabalho descreve um modelo conceitual para avaliar a provisão de serviços ecossistêmicos relacionados à água sob diferentes cenários de uso do solo na região de Matopiba, no Cerrado, a savana com maior biodiversidade do mundo e uma fronteira agrícola. Foram determinadas as variáveis do modelo (fatores diretos, fatores indiretos, componentes focais e respostas) e o *Nature Futures Framework* foi consultado para incorporar componentes socioeconômicos e feedbacks. Cenários futuros foram desenvolvidos considerando possíveis trajetórias de fatores antropogênicos e respostas de governança que podem impactar o uso do solo na região, incluindo a possibilidade de cumprimento total do Código Florestal e a implementação da Moratória da Soja na região. O modelo conceitual e os cenários apresentados no presente trabalho podem ser úteis para melhorar a compreensão das complexas interações entre fatores antropogênicos, serviços ecossistêmicos relacionados à água e suas possíveis implicações para os sistemas naturais e sociais da região. Decisões de governança serão críticas para manter os ecossistemas da região, os serviços fornecidos por eles, a cultura e tradição das pessoas historicamente inseridas na paisagem. Em reconhecimento da dependência da humanidade em relação à natureza, destaca-se a importância de inverter a maneira como os cenários são usualmente usados. Em vez de mensurar os impactos de diferentes políticas na natureza, cenários representando os resultados desejados para biodiversidade e serviços ecossistêmicos podem ser usados para informar como políticas podem garantir a integridade dos ecossistemas no futuro.

Palavras-chave: *Contribuições da natureza para as pessoas; cenários alternativos; Nature Futures Framework; política baseada na ciência; savana neotropical; Código Florestal; Moratória da soja; Matopiba.*

Introduction

Human activity has degraded over 75% of Earth's land surface, driving species extinction, intensifying climate change and undermining the well-being of two fifths of humanity (Scholes et al. 2018). In 2010, land degradation cost the equivalent of about 10% of the world's annual gross product through the loss of biodiversity and benefits provided by nature (Scholes et al. 2018). Therefore, one of the main challenges nowadays is to continue producing materials to support human systems, while maintaining the functionality of the global ecosystems and the provision of ecosystem services (i.e. the benefits that humans receive from nature that are essential for human activity and well-being; MEA 2005).

Ecosystem services include the availability of freshwater, which is finite in time and space and can be impacted by anthropogenic activities. Land use/land cover change (LULC) has negative impacts on water-related ecosystem service provision (Spera et al. 2016). LULC and the additional impacts of climate change make access to water one of the main challenges of the 21st century (U. N. General Assembly 2015). Many regions around the world are already facing water scarcity, while the demand for water resources is increasing (Veldkamp et al. 2017).

Brazil has 12% of the planet's freshwater reserves, most of the world's rainforests and an estimated 20% of global biodiversity (FAO 2015, Brasil 2017, 2018). This wealth of Brazilian natural capital brings great responsibilities as changes occurring within its territory can affect local, regional and global environmental equilibrium (Loyola 2014, Levis et al. 2020). Agriculture is one of the sectors that most impacts this natural capital and also the strongest sector of the Brazilian economy (Almagro et al. 2017). Demand for agricultural land is one of the main pressures contributing to land degradation and the loss of biodiversity and ecosystem services in Brazil (Bustamante et al. 2019). In addition, agricultural irrigation accounts for 67% of freshwater consumption, with irrigated area covering almost 7 Mha and expected to increase (Brasil 2018).

Much agricultural expansion is occurring in the Cerrado region, the second most extensive biome in South America and the most biodiverse Neotropical savanna in the world (Sano et al. 2010). The area destined to agriculture in the Cerrado nearly tripled between 2000 and 2016 (Mansur 2017). Despite being a biodiversity hotspot, the Cerrado has already lost 46% of its coverage (Strassburg et al. 2017). Only 7% of what remains is under environmental protection, leaving approximately 40% of remaining native vegetation available for legal deforestation (Soares-Filho et al. 2014; Strassburg et al. 2017). Agricultural expansion impacts biodiversity and ecosystem services provided by the Cerrado ecosystems and draws attention to the need to implement efficient and well-planned conservation actions (Vieira et al. 2018, Resende et al. 2019).

The region of the Cerrado known as the Matopiba should be prioritised for the safeguarding of biodiversity and ecosystems services. Despite containing the largest continuous area of native vegetation of the entire Cerrado (Miranda et al. 2014), the Matopiba region has emerged as a centre of agricultural expansion and deforestation in recent decades (Sano et al. 2019, Zalles et al. 2019). Between 2002 and 2014, about 68% of the expansion occurred by suppressing native vegetation (Garcia & Filho 2018). In 2017 the region was responsible for 11% of Brazil's soy production and as agricultural expansion is predicted to continue, demand for water in the Matopiba is expected to increase considerably (Ferrarini et al. 2019, de Barros & Stege 2019). Water scarcity is already a problem in this region and is expected to worsen as environmental conditions become warmer and drier according to climate projections

(Brasil 2018). Feedbacks between land use/land cover and climate change could also affect rainfall amounts and patterns, threatening the sustainability of agricultural production (Spera et al. 2016) and intensifying social conflicts over land and water.

Maintaining biodiversity and ecosystem services into the long term poses a great challenge. Policy responses to this challenge at the local and global scale may benefit from the use of integrated models that describe the drivers of change and their impacts on natural resources (Janse et al. 2015). Understanding and modelling the drivers of change, pressures and their dynamic links with biodiversity, ecosystem services and human well-being is thus essential to integrate science, society and stakeholders (Díaz et al. 2015). Models may aid the development of well-informed, science-based policies that explicitly consider biodiversity and ecosystem services, by evaluating alternative scenarios of policy options and their consequences for socio-ecological systems (Janse et al. 2015). Research to improve the sophistication of scenario modelling is necessary to the advancement of environmental policy that is capable of guaranteeing biodiversity and ecosystem services into the future.

Using the Matopiba region of Brazil as a case study this article has two main aims: i) to describe the development of a conceptual model that shows how anthropogenic drivers impact water-related ecosystem services, and ii) to develop future scenarios that consider the main governance options relevant to the study area. In order to develop this conceptual model and determine possible future scenarios, a Nature Futures Framework approach was used, considering values associated with water-related ecosystem services that encompass social (e.g. economic and utilitarian), cultural (e.g. traditional and Indigenous identities) and intrinsic values. These three ways of distinguishing the value of nature reflect the multiple ways that water-related ecosystem services can be understood and valued by diverse stakeholders in the Matopiba region. Whilst no actual modelling was undertaken in this study, the conceptual model and future scenarios presented here may be used to guide future studies that aim at scenario modelling in the region.

Material and Methods

1. Study Area

The study focused on the Matopiba region in the northern part of the Brazilian Cerrado that encompasses portions of the states of Maranhão, Tocantins, Piauí and Bahia (Miranda et al. 2014; Figure 1). The region covers approximately 73 million hectares (~8% of the Brazilian territory) originally composed by different types of vegetation, including grassland, shrubland, savanna and forest ecosystems (Miranda et al. 2014). Approximately 17% of the Matopiba is covered by protected areas, including those set for strict protection (IUCN categories I to III), sustainable use (IV to VI) and Indigenous lands (Embrapa 2015). The region's average annual temperature is above 25 ºC with an annual rainfall of between 1000mm and 1900mm (Alvares et al. 2013). In recent years the native vegetation of the Matopiba has been rapidly converted to agricultural activities (Figure 2), mainly mechanised soybean plantation (e.g. soy production in the region increased by 253% between 2000 and 2014; Carneiro & Costa 2016). Following this trend, Matopiba has become one of the last large-scale agricultural frontiers in the world (OECD/FAO 2015). In the coming decade Brazil is expected to become the world's largest producer of soybean (Cattelan & Dall'Agnol 2018) and agricultural expansion in the Matopiba is expected to continue at

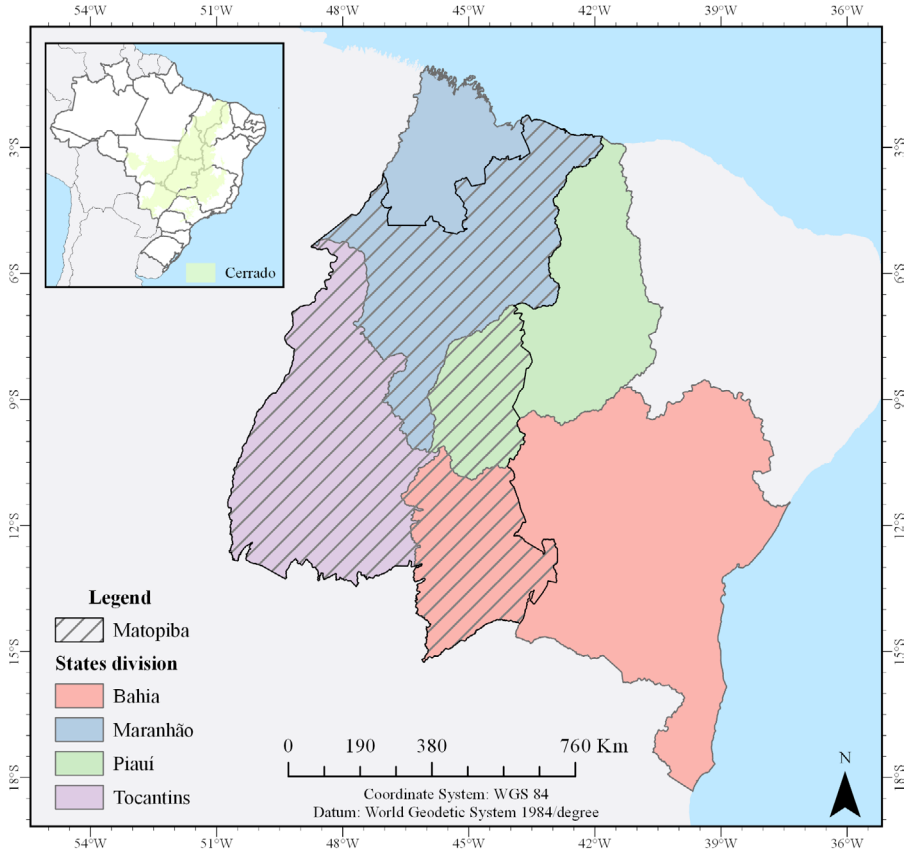
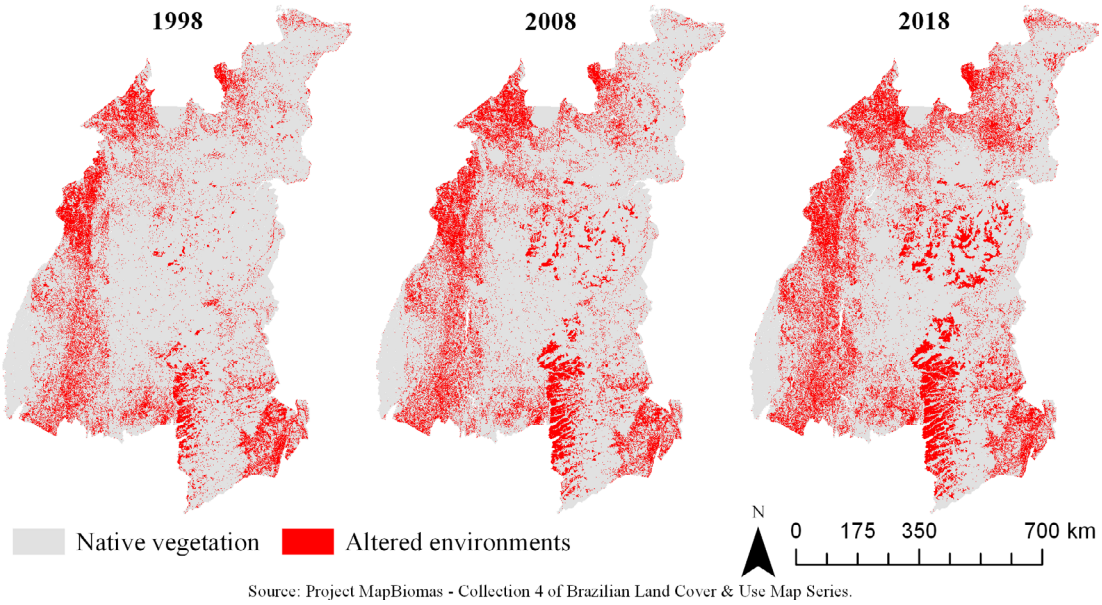


Figure 1. Location of the Matopiba region.



Source: Project MapBiomas - Collection 4 of Brazilian Land Cover & Use Map Series.

Figure 2. Land use/land cover changes in the Matopiba region over recent decades. Native vegetation includes remnants of forest, savanna and grassland ecosystems, while altered environments include mainly pasture and agricultural areas.

a rapid pace due to land availability, land costs, high productivity potential and continued demand for this commodity.

2. *Drawing a conceptual model*

A conceptual model of a social-ecological system can be defined as 'a concise summary in words or pictures of relationships between people and nature' (Díaz et al. 2015, p3). Models integrate key social and ecological components, and represent, in a simplified way, the interrelations between components. Drawing a conceptual model can be used to identify the primary components of interest within a system and the interrelationships that occur between those components, with the intention of identifying how changes in drivers may impact other components of the system (Díaz et al. 2015).

The conceptual model for the Matopiba region was developed following the guidance of prominent researchers during the scientific course "São Paulo School of Advanced Science on Scenarios and Modelling on Biodiversity and Ecosystem Services to Support Human Well-Being", which was held in São Pedro, São Paulo, Brazil, during two weeks in July/2019. These researchers presented different types of conceptual frameworks, scenarios and models associated with biodiversity, ecosystem services and human well-being that informed the construction of the model presented in this study. Throughout the event, findings were presented to all participants (~90 early-career researchers from different countries, cultures, and theoretical backgrounds) and ideas and suggestions were shared to improve our approach. Instructions and feedback were complemented by the authors' knowledge about the Matopiba region and literature review.

The focus of the conceptual model (presented in the results section) developed in this study was to assess the impact of agricultural expansion on nature, mainly on water-related ecosystem services and biodiversity. The development of the approach considered indirect drivers (i.e. underlying causes of change that are generated outside the ecosystem in question; Díaz et al. 2015); direct drivers (i.e. natural or anthropogenic factors that affect nature directly; Díaz et al. 2015); focal components (i.e. the main components of the system that are selected in order to measure the effects of changing drivers); and responses (i.e. the outcomes caused by the changes in the focal components). The links between each variable, including feedbacks among them, were investigated.

3. *Incorporating the Nature Futures Framework*

The Nature Futures Framework was used to identify how water-related ecosystem services could be valued according to nature perspectives, which reflect how different actors may perceive and relate to nature. The Nature Futures Framework was developed by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) and considers the different values and relationships that people have with nature, including cross-scale dynamics and socio-ecological feedbacks (Lundquist et al. 2017). The framework provides a methodology to incorporate different ways of valuing nature into decision-making (Schoolenberg et al. 2018). The *nature for nature* lens recognises the value of the preservation of nature's processes and the intrinsic value of natural systems, without human intervention. Through the perspective of *nature for people,* the value of nature is connected to the utilitarian functions of ecosystems. The *nature as culture* perspective recognises the integration of human and natural systems, in which humans are an integral part of nature and its functions.

4. *Future scenario development*

Exploratory scenarios were developed aiming to examine a range of potential trajectories of direct drivers for the Matopiba region (e.g. IPBES 2016). Specifically, alternative future scenarios were proposed, focusing on variations in the implementation of environmental policies (i.e. Forest Code, Soy Moratorium, management of protected areas/ Indigenous lands) and international demand for soybeans, as presented below and summarised in Table 1. These components were included in the scenarios because they contribute to determine future LULC

in the Matopiba region. Actual modelling was beyond the scope of this study, nonetheless these scenarios were useful to explore possible implications of political decisions for multiple socio-ecological variables. All five scenarios considered that climate change would occur following a unique climate change projection (e.g. the most probable climate change scenario based on current predictions; IPCC 2014). Using the same climate change projection maintains comparability among the five proposed scenarios and isolates the influence of LULC. Thus, five alternative future scenarios were proposed:

1) Business as usual scenario: considers that policies and other drivers of change that influence LULC in the region would not be changed and agriculture would continue to expand at current trends. This scenario considers that part of agricultural expansion implies illegal deforestation, in accordance with current rates and patterns. Indeed, compared to other regions such as the Amazon, environmental regulations in the Matopiba are less strict with fewer policies to prevent and monitor environmental degradation (Calmon 2017).

2) Forest Code scenario: considers that agricultural expansion will continue to occur, but in compliance with the Forest Code (formally recognised as the Native Vegetation Protection Law; Law nº 12651/2012), the main piece of Brazilian environmental legislation that guides LULC on private rural properties (Brancalion et al. 2016). The Forest Code defines the areas within private rural properties in which native vegetation must be maintained or restored: the Permanent Preservation Area (PPA) and the Legal Reserve (LR). PPA is comprised mainly of the margins of watercourses and areas with steep slopes and hilltops, aiming to conserve water resources and maintain geological stability within rural properties. The LR is an area within a rural property aimed at ensuring the sustainable use of natural resources, the conservation and rehabilitation of ecological processes, and the conservation of biodiversity. In the Matopiba region, landowners are obliged to set aside 20-35% of their property as LR (the highest percentage valid for properties that occur within the boundary of the Legal Amazon; Zakia & Pinto 2013). This scenario considers that PPA and LR in the Matopiba region would be properly maintained in accordance with the Forest Code. As a consequence, there will be no illegal deforestation, but still 40% of the native vegetation could be legally converted to agriculture (Soares-Filho et al. 2014).

3) Soy Moratorium scenario: considers that the Soy Moratorium would be implemented in the region, thus avoiding the conversion of native vegetation into soybean plantations. The Soy Moratorium is a zero-deforestation voluntary agreement signed by major players in the soybean production chain and implemented in the Brazilian Amazon (Gibbs et al. 2015). Several studies have shown that the Soy Moratorium has been effective in preventing conversion of native vegetation to soybean fields in the Amazon (Nepstad et al. 2014, Kastens et al. 2017, Gollnow et al. 2018). However, leakage to the Cerrado region may have occurred (Latawiec et al. 2015). Implementing the Soy Moratorium in the Cerrado would be particularly significant to prevent further deforestation in the Matopiba, as approximately 40% of soybean expansion in this region so far has occurred over native vegetation areas (Gibbs et al. 2015).

4) Utopia scenario: considers that global consumption of agricultural commodities will no longer increase (Schneider et al. 2010). Therefore, agricultural area would not expand in the Matopiba. In addition, Forest Code will be properly enforced and the network of protected areas would be expanded to 50% of the Matopiba's area, following the Half-Earth project proposal (Wilson 2016). Protected areas are effective in preventing deforestation and have a major role in protecting the remaining natural vegetation in the Cerrado (Carranza et al. 2014, Paiva et al. 2015, Brum et al. 2019). This scenario is based on the concepts discussed by Scarano (2019) about "deep" sustainability, which is characterised by "a world where people and nature live in full harmony by considering both long and short-term perspectives" (Scarano 2019, p. 53). Whilst this scenario represents a future that diverges from much current experience, it is important to identify the kind of future that humanity should strive for and the different pathways to achieve that future (Rosa et al. 2017).

5) Agribusiness scenario: considers a softening of national environmental policies according to bills presented by the current federal government. It considers the approval of bill n. 2362/19, which removes the requirement for LR within all private properties in Brazil (see

Table 1. Description of the five alternative scenarios.

	Business as usual scenario	Forest Code scenario	Soy Moratorium scenario	Utopia scenario	Agribusiness scenario
Forest Code	No changes in current enforcement	Full enforcement	Full enforcement	Full enforcement	Full enforcement, however extinction of Legal Reserves
Soy Moratorium	No implementation	No implementation	Implementation	Not applicable	No implementation
Protected areas/ Indigenous lands	No changes in the current coverage and management	No changes in the current coverage and management	No changes in the current coverage and management	Expansion of PA/ IL to 50% of the region's area	Legal permission to expand agriculture inside Indigenous land
Agriculture	Agricultural expansion under current trends	Agricultural expansion in accordance with the Forest Code	Agricultural expansion in accordance with the Forest Code and Soy Moratorium	No further expansion of agricultural areas	Strong agricultural expansion due to weakening of environmental policy
International demand for soybeans	Increasing demand, following the current trends	Increasing demand, following the current trends	Increasing demand, following the current trends	No changes in the current demand	Increasing demand, following the current trends

Metzger et al. 2019). In addition, this scenario considers that protections for Indigenous lands would be modified to allow the legal expansion of agriculture within Indigenous lands, considered in bill n. 191/20.

Results

1. The conceptual model

The conceptual model is presented in Figure 3. The focal components selected were water quality and quantity, a choice that reflects the critical role that water-related ecosystem services play in the development of the study region (Garcia & Filho 2018). The model includes three indirect drivers (commodity market, governance and technology) which affect the direct drivers (climate change and LULC). Commodity markets generate pressure on natural systems through the demand for primary resources, fostering or discouraging agricultural expansion (Marques et al. 2019). Governance (i.e. trends in the implementation and enforcement of regulation and legislation including the Forest Code, Soy Moratorium and establishment or degazetting of protected areas) can either intensify climate change and LULC or promote conservation through land protection and regulation of land use. Technological advancements might foster the transition from small-scale agriculture to mechanised agriculture, requiring the use of great extensions of land, along with the implementation of irrigation systems and the intensive use of pesticides and agrochemicals. Conversely, technological advances in agriculture can create the sustainable intensification of agriculture, increasing productivity such that pressure for expansion is eradicated (Latawiec et al. 2015).

Feedbacks among climate change and LULC were identified in the conceptual model. Climate projections for the region show a trend for increased mean temperature, decreased daily and annual precipitation and lower atmospheric humidity, leading to even dryer conditions and, in the long term, desertification (Marengo & Bernasconi 2014). These expected changes can lead to the unsuitability of areas for growing crops, displacing agricultural expansion in response to the changing climate (FAO 2016). Moreover, as the conversion of native Cerrado vegetation by agriculture decreases the water balance, LULC might affect precipitation in the region (e.g. Spera et al. 2016). LULC also modifies carbon stocks in vegetation and soil, contributing to climate change. Climate change and LULC in turn affect water quality and water quantity, the model's focal components (Nobre et al. 2020). These changes might negatively affect agricultural production, water catchment runoff and ecosystem services (Marengo & Bernasconi 2014).

Climate change can affect water quality and quantity in several ways, including increased temperatures, seasonal variability of precipitation, and evapotranspiration or decreased annual rainfall (Sun et al. 2008; Carpenter et al. 2011; Nunes et al. 2017). Higher water temperatures and less precipitation can lead to a reduction in water yield, especially during low flow seasons, thus affecting the timing and inflow of water to reservoirs (De Lucena et al. 2009; Bangash et al. 2013; Neupane et al. 2015; Van Vliet et al. 2016). Seasonal changes in precipitation can lead to greater erosion and nutrient export, thus causing siltation of reservoirs (Nunes et al. 2017). Increased nutrient loading and warmer water temperatures, can favour the proliferation of blooms of cyanobacteria (Paerl & Paul 2012; Bonilla et al. 2016) and threaten the persistence of aquatic organisms due to less dissolved oxygen and increased pollutant load (Carpenter et al. 2011). As a result, the provision of drinking and irrigation water, habitat for biodiversity, and hydropower generation can be hampered by changes in water quality and quantity caused by the adverse effects of climate change. The impairment of freshwater resources can cause local land conflicts by emphasising inequalities and forcing migration (Reuveny et al. 2007; Scheffran & Battaglini 2011).

LULC might also have several consequences on water quality and quantity (Vitousek 1997; Marques et al. 2019). For

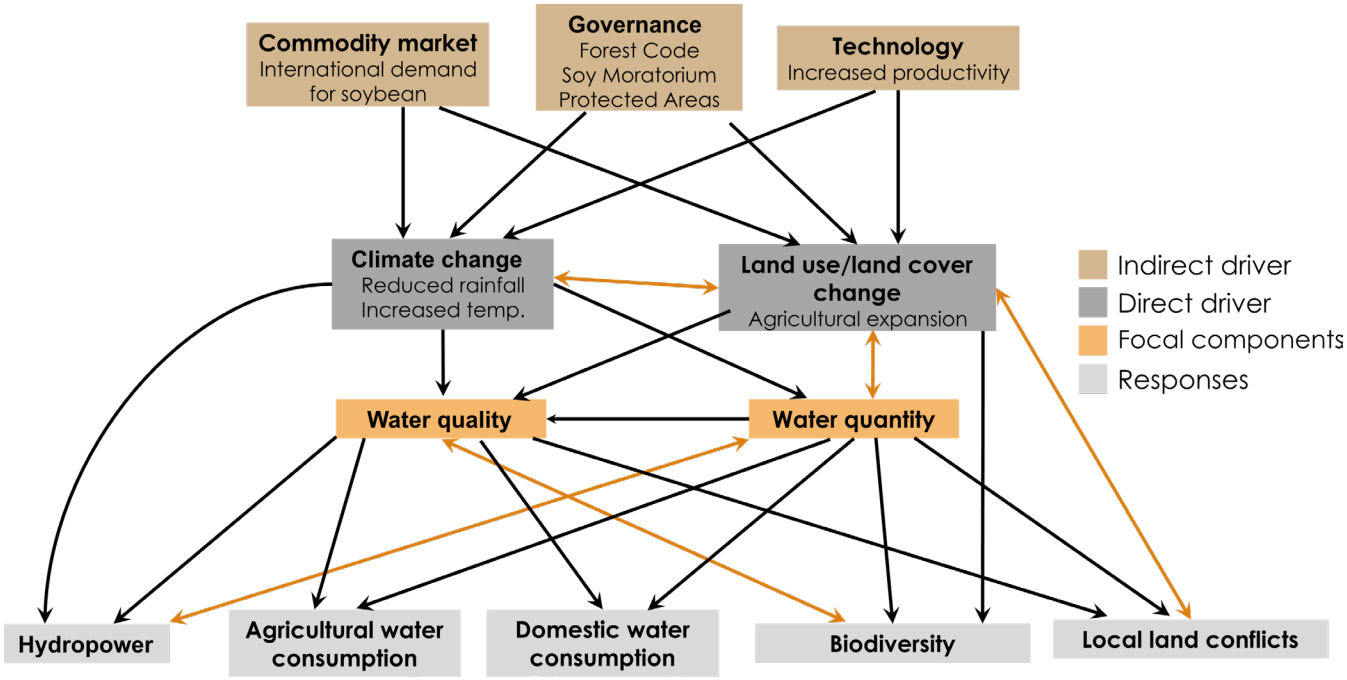


Figure 3. Conceptual model describing the focal components, drivers, and responses related to water quality and quantity in the Matopiba region of Brazil. Arrows represent possible relationships among variables. Feedback relationships are represented by orange arrows.

example, the conversion of natural habitats to agriculture might alter the patterns of evapotranspiration, runoff and groundwater recharge (Sun et al. 2008; Carpenter et al. 2011; Nunes et al. 2017). Fertilisers and other agrochemicals are sources of nutrients and other pollutants; therefore, soil erosion and runoff contribute to exporting them to water (Schilling et al. 2008). Nutrient enrichment from agricultural sources can favour the proliferation of cyanobacterial blooms, affecting domestic water consumption and aquatic biodiversity (Paerl & Otten 2013; Doubek et al. 2015). In addition, LULC might be associated with the increased water demand for irrigation and hydropower generation, which is met through increased diversions and impoundments (Vitousek et al. 1997). Expansion of crops can also push smallholders and Indigenous and traditional communities to marginal lands with scarce resources, which can lead to conflicts and disputes (Mbonile 2005; Sauer 2018).

Therefore, the two direct drivers (LULC and climate change) can drive reductions in water quality and quantity, affecting water potability and aquatic biodiversity and potentially causing conflicts related to the availability of clean water. Changes in water quantity might also affect water quality. Changes in both parameters (water quality and quantity) may impact human activities (i.e. hydropower, agricultural and domestic water consumption), biodiversity and land conflicts, which were identified as responses in the conceptual model.

2. *The Nature Futures Framework perspective*

Considering that the region encompasses different types of social groups, including Indigenous and traditional communities, smallholder family farmers and more recently large-scale agribusiness farmers, the potential values associated with a healthy hydric system could vary a lot. Thus, different values could be associated with the water-related ecosystem services included in the conceptual model (Figure 4). In terms of the utilitarian perspective of nature for society, water-related ecosystem services can be valued for the energy offered through hydropower, water for agricultural irrigation and domestic use and the tourism opportunities provided by the river system. When viewing nature as having intrinsic value through the nature for nature lens, the important aspects include the maintenance of ecosystem function and biodiversity and the regulation of the water cycle. Nature as culture provides a perspective in which water quality and quantity can be valued as providing opportunities for learning and inspiration, maintaining culturally important species and supporting the identities of people with a long history in the region. Clashes in ways of understanding and valuing nature by actors coexisting and utilising the same land, coupled with unequal access to resources can lead to conflict for land and water.

3. *Predicted outcomes of future scenarios*

The five scenarios proposed in the present study could generate remarkably different outcomes in terms of the rate of agricultural expansion, water quality and quantity, land and water conflicts and biodiversity. Whilst performing scenario modelling was not within the scope of this article, it was possible to predict results that may arise from each scenario based on a literature review and authors' knowledge of Brazilian environmental policies. The predicted outcomes of each scenario are described below and trends summarised in Figure 5.

In the "Business as usual" scenario, the increased demand for water and runoff of agricultural inputs could impair biodiversity and the provision of water-related ecosystem services. It is expected that poor compliance with the Forest Code would result in high levels of deforestation (Roriz et al. 2017, Soterroni et al. 2018). Soterroni and colleagues (2018) suggested that weak enforcement of the Forest Code in Brazil would result in deforestation rates similar to those of a scenario without this mechanism in place. Agricultural expansion in the Matopiba region would lead to high erosion rates, which, beyond impacting on river systems, can affect agricultural productivity (Gomes et al. 2019). Agricultural expansion may exacerbate social inequality as natural and economic resources are unevenly distributed among the agribusiness sector and Indigenous and traditional communities and other regional actors. Land and water conflicts would be expected to increase.

In the "Forest Code" scenario, the rate of LULC would probably decrease due to an absence of illegal deforestation, leading to a slight increase in the biodiversity conservation and provision of water-related

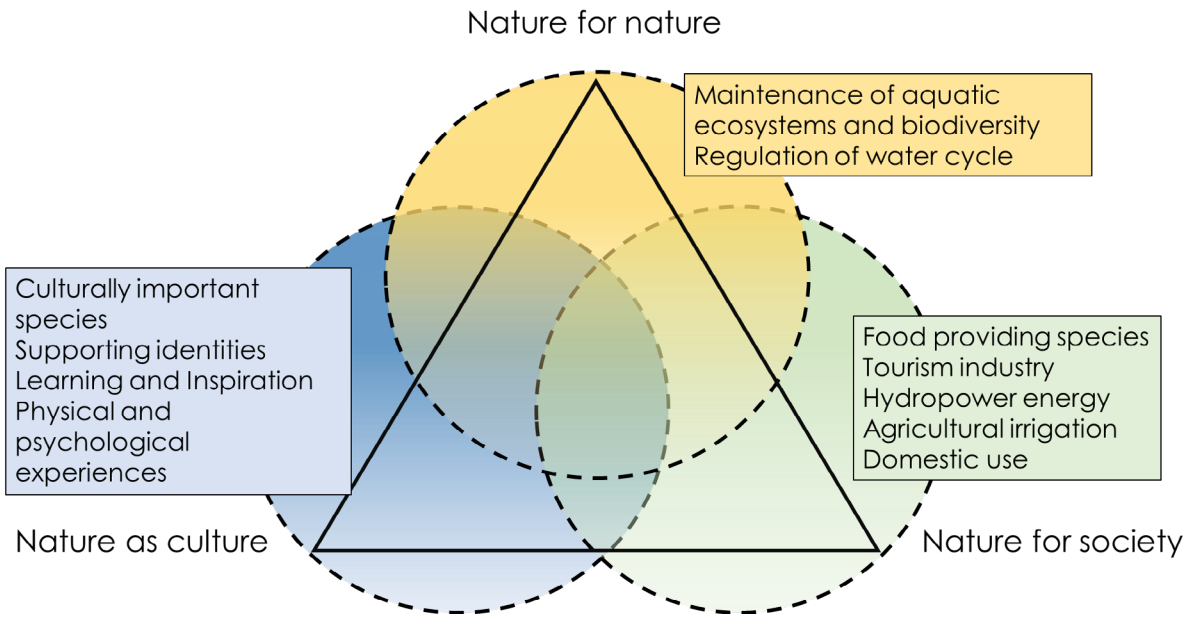


Figure 4. Values of nature according to different perspectives of water-related ecosystem services in the Matopiba region.

ecosystem services when compared to the "Business as usual" scenario. However, in the Matopiba region there is a surplus of native vegetation that can be legally cleared, so even with Forest Code enforcement full benefits for water security and biodiversity may not be realised (Vieira et al. 2018). Moreover, the riparian widths for rivers introduced by the Forest Code, after revisions approved in 2012, may be insufficient to protect water quality (Valera et al. 2019). Under this scenario, conflicts for land and water may still occur. Even when undertaken in compliance with the Forest Code the expansion of agricultural activities may impact on livelihoods and access to resources of other regional actors.

In the "Soy Moratorium" scenario, the expansion of soybean production would not imply the conversion of native vegetation. Around 40% of the remaining Cerrado native vegetation could be legally converted to agriculture in the absence of the Soy Moratorium (Strassburg et al. 2017), so its implementation is an urgent matter. The Moratorium could create great benefits for the conservation of Matopiba, as 86% of soy expansion is expected to occur within the Cerrado region until 2050 (Soterroni et al. 2019). The native vegetation maintained through the implementation of the Soy Moratorium could reduce the rate of soil erosion, improve water quality indicators, and increase biodiversity conservation when compared to the "Business as usual" scenario. Under this scenario LULC would be reduced, generating less land and water conflicts

In the "Utopia" scenario the expansion of agricultural area will be very low (or even zero) due to the reduction of international demand for soybeans and environmental policies, thus the provision of water-related ecosystem services and biodiversity conservation would improve significantly compared to the "Business as usual" scenario. The enforcement of the Forest Code and increase in protected area would result in a larger proportion of land with native vegetation, contributing to the provision of water-related services. By allowing increased water infiltration and storage, natural vegetation will secure water supply in different seasons. Landscape composition is related to surface water quality, and several studies indicate that larger percentages of forest in the watershed are correlated with better water quality (Qiu & Turner 2015, Huang et al. 2016). Following strong changes in the development pattern of the region, a reduction in land and water conflicts between agribusiness, Indigenous and traditional peoples and other stakeholders could be expected.

In the "Agribusiness" scenario, the softening of national environmental policies could lead to a higher rate of LULC than seen in the "Business as usual" scenario. Agriculture could expand extensively in Matopiba, including into Indigenous territories. If LRs were revoked, about 29% of the remaining vegetation in Brazil could be legally cleared, and the Cerrado could be reduced to only 13% of its original extension of native vegetation cover (Metzger et al. 2019). As a result, biodiversity and ecosystem services would be drastically affected due to the large loss of natural vegetation from private lands (Metzger et al. 2019). Without natural vegetation, unsustainable agriculture practices would generate high sediment loads, nutrients and other pollutants that would enter water bodies. Moreover, land and water conflicts may be exacerbated due to unregulated agricultural expansion in the absence of robust environmental policies, potentially affecting Indigenous and traditional livelihoods and well-being.

Discussion

The reduction of water availability due to the combination of LULC and climate change, along with an accompanying increase in demand for water resources for agriculture amongst other uses is causing severe competition for this resource in the Matopiba region (Pousa et al. 2019). The conceptual model proposed in the present study might be useful to improve understanding of the complex interaction among anthropogenic drivers, water-related ecosystem services and their multiple potential repercussions for natural and social systems. In turn, the alternative future scenarios described here demonstrate that governance decisions will be critical to maintaining the Cerrado biome, the services it provides and the culture and tradition of the people historically embedded in the landscape.

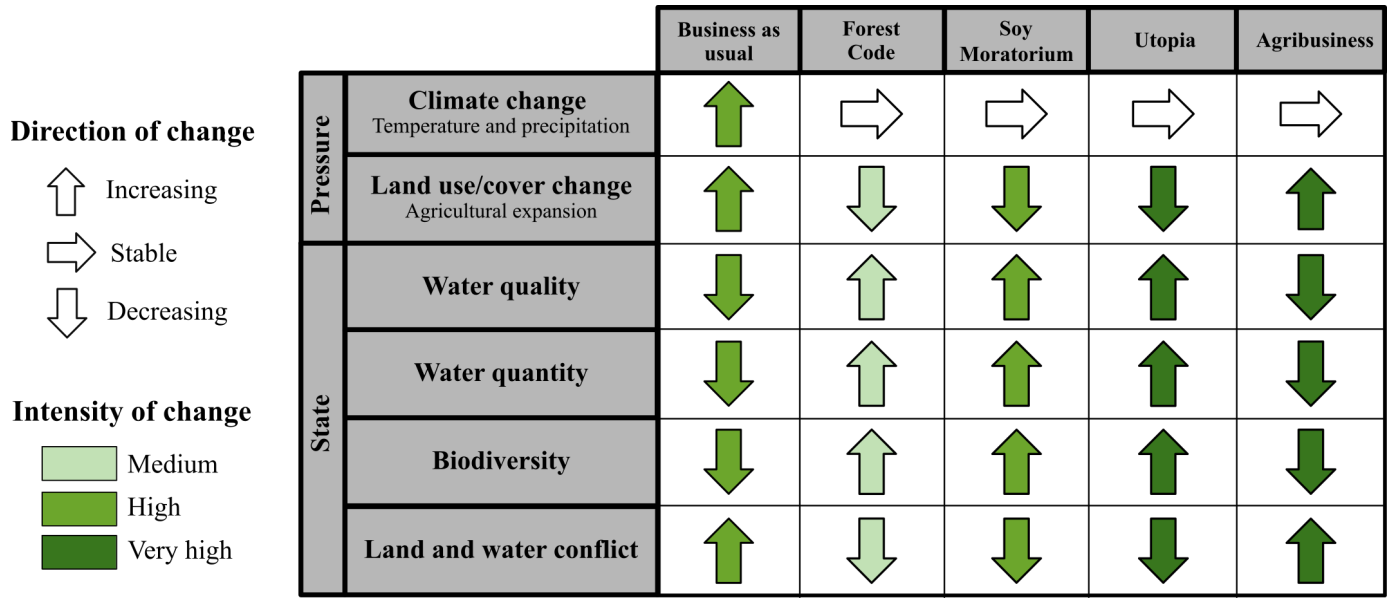


Figure 5. Predicted trends in changes in pressures and state under each scenario.

The use of scenario modelling delivers decision-makers a window into the future, to observe the outcomes for a range of socioenvironmental indicators that have implications for human well-being (Nicholson et al. 2019). In this case study, both the "Business as usual" and "Agribusiness" scenarios imply drastic reductions in the provision of water-related ecosystem services, biodiversity and also have impacts on regional stakeholders such as Indigenous groups and traditional communities. The "Forest Code" and "Soy Moratorium" scenarios generate positive outcomes for water-related ecosystem services and conflict reduction, however not to the same extent as the "Utopia" scenario. According to these hypothesised predictions, governance measures including Forest Code enforcement coupled with the implementation of the Soy Moratorium are minimum requirements for guaranteeing the protection of Cerrado ecosystems and associated ecosystem services and biodiversity.

1. Challenges in incorporating complex realities into models

The process of creating a conceptual model to assess the impacts of direct and indirect drivers on biodiversity and ecosystem services poses several challenges. Primarily there is the intrinsic limitation of all conceptual models to represent complex realities, given the impossibility of the inclusion of all variables and all possible relationships in one single model. Further challenges arise in the inclusion of variables that are difficult to measure or quantify, such as well-being or cultural identity. Many studies emphasise that the notion of value should not be restricted to mere instrumental values but embrace a larger range of values, including those related to supporting identities and culture (e.g. Jax 2019). Cultural services can be intangible and may include spiritual and cultural identification, recreation opportunities or heritage values (Bray et al. 2019). Despite the challenges of including multiple ways of valuing nature into models this is essential to improve understanding of the complex relationships and feedbacks that may occur.

It is important to recognise that land and water-related conflicts represent just one part of the many issues that threaten human well-being; there is a huge knowledge gap on how to incorporate human well-being indicators into research and modelling (Pires et al. 2018). In the Matopiba region, the well-being of traditional and Indigenous local populations suffers as they struggle with land grabbing and water conflicts related to soybean agriculture expansion. The land rights of traditional and Indigenous groups are extremely difficult to express in data that can be incorporated into scenario modelling because land tenure in the region is mostly informal, based on customary and continuous land occupation over generations (Pitta & Vega 2017). Furthermore, already existing conditions of land-expropriation and population expulsion driven by large-scale agricultural expansion are prone to aggravate under climate change effects such as water scarcity (Pitta & Vega, 2017). This may directly affect Indigenous and smallholder communities by forcing them to diversify their livelihoods or migrate and abandon their original territory, implying deep cultural consequences that cannot be measured by indices such as Gross Domestic Product (GDP). Careful considerations need to be made when attempting to include human well-being to models and in terms of deciding what types of indicators should be used. Alternative indicators that explicitly include natural and social aspects should be fostered, using as a basis examples such as the Human Development Index (HDI), Multidimensional Poverty Index, Inequality-adjusted Human Development Index, Gender Inequality Index (UNDP, 2018) or the Genuine Progress Indicator (Andrade & Garcia 2015).

2. Using scenarios to guarantee ecosystem service provision

Whilst the incorporation of the diversity of nature's values into scenario modelling is still incipient, it is an endeavour that can improve the sophistication of our responses to complex problems. In this way, the Nature Futures Framework aims at informing the development of positive scenarios, where humans and nature thrive together, addressing the multiple visions and values of nature (Rosa et al. 2017). A challenge faced throughout the elaboration of this work was how to develop scenarios that represent a future that humanity could strive for, aligned with the Nature Futures Framework. Developing the "Utopia" scenario was an exercise that reflected this, with a focus on valuing nature so as to ensure the provision of ecosystem values across all perspectives into the future. Indeed, with the application of sustainable agricultural practices, production from the region could remain the same or increase, even whilst conservation measures were enforced. The "Utopia" scenario determined nature-centred objectives and then established the changes in governance needed to achieve them, rather than supposing policy changes and analysing their impacts. When the focus is placed on maintaining biodiversity and ecosystem services it reveals the drastic policy and societal changes that need to be made. Nature conservation must be central to policy formation, including the creation of policy options that represent a future that society should aim towards, where human systems continue to be supported by the services provided by natural systems (Rosa et al. 2017).

Conclusion

With critical ecological thresholds being crossed, the decisions that are taken by policy-makers in the coming decade may cause or avoid irreversible impacts for future generations, either placing in jeopardy the natural systems on which humanity depends or guaranteeing their survival. The elaboration of scenarios that intend to deliver the biodiversity and ecosystem services outcomes necessary to maintain Earth's life support systems allows insights into the opportunities and barriers that exist in defining policy, and more broadly, in transforming society to a model of existence that occurs within the limits determined by our finite Earth. As such, this study intended to shine a light on the possible pathways available to prevent the destruction of the Cerrado biome for short-term gain and provide insights into how the incorporation of the multiple values of nature can inform spatial planning and policy responses to guarantee the future of the world's most biodiverse savanna.

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Author Contributions

Fernando de Moura Resende: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Lara A. Cornejo Denman: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Gracie Verde Selva: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Ligia Maria Barrios Campanhão: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

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Yohana Gisell Jimenez: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Edberto Moura Lima: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Julia Niemeyer: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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Inventory

Dragonflies and damselflies from the West of Minas Gerais, Brazil: checklist and new records

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Abstract: The knowledge about the richness and distribution of Brazilian dragonflies is still being unveiled. Over the years, inventories, reviews, and descriptions have been made. These contributions, apart from the taxonomic value, also provide valuable data on the occurrence of species and their distributions, which are rarely accompanied by notes about natural history and behavior. Keeping this legacy in mind, we collected dragonflies between 2011 and 2019 in Minas Gerais state, which resulted in the registration of 90 species, 41 genera and 11 families. Our results also increase distribution data, an important tool for conservation actions, and provide additional information about habitat and biology of species.
Keywords: *Zygoptera, Anisoptera, biodiversity, species list, inventory.*

Libélulas do Oeste de Minas Gerais, Brasil: lista de espécies e novos registros

Resumo: O conhecimento sobre a riqueza e distribuição das libélulas do Brasil ainda está sendo desvelado. Ao longo dos anos, inventários, revisões e descrições foram feitas. Essas contribuições, além do valor taxonômico, também fornecem um conjunto de dados precioso sobre a ocorrência das espécies e suas distribuições, estas que raramente são acompanhadas de anotações sobre história natural e comportamento. Mantendo este legado em mente, nós realizamos coletas de libélulas entre 2011 e 2019 no estado de Minas Gerais, o que resultou no registro de 90 espécies, 41 gêneros e 11 famílias. Nossos resultados aumentam os dados de distribuição, uma ferramenta importante para ações de conservação, e fornecem informações sobre o habitat e a biologia das espécies.
Palavras-chave: *Zygoptera, Anisoptera, biodiversidade, lista de espécies, inventário.*

Introduction

Mainly in the last 80 years, the efforts spent on taxonomic studies (Santos 1944, 1945, 1950, Machado 1964, 1985, Machado et al. 1991, Lencioni 2005, 2006, 2017) and surveys (Dalzochio et al. 2011, Calvão et al. 2014, Vilela et al. 2016, Koroiva et al. 2017a, Koroiva et al. 2017b, Rodrigues & Roque 2017) helped to cover gaps on knowledge of Brazilian odonates. Of the over 6000 hitherto described Odonata species, about 1700 are known to occur in the Neotropical region, and over 800 are recorded for Brazil (von Ellenrieder 2009, Neiss 2012). Despite these efforts, there are many species yet to be described.

In the past five years, most of the surveys generated taxonomic and distributional novelties. In a recent expedition (Oct-Nov 2015) to Chapada dos Guimarães over 100 Odonata species, one of them a new species described and two larvae of *Argia* (Odonata:Coenagrionidae) were recorded (Vilela, et al. 2018a,b, Cezário et a. 2018). Furthermore, Calvão et al. (2014) recorded five species new to Mato Grosso State, Brazil; Dalzochio et al. (2018) reported 182 species and seven new records to the state of Rio Grande do Sul and Rodrigues & Roque (2017) recorded 33 species new for the state of Mato Grosso do Sul.

In the state of Minas Gerais (MG), however, few studies aimed to list Odonata species. Machado (1998) compiled records of 218 species for the entire state. Ferreira-Peruquetti & de Marco Jr (2002) found 17 species in the municipality of Viçosa. Souza et al. (2013) recorded 57 Odonata species in the Baú Forest, municipality of Barroso, and Bedê et al. (2015) collected 128 species in Serra de São José. More recently, Machado & Bedê (2015) described nine new species from a small area in Serra da Canastra, and Vilela et al. (2016) recorded three new species for the state, including one new to science (Guillermo-Ferreira et al. 2016).

Distributional studies are also important under a conservationist point of view since to determine if a given area needs conservational actions, the local fauna have to be taken into account. In this sense, the International Union for Conservation of Nature (IUCN 2019) relies on several types of species data, such as population size and distributional range, in order to assess the conservation status of species around the globe. IUCN is a global program for evaluating the conservation status of plant and animal species and providing some information on species habitat and biology can help to increase those conservationist actions (IUCN 2019). However, if there is a gap on the distributional data of a given species, it makes the IUCN work difficult or even impossible, disabling actions that may be taken towards the conservation of the species and its habitat. Furthermore, considering the last two great ecological disasters caused by mining in Minas Gerais (see Freitas et al. 2019), studies on the local biodiversity are crucial to know what we lose with such environmental crimes (e.g. MMA/IBAMA 2015).

Not only the species are understudied, but also some phytophisiognomies are almost unexplored. In the west of Minas Gerais, the predominant biome is the Cerrado, which presents a great array of freshwater ecosystems. Within this biome, the Veredas play an important role on the hidrology, being consisted by permanently water saturated soil and a dense vegetation, including the palm tree *Mauritia flexuosa* L (Fonseca 2005). Additionally, Veredas are an important source of shelter and food from insects to fishes and birds, playing an important role on the ecological balance in the Cerrado. Odonates are little explored within such areas, despite recent studies show that this ecosystem holds a great number of species of the order (Vilela et al. 2016; Barbosa et al. 2019; Borges et al. 2019).

The main objective of this study is to increase the knowledge of the geographical distribution of Odonata species.. For this, here we compile data on species from the western part of Minas Gerais State and make our database available to the academic community. In summary, our study aimed to contribute to the species conservation actions, such as the IUCN Red List of Threatened Species™ and the Latin-American Odonatological Society evaluations, which many times rely on species distributional data for assessments.

Material and methods

1. Field sampling sites and methodology

Altogether, we surveyed 49 localities in ten municipalities (Figure 1):

- Campina Verde (Altitude 494m): Chácara (CVC, -19.5476, -49.4936; small pond, formed by the damming of a Vereda, Figure 2d) and Granja (CVG, -19.5357, -49.5062; small pond connected to a Vereda), both sampled in February 2013.
- Guarda-Mor (Altitude 616m): Ponto 1 (GMP1, -17.7828, -47.1301; small stream) and Ponto 2 (GMP2, -17.7726, -47.1332; small stream), both sampled in December 2014.
- Ituiutaba (Altitude 605m): Lagoa Temporária (ITBL, -18.9776, -49.4103; temporary pond) in April 2014; Ribeirão São Lourenço (ITBSL, -18.9853, -49.4179 and -19.0611,-49.3213; medium order stream, Figure 2e) sampled in December 2013 and April 2014; Rio Tijuco (ITBT, -18.9418,-49.4768; -18.9209,-49.5664 and -18.9525,-49.3377; medium sized river, Figure 2f) sampled in December 2011 and March 2012; Estância Paraíso (EPA, -18.9522, -49.3399; small stream connected to a river, Figure 2g) sampled in April 2014.
- Matutina (Altitude 1060m, Figure 2h): Matutina 1 (MAT1, -19.1377, -46.0669; small stream connected with a Vereda), Matutina 2 (MAT2, -19.1251, -46.0568; small pond), Matutina 3 (MAT3, -19.1563, -46.0369; small stream) and Matutina 4 (MAT4, -19.1221, -46.0673; small stream) all sampled in March 2015.
- Paracatu (Altitude 688m): Ranchão (PAR, -16.8608, -46.9811; stream connected with a Vereda, Figure 2c) sampled in July 2014.
- Prata (Altitude 631m): Rodovia (PRA, -19.3210, -48.9454; stream connected with a Vereda) sampled in October 2012.
- São Roque de Minas, Serra da Canastra (Altitude 819-1300m): Cachoeira Rio do Peixe (CRP, -20.2569, -46.4096; small stream by a waterfall, Figure 2a), Aqueduto (AQD, -20.2648, -46.3968; stream near to a Vereda), Riacho Costela de Vaca (RCV, -20.2658, -46.3957; stream near to a Vereda), Cerradão (CER, -20.1914, -46.3858; stream near to a Vereda, Figure 2b), Barro Sujo (BS, -20.2145, -46.3808; small stream), Cerca elétrica (CE, -20.2385, -46.3847; stream near to a Vereda), Espraiado (Subida) (ESS, -20.2411, -46.3857; stream near to a Vereda), Rio São Francisco (RSF, -20.3330, -46.4361; large river), Água Branca (AGB, -20.2922, -46.3658; small stream), Cachoeira da Chinela (CHI, -20.3002, -46.3955; stream by a waterfall), Casca D'anta (CCD, -20.2974, -46.5227; stream by a waterfall), Rolinho (RL, -20.1706, -46.5615; small stream near a Vereda), Nascente (NAS, -20.2433, -46.4463;

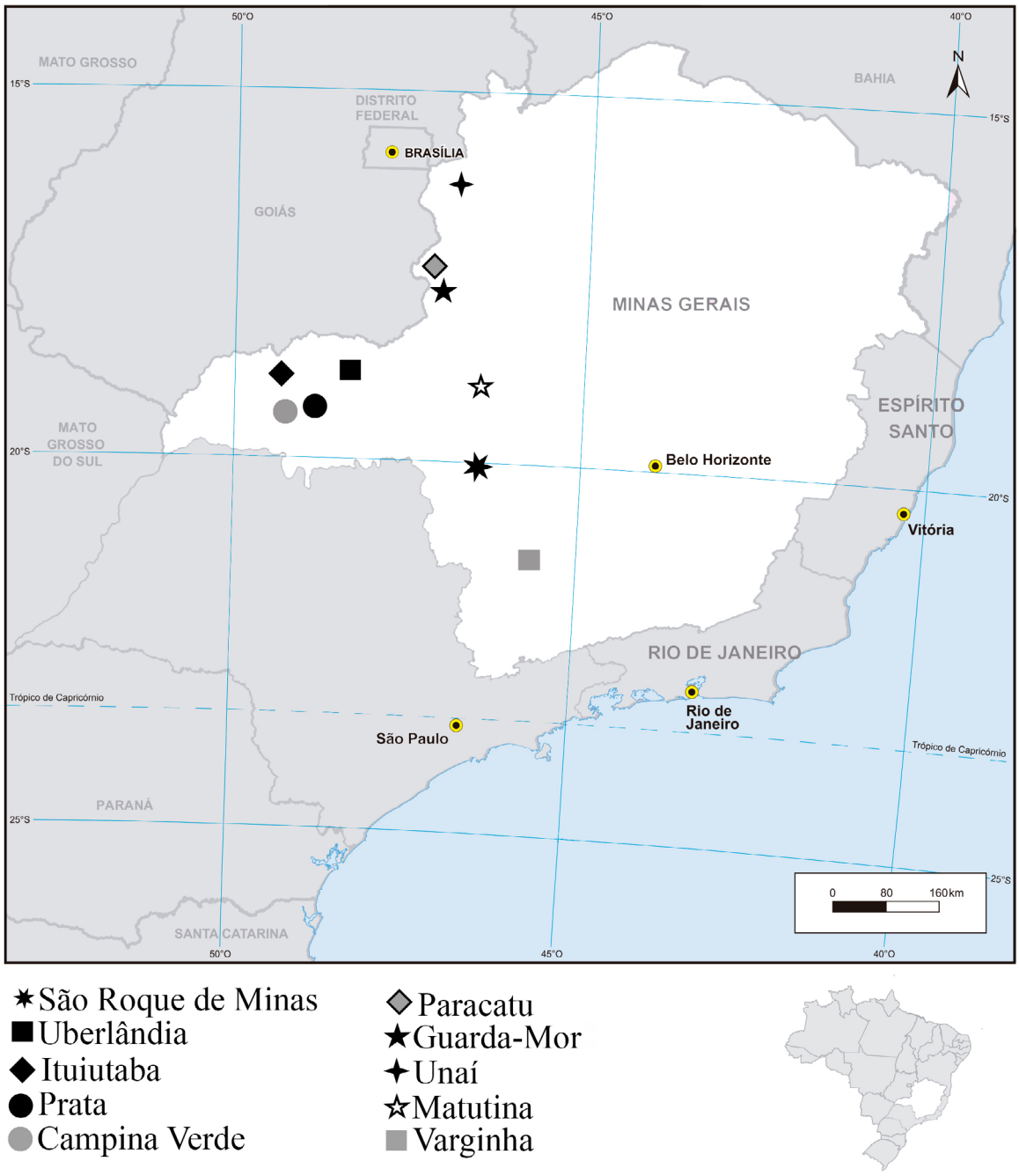


Figure 1. Map of Minas Gerais state, southeast Brazil, showing the ten sampled municipalities.

small stream connected to a Vereda), Ponte 1 (PO1, -20.2402, -46.5875; small stream connected to a Vereda), Ponte 2 (PO2, -20.2325, -46.6083; small stream connected to a Vereda), Quintal da Canastra (QUI, -20.3282,-46.5038; large pond), Cachoeira da Capivara (CPV, -20.6287,-46.2863; large stream by a waterfall), Lago Tio Zezico (ZZC, -20.3121,-46.5319; small pond), Córrego Tio Zezico (ZZC, -20.3116,-46.5324; stream), Lago P31 (P31, -20.1656,-46.6877; two small ponds within a Vereda), Riacho Sr. Vicente (VCT, -20.3033,-46.5492; ; small stream connected to a Vereda), Córrego Guariba (GUA, -20.3017,-46.5483; small stream near a Vereda), Córrego Passageiro (PSG, -20.2668,-46.5554; small stream with rocky bottom), Córrego Rasga Canga (CAN, -20.1761,-46.5603; stream by a waterfall), Portaria Sul (SUL, -20.3063,-46.5236; small stream), Portaria 2 (PR2, -20.1523,-46.6605; small stream by a waterfall), Centro de Visitantes (VIS, -20.2541,-46.4168; small stream) sampled in May and October 2017, March and November 2018 and April 2019.

- Uberlândia (Altitude 863m): Marileuza (UDI,-18.8712, -48.2481; small stream near a Vereda, which nowadays is turning to a habitation area) sampled in February 2015.

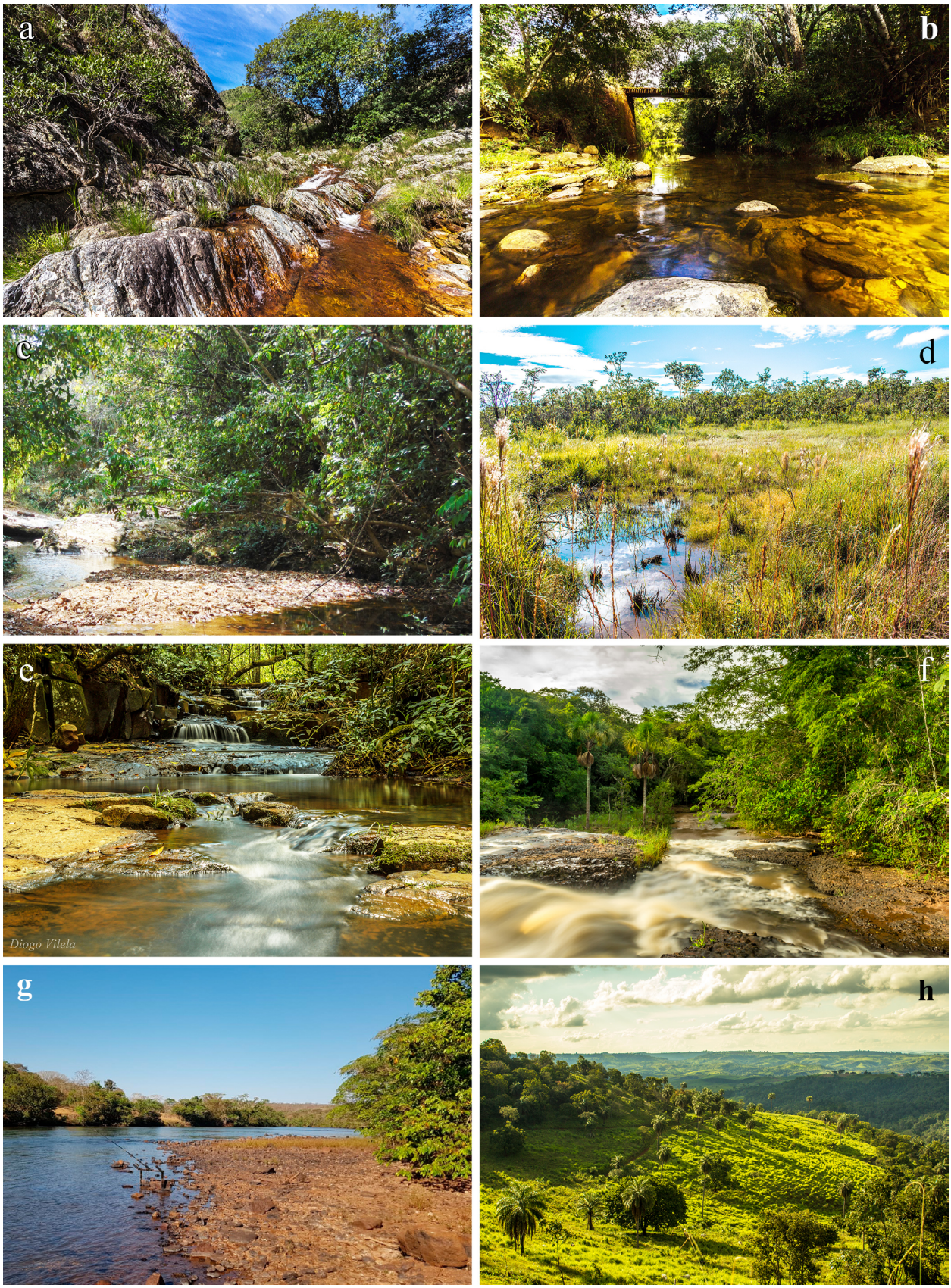


Figure 2. Some of the sampled sites in this study: a. Cachoeira Rio do Peixe (CRP), São Roque de Minas; b. Cerradão (CER), São Roque de Minas; c. Ranchão (PAR), Paracatu; d. Chácara (CVC), Campina Verde; e. Ribeirão São Lourenço (ITBSL), Ituiutaba; f. Rio Tijuco (ITBT), Ituiutaba; g. Estância Paraíso (EPA), Ituiutaba; h. Landscape between Matutina 3 (MAT3) and Matutina 4 (MAT4), Matutina.

- Unaí (Altitude 640m): Lagoa-Riacho (UNAI, -16.4822, -47.4149; medium order river and a pond) sampled in July 2014.
- Varginha (Altitude 915m): Sítio Juriti (SRI, -21.5854, -45.4070; small pond), Carro Velho (CAR, -21.5901, -45.3721; small stream), Lagoa Soberana de Minas Jorge (JOR, -21.6289, -45.4342; small stream and pond), Faz. Tachos (TCH, -21.6154, -45.4803; small stream) sampled in June 2018.

The collections were made *ad libitum* in different hours of the day, for at least one hour per site, always between 8:00 to 14:00h. An entomological net was used to collect the specimens and they were placed in individual paper envelopes. The collection authorization process was issued by IBAMA, through SISBio system under the numbers 53026-3 and 54386-6. The identifications were made using the keys of Lencioni (Lencioni 2005, 2006, 2017) and Garrison et al. (2006, 2010). The specimens collected are deposited in the Laboratory of Ecological Studies on Ethology and Evolution (LESTES, UFSCar), São Carlos, São Paulo and in the personal collection of Frederico Lencioni in Jacareí, São Paulo.

During fieldwork, we observed and noted the following behavioral traits: (i) territoriality status, (ii) mate-guarding behavior and (iii) oviposition behavior. Such behavioral traits are important because they reveal important aspects of reproductive tactics, habitat occupancy and selection, competition and even larval development (Corbet 1999).

When not possible to notice behavioral traits on the moment of collections, we searched for such information on the literature on two online platforms (Google scholar: https://goo.gl/MtXqZN; Scopus: https://goo.gl/2F36gs) with the terms "*species name*", "behavior", "behaviour". The terms were used all together, in different orders and separately along with the species names. For example: "*Tigriagrion aurantinigrum*" "behavior" "behaviour" or solely "*Tigriagrion aurantinigrum*".For every sampled species, we checked the IUCN conservation status (iucnreslist.org) (IUCN 2019). When a species is assessed by specialists, a code is given to represent its conservational status. For example, if a species is lacking distributional data and nothing much is known of its conservational situation, it is given to it a data deficient status, or DD. Other classification status are: LC (least concern), when a species is well distributed, occurring in many localities, including protected areas; NT (near threatened), when its assessment indicates any degree of conservational threat, usually applied to species occurring near expanding urban areas, which can be threatened in a near future; VU (vulnerable), species facing extinction risk in nature, with a limited distributional range (<5000 km²) in areas threatened by human activities; CR (critically endangered), species inhabiting areas less than 100 km², occurring in usually one locality, often threatened by human activities.

The map was adapted from IBGE - Brazilian Geography and Statistics Institute (2019) using Adobe Photoshop 2017.1.1. Habitus scan of species was made using an EPSON V600 Perfection and posterior plate assembling using Adobe Photoshop 2017.1.1. Photographs of the sampling sites were all made by the authors, except for (Fig. 3g), courtesy of Edson Soares dos Santos.

Results

1. *Sampled species*

We collected individuals from 11 families, 41 genera and 90 species (Table 1; Figure 3a−l). The family Libellulidae was the most representative of Anisoptera, with 13 genera and 27 species, whereas Coenagrionidae was the most specious family of Zygoptera, with 12 genera and 35 species (Table 1). PAR was the most speciose site with 16 records, whereas NAS recorded 15 species and ITBT and UNAI recorded 14 species each. On the other hand, VIS and RL were the least specious site with one species each (Table 2).

Table 1. Representation of each collected family by genera and species in 49 sampling points distributed in the State of Minas Gerais, Brazil.

Anisoptera		**Number of genera**	**Number of species**
	Aeshnidae	5	5
	Corduliidae	1	1
	Gomphidae	3	4
	Libellulidae	13	27
Zygoptera			
	Calopterygidae	2	7
	Coenagrionidae	12	35
	Dicteriadidae	1	1
	Heteragrionidae	1	4
	Lestidae	1	3
	Megapodagrionidae	1	1
	Protoneuridae	1	2
Total	11 Families	41	90

Furthermore, Machado (1998) reported 218 Odonata species to Minas Gerais state. Therefore, adding new species descriptions (n = 29) and new records (n = 22) since 1998, the number raises to 269 species to Minas Gerais (Table 3).

2. *First records and new species*

We found two new records of odonate species for Minas Gerais, one belonging to Coenagrionidae and the other to Calopterygidae: *Neoneura waltheri* Selys and *Hetaerina hebe* Selys, respectively. Also, we found a new species from the Heteragrionidae family: *Heteragrion denisye* Vilela, Koroiva and Guillermo-Ferreira.

Hetaerina hebe Selys, three males (Figure 3h): This species is recorded in the states of Rio de Janeiro (Santos 1970) and São Paulo (Lencioni 2017). Our specimens of *H. hebe* were found in streams with channel shading by riparian vegetation and presence of rapids in sampling sites of Varginha and Serra da Canastra. We have noticed females perform endophytic oviposition.

Neoneura waltheri Selys, one male (Figure 3i): *Neoneura waltheri* occurs in Brazil and Argentina. There are records of this species in the

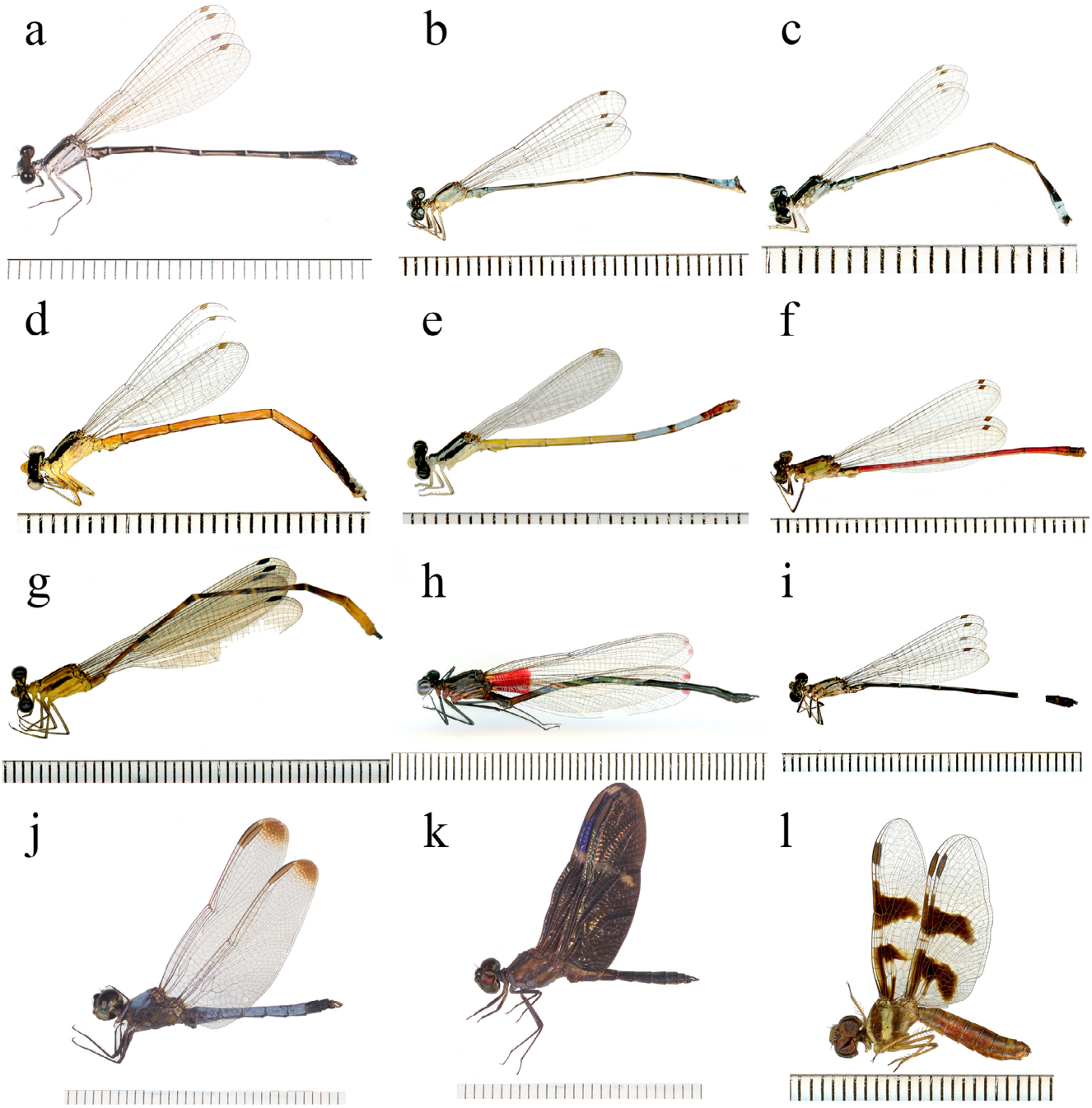


Figure 3. Habitus scan of some species sampled in our expeditions: a. *Argia lilacina* Selys; b. *Acanthagrion aepiolum* Tennessen; c. *Ischnura capreolus* Hagen; d. *Minagrion waltheri* Selys; e. *Minagrion franciscoi* Machado & Bedê; f. *Oxyagrion chapadense* Costa; g. *Heteragrion triangulare* Hagen in Selys; h. *Hetaerina hebe* Selys; i. *Neoneura waltheri* Selys; j. *Erythrodiplax ana* Guillermo-Ferreira, Vilela, Del-Claro & Bispo; k. *Zenithoptera lanei* Santos; l. *Perithemis mooma* Kirby.

states of Rio de Janeiro and Paraná. Specimens collected at the margins of the Tijuco River in Ituiutaba were perched in a clump of *Elionurus* sp. Jurzitza (1981), made some observations on specimens in National Park of Iguazu, Argentina. We have noticed females perform endophytic oviposition in tandem with the male, at running waters.

Heteragrion denisye Vilela, Koroiva and Guillermo-Ferreira, one male: this species was recently described (Vilela et al. 2019) inhabiting altitude fields within the Serra da Canastra National Park. We only found one specimen despite sampling the type location in two occasions. This species is peculiar because was found in small bushes in an open area, whereas other *Heteragrion* species are known to inhabit shaded areas with gallery woods.

3. *Endemic and peculiar species*

In addition to these records, we collected some of the endemic species of Serra da Canastra described by Machado & Bedê (2015),

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Table 2. Sampled localities with the respective number of species collected on each site.

Locality	Code	N. Species
Paracatu	PAR	16
Nascente	NAS	15
Rio Tijuco	ITBT	14
Unaí	UNAI	14
Ribeirão São Lourenço	ITBSL	12
Marileuza	UDI	12
Matutina Ponto 2	MAT2	10
Quintal da Canastra	QUI	10
Cachoeira da Capivara	CPV	9
Cachoeira Rio do Peixe	CRP	9
Aqueduto	AQD	8
Cerradão	CER	8
Rio São Francisco	RSF	8
Lago Tio Zezico	LZZ	8
Córrego Tio Zezico	ZZC	7
Carro Velho	CAR	7
Fazenda Sr. Gilberto	GIL	7
Granja	CVG	7
Guarda Mor Ponto 1	GMP1	7
Matutina Ponto 4	MAT4	7
Prata	PRA	7
Lago P31	P31	6
Guarda Mor Ponto 2	GMP2	6
Matutina Ponto 1	MAT1	6
Riacho Costela de Vaca	RCV	6
Espraiado (Subida)	ESS	6
Cachoeira da Chinela	CHI	6
Lagoa Temporária	ITBL	5
Matutina Ponto 3	MAT3	5
Ponte 1	PO1	5
Ponte 2	PO2	5
Riacho Sr. Vicente	VCT	5
Fazenda dos Tachos	TCH	4
Chácara	CVC	4
Barro Sujo	BS	4
Casca D'Anta	CCD	4
Cerca	CE	4
Córrego Guariba	GUA	4
Córrego Passageiro	PSG	4
Córrego Rasga Canga	CAN	4
Portaria Sul	SUL	4
Portaria 2	PR2	3
Sítio Juriti	SRI	3
Lagoa S. M. Jorge	JOR	3
Água Branca	AGB	3
Alojamento (P17)	P17	2
Estância Paraíso	EPA	2
Centro de Visitantes	VIS	1
Rolinho	RL	1

Table 3. List of new Odonata species and new records to the state of Minas Gerais, published after 1998.

Author	Year	Type of data	Number of records
Machado	2000	New species	1
Costa et al.	2000	New species	1
Machado	2002	New species	1
Tennessen	2004	New species	1
Machado	2005a	New species	1
Machado	2005b	New species	1
Garrison	2006	New species	1
Machado	2006	New species	1
Machado & Bedê	2006	New species	1
Machado	2007a	New species	1
Machado	2007b	New species	1
Pessacq & Costa	2007	New species	2
Costa et al.	2009	New species	1
Santos et al.	2010	New species	1
Machado	2010	New species	1
Almeida et al.	2013	New record	1
Machado	2014	New species	1
Machado	2015	New species	1
Machado & Bedê	2015	New species	7
Bedê et al.	2015	New records	6
Guillermo-Ferreira et al.	2016	New species	1
Vilela et al.	2016	New record	1
Pinto & Almeida	2016	New species	1
Ávila-Júnior et al.	2017	New species	1
De Souza et al.	2017	New records	7
Borges et al.	2018	New records	1
Barbosa et al.	2019	New records	6
Vilela et al.	2019	New species	1
This study		New records	2
		Total	**51**

such as *Franciscagrion franciscoi* Machado & Bedê, *Franciscagrion longispinum* Machado & Bedê, *Franciscobasis franciscoi* Machado & Bedê, *Franciscobasis sonia* Machado & Bedê, *Minagrion franciscoi* Machado & Bedê (Fig. 2e) and *Oxyagrion franciscoi* Machado & Bedê. Despite the extensive sampling effort throughout western region of Minas Gerais, these species remain restricted to the Serra da Canastra National Park.

Given our large sampling size, some hard to sample species were collect in Serra da Canastra such as *Limnetron debile* Karsch and *Neocordulia volxemi* Selys, both at sites with running water and little shaded areas. Additionally, the larvae of *Castoraeschna corbeti* Carvalho, Pinto & Ferreira, a possible new Libellulidae species and the hitherto undescribed female of *Mnesarete rhopalon* Garrison were also sampled.

4. *Behavioral and ecological traits*

As most of the collections were made in the course of an hour, freshwater habitat selection was the only ecological trait that could be inferred for all species. **We emphasize that some of the observed traits were already reported in the literature and the data observed by us are highlighted in bold** (Table 4).

Data on behavioral traits are derived from personal observations or from literature: territoriality status, mate-guarding behavior and oviposition behavior. Of all traits possible, however, 168 (63%) were not found on the literature or observed in our field study (*i.e*. ND). Moreover, 40 (45%) of all species had no behavioral information available. Territoriality was the most representative trait, determined for

Table 4. Odonata species collected in this study with information about freshwater habitat selection, territoriality status, mate-guarding (MGB) and oviposition behavior. LE: lentic habitat; LO: lotic habitat; FA: female alone; IT: in tandem; NC: no contact; T: territorial; NT: non-territorial; EX: exofitic oviposition; END: endofitic oviposition; PE: percher; FL: flier; IUCN Status: LC (least concern), DD (data deficient); ND: no data recorded in the study area or literature. * First record to Minas Gerais State; ** Under evaluation by IUCN specialists. **Traits in bold were observed in this study**.

Species	Habitat	Territoriality	MGB	Oviposition	IUCN status	Sampled localities	References other than this study
Acanthagrion aepiolum	**LO**	ND	ND	ND	ND	CER, GMP1, MAT2, MAT4, PAR, GIL	Tennessen, 2004; von Ellenrieder & Garrison, 2007; Muzón et al. 2008
Acanthagrion gracile	**LO, LE**	ND	IT	**END**	ND	CER, CVG, ESS, GMP1, MAT3, PAR, SRI, CAR, TCH, QUI, LZZ	Paiva-Silva et al. 2010; Lencioni, 2011; Calvão et al. 2014; Nobre & Carvalho, 2014
Acanthagrion lancea	**LO, LE**	**NT**	**FA**	**END**	ND	CVG, ITBSL, MAT4, PAR	von Ellenrieder & Garrison, 2007; von Ellenrieder, 2009b; Paiva-Silva et al. 2010; Vilela et al. 2016
Acanthagrion temporale	**LO, LE**	ND	ND	ND	ND	RSF, P31	Leonard, 1977; Souza, 2003
Acanthagrion truncatum	**LE**	NT	**IT**	**END**	LC	MAT2, MAT4, QUI, LZZ	von Ellenrieder, 2009; Guillermo-Ferreira & Del-Claro, 2012a, 2013; Vilela et al. 2016
Allopodagrion contortum	**LO**	ND	ND	ND	LC	GUA, VCT	von Ellenrieder, 2009
Archaeogomphus infans	**LE**	ND	ND	ND	ND	ZZC	Barbosa et al. 2019
Anax amazili	**LE**	ND	ND	END	ND	GMP2	Convey, 1989; von Ellenrieder & Garrison, 2007
Argia claussenii	**LO**	ND	ND	ND	ND	CPV, GUA, VCT	Lencioni, 2017
Argia croceipennis	**LO**	ND	ND	ND	LC	NAS	Costa et al. 2008; von Ellenrieder, 2009; Dalzochio et al. 2011
Argia lilacina	**LO**	ND	ND	ND	ND	AQD, RCV, CER, CE, CRP, CHI, CAR, PO2, PR2	Machado, 1988; Machado & Bedê, 2015
Argia modesta	**LO**	ND	ND	ND	ND	CPV, VIS, SUL, ZZC, CAN, VCT, PR2	Ferreira-Peruquetti, & Trivinho-Strixino, 2003
Argia mollis	**LO**	ND	ND	ND	ND	CAR, GIL, SUL, CAN	Cezário et al. 2018
Argia reclusa	**LO**	T	**IT, FA**	**END**	ND	ITBT, MAT1, MAT2, PAR, EPA, GIL, TCH, CPV	Guillermo-Ferreira & Del-Claro, 2012b; Vilela et al. 2016
Argia smithiana	**LO**	ND	ND	ND	ND	CRP, ITBSL, ITBT, MAT2, CPV	Vilela et al. 2016
Argia tamoyo	**LO, LE**	ND	ND	ND	ND**	AQD, CRP, RCV, CER, ESS, RSF, AGB, CHI, CAN	Dalzochio et al. 2011
Brechmorhoga praedatrix	**LO**	ND	ND	ND	LC	CPV	Fleck, 2004; von Ellenrieder, 2009
Cacoides latro	**LE**	ND	ND	ND	ND	GMP2	Borges et al. 2019
Castoraeschna januaria	**LO**	ND	ND	ND	ND	CRP, P17	Carvalho et al. 2009
Coryphaeshna adnexa	**LE**	ND	ND	ND	LC	UNAI	von Ellenrieder & Garrison, 2007; Paulson, 2009; Vilela et al. 2016
Cyanallagma ferenigrum	**LE**	**T**	ND	END	DD	MAT4	von Ellenrieder, 2009a; Vilela et al. 2016
Diastatops obscura	**LE**	T	**NC**	**EXO**	ND	CVC	Vilela et al. 2016
Epipleoneura machadoi	**LO**	ND	**IT**	**END**	ND	UNAI	Rácenis, 1960; Lencioni, 2017

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Continuation Table 4.

Species	Habitat	Territoriality	MGB	Oviposition	IUCN status	Sampled localities	References other than this study
Epipleoneura williamsoni	**LO**	NT	**IT**	**END**	LC	ITBSL, UNAI	von Ellenrieder, 2009; Vilela et al. 2016
Erythemis credula	**LE**	ND	ND	ND	ND	ITBT	Vilela et al. 2016
Erythemis vesiculosa	**LE**	ND	FA	END	LC	GMP2, UDI, UNAI	von Ellenrieder & Garrison, 2007; Paulson, 2009; Vilela et al. 2016
Erythrodiplax ana	**LE**	T	**NC**	**EXO**	ND**	NAS, CCD	Guillermo-Ferreira et al. 2016; Vilela et al. 2016
Erythrodiplax castanea	**LE**	ND	ND	ND	ND	AQD, CAR, JOR, CPV, ZZC, QUI	Brooks, 1989; von Ellenrieder, 2011; Monteiro-Junior et al. 2013; Borges et al. 2019
Erythrodiplax fusca	**LO, LE**	T	NC	EXO	ND	GMP1, ITBL, ITBT, MAT3, PAR, UDI, AQD, CER, RSF	Convey, 1989; Louton et al. 1996; Paiva-Silva et al. 2010; Nobre & Carvalho, 2014; Vilela et al. 2016
Erythrodiplax juliana	**LE**	T	NC	EXO	LC	ITBL, MAT2, PAR, CRP, AQD, RCV, ESS	von Ellenrieder, 2009; Vilela et al. 2016
Erythrodiplax latimaculata	**LE**	T	NC	EXO	ND	GMP1, ITBT, MAT2, MAT3, UNAI	Calvão et al. 2013; Vilela et al. 2016
Erythrodiplax lygaea	**LE**	ND	**FA**	**EXO**	LC	CAN	von Ellenrieder, 2009
Erythrodiplax pallida	**LO, LE**	ND	ND	EXO	LC	NAS	Costa et al. 2001; von Ellenrieder, 2009; Del Palacio & Muzon, 2016
Erythrodiplax umbrata	**LE**	T	FA	EXO	ND	CVG, PAR, PRA, UDI, UNAI	Garcia-Diaz, 1937; Convey, 1989; Paulson, 1998; Von Ellenrieder & Garrison, 2007; Vilela et al. 2016
Franciscagrion franciscoi	**LO, LE**	NT	**IT**	**END**	ND**	NAS	Machado & Bedê, 2015
Franciscagrion longispinum	**LO, LE**	NT	ND	ND	ND**	NAS	Machado & Bedê, 2015
Franciscobasis franciscoi	**LO, LE**	NT	ND	ND	ND**	NAS	Machado & Bedê, 2015
Franciscobasis sonia	**LO, LE**	NT	ND	ND	ND**	NAS	Machado & Bedê, 2015
Heliocharis amazona	**LO**	T	ND	ND	ND	ITBSL, PAR	Dunkle, 1991; Louton et al. 1996
Hetaerina hebe*	**LO**	T	ND	**END**	LC	TCH, SUL, VCT	von Ellenrieder, 2009
Hetaerina longipes	**LO**	T	ND	ND	ND	ITBT, PAR	Pestana et al. 2018
Hetaerina rosea	**LO**	T	IT, NC	EXO	ND	ITBSL, ITBT, MAT3, PAR, EPA, CAR, GIL, CPV, ZZC	Von Ellenrieder & Garrison, 2007; Paiva-Silva et al. 2010; Guillermo-Ferreira & Del-Claro, 2011; Vilela et al. 2016
Hetaerina simplex	**LO**	ND	ND	ND	ND**	CRP, AQD, RCV, CER, BS, ESS, RSF, AGB, CHI, PSG, CCD, QUI, NAS, PO2, PR2	Garrison, 1990; Lencioni, 2017
Heteragrion aurantiacum	**LO**	T	ND	ND	LC	MAT2, UNAI	Von Ellenrieder, 2009
Heteragrion denisye	**LO**	ND	ND	ND	ND	PO2	Vilela et al. 2019
Heteragrion gracile	**LO**	ND	ND	ND	ND	CAR, SUL	Machado, 2006; Lencioni, 2013
Heteragrion triangulare	**LO**	ND	ND	ND	ND	CER, GUA	This study
Homeoura chelifera	**LO**	NT	IT	ND	ND	MAT4, JOR	von Ellenrieder & Garrison, 2007; Paiva-Silva et al. 2010; Vilela et al. 2016
Idiataphe longipes	**LE**	ND	ND	ND	ND	ZZC, QUI	Oldrini & Mascarenhas, 2005; Borges et al. 2019
Ischnura capreolus	**LE**	NT	**FA**	**END**	ND	MAT2, MAT4, PRA, UDI, UNAI, RSF, JOR, LZZ	Paiva-Silva et al. 2010; Nobre & Carvalho, 2014; von Ellenrieder & Garrison, 2007; Vilela et al. 2016; Vilela et al. 2017
Ischnura fluviatilis	**LE**	**NT**	FA, NC	ND	LC	GMP1, PRA, UNAI	von Ellenrieder & Garrison, 2007; von Ellenrieder, 2009

Continuation Table 4.

Species	Habitat	Territoriality	MGB	Oviposition	IUCN status	Sampled localities	References other than this study
Lestes auritus	**LE**	ND	IT	ND	LC	UDI	von Ellenrieder, 2009; Renner et al. 2016a
Lestes bipupillatus	**LE**	NT	ND	ND	ND	P31	Cardoso-Leite et al. 2014
Lestes forficula	**LE**	NT	IT, FA	END	ND	CVG, ITBL, MAT2, PRA, UNAI, QUI, P31	Garcia-Diaz, 1937; Von Ellenrieder & Garrison, 2007; Nobre & Carvalho, 2014
Limnetron debile	**LO**	ND	ND	ND	ND	P17	Santos, 1970; Assis et al. 2000
Macrothemis imitans imitans	**LO**	ND	ND	ND	ND	SRI, GIL, CPV	Salgado et al. 2013
Micrathyria hesperis	**LE**	ND	NC	ND	ND	CVG, GMP1, PAR	Von Ellenrieder & Garrison, 2007; Paiva-Silva et al. 2010; Vilela et al. 2016
Micrathyria ocellata dentiens	**LO**	ND	ND	ND	ND	SRI	Costa et al. 2002
Micrathyria spuria	**LO**	ND	ND	ND	LC	QUI	Costa et al. 2002; von Ellenrieder, 2009
Micrathyria stawiarskii	**LO, LE**	ND	ND	ND	LC	CPV, NAS, CCD, PO1	Costa et al. 2002; von Ellenrieder, 2009
Minagrion franciscoi	**LO, LE**	NT	ND	ND	ND**	NAS, PO1	Machado & Bedê, 201
Minagrion waltheri	**LE**	NT	ND	ND	LC	ITBSL, MAT1, PO1, PO2	von Ellenrieder, 2009; Vilela et al. 2016
Mnesarete guttifera	**LO**	T	ND	ND	LC	AQD, RCV, CER, BS, CE, ESS, RSF, AGB, CHI, CRP, ZZC, VCT	Garrison, 2006; von Ellenrieder, 2009
Mnesarete pudica pudica	**LO**	T	FA	END	ND	CVG, ITBSL, ITBT	Guillermo-Ferreira & Bispo, 2012; Vilela et al. 2016
Mnesarete rhopalon	**LO**	T	ND	ND	ND**	CHI, CRP, CCD	Garrison, 2006
Neocordulia volxemi	**LO**	ND	ND	ND	DD	GUA	von Ellenrieder, 2009
Neoneura sylvatica	**LO, LE**	ND	IT	END	ND	ITBSL, UNAI	Paiva-Silva et al. 2010; Nobre & Carvalho, 2014; Vilela et al. 2016
Neoneura waltheri*	**LO**	ND	**IT**	**END**	ND	ITBT	Jurzitza, 1981; Garrison, 1999
Oligoclada abbreviata	**LE**	ND	ND	ND	LC	CVG, GMP1, ITBL, PAR, QUI	von Ellenrieder, 2009
Orthemis aequilibris	**LE**	ND	NC	EXO	ND	GMP2, ITBT	von Ellenrieder & Garrison, 2007
Orthemis discolor	**LE**	T	NC	EXO	ND	GMP2, ITBL, ITBT, MAT1, MAT2, MAT3, PRA, UDI, ESS, LZZ	von Ellenrieder & Garrison, 2007; Paiva-Silva et al. 2010
Oxyagrion basale	**LE**	ND	ND	ND	ND	CRP, AQD, RCV, CER, BS, CE, ESS, RSF, CHI, GIL, PSG, LZZ	Hanauer et al. 2014
Oxyagrion chapadense	**LO**	ND	ND	ND	ND	PAR, NAS	Calvão et al. 2014; Tennessen, 2015
Oxyagrion franciscoi	**LO**	ND	ND	ND	ND**	PSG	Machado & Bedê, 2015
Oxyagrion hempeli	**LO**	ND	ND	ND	ND	RL, PO1	Costa et al. 2010; Renner et al. 2016b
Oxyagrion impunctatum	**LO**	ND	ND	ND	ND	NAS, PSG	Costa, 1981
Oxyagrion microstigma	**LE**	T, NT	IT	END	ND	ITBT, UDI, UNAI, NAS, PO1, PO2, QUI, P31, LZZ	Vilela et al. 2016
Oxyagrion santosi	**LE**	ND	ND	ND	ND	UDI, NAS, PO2	Costa et al. 2000; Borges et al. 2019
Oxyagrion terminale	**LE**	ND	ND	ND	ND	CER, CE, CAR, TCH	Capitulo, 1996; Von Ellenrieder & Garrison, 2006; Hanauer et al. 2014

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Continuation Table 4.

Species	Habitat	Territoriality	MGB	Oviposition	IUCN status	Sampled localities	References other than this study
Pantala flavescens	**LE, LO**	T, NT	NC, FA, IT	EXO	LC	CVC, GMP2, ITBSL, PRA	Convey, 1989; Dumont, 1991; Mitra, 2000; von Ellenrieder & Garrison, 2007; Paiva-Silva et al. 2010
Perithemis lais	**LE**	T	ND	ND	LC	CVC, PAR	von Ellenrieder, 2009
Perithemis mooma	**LE**	T	ND	ND	ND	CVC, ITBSL, MAT1, PAR, PRA, UDI, LZZ	Louton et al. 1996; Von Ellenrieder & Garrison, 2007; Paiva-Silva et al. 2010; Pinto et al. 2013
Progomphus costalis	**LO**	ND	ND	ND	LC	NAS	Belle, 1973; von Ellenrieder, 2009
Progomphus intricatus	**LO**	ND	ND	ND	LC	ZZC	Belle, 1973; von Ellenrieder 2009; Dalzochio et al. 2011
Telebasis carmesina	**LE**	NT	IT	END	LC	ITBT, PAR, UDI, UNAI, BS, RSF, QUI, P31, LZZ	von Ellenrieder, 2009
Telebasis coccinea	**LE, LO**	ND	ND	ND	ND	UDI	Garrison, 2009; Calvão et al. 2018; Borges et al. 2019
Tholymis citrina	**LE, LO**	ND	ND	ND	LC	UNAI	Fleck et al. 2004; Paulson 2017
Tigriagrion aurantinigrum	**LO**	T	ND	ND	ND	ITBSL, ITBT, MAT4, GIL	Paiva-Silva et al. 2010; Vilela et al. 2016
Tramea calverti	**LE**	ND	ND	ND	LC	P31	Paulson, 2017; Borges et al. 2019
Zenithoptera lanei	**LE**	NT	IT, NC, FA	EXO	ND	ITBT, MAT1	Vilela et al. 2016

38 (42%) of the species. Mate-guarding behavior (MGB) and oviposition were determined for 31 (35%) species (Table 4).

5. IUCN status

The IUCN conservational status was available for only 28 (31.5%) of the sampled species. Most of the evaluated species (26 out of 28) were assessed as being Least Concern by IUCN classification, whereas for *Cyanallagma ferenigrum* de Marmels and *Neocordulia volxemi* Selys are classified as Data Deficient (DD) (Table 4).

Discussion

After this study, with 269 recorded species, Minas Gerais is the Brazilian State with the second highest number of Odonata species, considering that Rio de Janeiro has recorded 280 species (Costa & Santos 2000), followed by São Paulo, 251 species (Costa, Machado, et al. 2000), Mato Grosso do Sul, 209 species (Rodrigues et al. 2018, Koroiva et al. 2017b), Rio Grande do Sul, 182 species (Dalzochio et al. 2018), and Goiás and the Distrito Federal, 152 species (Nóbrega & De Marco 2011). Obviously, such numbers reflect the areas where most Brazilian odonatologists explored, and the northern States of Brazil may concentrate an even higher number of species.

Concerning the sampled areas, 18 of the 49 sites were at or near Veredas, 24 areas were consisted of streams, rivers and waterfalls, and only seven of them were ponds. This consists, so far, in the most extensive (in number of species recorded and sampled areas) study of odonates in the State of Minas Gerais. Among the sampled sites, the Veredas were mostly well preserved, however few (five out of 18) of them were placed in protected areas. In fact, the Vereda in Uberlândia (UDI) is already threatened by a urbanization project with housing activities. Such anthropic pressure may permanently impact on the faunal composition of this and other unprotected areas, as Vereda areas do not regenerate after a severe disturbance (Guimarães et al. 2002; Oliveira et al. 2009).

Bearing in mind the information on species behavior, we provide a list of behavioral traits of our focal observations and the ones found in the literature. Despite being available for 55% of the sampled species, most of the information on species biology is underexplored, what requires data from more than one source per species to build a more complete behavioral perspective. Considering that only 40 of 90 species have biological information, it is important to know how much to we must advance in this sense. Although neglected, behavioral diversity is an important species feature, for it reveals a cryptic biodiversity (Cordero-Rivera 2017). For instance, for species that are morphologically similar but behave in different ways, the behavioral repertoire can be a distinguishable trait between them (Guillermo-Ferreira & Bispo 2012, Cordero-Rivera 2017).

Here, we also show that few species were assessed regarding their conservational status. Considering the current measures from the Latin-American Odonatological Society and IUCN to assess all Latin-American odonate species, our results make a great contribution to this effort. The IUCN evaluations require data of distribution ranges, altitude of occurrence, population status, and biological data (IUCN 2019). Therefore, the more information one can gather about a species, more precisely it can be evaluated. In our study, only 31.5% of the sampled species were already assessed by IUCN. Most of these species fit in the Least Concern category, which means that, although some of the species may be widespread and out of risk (IUCN 2019), others that

were not assessed may be under threat. For *Cyanallagma ferenigrum* de Marmels and *Neocordulia volxemi* Selys, the status appears as Data Deficient, which means that, at the moment of the assessment, the data available for evaluation were insufficient to set a conservational status to these species (IUCN 2019). Our records for this two species and the others that were not assessed will help in ongoing assessments. The results presented here respect the guidelines of the Latin-American Odonatological Society and are being used to assess Neotropical species conservation status. Finally, we suggest that research focus on studies of natural history and distributional ranges that cover understudied species (Data Deficient and unevaluated species) in the Cerrado biome (mainly on Veredas) to ensure a broader perspective on the Neotropical odonate fauna.

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Author contributions

Diogo Silva Vilela: Contribution to data collection and manuscript preparation. Substantial contribution in the concept and design of the study. Contribution to critical revision, adding intelectual content.

Ricardo Koroiva: Contribution to data collection and manuscript preparation. Substantial contribution in the concept and design of the study. Contribution to critical revision, adding intelectual content.

Thiago Henrique Azevedo Tosta: Contribution to data collection and manuscript preparation. Contribution to critical revision, adding intelectual content.

Marcos Carneiro Novaes: Contribution to manuscript preparation. Contribution to critical revision, adding intelectual content.

Rhainer Guillermo-Ferreira: Contribution to data collection and manuscript preparation. Contribution to critical revision, adding intelectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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Article

Development of a conceptual framework for the management of biodiversity and ecosystem services in the Mexican Caribbean

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Abstract: Coral reefs and mangroves support rich biodiversity and provide ecosystem services that range from food, recreational benefits and coastal protection services, among others. They are one of the most threatened ecosystems by urbanization processes. In this context, we developed a conceptual framework for the management of biodiversity and ecosystem services for these coastal environments. We based our workflow on two sections: "Information base" and "Governance" and use the Puerto Morelos Coastal region as a case study for coastal protection. Puerto Morelos is between two of the most touristic destinations of Mexico (Playa del Carmen and Cancun) that has experienced an increase of population in the past four decades resulting in an intensification of multiple threats to its ecosystems. We characterized the two ecosystems with a "Management Units" strategy. An expert-based ecosystem services matrix was also described in order to connect mangroves and coral reef ecosystems with the multiple beneficiaries. Then an ecosystem model (conceptual model and Global Biodiversity model) was developed. The conceptual model was useful in understanding the interplay processes between systems regarding the ecosystem service of "Coastal Protection". The Global Biodiversity model evidenced the human-induced shifts in the biodiversity for mangrove and coral reefs ecosystems. Also, a projection for 2035 of "best" and "worst" scenarios was applied using GLOBIO3. A DPSIR conceptual framework was used to analyze environmental problems regarding ecosystem services maintenance. Finally, we evaluated a set of policies associated with these ecosystems that favor coastal protection integrity. This framework facilitates the identification of the most relevant processes and controls about the provision of coastal protection service. It can also be useful to better target management actions and as a tool to identify future management needs to tackle the challenges preventing more effective conservation of coastal environments.

Keywords: *Ecosystem services; Framework; Future scenarios; Marine; Public policies.*

Desenvolvimento de um roteiro conceitual para a gestão da biodiversidade e dos serviços ecossistêmicos no Caribe mexicano

Resumo: Recifes de coral e manguezais possuem rica biodiversidade e fornecem serviços ecossistêmicos, tais como, alimento, recreação, proteção costeira, entre outros. Esses ecossistemas encontram-se entre os mais ameaçados pelos processos de urbanização. Nesse contexto, desenvolvemos um roteiro conceitual para a gestão da biodiversidade e dos serviços ecossistêmicos desses ambientes costeiros. Organizamos nossa sequência de passos de trabalho em duas seções: "Base de informações" e "Governança" e usamos a região costeira da cidade de Puerto Morelos (México) como um estudo de caso para analisar o serviço de proteção de costa. Puerto Morelos encontra-se entre dois dos destinos mais turísticos do México (Playa del Carmen e Cancún), e portanto sua população vem aumentando nas últimas quatro décadas, resultando na intensificação de múltiplas ameaças para os ecossistemas. Primeiramente, caracterizamos os dois ecossistemas identificando-os como "Unidades de Gestão", detalhando seus principais componentes e processos. Através de uma "Matriz de serviços ecossistêmicos", construída com base na opinião de especialistas, foram sistematizados os principais serviços ecossistêmicos prestados pelos manguezais e recifes de corais aos múltiplos beneficiários. Em seguida, foi desenvolvida uma modelagem do sistema (e ecossistemas) através de sua representação na forma de um modelo conceitual e um modelo numérico de Biodiversidade Global. O modelo conceitual facilitou a compreensão dos processos de interação entre sistemas em relação ao serviço "Proteção Costeira". O modelo numérico evidenciou as mudanças induzidas pelo homem na biodiversidade dos ecossistemas de manguezal e recifes de coral. Além disso, uma projeção dos cenários "melhor" e "pior" foi desenvolvida para 2035 usando GLOBIO3. A Estrutura conceitual DPSIR foi aplicada para analisar problemas ambientais relacionados à manutenção dos serviços ecossistêmicos. Finalmente, avaliamos um conjunto de políticas públicas associadas a esses ecossistemas e que favorecem a integridade da proteção costeira. Portanto, o roteiro facilitou a identificação dos principais processos e controles para a provisão de um serviço ecossistêmico. Além disso, pode ser útil para direcionar melhor as ações de gerenciamento, bem como, uma ferramenta para identificar necessidades futuras de planejamento e gestão para enfrentar desafios que permitam uma conservação mais eficaz dos ambientes costeiros.
Palavras-chave: *Cenários futuros, Marinho, Políticas públicas; Roteiro; Serviços ecossistêmicos.*

Introduction

Coastal and marine ecosystems are the most productive environments on the planet (MEA 2005) and are also the most threatened by the urbanization process. It is estimated that about one-third of mangrove forests and one-tenth of coral reefs in the world have been lost (Brown 2006). The list of ecosystem services provided by these environments is extensive (see Barbier et al. 2008, Liquete et al. 2013, Barbier 2016, Guannel et al. 2016) and includes water, food, climate regulation, nutrient cycling and different recreational, spiritual and aesthetic benefits (MEA 2005, TEEB 2010a, TEEB 2010b, Diaz et al. 2018). It is essential to understand the effects of the urbanization process on such relevant areas given that these are uniquely productive and biodiverse ecosystems providing ecosystem services to support human well-being.

The 'Ecosystem Services' concept has evolved over the years with definitions on either the ecological basis and the socio-economic uses (Granek et al. 2010). According to MEA (2005), it can be defined as "benefits that people derive from ecosystems". It also can be defined as the main benefits (e.g. services, materials, provision) that the ecosystem provides to the socio-economic activities that are dependent on it. In order to manage and to conserve the ecosystems (and their services), incorporating both conservation and development, Ecosystem-Based Management (EBM) has been proposed as a valuable strategy (Barbier et al. 2008). This approach focuses on ecosystem services since they reflect social goals, values, desires, and benefits. The inclusion of ecosystem services into holistic management strategies improves management by better capturing the diversity of positive and negative human-natural interactions and making explicit benefits to society (Kelble et al. 2013). The EBM approach deals with the management and the sustainability of human activities to maintain the ecosystem services generated by coastal ecosystems (McLeod & Leslie 2009, Dasí 2011, Arkema et al 2015).

The anthropogenic threats that result from different human activities are numerous and particularly harmful to coastal ecosystems, which are influenced by activities on land (terrestrial and freshwater), along the coasts, and in the ocean (Halpern et al. 2008). According to Halpern et al. (2008), when management planning and implementation within a sector considers the effects of an activity on a habitat or other ecosystem components, it is only to the overall goals for that sector. However, a holistic view of multiple impacts affecting the entire ecosystem is necessary for effective management of several ecosystem services.

Coastal ecosystem responses to climate change and anthropic stressors are extensively studied, showing changes in ecosystems landscape and biodiversity (Duke et al. 2007, Barbier et al. 2008, Feller et al. 2017). However, management actions on the whole coastal landscape have been infrequent (Hoegh-Guldberg et al. 2008, McClanahan et al. 2015, Weijerman et al. 2015). Accordingly, an EBM framework is useful to mitigate the current and potential impacts of urbanization on coastal ecosystems. Mangroves and coral reefs, for example, are coastal systems that are impacted by overexploitation of fishery stocks, habitat degradation by human activities, SCUBA diving and boating, aquaculture, water pollution and eutrophication, land conversion, invasive species and the effects of climate change (Figure 1) (FAO 2008, Feller et al. 2017, IUCN 2018, Pelage et al. 2018). These drivers threaten the socioeconomic sustainability of activities derived from the coastal ecosystem services and could cause, in some cases, severe ecological losses at different spatio-temporal scales (Duke et al. 2007, Feller et al. 2017).

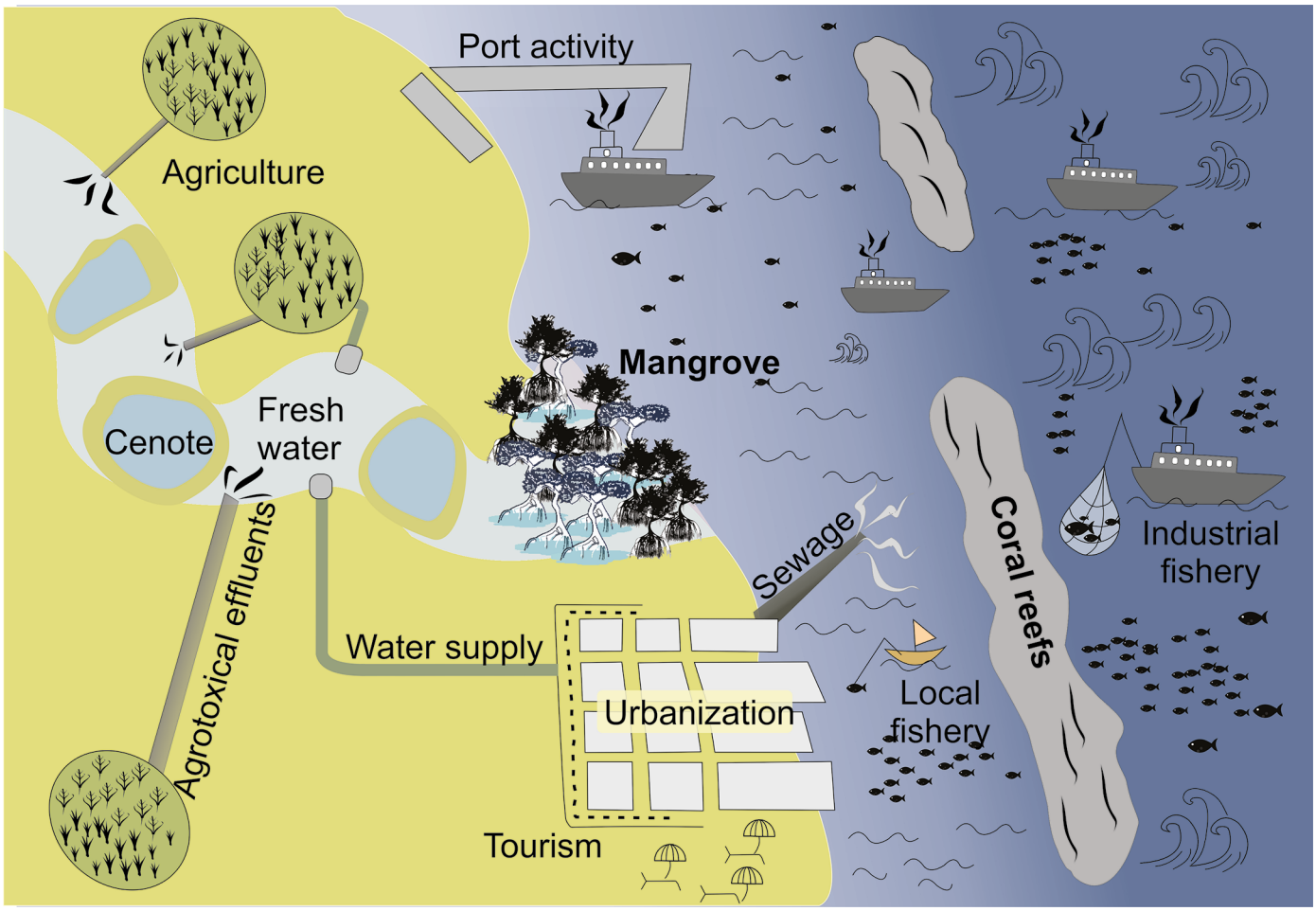


Figure 1. Representation of the anthropogenic impacts on coastal ecosystems. This scheme is based in Puerto Morelos, Mexico system and its human activities. The main anthropogenic impacts in Puerto Morelos are: sewage, urbanization (tourism, land-use change), fisheries and port activities.

In this context, the principles of EBM have often been defined and applied to these ecosystems to aid their conservation and optimize decision-making strategies (Yáñez-Arancibia et al. 2013). EBM may help to maintain ecosystem services by identifying possible scenarios that can be adopted by policy/decision-makers thereby encouraging sustainable development.

In order to apply and describe some insights of the EBM strategy, we used the case study of Puerto Morelos, a town in the south-east of Mexico. This town is located in the Mexican Caribbean, a popular tourist destination experiencing a rapid urbanization process. In Puerto Morelos is located the national park *Parque Nacional Arrecife de Puerto Morelos* (PNAPM), which hosts a mosaic of ecosystems (such as wetlands, seagrass, coastal lagoons, coral reefs, and mangroves), resulting in one of the most biodiverse regions of the Caribbean (Miloslavich et al. 2010). Mexico has a legal framework for coastal ecosystems that include laws, official norms, and programs that establish the regulations for the conservation, sustainable use and restoration of coastal wetlands in mangrove areas. For the coral reefs ecosystems, there are guidelines promoted by the Management Program of Puerto Morelos National Park (INAFED 2019). There is also the International MRS Leadership Program for sustainable use of resources, that through the Safeguard Zone, called Coral Reefs of the Gulf of Mexico and the Mexican Caribbean, encourages partial reef protection, since hydrocarbon exploration and extraction activities are prohibited (Costanza et al. 2014, Perez-Cervantes et al. 2017). In addition, the production of technical and scientific data about components and processes (i.e. biological, ecological, social and economic) for coral reef and mangrove ecosystems across the Caribbean has increased exponentially in recent years.

Given the above statements, it becomes increasingly necessary to apply scenarios for identifying future strategies capable of promoting conservation actions, sustainable use and avoid habitat degradation. Additionally, it is pivotal to assess whether the changes in biodiversity and ecosystem services, driven by socio-economic pressures, are covered by robust protection policies. In this context, this study aims to design and describe a pathway to develop an EBM framework for coastal ecosystems. This article examines practical experimentation of the intersections between science and policies for the mangroves and coral reefs in Puerto Morelos, Mexico. We use available data for strengthening policy formulation and implementation by decision-makers. This could help ensure the conservation and sustainable use of ecosystem services in coastal regions, enhancing the ecological relevance and human well-being.

Material and Methods

1. Study area

The case study was performed for Puerto Morelos, in the north of Quintana Roo state, Mexico. This town is located between Cancun and Playa del Carmen, which are the most popular coastal tourist destinations of Mexico in the Caribbean (Coronado et al. 2007) (Figure 2). Puerto Morelos retains part of its original features as a fishing village. In addition, the massive tourism it received in the recent years, impacts from urbanization, agriculture and drainage are already noticeable (Figure 1). The coral reef barrier is a touristic attraction and is protected by the Parque Nacional Arrecife de Puerto Morelos (PNAPM) (located between 20º0'0"N, 86º53'14.4"W and 20º48'33"N, 86º46'38.9"W), which covers an area of 9066 ha (SEMARNAT 2016). The Puerto Morelos reef extends parallel to the coast with three structural zones; (i) The reef lagoon, between the reef and the coast, with the bottom mainly covered by seagrass macroalgae and calcareous sand; ii) The reef ridge, between the lagoon area and the reef, covering the larger area with scleractinian coral diversity, and areas with grassland and seaweed; and, iii) The frontal reef, found in shallow waters, covered by corals and coral rubble and dominated by the species *Acropora palmata* (Lamarck 1816) (Jordan-Dahlgren 1979, Sánchez-Quinto & Falcon 2019). Economically, around 60% of the local population depends directly or indirectly on the reef's ecosystem benefits services. Among the various ecosystem services that coral reefs provide, the economic activities related to the categories of cultural and supporting ecosystem services stand out the most. The main users of these services are nautical tourists (looking to dive, do snorkeling and fishing, etc.) and fishermen (Figure 1).

Due to the location and natural attractions, Puerto Morelos' population has been growing rapidly. Between 1980 and 2010, the population has increased from 222 to 9188 inhabitants (Jordán-Dahlgren & Rodriguez-Martinez 1998, Carabias-Lillo 2000, INEGI 2010, Gomez 2020), and currently reached approximately 37000 inhabitants (INAFED 2019). This fast population increase is not always followed by basic infrastructure services (such as sewage treatment, land use regulation, etc.) and could lead to coastal ecosystems degradation. The sewage treatment is limited and most of the population are served by septic tanks. The remaining waste is taken to one of the three primary treatment plants where the water is treated and pumped about 60 m deep into the soil (Hernández-Terrones et al. 2011).

The two villages (coastal/touristic and urban/local population zones) of Puerto Morelos are surrounded by coastal vegetation including mangroves, and the increasing population threatens this ecosystem as well. Tourism has increased so quickly in recent years that hotel capacity grew from 3638 to 5500 rooms between 2008 and 2018, reaching more than 7000 rooms by 2020 (Comunicación Social de Puerto Morelos 2019, Gomez 2020).

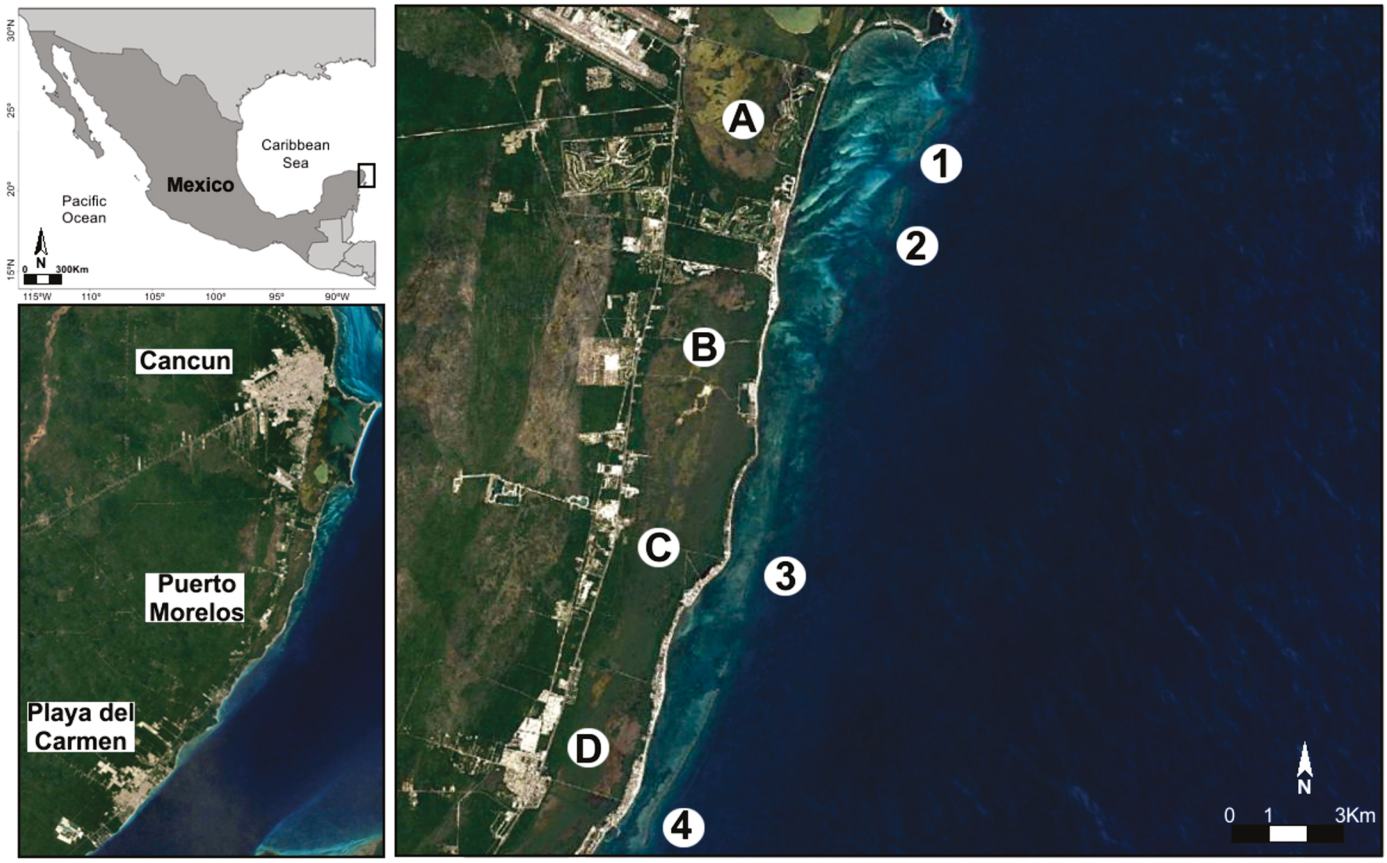


Figure 2. Study area. Upper left panel: Mexico with a highlight in the study area; Bottom left panel: Satellite Image of Puerto Morelos showing its proximity with two main touristic localities (Cancun and Playa del Carmen); and Right panel: Location of Puerto Morelos, Quintana Roo in the Mexican Caribbean, where (A), (B), (C) and (D) show the areas used in the GLOBIO3 model to calculate the vegetation cover. The numbers represent the location of the coral reef areas: (1) Limones, (2) Bonanza, (3) Tanchacte, and (4) Jardines. Source: Google Earth (Landsat/Copernicus).

Moreover, it is expected that the construction of 2000 residential units and eight lodging centers nearby a protected land, constituted for forests of red mangrove (*Rhizophora mangle*) (Linnaeus 1753), button mangrove (*Conocarpus erectus*) (Linnaeus 1753) and chit palms (*Thrinax radiata*) (Lodd 1830) (CONABIO-CONANP-TNC-Pronatura 2007) will start soon. Moreover, similar to the urban areas described, most hotels do not have proper sewage treatment with the larger hotels pumping the treated water into the aquifer (70 - 100 m).

2. *Practical experimentation strategy*

The methodological approach used for Puerto Morelos in this study was partially based and adapted from Asmus et al. (2018). In order to establish an ecosystem information base that supports integrated management, our method consisted of four sections: 1) the identification of ecosystems as management units; 2) the identification of the ecosystem services (ESM); 3) the ecosystem modeling (Conceptual model and Global Biodiversity model); and 4) the identification of the management sectors (DPSIR and Policy assessment). (Figure 3).

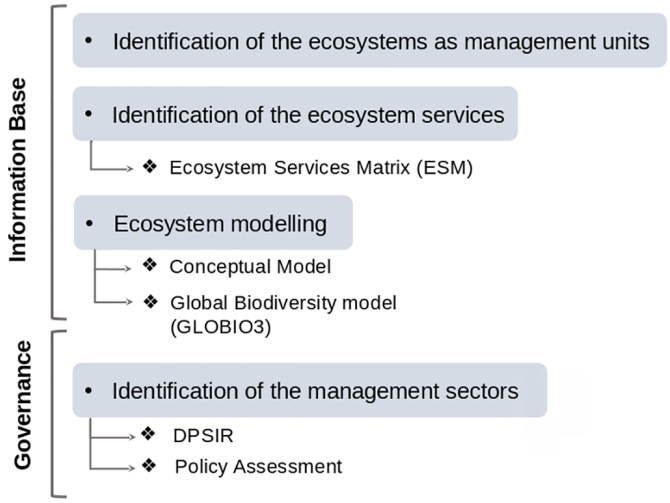


Figure 3. Methodological sections adapted for Puerto Morelos study case, modified from Asmus et al. (2018), . Within the information base section we followed: the identification of the ecosystems as management units; the identification of the ecosystem services (ESM); and the ecosystem modelling (Conceptual model and Global Biodiversity model). Within the Governance section, we included the identification of the management sectors (DPSIR and Policy assessment).

In all sections, a comprehensive bibliographic review was performed to guarantee the theoretical basis, revealing the concepts and definitions that guided the scope of the investigation and results interpretation. The main ecosystem service provided by mangroves and coral reefs identified was "Coastal Protection". These two ecosystems protect coastal areas and their population from the effects of waves, storms, rising seas, among others. Through these sections, the elements in the ecosystem information base are defined to understand the ecosystems and the different connections between their main components and processes responsible for coastal protection. The last two subsections (DPSIR and Policy Assessment) bring the elements of management and governance that result from an analysis of the ecosystem information base, together with assessments of existing policies for ecosystem protection and management. Nevertheless, the definition of values and qualities from Asmus et al. (2018) were omitted given the theoretical scope of this proposal, as we have not worked directly with the social actors to understand their perception of values in relation to services that might benefit their local communities.

2.1. *Identification of ecosystems as "Management Units"*

To identify and characterize the focal coastal ecosystems (i.e. mangrove and coral reefs) as management units, we applied a strategy to capture the knowledge of different experts on a particular topic, a commonly used procedure to fill gaps in scientific research (Krueger et al. 2012, Martin et al. 2012, Nordlund et al. 2016). We used this approach to acquire information on ecosystems and the different aspects related to socioeconomic activities (ecosystem services, uses and benefited actors), as well as initiatives and strategies for coastal management in Puerto Morelos.

2.2. *Ecosystem Services Matrix (ESM)*

Following the identification of ecosystems as "management units", we developed an ESM. The ESM was developed in order to visualize the connection between mangrove and coral reef ecosystems and their diverse beneficiaries, taking into account the activities developed in each ecosystem and the use of ecosystem services for human well-being. First, we identified the different services provided by each ecosystem, recognizing its corresponding ecosystem service category based on the Millennium Ecosystem Assessment (MEA 2003) classification. The four categories are: 1. Support: those required for the maintenance of other ecosystem services, such as nutrient cycling and ecological corridors; 2. Provision: products obtained from ecosystems (such as food, wood and medicinal products); 3. Regulation: related to the regulatory characteristics of ecosystems (such as air quality maintenance, erosion control and climate); and, 4. Cultural: related to human values and behaviors linked to ecosystems (such as contemplative and spiritual values and social relations). Second, the various benefits and beneficiaries were listed. Finally, all the information collected was organized in a table, allowing for the identification of the different ecosystem services from mangroves and coral reefs and their importance to people in the study area.

2.3. *Conceptual model*

Once the management units were characterized and the main ecosystem service identified, we developed a conceptual model (Figure 4). The diagram of the conceptual model was drafted to understand the interplay of the coastal processes, namely, the ecosystem services of "Coastal Protection" and interactions with the ecosystems and the environmental and socio-economic components. The structure of the conceptual model allows an understanding of the system in its organizational base, where several simultaneous processes occur. After mapping the ecosystems and their services, as well as the actors involved, and how they interact with the ecosystems, the conceptual model was also used to understand the methods developed in this proposal, by describing the processes through a diagram (Figure 4), as follows:

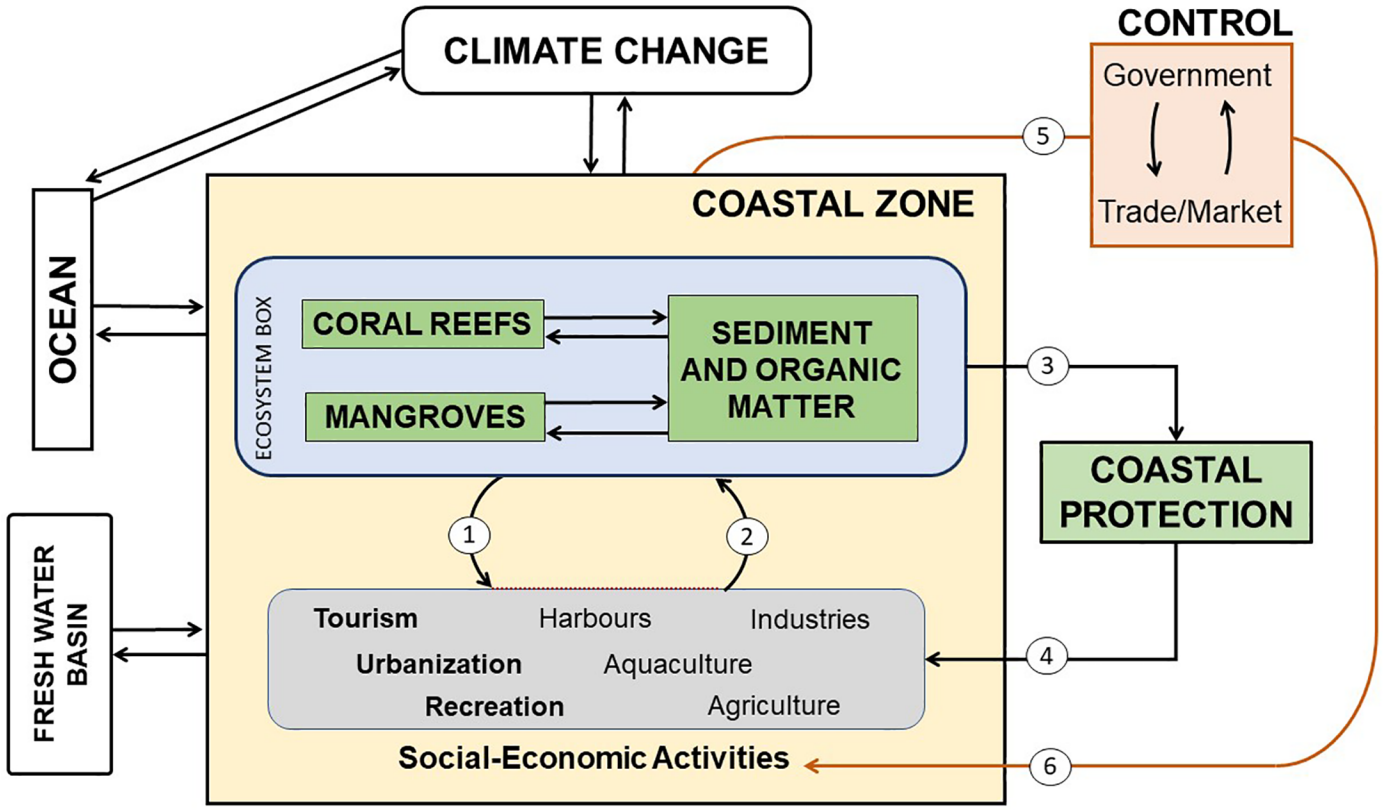


Figure 4. Conceptual model representing the main components (boxes) and processes (numbered circles), based on the coastal protection, as the main ecosystem service in analysis in Puerto Morelos, Mexico. Six processes within the Coastal Zone (orange box) were identified (black arrows indicate direct interaction). Process 1: Ecosystem services provided by mangroves and coral reefs to society (blue box). Process 2: Pressures and the drivers affecting mangroves and coral reefs (grey box). Processes 3 and 4: The connection between the ecosystems and the activities in the coastal zone that directly affects the coastal protection service (green box). Processes 5 and 6: The ecosystem-based information used as a tool to support government management decisions (orange line and orange box) and the creation of new policies aiming the conservation of ecosystems (orange arrow).

Process 1: Refers to services provided by mangroves and coral reefs to society. An Expert-Based Ecosystem Services Matrix, Global Biodiversity model, and DPSIR framework were applied as tools for the characterization of the ecosystems within Puerto Morelos.

Process 2: The activities carried out in the coastal zone can impact ecosystems and thereby affect (even causing loss) on the "coastal protection" service. Therefore, we identified some of the main pressures and drivers affecting mangroves and coral reefs. Despite the fact that climate change is an important driver, in this study we focused on direct human-effects (mainly the urbanization process) to evaluate how these activities cause pressure in the ecosystems and threaten their services. The DPSIR framework and the GLOBIO model were used to link the current state of the ecosystems with potential future scenarios.

Processes 3 and 4: The connection between the ecosystems and the activities in the coastal zone affects directly the coastal protection service, among others coastal ecosystem services. Hence, to identify these influences on human well-being (benefits and actors benefited), we used an Expert-Based Ecosystem Services Matrix, which provides a qualitative database for the analysis. Moreover, a DPSIR framework, policy assessment and a Global Biodiversity model are crucial to identify the best scenario as possible for maintaining the coastal protection service.

Processes 5 and 6: All the characterization from the Expert-Based Ecosystem Services Matrix, the Global biodiversity model, the DPSIR and policies, were used to obtain the ecosystem-based information. The policies could be used as a tool to support government management decisions (Process 5). Thus, the government will have the background information to reinforce or enact new policies in order to conserve ecosystems and their ecosystem services (such as coastal protection) (Process 6).

2.4. Global Biodiversity Model

The next step was to identify the pressures over the biodiversity of both mangrove and coral reefs ecosystems. For this, we applied the Global Biodiversity model (GLOBIO3; Alkemade et al. 2009) as a proxy for understanding the impacts of ecosystem degradation on the 'Coastal Protection' service by modeling the loss of biodiversity in both ecosystems over a decade and for predicting future scenarios (optimistic and pessimistic) for the next two decades. The mean species abundance (MSA) relative to their abundance in a reference condition is used as an indicator of biodiversity. The MSA computes the average of remaining species abundance in disturbed circumstances in relation to the equivalent in an undisturbed control condition by scaling between one (undisturbed or primary ecosystem) and zero (disturbed ecosystem). The driver of biodiversity loss considered herein for terrestrial ecosystems (mangroves) is land-use change (MSALU). For the coral reefs, we used a similar approach using coral cover change to assess the impacts of human activities on this ecosystem. MSA values are categorized as follows: $0 \leq 0.20$ low; 0.21 – 0.40 relatively low; 0.41 – 0.60 medium; 0.61 – 0.80 relatively high; and $0.81 \leq 1$ high (Trisurat et al. 2010).

Our framework includes terrestrial (coastal vegetation) and marine (coral reefs) ecosystems. The coastal vegetation was defined as 'mangroves' since mangrove species, such as *R. mangle*, *Laguncularia racemosa* (Volkmar 1979), *Avicennia germinans* (Linneo 1764), and *C. erectus,* are the dominant vegetation in the analyzed area. Although occurring in surrounding vegetation in a smaller proportion (evergreen tropical forest) (Vázquez-Lule et al. 2009), we restricted the term naming mangroves as the main terrestrial ecosystem supplier for coastal protection (our target ecosystem service). For analyzing mangroves data, we selected an inland area in front of the reef barrier using Landsat images from Google Earth Professional , and determined four adjacent areas of 5 km² inside the selected inland area (Figure 2). We set the reference condition as 2005 and calculated the total area of mangroves cover (i.e. the undisturbed area) using the polygon tool. Additionally, we considered the other areas with more than 80% built up disturbed as urbanized, even if it still had some sort of sparse vegetation between constructions, following the same parameters of the GLOBIO3 (Alkemade et al. 2009). To obtain MSA values for each area, we multiplied the total area (in km²) of each category (i.e. intact forest or urbanized area) to the corresponding MSA_{LU} values from Alkemade et al. (2009) (i.e. vegetated areas - 1.0; built-up areas - 0.05). Both values were then summed and divided by the total area (5 km²), generating a MSA value ranging from 0 to 1. Cumulative changes were thus computed to the reference condition in 2005, as well as for the years of 2008, 2011 and 2014.

Concerning the marine system, for the coral reefs we considered the reduction of coral cover in four different areas: Limones, La Bonanza, Tanchacte, and Jardines (Figure 2). GLOBIO3 is designed mainly for terrestrial ecosystems, with an adaptation available for inland water ecosystems (Janse et al. 2015) allowing us to modify some analysis to be useful for marine ecosystems as well. Instead of analysing satellite images, our proposed modification relied on a meta-analysis of published data on the different areas of coral reef cover in the same years used for mangroves (2005, 2008, 2011, 2014). Therefore, the coral cover was analysed for the same years as mangroves, using data obtained from Banaszek & Álvarez-Filip (2014) and Álvarez-Filip & Banaszek (2016).The percentage of area with and without coral cover was also used. To obtain the MSA values for each area, we adapted the resilience index estimated by Ladd & Collado-Vides (2013) for each of the four sites studied. These indexes applied local empirical data based on broad and local-scale indicators that influence ecological processes, anthropogenic impacts, biological variables and physical variables of coral reefs. These include 'Fishing Pressure', 'Contamination/Pollution (%N and N:P)', 'Land-based Anthropogenic Impacts ($\delta^{15}N$)', 'Anthropogenic Physical Impacts (Tourism Intensity)', 'Herbivore Biomass', 'Abundance of Invasive Species', and so on (see Ladd & Collado-Vides 2013 and the original concept in Maynard et al. 2011). Scores obtained from the resilience index (which ranges from 0 to 100) were weighted from 0 to 1 and assigned into coral-MSA values. We considered the areas with coral cover to have the highest coral-MSA (i.e. 1.0, as those areas are equivalent to an intact forest) and the areas without coral cover were multiplied by the resilience index equivalent to the area of study (Limones: 0.94; La Bonanza: 0.68; Tanchacte: 0.75; and Jardines: 0.82). Thus, values of each coral reef were summed and divided by the total area, resulting in the MSA value for the coral reef.

After modeling values for both terrestrial and marine ecosystems over the last decade, we also generated two future scenarios for both ecosystems. The scenarios were projected to 2035, two decades after the observed values in order to make predictions of optimistic and pessimistic scenarios, and to consider a period where more effective ocean governance is implemented by taking actions to mitigate biodiversity loss (Figure 5).

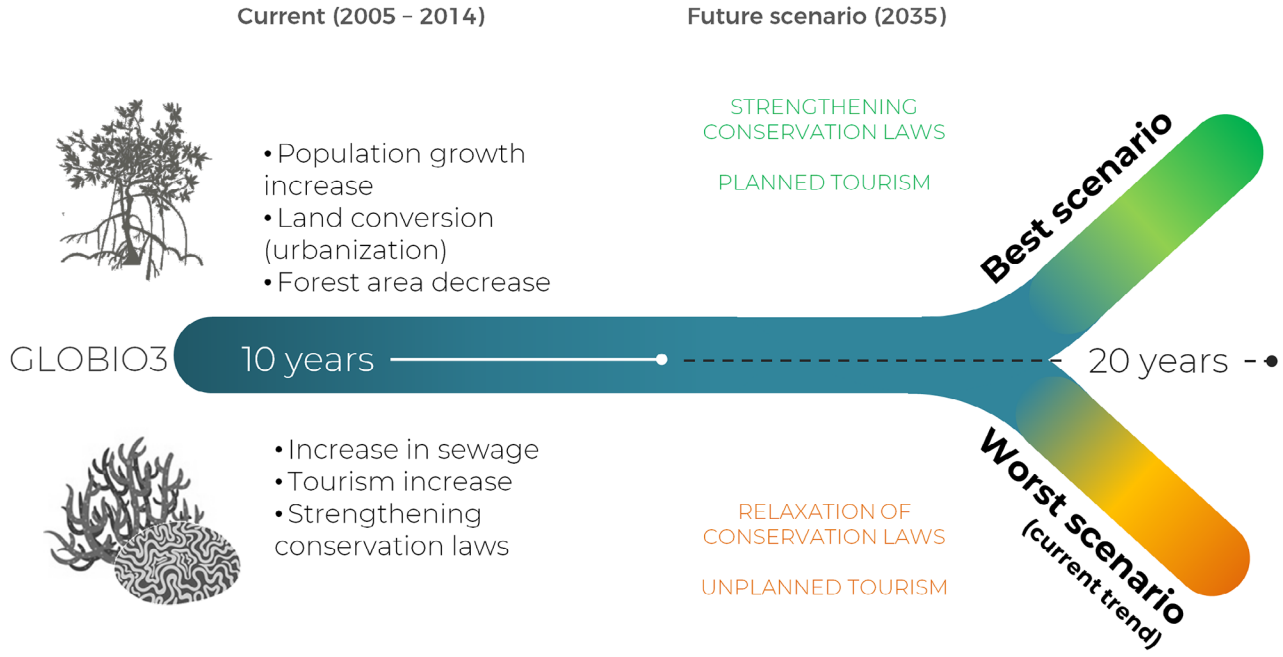


Figure 5. Theoretical past and future scenarios for mangroves and coral reefs in Puerto Morelos. In light grey, besides draw schemes (mangrove and corals) are the "current"conditions (left), representing the changes in vegetation and coral cover for the last 10 years (see GLOBIO3 results). The two future scenarios representing projections for a Best Scenario' (top, in green) in which conservation laws are strengthened and Puerto Morelos acts towards sustainable policies; and a 'Worst Scenario', which is the maintenance of current actual policies (bottom, in reddish).

Given the above, we projected: (1) the effects of policy implementation for sustainable development (best scenario - 2035-B); and, (2) the effects of maintenance of current policies (worst scenario - 2035-W).

To project the best scenario (2035-B) for mangrove vegetation, we calculated an increase of 10% of the vegetated area compared to the last assessed year (2014) and calculated the expected MSA to 2035. The National Policy of Seas and Coasts of Mexico includes regulation on the need of reverting the damage inflicted to marine and coastal ecosystems. Furthermore, this is a possible scenario since technology has been developed for mangrove rehabilitation with improved results and reduction of costs (see Dale et al. 2014 for a revision on this theme). We consider that this value could be achieved if conservation policies were applied in the following years (i.e. through mangrove restoration). For coral reefs, we calculated the gain of coral cover in 10 years (from 2005 to 2014) for Limones, which had the highest coral cover recovery (25%) according to Álvarez-Filip & Banaszek (2016). This value was divided by 10 (according to the period 2005-2014), representing an annual cover recovery of 2.5%. We then applied this value of annual coral cover increase in all studied areas for the period of 2015 to 2035, obtaining the coral cover for the best future scenario. We considered the 25% value due to empirical data occurring in the last decade, that represents a realistic recovery value under compliance of coral reef conservation policies and actions. However, it is important to note that this "best scenario" may be conservative, as a 25% increase occurred in circumstances of little effort invested for conservation of coral areas in Puerto Morelos. Finally, to project the worst scenario (2035-W) for both mangrove and coral reefs, we calculated the linear regression equation (based on the MSA values from 2005, 2008, 2011 and 2014) and projected the trend to 2035. Finally, we named this scenario 'worst' because our data analysis reveals a trend in relaxation of conservation laws and unsustainable tourism.

2.5. Drivers – Pressures – State – Impact – Response (DPSIR) framework

The DPSIR framework was performed in the identification of the management sectors to analyze environmental problems regarding ecosystem services maintenance. DPSIR is a conceptual framework model widely applied to different case studies in management to solve problems involving environmental changes driven by socio-economic pressures with the required actions to mitigate adverse impact on ecosystem goods and services (Zaldívar et al. 2008, Gari et al. 2015, Patricio et al. 2016). In our specific case study, the DPSIR model was elaborated for "coral reefs" and "mangroves" ecosystems, identifying the socio-economic activities that are direct and/or indirect forces generating transformations of these environments (Tourism/ Recreation, Urbanization, Fishing, Port Activity). The "drivers" were considered as possible activities that substantially affect the coastal environments. The "pressures" were considered as the anthropogenic factors inducing environmental changes. The "state" was considered to be the conditions that generate pressures on each part of the environment. The "impacts" correspond to the negative effects of the pressures in these ecosystems. Finally, "response" encompasses the solutions proposed to mitigate or modulate the effects of the "drivers" in the ecosystems.

2.6. Policy assessment

To provide the required knowledge for the governance stage, we first identified and compiled the Mexican government's environmental management tools, including the legal and normative instruments related to the studied ecosystems. These policies were assessed adopting three groups of indicators in which the legal framework were addresses: i) incorporation of ecosystem services approach (defining or not guidelines and actions about coral reefs and coastal vegetation); ii) association with economic activities and land/marine use change (urbanization, ports and navigation, tourism, fisheries); and, iii) attention to climate change effects. We then analyzed the policies related to our study case in three different levels of management: Federal (Mexico), Regional (Quintana Roo State) and Local (Puerto Morelos Municipality). The analysis of the legal framework was focused on policies and tools that directly or indirectly support conservation and sustainable management of marine and coastal areas in Mexico (coral reefs and mangroves as the main target); and/or address anthropogenic and natural drivers of change in these systems.

This evaluation of the legal framework enables support to decision-making processes and defines scenarios of conservation policies while identifying gaps in current design of the management instruments. It also assesses possible options to address policy formulation and implementation to further sustainable development.

Results

The designed pathway to catalyze the development of ecosystem-based management framework for coastal ecosystems and applied in the mangroves and coral reefs ecosystems in the National Reef Park of Puerto Morelos is described as follows:

1. Identification of ecosystems as "Management Units"

Mangrove forest global distribution occurs in a transition zone between terrestrial (low-lying coastal areas) and marine (inter-tidal zones) ecosystems and are confined between subtropical latitudes, generally delimited by the 20° C isotherm of seawater (Alongi 2009). Mangroves are highly productive ecosystems, host a great biological diversity (several species of birds, fish, crustaceans, molluscs, amphibians and others), and provide a wide variety of ecosystem goods and services for human well-being and coastal and marine ecosystems. For instance, mangrove forests provide feeding, shelter and nursery for biodiversity; raw materials (fuel and wood), fishery production supporting, aesthetic and recreation services, flood control, saline intrusion mitigation, erosion control, coastal protection, water quality, and maintenance of natural processes such as sedimentation and responses to sea level changes (Valiela 2001, SEMARNAT 2003, CONABIO 2006). Mexico is the fourth most mangrove-rich country with cumulative percentages of about 741,917 ha (Giri et al. 2011). In turn, the Yucatan Peninsula Region accounts for 55% (423,751 ha) of the total mangrove extension. These forests are predominantly composed of four halophyte tree species (tolerant to salinity) (*R. mangle*, *L. racemosa*, *A. germinans* and *C. erectus*).

Coral reef ecosystems are globally confined between the Tropics of Cancer and Capricorn (Dubinsky & Falkowski 2011). Coral reefs are marine communities of shallow waters near the coast, dominated by a great diversity of corals, algae, invertebrates, microbes and fishes (Lesser et al. 2018, Sánchez-Quinto & Falcon 2019).

They have ecological importance in coastal dynamics by preventing erosion and decreasing the force of waves, as well as being the most effective protection structure against the strong effects of tropical storms and hurricanes. Corals are essential within the ecosystem since they carry out different functions as primary producers, reef builders, filters and predators. Coral reefs also provide several ecosystem services related to breeding, shelter, feeding and reproduction of many species of invertebrates and vertebrates with commercial importance for the Mexican population (Moberg & Folke 1999, Woodhead 2019). In addition, they provide recreational activities, coastal protection, soil formation, climate mitigation, aesthetic and cultural benefits, among many others. In the Yucatan Peninsula, the distribution of corals is found from Contoy Island to Banco Chinchorro. In the National Reef Park of Puerto Morelos, corals form barrier reefs parallel to the coast (Coronado et al. 2007, Aguilar et al. 2008).

2. *Identification of the Ecosystem Services (Ecosystem Services Matrix)*

The systematization of the collected information into the Ecosystem Services Matrix revealed 16 services provided by mangroves and 14 services by coral reefs (Table 1). The matrix also shows that several social actors are benefited by ecosystem services, ranging from fishermen to local community to pharmaceutical industry. The highest number of beneficiaries (six) registered was related to the regulation ecosystem services category as the services of "sediment regulation", "hydric balance", "carbon sequestration and storage" and "extreme events mitigation" which encompass benefits such as water quality, flood control, erosion control and coastal protection. These provide extremely important contributions to the sustenance and maintenance of all activities developed inside and adjacent to the study area.

3. *Conceptual model*

The conceptual model shows a fragment of the coastal zone with the presence of ecosystems (coral reefs and mangroves) and different socioeconomic activities (such as: tourism, urbanization, recreation, etc.) (Coastal Zone box) (Figure 4). Although these activities obtain benefits from ecosystems through the provision of several products and services (Process 1), they act as Drivers, affecting the ecosystems and their benefits (Process 2). One of the important services that coral reefs and mangroves provide through their functions (Ecosystem box) is "coastal protection" (Process 3), which facilitates the development of diverse socioeconomic activities and in turn, benefit different social actors (such as: citizens, tourists, fishermen, port workers, among others.) (Process 4).

The ecosystem-based information, including all the ecological and socioeconomic relationships, supports management (Process 5).

Table 1. Ecosystem services matrix for the mangroves and coral reefs in Puerto Morelos, Mexico. The matrix components are based on MEA 2003.

	MEA	SERVICES	BENEFITS	BENEFITED ACTORS
MANGROVES	Support	Base for biodiversity, nursery, nutrient cycling, physical space	Ecosystem itself and fisheries activities	Fishermen; General and local community
	Regulation	Sediments regulation (retention and export), nutrients and sediments filtration, hydric balance, carbon sequestration and storage, moderation of extreme events storm protection	Water quality; flooding control, erosion control (shoreline stabilization), climate control (mitigation and adaptation); air and soil quality; coastal protection, storm protection	General and local community; Urbanization; Tourism; Port sector; Fishermen
	Provision	Medicinal resources, biomass production, vegetable fibers, timber, sediment stock, wood	Raw materials for pharmacy, fisheries, agriculture and construction	Pharmaceutical Industry, Fishermen General and local community,
	Cultural	Landscape, social relationships and spiritual values	Education, tourism, recreation, fisheries activities, identity, contemplation	General and local community, NGO's, educational institutions
CORAL REEFS	Support	Base for biodiversity, nursery, nutrient cycling, soil formation	Ecosystem itself	Fishermen, General and local community
	Regulation	Sediments regulation (retention and export), nutrients and sediments filtration, hydric balance, carbon sequestration and storage, moderation of extreme events	Water quality; flooding control, erosion control (shoreline stabilization), climate control (mitigation and adaptation); air quality; coastal protection, storm protection	General and local community; Urbanization; Tourism; Port sector; Fishermen
	Provision	Medicinal resources, raw material production; limestone, calcareous rocks and sandstone production (sediment stock)	Raw materials for pharmacy, fisheries, and construction	Pharmaceutical , Industry, Fishermen General and Local community,
	Cultural	Landscape, social relationships, spiritual values	Education, tourism, recreation, fisheries activities, identity, contemplation	General and local community, NGO's, educational institutions

Therefore, allow the regulation of human activities by maintaining the ecosystems, their functions and services in a sustainable manner. Furthermore, this understanding helps to support government coastal decision-making policies (Process 6) (Figure 5).

4. Global Biodiversity Model

The analysis revealed the negative impact of land-use change over coastal ecosystems of Puerto Morelos. The overall MSA value for mangroves in the reference condition (2005) was on average 0.93 and gradually decreased to 0.81, 0.79, and 0.75 in 2008, 2011 and 2014, respectively. The land conversion contributed to a reduction in MSA in all mangroves areas, representing a loss of 18.6% in relation to the reference condition. This loss was more intensive in the northern than in the southern area. In 2005, the northern area (area A) had a high MSA, followed by a steep decline in 2008, lowering from high MSA class to relatively high. In the following years, the value remained constant. Area B showed a persistent reduction in the MSA value and went from high to relatively high class. Despite the MSA values decrease observed in areas C and D, they remained in the high class in relation to the reference year (Table 2).

Regarding future projections, vegetation would increase to 0.82 on average in the most optimistic scenario (high MSA class), while it would decrease to 0.42 in the most pessimistic scenario (medium MSA class). In addition, the northernmost area is the one with lower MSA class in both optimistic and pessimistic scenarios, being in relatively high and low classes, respectively. This is followed by area B, that could rise to high MSA class in the best scenario, while it can decrease to relatively low class in the worst scenario. Areas C and D would maintain high MSA classes in the best scenarios, while they can decrease to relatively high and medium classes in the worst scenario, respectively (Table 2).

The overall average MSA value of coral reefs remained constant through the years. In the reference condition, the MSA value was 0.82. There was a slight increase to 0.83 in 2008, followed by a small decrease to 0.81 in 2011, and then a recovery to 0.83 in 2014 (Table 2). Specifically, the northernmost area (i.e. Limones) maintained the MSA values constant onto high class throughout the studied period, followed by the southernmost area (i.e. Jardines), also with high MSA class throughout the years. On the other hand, Tanchacte remained with a relatively high MSA class through the years, similar to what was observed in La Bonanza, that showed the lower MSA values.

The constant values of MSA class can also be observed in future projections. On average, coral reefs could maintain MSA classes of 0.83 and 0.81 in the best and worst scenarios, respectively. The area of Limones would be the most constant in biodiversity irrespectively of the scenario, since they will keep with high MSA values in both best and worst projections. The same pattern is observed for Jardines, while Tanchacte and La Bonanza would remain in a relatively high class in both scenarios, with lower values in La Bonanza (Table 2).

5. DPSIR

The socio-economic activities such as tourism/recreation, urbanization, fishing, ports and climate change as a driver of socio-economic impacts, were defined through the literature review performed in the identification of the management sectors section and in consulting the Management Program of Puerto Morelos coral reef National Park (INEGI/INE 2000). The primary local policy related to the study area was considered and addressed as 'drivers' (Table 3) in the analysis. With regard to the Tourism/Recreation driver, the identified pressure was the modification on the health condition of ecosystems. This pressure acts by altering the cover, diversity and complexity of the ecosystems ('state'). As a consequence ('impact'), reduction of ecosystems services and benefits (support, provision, regulation and cultural) occurs. As a 'Response', policing, ecotourism promotion (with appropriate or local guides), educational efforts, monitoring programs, local government actions and policy efforts for integrated management (public and private) are suggested.

Table 2. MSA values for mangroves and coral reefs of different areas obtained through the GLOBIO3 model for the period from 2005 to 2014. MSA values were classified into five classes that range from high (with higher intactness) to low.

a) Mangroves MSA						Future scenarios	
Site	**Area (km²)**	**2005**	**2008**	**2011**	**2014**	**2035-B**	**2035-W**
A	**25**	0.87	0.61	0.61	0.61	0.66	0.11
B	**25**	0.99	0.9	0.88	0.77	0.84	0.36
C	**25**	0.94	0.89	0.89	0.83	0.91	0.62
D	**25**	0.91	0.82	0.78	0.81	0.89	0.60
b) Coral reef MSA						**Future scenarios**	
Site	**Area (m²)**	**2005**	**2008**	**2011**	**2015**	**2035-B**	**2035-W**
Limones	**216.97**	0.95	0.95	0.95	0.95	0.96	0.95
La Bonanza	**273.02**	0.70	0.73	0.69	0.71	0.72	0.70
Tanchacte	**165.76**	0.78	0.79	0.78	0.78	0.80	0.77
Jardines	**75.21**	0.86	0.85	0.84	0.84	0.86	0.81

MSA Class

0.81 ≤ high ≤ 1	0.61 ≤ relatively high ≤ 0.8	0.41 ≤ medium ≤ 0.6	0.21 ≤ relatively low ≤ 0.4	0.2 ≤ low

Table 3. DPSIR (Drivers-Pressures-State-Impacts-Response) framework for the coastal protection ecosystem services in Puerto Morelos, Mexico.

DRIVERS	PRESSURE	STATE	IMPACTS	RESPONSE	POLICIES
Tourism/ recreation	Modification on the ecosystems (health, pollution) and integrity	Modification of the cover, diversity, complexity	Reduction of ecosystems services and benefits (support, cultural, provision and regulation)	Fiscalization, Ecotourism promotion (guides), Educational efforts, Monitoring programs, Local government, Policy efforts for integrated management (public and private)	*Current*: Sustainable Tourism Agenda of Quintana Roo / Puerto Morelos Reef National Park Management Program. *Desirable*: Sustainable tourism certification / Marine Spatial Planning.
Urbanization	Modification on the ecosystems (health, pollution) and integrity	Modification of the cover, diversity, complexity	Reduction of all ecosystems services and benefits	Coastal Management program, Government participation, Educational efforts	*Current*: National Sustainable Development Policy for coasts and oceans / General Law of Ecological Balance and Environmental Protection / Regulations for the Use and Exploitation of the Territorial Sea, Navigable Waterways / Municipal Programs. *Desirable*: Land Use Master Plan / environmental licensing based on ecosystem services.
Fisheries activities	Modification on the ecosystems (health, pollution) and integrity; Modification in the fishery stocks	Modification of the cover, diversity, complexity; Modification in the fishery community	Reduction of ecosystems services and benefits (provision of food, biomass, support, biodiversity, cultural identities, amenities)	Educational efforts, Fiscalization, Fisheries policy (fishery restrictions), Monitoring programs	*Current*: Puerto Morelos Reef National Park Management Program / National Sustainable Development Policy for coasts and oceans, Regulations for the Use and Exploitation of the Territorial Sea, Navigable Waterways / General Law of Ecological Balance and Environmental Protection. *Desirable*: Marine Spatial Planning.
Ports and navigation	Modification on the ecosystems (health, pollution) and integrity	Modification of the cover, diversity, complexity; Biological invasions	Reduction of all ecosystems services and benefits	Ports regulation, Coastal management planning (Port Management), Capacitation of the port staff	*Current*: National Sustainable Development Policy for coasts and oceans, Regulations for the Use and Exploitation of the Territorial Sea, Navigable Waterways / General Law of Ecological Balance and Environmental Protection / Sustainable Tourism Agenda of Quintana Roo / Puerto Morelos Reef National Park Management Program. *Desirable*: Marine Spatial Planning / environmental port licensing based on ecosystem services.
Climate change	Modification on the ecosystems (health, pollution, pH decrease, temperature increase, diseases) and integrity	Modification of the cover, diversity, complexity	Reduction of all ecosystems services and benefits	Education efforts, Coastal Management planning, Government policies for climate change mitigation	*Current*: State Programme of Action on Climate Change Quintana Roo. *Desirable*: Local environmental diagnosis of climate change effects (Puerto Morelos).

The Urbanization driver was similar to the Tourism/Recreation driver for the pressure and state categories. However, the reduction of all ecosystem services and benefits were identified as impacts. As a response to this driver we proposed a Coastal Management program with Government participation and educational efforts programs for residents and tourists. For the Fisheries activities driver, the pressure and the state categories were also similar to the Tourism/Recreation and Urbanization drivers. Furthermore, the inclusion of the fish community/stock alteration was included. Some of the impacts identified for this driver were; the reduction of ecosystem services and benefits like provision of food, biomass, support, biodiversity, cultural identities and amenities. A potential response to this driver could be educational efforts, environmental policing, fisheries policy (fishery restrictions) and monitoring programs. The ports and navigation driver showed a similar pattern regarding the categories of pressure and state, but including also the impact of potential biological invasion by non-native organisms.

The impacts detected were also the reduction of all ecosystem services and benefits, and the potential responses proposed are a strict ports regulation with a proper coastal management planning (port management) and the capacitation of the port staff. Finally, the last driver identified was Climate Change. Several modifications on the ecosystems affecting their health condition (such as pollution, pH decrease, temperature increase and diseases, among others) were identified as Climate Change pressures. This driver affects the state causing modification of the coral and mangroves cover, diversity and complexity. The impacts involved include the reduction of all ecosystem services and their benefits. The response proposed are the reinforcement of education and a proper coastal management planning, with the support of Government policies focused on climate change mitigation.

6. *Policy assessment*

The legal framework evaluation allowed the identification of seven policies and tools related to support conservation and sustainable management of marine and coastal areas of Mexico, as well as planning for mitigation and/or avoidance of impacts arising from the ecosystems-change drivers mentioned above. Among these policies (three work on national level, two on state level and two on local level), there are variations on the degree of inclusion of the different agents of change and pressures on coastal areas. (Figure 6).

List of policy and management tools	Governance level	Evaluated policies and management actions covering coral reef and/or coastal vegetation features under drivers pressures					
		Incorporation of ecosystem service approach	Correlation with economic activites and land/marine use				Correlation with climate Change effects
			Urbanization	*Ports and harbours*	*Fisheries*	*Tourism*	
Política Nacional de Desarrollo para Costas y Océanos (2006)	F	→	↗	↗	↗	↗	↗
Ley General del Equilibrio Ecológico y Protección al Ambiente (1983)	F	→	↗	↘	↗	↗	↗
Reglamento del Mar Territorial y Zona Federal Marítimo Terrestre (1991)	F	↘	↗	↗	↘	→	↘
Programa Estatal de Acción ante el Cambio Climático Quintana Roo (2013)	S	↗	↗	↘	↘	↗	↗
Agenda de Turismo Sustentable de Quintana Roo (2014)	S	→	↗	↘	↘	↗	↘
Programa de Manejo de Parque Nacional Arrecife de Puerto Morelos (2000)	L	↗	↗	↗	↗	↗	→
Programas Municipales Puerto Morelos (2016-18)	L	↗	↗	↘	↗	↗	↘

Figure 6. Policy framework assessment. Seven policies and tools applied in Puerto Morelos. F corresponds to Federal level, S to State level and L to local, Puerto Morelos level. Green arrows correspond to presence/application, yellow arrows correspond to mentioned but partially attended, and red arrows correspond to absence/not attended.

In all the policies, urbanization and tourism activity processes were identified as drivers associated with land use and coastal changes. Comparing the seven policies analysed, only three of them have integrated in their guidelines ecosystem services. Three others mentioned management efforts but do not explicitly discuss ecosystem services while the last one did not mention any ecosystem services. The ports, navigation and fisheries drivers were included in marine related policies exclusively, although it could be directly associated with climate change agenda and conservation laws. The effects of climate change were addressed in three policies and laws of the management framework. The "*Programa de Manejo Parque Nacional Arrecife de Puerto Morelos"* (Puerto Morelos Reef National Park Management Program) and *"Política Nacional de Desarrollo Sostenible para costas y océanos"* (National Sustainable Development Policy for coasts and oceans) policies were broader for considering most of the analyzed drivers.

Discussion

This study resulted in a low cost and easily applicable workflow to generate an Ecosystem-Based Management (EBM) framework for coastal ecosystems. This approach allowed us to identify the main ecosystem services, their current state and their pressures. Our case study from the Caribbean mangrove and coral reef ecosystems (Puerto Morelos, Mexico) is an explicit example of how recent socio-economic pressures are altering coastal ecosystems. This workflow was first developed using an 'ecosystem information base' that systematizes relevant information about the studied ecosystems. It later analyzes the current policies and their effectiveness. To construct the information base, we used different strategies, such as analysing the ecosystems as "Management Units" which revealed a high complexity of socio-economic activities depending on these ecosystems. Also, we used an ecosystem services matrix (ESM), that assisted in the characterization and identification of ecosystem services of the study area (Geange et al. 2019). According to Jacobs et al (2015), matrix approaches have weaknesses such as inferior methodological transparency, uncertainties with regard to the quality of the results, low replicability and lack of reliability. The use of ESM to complement other methodologies becomes important to reinforce additional assumptions about future potential provision of ecosystem services (IPCC 2001). Given the above, we constructed a Conceptual Model to understand the interplay coastal processes, and then modelled past biodiversity loss and predictions of future scenarios in both mangroves and coral reefs ecosystems using the GLOBIO3 model. Finally, we evaluated the governance section in the DPSIR framework and Policy Assessment.

The conceptual model pointed to two main pieces of information: the framework steps (methodology) and the processes occurring in coastal ecosystems (results). It was helpful by connecting the different processes that occur in these coastal systems (biological and social interactions), which facilitates the understanding of how each process can be evaluated. As a result, it decoupled the several 'pieces' of the systems allowing identification of the gaps where management action is needed. This work indicated that services provided by mangrove and coral reef ecosystems (i.e. climate regulation, food supply, landscape, among others) simultaneously are basis and support for the socio-economic activities of the region. Indeed, these systems not only protect biodiversity but also the coastal land, essential for human development (Douvere 2008). It is important to note that the conceptual model adopted simplifies a complex set of human activities and marine ecosystem services. Additionally, it does not map other products, such as social benefits and tax payments. Among the ecosystem services provided by both ecosystems, only 'coastal protection' was evaluated due to its importance for the development of socio-economic activities on coastal land and sea. Mangroves reduce the water flow speed and the roots hold sediments, increasing the coastline, while coral reefs dissipate the energy of waves, decreasing the energy flow to the land and reducing coastal erosion (Spalding et al. 2014), providing coastal protection.

The GLOBIO3 model clearly showed pressures on mangrove systems, leading to biodiversity loss from 2005 to 2014. Among the activities affecting the mangrove cover in Puerto Morelos, land conversion by tourism and urbanization was considered the major one prompted by the construction of hotels, resorts, and houses, affecting coastal protection (Rodríguez-Martínez 2008, Costanza et al. 2014, Spalding et al. 2014). Despite this reduction in mangrove area, the studied areas still maintained a considerable mangrove cover. Similarly, a previous study conducted in the same area, showed about 27% of mangrove loss from 1981 to 2005, but just 1% from 2005 to 2010 (Vázquez-Lule et al. 2009). This relatively low suppression of mangroves could be due to the increase of public policies in recent years and sustainable land use land cover (LULC) strategies (see Figure 6 for an overview of policies). However, the socio-economic pressures are expected to keep increasing in Puerto Morelos region, and, if it continues leading to mangrove suppression at the same pace over the next two decades (our worst scenario), the ecosystem services provision will be threatened (Koch et al. 2009, Duke et al. 2007, Taylor et al. 2018). A better path to take for the next 20 years would be our best scenario, in which communities and government work together to develop strategies and policies to low cost and feasible mangrove restoration, in order to better cope with land-use change (Dale et al. 2014).

In contrast to mangroves, the coral reef biodiversity loss indexes kept constant during the last decade (see also Banaszek & Álvarez-Filip, 2014, Álvarez-Filip & Banaszek, 2016) and will remain the same in the next 20 years to our both pessimistic and optimistic scenarios. It seems likely that the recent reduction of coral degradation might be a result of conservation actions and novel policies, especially regarding the Puerto Morelos Coral Reef National Park management plan. However, the good state of the corals revealed by GLOBIO3 could also be due to analytical issues. That is, because there is no reliable model programs for marine environments and our GLOBIO3 adaptation used high resilience indexes that generated higher MSA values, overestimating the overall coral quality from some areas, such as La Bonanza (Ladd & Collado-Vides, 2013, Álvarez-Filip & Banaszek, 2016). Moreover, it is possible that other drivers not considered in the projections (e.g. the increase in sewage, climate change, diseases, ocean acidification), could affect the health of coral organisms and their distribution in the future (Fine & Tchernov 2007, Sutherland et al. 2010, Hughes et al. 2017). The mangrove and coral reef cover projections demonstrate that the efforts must continue to maintain the conservation of these ecosystems. Therefore, the cumulative impacts on both ecosystems require the attention of stakeholders (e.g. governmental institutions, environmental managers, civil society, among others) to remain updated and to develop new policy-oriented governance from scientific-based analysis with the support of different stakeholders, in order to improve the ocean health and the quality of coastal ecosystems.

The DPSIR framework (identification of the management sectors) complements the ecosystem modeling section by revealing that the main drivers to both coastal ecosystems are linked to the urbanization processes (tourism/recreation, urbanization, fisheries activities, ports and navigation). Even when compared to the economic and social benefits derived from such activities, human activities are affecting the quality of life of surrounding residents and visitors, since pressures produce changes in the state of ecosystems and the impacts they generate over ecosystem services are directly related to the quality of the environment. The responses identified to these drivers constitute suggestions for sustainable development in order to maintain the provision of ecosystem services. Tallis et al. (2010) highlight the need to structure applicable and balanced governance agendas to address the complex issues associated with coastal systems. Multi-specific planning and management proposals can help to better understand and address this challenge.

The survey of policies was the final step (identification of the management sectors) to create a legal framework that would precede governance actions. This was particularly complex as (1) policies work on different levels of governance, (2) information is usually dispersed, and (3) most policies are focused on sectoral activities instead of an integrated perspective. At the federal level, Sustainable Coastal and Marine Management Policy (SEMARNAT 2006) is the only instrument that functions as an integrative policy. That is, several other instruments and laws emphasized specific drivers and failed to correlate the synergistic impacts on the environment (especially considering the climate change effects). The state management framework functions by considering the main drivers, threats and natural features of its coastal zone. It also develops guidelines and programs indicating the actions that shall be accomplished. At the regional scale (Quintana Roo state) policies contemplate two of the main drivers of pressure in coastal ecosystems: climate change and tourism, which are related with urbanization. Another important effort identified, but not included in the Mexican legal framework, is the "Good Practices for Climate Change Adaptation project, Mexico, Quintana Roo State" (Silva et al. 2019, UN 2019). This effort has a focus on the management of land conversion, which is the current main driver of changes (directly or indirectly) over mangrove and coral reef ecosystems. Finally, a federal environmental tool applied on a local scale has been directing its efforts for conservation of Puerto Morelos coral reefs through the delimitation of the Coral Reef National Park and its management plan (Carabias-Lillo 2000).

The integration of ecosystem services knowledge into these policies is a valuable approach to incorporate the relationship between values and benefits delivered by the ecosystems and the different social activities (Santos-Martín et al. 2015). Indeed, there are some examples of successful coastal management practices that incorporated ecosystem services in their decisions (Luisetti et al. 2011, Guerry et al. 2012, Kelble et al. 2013). For example, in Belize, the Integrated Coastal Zone Management Plan allows the continuous use of the ocean, such as coastal development and aquaculture, but in high risk areas, the natural habitats reduction is limited up to 20% (Arkema et al. 2014). In addition, there should be incentives to update and adapt current policies to be able deal with potential new sources of and increases in drivers of pressure in the next years, given that the population growth in Puerto Morelos is not being addressed adequately by these policies. This lack of attention to population growth may result in the intensification of pressures on the ecosystems (Hernández-Terrones et al. 2011). It follows that an integrated coastal management must be linked with public policies for sustainable development of people and spaces (socio-ecological systems) with the participation of different stakeholders (Muñoz 2020). The Puerto Morelos Coral Reef National Park has a great potential of awareness and knowledge from the population about the importance of reef ecosystems for the society. An environmental licensing based on ecosystem services (for ports, urbanization and tourism facilities) added to a local Land Use Master Plan and an international sustainable tourism certification is recommended. Finally, a Marine Spatial Planning (MSP) may contribute to harmonizing those activities who depend on, use and disturb the marine and coastal environment (Ehler & Douvere 2009, Collie et al. 2013).

Although the present study contributes to the advancement of approaches based on marine ecosystems, it also identified some caveats and limitations that require improvement. For instance, some processes that also occur in the coastal zone were not considered by the conceptual model and the scenario projections. The decision to omit these processes was taken owing to the amount of information required to incorporate many processes, as well as reducing the complexity of the models and making them more understandable. Focusing on only one service (coastal protection) and its main driver (urbanization) made possible a well-grounded understanding about the overall problem and development of solutions to the principal issues of mangroves and coral reef losses in the region. Moreover, despite the fact that GLOBIO3 models have been developed for terrestrial systems (Alkemade et al. 2009), in this study we were able to adapt land-use change to coral reef's cover. These promising approaches require support from scientific communities to develop a suitable solution applicable to marine environments so as to avoid model biases. Although improvements should be made to create a more reliable model and future predictions for these systems, the adaptations applied in this study were worthwhile and provided us with a broader view of the issue. Despite these limitations in some specific parts of our EBM framework, the complementary pathway used in this study leads us to have a general understanding for strengthening decision-makers/policy formulation and implementation which will assist in ensuring sustainable development and maintenance of ecosystem services in coastal regions. It is worth noting that through a collaborative process, which involved several researchers with different backgrounds, it was possible to create this framework as a more comprehensive and complete tool. Given the global trends in biodiversity loss due to anthropogenic impacts (IPBES 2019), and the increasing pressure of climate change on ecosystems (IPCC 2014), the development of new models to ascertain the health and sustainability of coastal ecosystems has increased relevance, especially those that include the use of policies which take into account different areas of knowledge and cultural backgrounds. Therefore, this type of collaborative approach is essential to face the challenges that arise in the Anthropocene era (Berkes 2017).

Overall, this report revealed relationships between ecosystems with other elements such as services and beneficiaries, as well as human and natural drivers. The proposed strategy ties key scientific information necessary to understand the functioning of the ecosystems involved. The conceptual model evidenced the ecosystems interplay through main components and processes. The empirical model assessed the quantitative effects of coastal and marine activities and land-use change on the ecosystems.

Seven potential policies and tools from three different governance levels can be potentially used in an integrated ecosystem approach. We highlight possible shortcomings in current laws, which should be considered when expanding the formulation and implementation of public policies toward environmental governance good practices. The future of the ocean depends on successful immediate implementation of a comprehensive governance framework that moves away from a sectoral management approach to an integrated one (Foley et al. 2010). Marine ecosystems are still poorly studied concerning their ecosystem services. It is, therefore, relevant to understand all the range of services provided by these systems and evaluate (and value) the costs of degrading and losing them (Spalding et al. 2014). Mangrove and coral reef ecosystems in Puerto Morelos were used as an example to demonstrate how it is possible to design and develop a workflow with integrated disciplines information for the development of an EBM. We suggest that stakeholders (e.g. all governmental institutions, second sector and the local society) propose viable science-based solutions to improve the marine ecosystem health through EBM underpinning the source of ecosystem services benefits for the local communities and the whole social system.

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Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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Inventory

Fishes community composition and patterns of species distribution in Neotropical streams

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Abstract: The ichthyofauna of streams in the Neotropical region is not yet fully known. This study aims to investigate the ichthyofauna composition of six streams of the Ijuí River sub-basin, Rio Grande do Sul State, inserted in the Uruguay River basin, as to contribute to the knowledge of fishes species richness and distribution in the south of Brazil. Sampling was carried out between July 2015 and May 2016, bimonthly, using the technique of electric fishing to collect the fishes. Spatial variations (per sampled stream) in the ichthyofauna composition were tested with a permutational multivariate analysis of variance. In total, we collected 5,029 individuals from 55 species, 13 families and five orders. From these species, 17 are endemic to the Uruguay River basin. Five species alone represented approximately 70% of the ichthyofauna abundance sampled. Our hypothesis that the fish community composition is not homogeneous along the streams sampled was confirmed and we observed that species complexity increases from the upstream closest area to the downstream according to the river continuum concept.
Keywords: *Abundance, Characidae, Heptapteridae, Loricariidae, Richness, Uruguay River basin.*

Composição da comunidade de peixes e padrões de distribuição de espécies em riachos Neotropiacais

Resumo: A ictiofauna de riachos na região Neotropical ainda não é totalmente conhecida. Este estudo objetiva investigar a composição da ictiofauna de seis riachos da sub-bacia do rio Ijuí, estado do Rio Grande do Sul, inseridos na bacia do rio Uruguai, de forma a contribuir no conhecimento da riqueza e distribuição de espécies de peixes no sul do Brasil. A amostragem foi realizada entre julho de 2015 e maio de 2016, bimestralmente, utilizando a técnica da pesca elétrica. Variações espaciais (por riacho amostrado) na composição da ictiofauna foram testadas com uma análise de variância multivariada permutacional. No total, coletamos 5029 indivíduos de 55 espécies, 13 famílias e cinco ordens. Destas espécies, 17 são endêmicas da bacia do rio Uruguai. Cinco espécies sozinhas representaram aproximadamente 70% da abundância da ictiofauna amostrada. Nossa hipótese de que a composição da comunidade de peixes não é homogênea ao longo dos riachos amostrados foi confirmada e observamos que a complexidade das espécies aumenta de áreas à montante em direção à jusante, conforme o conceito do rio contínuo.
Palavras-chave: *Abundância, bacia do rio Uruguai, Characidae, Heptapteridae, Loricariidae, Riqueza.*

Introduction

The ichthyofauna of the Neotropical region comprises 4,475 valid species, and perhaps more than 1,550 undescribed ones (Reis 2013). It is estimated that there are 6,025 species and that this number could be surpassed, overcoming the 8,000 species (Schaefer 1998, Reis 2013). In South America, this ichthyofauna occupies a variety of habitats, from large rivers to small and medium-sized streams, swamps, lagoons, high altitude lakes, among others (Vari & Malabarba 1998, Reis 2013).

Among the habitats occupied by the ichthyofauna, streams are known as lotic environments, with unidirectional water flows from headwaters to mouth and may have non-persistent flooding areas during rainy seasons (Esteves & Aranha 1999, Uieda & Castro 1999). They are known to have a wide variety of mesohabitats due to environmental gradients ranging from rocky riffles and runs to sandy pools and backwaters, in addition to a variety of marginal vegetation in the stream bank (Araújo-Lima et al. 1995, Esteves & Aranha 1999). In southern and southeastern Brazil, the streams may present high dissolved oxygen concentration and large seasonal temperature variation, with influence of drainage basin geomorphology under abiotic components as transparency, pH and conductivity (Araújo-Lima et al. 1995, Esteves & Aranha 1999).

The streams have high biological diversity and great importance in maintaining the integrity of the entire ecosystem (Meyer et al. 2007). These environments frequently present isolated populations of fish, often undescribed, with a high degree of endemism (Langeani et al. 2007, Reis 2013, Vidotto-Magnoni et al. 2015). The assessment of species in these sites contributes, therefore, to the understanding of the distribution of the species already described and to the description of new taxa (Pereira et al. 2014). Studies of species distribution assist in estimating changes in habit susceptibility to anthropogenic impacts that influence the composition of aquatic communities and are useful in the definition of priority areas for conservation (Bailly et al. 2016, Rose et al. 2016).

Freshwater ecosystems are particularly vulnerable to anthropogenic impacts that often promote the proliferation of some populations in the face of the decline, or even the extinction of others (Agostinho et al. 1999, Bailly et al. 2016). In streams, the susceptibility to these impacts may be higher because of the reduced size of these habitats and the sensitivity of microhabitats (Galves et al. 2009, Bonato & Fialho 2016). The fishes community is an indicator of the biological integrity of freshwater systems (Moore et al. 1997) and the knowledge of streams ichthyofauna is an informative tool to propose mitigation measures to these impacts (Vidotto-Magnoni et al. 2015). In the hydrographic region of River Uruguay, Brazil, anthropogenic impacts consist mainly on the environmental degradation in areas of high population and industrial density caused by agricultural activities, by the construction of hydroelectric dams, with the disappearance of lotic environments, and by the constant introduction of exotic species (Malabarba et al. 2009).

The Uruguay River is one of the main tributaries of the La Plata River basin which, in South America, comprehends the second largest drainage system, behind only the Amazonas (Cappato & Yanosky 2009). The Uruguay River has an extension of 2,200 km (ANA 2016) with a drainage area of about 365,000 km^2 (Di Persia & Neiff 1986, Albert & Reis 2011). Its main tributaries are the Negro River, Quaraí River, Ibicuí River and Ijuí River (Carvalho & Reis 2009). The ichthyofauna of the Uruguay River drainage system comprises about 275 species known; from these, 78 (28%) are endemic (Bertaco et al. 2016).

The "river continuum concept" proposed by Vannote et al. (1980) explains the distribution pattern of fishes fauna following the upstream-downstream gradient. This theory describes the structure and functions of communities along river systems, considering gradients of physical factors, formed by the drainage network, which include energy input, organic matter transport and use by macroinvertebrates functional feeding groups (Vannote et al. 1980). In addition, this concept proposes that community complexity increases from upstream to downstream, with the alteration on the composition of species and trophic guilds being influenced by continuum gradients (Vannote et al. 1980).

This study aims, therefore, to evaluate the composition of the fishes community and the pattern of species distribution in streams located along a longitudinal gradient (upstream-downstream) in the hydrographic sub-basin of the Ijuí River, tributary of Uruguay River, intending to contribute to the knowledge of the richness and abundance of species in this region of the south of Brazil. The hypothesis is that the composition of the fishes community is not homogeneous along the streams sampled, and that its complexity increases from the upstream closest area to the downstream (mouth of the Ijuí River sub-basin in the Uruguay River basin), according to the "river continuum concept".

Material and Methods

Collections were carried out in six streams, located in rural areas of the Ijuí River sub-basin, at the northwest region of the Rio Grande do Sul State, southern Brazil. With a drainage of 10,649.13 Km², it is located in the middle portion of the Uruguay River hydrographic network (FEPAM 2016) (Figure 1). In order to sample different portions of the Ijuí River sub-basin (high, middle and low), chosen streams were distributed along the longitudinal gradient, from upstream to downstream areas, near the mouth of the Ijuí River sub-basin in the Uruguay River (Figure 1). From the sampled streams, two are locate in an upper portion of the sub-basin: stream 1 (28°18'58.4''S, 53°54'17.9''W) (Figure 2a) and stream 2 (28°25'56.2''S, 53°58'14.9''W) (Figure 2b); two are in the mid portion: stream 3 (28°12'06.2''S, 54°13'06.9"W) (Figure 2c) and stream 4 (28°23'41.5''S, 54°27'05.9''W) (Figure 2d); and two are in the lower portion: stream 5 (28°13'40.8''S, 54°57'24.8''W) (Figure 2e) and stream 6 (28°10'13.5''S, 55°03'57.4''W) (Figure 2f). Anthropogenic activities developed nearby the streams consist mainly in agriculture (soybean crops) and cattle farming, with swine farming in the corresponding area to the stream 4. The riparian vegetation, next to the streams, is poorly preserved at all sampling sites, corresponding to narrow tree lines running along the streams, often less than 5m width.

Biological samples were collected bimonthly, from July 2015 to May 2016, summing up six capture expeditions for each stream (July, September, and November 2015, and January, March, and May 2016). Fishes were collected using the electric fishing technique, in an extension of 100m in each stream, for the period of an hour. Fieldwork and sampling were carried out under a scientific collection permit (Permit Number 48291-1) issued by the Instituto Chico Mendes de Conservação da Biodiversidade, Ministério do Meio Ambiente, Brasília – Distrito Federal, Brazil. This study was conducted in accordance with protocols approved in their ethical and methodological aspects, for the

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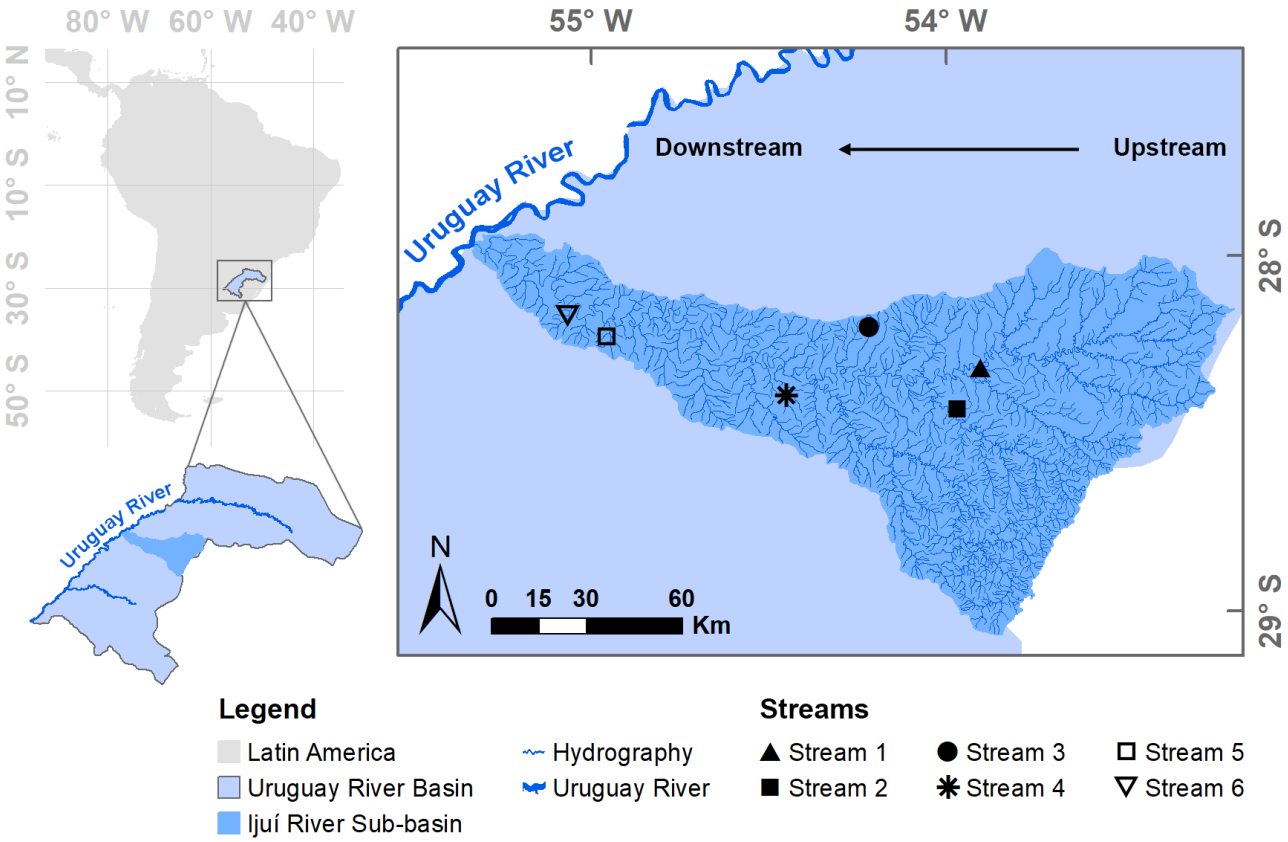


Figure 1. Location of the sampled streams in the Ijuí River sub-basin and its respective position into the Uruguay River hydrographic basin, Brazil.

use of fish, by the Ethics Committee on Animal Use of the Universidade Federal do Rio Grande do Sul, Brazil (Permit Number 35495).

In the field, individuals were anesthetized and euthanized with eugenol 10% (Jenkins et al. 2014) and fixed with formalin 10%. In the laboratory, specimens were selected and identified before being preserved in alcohol 70%. Species identification was made according to criteria of the literature (Buckup & Hahn 2000, Casciotta et al. 2002, Lucena 2007, Ghazzi 2008, Carvalho & Reis 2009, Malabarba et al. 2015) and specialists. The classification and nomenclature followed Eschmeyer et al. (2018) and Betancur-R et al. (2017) for Cichlidae. Voucher specimens were deposited in the ichthyologic collection of the Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Brazil. The fish community was described considering the abundance (number of individuals collected) and richness (number of species).

Spatial variations (for each sampled stream) on the ichthyofauna composition were tested using the permutational multivariate analysis of variance (PERMANOVA; $\alpha < 0.05$), based on a dissimilarity matrix constructed with the Bray-Curtis index (Anderson 2001, Anderson et al. 2011, Borcard et al. 2011). Abundance data were standardized using $\log_{10}(y+ 1)$ (Legendre & Legendre 1998, Anderson et al. 2011). The Bray-Curtis index was chosen as it considers the abundance data and enables the exclusion of joint absences (Anderson et al. 2011). This decision was made because we did not consider two samples to be more similar due to the sharing of absence of a particular species, since we do not have *a priori* information if the species does not actually exist in the local, or was simply not captured (Anderson et al. 2011). The pattern of species spatial distribution, if identified with the PERMANOVA, was visualized with a principal coordinates analysis (PoCA), using a dissimilarity matrix made with the Bray-Curtis index (Legendre & Legendre 1998, Borcard et al. 2011). In the PCoA graph presenting the species composition along the sampled streams, only those species that contributed with a minimum of 10% of the explanation of the data distribution (eigenvectors $\geq \pm 0.10$) were shown, for the first two axis, in order to improve the visualization of distribution patters and avoid visual pollution. In the PCoA graph presenting the distribution of fish families, all species were shown. Statistical tests were carried out using R Project for Statistical Computing software, version 3.4.1. with the Vegan statistical package, version 2.4-5 (Oksanen et al. 2017).

Results

The ichthyofauna found in the six sampled streams in the Ijuí River basin is distributed within five orders, 13 families, 33 genera and 55 species, totalizing 5,029 individuals sampled (Table 1). The orders Characiformes and Siluriformes presented five families each, while Cichliformes, Gymnotiformes and Synbranchiformes were represented by a single family. The order Siluriformes was the most abundant in number of collected individuals (3,051 specimens), representing 60.68% of the total sampled, distributed within 17 genera. Characiformes presented the highest richness (23 species) and the second highest abundance (36.85% of individuals collected), comprised by 11 genera. Cichliformes had eight species and 1.25% of the total abundance,



Figure 2. Sampling sites in the streams of the Ijuí River sub-basin, Brazil. Upper portion (upstream): (**a**) Stream 1 and (**b**) Stream 2; mid portion (midstream): (**c**) Stream 3 and (**d**) Stream 4; lower portion (downstream): (**e**) Stream 5 and (**f**) Stream 6.

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Table 1. List of occurrence and abundance of species of the ichthyofauna sampled in six streams in the Ijuí River sub-basin, Brazil. a Species endemic to the Uruguay River basin.

Taxa	Upper portion		Mid portion		Lower portion		Total	% of total	Voucher
	Stream 1	Stream 2	Stream 3	Stream 4	Stream 5	Stream 6			
CHARACIFORMES							1853	36.85	
Characidae							791	15.73	
Astyanax abramis (Jenyns 1842)					4	19	23	0.46	UFRGS 22179; 22180; 22182; 22187; 22373
Astyanax aramburui Protogino, Miquelarena & López 2006					4	11	15	0.3	UFRGS 21981; 21985; 21997; 21998
Astyanax eigenmanniorum (Cope 1894)					3	1	4	0.08	UFRGS 21967; 21993
Astyanax lacustris (Lütken 1875)	12	41	2	2	13	81	151	3	UFRGS 21968; 21969; 21970; 21974; 21984; 21991; 21995; 22002; 22076; 22178; 22181; 22183; 22184; 22185; 22186; 22188; 22189; 22190; 22191; 22192; 22193; 22194; 22372; 22374
Astyanax laticeps (Cope 1894)			7	1			8	0.16	UFRGS 21971; 21976; 21987; 21992
Astyanax ojiara Azpelicueta & Garcia 2000	1	12	1				14	0.28	UFRGS 22473; 22477; 22723; 22724; 22725; 22726
Astyanax paris Azpelicueta, Almirón & Casciotta 2002				7		13	20	0.4	UFRGS 21927; 21928; 21929
Astyanax saguazu Casciotta, Almirón & Azpelicueta 2003					5	15	20	0.4	UFRGS 21919; 21980; 21982; 21986; 21988
Astyanax sp.					1	7	8	0.16	UFRGS 21972; 21990; 21994
Astyanax xiru Lucena, Castro & Bertaco 2013		2		1	2	7	12	0.24	UFRGS 21975; 21983; 21989; 21999; 22000; 22001; 22003
Bryconamericus iheringii (Boulenger 1887)	3	75	21	18	98	125	340	6.76	UFRGS 22478; 22481; 22544; 22702; 25454; 25456
Bryconamericus uporas Casciotta, Azpelicueta & Almirón 2002[a]	9	5	34	41	1	9	99	1.97	UFRGS 22479; 22480; 22703; 22713; 22714; 25449
Diapoma uruguayense (Messner 1962)[a]						3	3	0.06	UFRGS 22474
Galeocharax humeralis (Valenciennes 1834)					1		1	0.02	UFRGS 25405
Hyphessobrycon luetkenii (Boulenger 1887)				1		9	10	0.2	UFRGS 22475; 22476
Hyphessobrycon togoi Miquelarena & López 2006			1				1	0.02	UFRGS 22472
Oligosarcus sp.						2	2	0.04	UFRGS 25450
Piabarchus stramineus (Eigenmann 1908)	1				47	12	60	1.19	UFRGS 22699; 22704; 22715
Crenuchidae							976	19.41	
Characidium pterostictum Gomes 1947	10	68	162	196	328	207	971	19.31	UFRGS 24564; 24565; 24566; 25425; 25426; 25427
Characidium tenue (Cope 1894)					5		5	0.1	UFRGS 25385; 25397

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Continuation Table 1.

Taxa	Upper portion		Mid portion		Lower portion		Total	% of total	Voucher
	Stream 1	Stream 2	Stream 3	Stream 4	Stream 5	Stream 6			
Curimatidae							1	0.02	
Steindachnerina biornata (Braga & Azpelicueta 1987)		1					1	0.02	UFRGS 25460
Erythrinidae							5	0.1	
Hoplias malabaricus (Bloch 1794)		2			2	1	5	0.1	UFRGS 25355
Parodontidae							80	1.59	
Apareiodon affinis (Steindachner 1879)					77	3	80	1.59	UFRGS 25363; 25367
SILURIFORMES							3051	60.67	
Callichthyidae							94	1.87	
Corydoras longipinnis Knaack 2007		94					94	1.87	UFRGS 22177; 25433; 25452
Heptapteridae							1312	26.09	
Cetopsorhamdia iheringi Schubart & Gomes 1959	20						20	0.4	UFRGS 25402; 25409
Heptapterus mandimbusu Aguilera, Benitez, Terán, Alonso & Mirande 2017	23			66		1	90	1.79	UFRGS 25357; 25366; 25373; 25408
Heptapterus mustelinus (Valenciennes 1835)	145	358	69	115	186	214	1087	21.61	UFRGS 21107; 21955; 25434; 25435; 25436; 25437; 25438; 25447
Heptapterus sp1	23						23	0.46	UFRGS 25400; 25401; 25404; 25455
Rhamdella longiuscula Lucena & da Silva 1991[a]					2		2	0.04	UFRGS 25362
Rhamdia aff. *quelen* (Quoy & Gaimard 1824)	21	22	7	11	19	10	90	1.79	UFRGS 25440; 25441; 25442; 25443; 25444; 25448; 25451
Loricariidae							1464	29.11	
Ancistrus taunayi Miranda Ribeiro 1918[a]	101	198	119	132	115	35	700	13.92	UFRGS 25350; 25358; 25364; 25371; 25372; 25375; 25403
Eurycheilichthys pantherinus (Reis & Schaefer 1992)[a]			3				3	0.06	UFRGS 21811; 21978
Hemiancistrus fuliginosus Cardoso & Malabarba 1999	84	31	11	57	44	43	270	5.37	UFRGS 25360; 25361; 25370; 25391; 25395; 25396; 25459
Hisonotus aky (Azpelicueta, Casciotta, Almirón & Koerber 2004)[a]			2	4		2	8	0.16	UFRGS 25381; 25382; 25383
Hypostomus commersoni (Valenciennes 1836)	3	10			5	4	22	0.44	UFRGS 25354; 25410
Pareiorhaphis hystrix (Pereira & Reis 2002)	45	7	120	179	1		352	7	UFRGS 25359; 25369; 25374; 25392
Pareiorhaphis sp.[a]	1						1	0.02	UFRGS 21977
Rineloricaria reisi Ghazzi 2008[a]	2						2	0.04	UFRGS 25353; 25412
Rineloricaria sanga Ghazzi 2008[a]	1	31	5	6	3	16	62	1.23	UFRGS 25418; 25419; 25420; 25421

Continuation Table 1.

Taxa	Upper portion		Mid portion		Lower portion		Total	% of total	Voucher
	Stream 1	Stream 2	Stream 3	Stream 4	Stream 5	Stream 6			
Rineloricaria stellata Ghazzi 2008[a]			12				12	0.24	UFRGS 25416; 25417
Rineloricaria zaina Ghazzi 2008[a]	13	7	8	3		1	32	0.64	UFRGS 25413; 25414; 25415
Pseudopimelodidae							97	1.93	
Microglanis malabarbai Bertaco & Cardoso 2005[a]	27		41	15	11	3	97	1.93	UFRGS 20253; 20254; 25376; 25380; 25387; 25388; 25389; 25390; 25394
Trichomycteridae							85	1.69	
Ituglanis sp.	2						2	0.04	UFRGS 21920; 21921
Scleronema sp.[a]		1		6	38	16	61	1.21	UFRGS 21958; 21959; 21961; 21962; 21963; 21964; 21965; 21966; 21973; 21979; 22579; 22583; 22584; 22585; 22586; 22587; 22588; 22589
Trichomycterus perkos Datovo, Carvalho & Ferrer 2012	4		18				22	0.44	UFRGS 25377; 25378; 25379; 25393; 25399; 25422; 25423; 25424
GYMNOTIFORMES							39	0.78	
Gymnotidae							39	0.78	
Gymnotus cuia Craig, Malabarba, Crampton & Albert 2018		33	4	1	1		39	0.78	UFRGS 25429; 25445; 25446
CICHLIFORMES							63	1.25	
Cichlidae							63	1.25	
Crenicichla hadrostigma Lucena 2007[a]	1						1	0.02	UFRGS 25458
Crenicichla lepidota Heckel 1840	1		1		3	1	6	0.12	UFRGS 25356; 25384; 25406; 25407
Crenicichla missioneira Lucena & Kullander 1992[a]	3				2	2	7	0.14	UFRGS 25351; 25431
Crenicichla scottii (Eigenmann 1907)[a]			1	2	4	7	14	0.28	UFRGS 25457
Crenicichla sp.						3	3	0.06	
Crenicichla tendybaguassu Lucena & Kullander 1992	1						1	0.02	UFRGS 21996
Geophagus brasiliensis (Quoy & Gaimard 1824)	2	12					14	0.28	UFRGS 25368; 25386; 25432; 25439; 25461
Gymnogeophagus constellatus Malabarba, Malabarba & Reis 2015[a]					3	14	17	0.34	UFRGS 25453
SYNBRANCHIFORMES							22	0.44	
Synbranchidae							22	0.44	
Synbranchus marmoratus Bloch 1795	16		1		4	1	22	0.44	UFRGS 25352; 25365; 25398; 25411; 25428; 25430
Total	575	1010	650	864	1032	898	5029		

followed by Gymnotiformes and Synbranchiformes, with one species each, and 0.78% and 0.44% of the total number of collected specimens, respectively (Table 1). From the 55 fish species collected, 17 are endemic to the Uruguay River hydrographic basin and no exotic species were collected (Table 1).

Characidae had the highest number of species recorded, 18, followed by Loricariidae, Cichlidae, Heptapteridae, and Trichomycteridae, with 11, eight, six and three, respectively. In relation to the total of individuals captured, the most representative families were Loricariidae (29.11%), Heptapteridae (26.09%), Crenuchidae (19.41%) and Characidae (15.73%). The species with the highest number of individuals collected were *Heptapterus mustelinus* (Valenciennes 1835) (21.61%), *Characidium pterostictum* Gomes 1947 (19.31%), *Ancistrus taunayi* Miranda Ribeiro 1918 (13.92%), *Bryconamericus iheringii* (Boulenger 1887) (7.00%) and *Pareiorhaphis hystrix* (Pereira & Reis 2002) (6.76%), representing together approximately 70% of the ichthyofauna abundance. The abundance of the other species was inferior to 6% for each taxon (Table 1).

The distribution of species and the representativity of families were not homogenous throughout the altitudinal gradient of the Ijuí River sub-basin (Figure 3-4). A pattern of spatial variation on the ichthyofauna composition was detected, with differences in richness and species abundance from upstream (upper portion of the sub-basin) to downstream areas, near the mouth in the Uruguay River (sub-basin lower portion) according to PERMANOVA results (Df: 5, pseudo-F: 10.29, R^2: 0.63, p: 0.0001), which indicates that species distribution does not occur randomly. The streams were more similar to each other regarding the ichthyofauna composition, according to the geographical location along the sub-basin (upper, mid, and lower portion) (Figure 3). Species richness varied between sampled streams, detecting a higher number of species in the lower portion of the sub-basin: 34 in stream 6 and 31 in stream 5. In the sub-basin mid portion, stream 3 and stream 4 presented 23 and 21 species, respectively, while in the upper portion were recorded 28 species in the stream 1 and 20 in the stream 2.

The most abundant species although appearing in all sampled sites, contributed to the segregation of the streams in the Principal Coordinates Analysis (Table 2; Figure 3). *Ancistrus taunayi* and *H. mustelinus* were associated with the upper portion of the sub-basin (streams 1 and 2), *P. hystrix* was associated to the mid portion (streams 3 and 4), while *B. iheringii* and *C. pterostictum* were linked to the stream in the lower areas (streams 5 and 6). Less abundant species also contributed to this segregation, the most important being, according to the PCoA eigenvectors (Table 2): *Corydoras longipinnis* Knaack 2007, Callichthyidae family, recorded only in the upper portion of the sub-basin, with 92 individuals collected in the stream 2, and *Gymnotus cuia* Craig, Malabarba, Crampton & Albert 2018, with approximately 85% of the individuals collected in this same location; *Bryconamericus uporas* Casciotta, Azpelicueta & Almirón, 2002 and *Microglanis malabarbai* Bertaco & Cardoso, 2005, with 76% and 58%, respectively, of individuals collected in the mid portion of the sub-basin (streams 3 and 4); and *Scleronema* sp., with 89% of the specimens collected in the lower portion (stream 5) (Figure 3).

A pattern in the representativity, abundance, and number of species and families in Characiformes, Siluriformes and Cichliformes is observed in relation to the second axis of PCoA (Figure 4). Siluriformes richness was higher in the upper portion of the Ijuí River sub-basin (streams 1 and 2), with 18 out of 22 collected species occurring in the area, from which six have been exclusive to it (considering only this study data). Stream 1 (upper portion) presented the highest richness of Siluriformes (16 species) and the highest number of this order taxa with exclusive occurrence, namely: *Cetopsorhamdia iheringi* Schubart & Gomes 1959; *Pareiorhaphis* sp.; *Rineloricaria reisi* Ghazzi 2008; *Ituglanis* sp.; and Heptapteridae (identified only at family level). Siluriformes richness declined along the sub-basin, with 14 species recorded in the mid portion (streams 3 and 4) and 13 in the lower portion (streams 5 and 6) of Ijuí River (Figure 4).

The highest representativity of the Characiformes order occurred within the Characidae family, in the lower portion of the sub-basin (streams 5 and 6). Of the 18 species captured, 15 occurred in this area and eight were recorded exclusively for these two sampled streams (data from this study only). Likewise, the Cichliformes of the Cichlidae family are associated with the lower portion of the sub-basin, where their greatest abundance appeared (streams 5 and 6) (Figure 4).

Discussion

The species richness found in the streams of the Ijuí River sub-basin follows the pattern of freshwater fishes in the Neotropical region, with Characiformes and Siluriformes as the richest orders in number of species (Lowe-McConnell 1999, Malabarba & Malabarba 2014). Our hypothesis that the fish community composition is not homogeneous along the streams sampled was confirmed and we observed that species complexity increases from the upstream closest area to the downstream according to the river continuum concept. The latitudinal variation of the richness within the Ijuí River sub-basin, smaller in the upstream streams (closer to the headwaters of the sub-basin), increasing towards the mouth in Uruguay River (streams 5 and 6), is an expected pattern, according to the "river continuum concept" proposed by Vannote et al. (1980). Although, upstream and midstream areas present virtually the same (or higher) number of species, the richness has increased considerably towards the streams located in the lower portion of the basin (downstream) and we believe this is due to the influence of the Uruguay River, located very close to streams 5 and 6. According to the river continuum concept, the complexity of community structure and function increases along a river system as the increases of the complexity of the physical gradients dynamics formed by a drainage network (Vannote et al. 1980). Furthermore, the three streams with the smallest longitude (streams 1, 3 and 6) in relation to the correspondent streams (streams 2, 4 and 5), which occupy the same portion in the sub-basin (upper, mid, and lower) presented a higher number of species, respectively.

The knowledge about the influence of the global longitudinal gradient on the distribution of species richness is well established and, for freshwater fishes, remains the same even in anthropomorphized habitats, such as in large spatial reservoirs, although this distribution is better explained by the overlapping of factors, rather than a single hypothesis (Brown 2014, Bailly et al. 2016). For freshwater fishes, the species richness tends to decrease within the latitude and increase along the longitudinal fluvial gradients (Osborne & Lewis 1992, Ibañez et al. 2009, Bailly et al. 2016) (same pattern found in our samplings). The further away from the headwaters, within a hydrographic basin, the greater the species richness, as new species are added downstream more easily

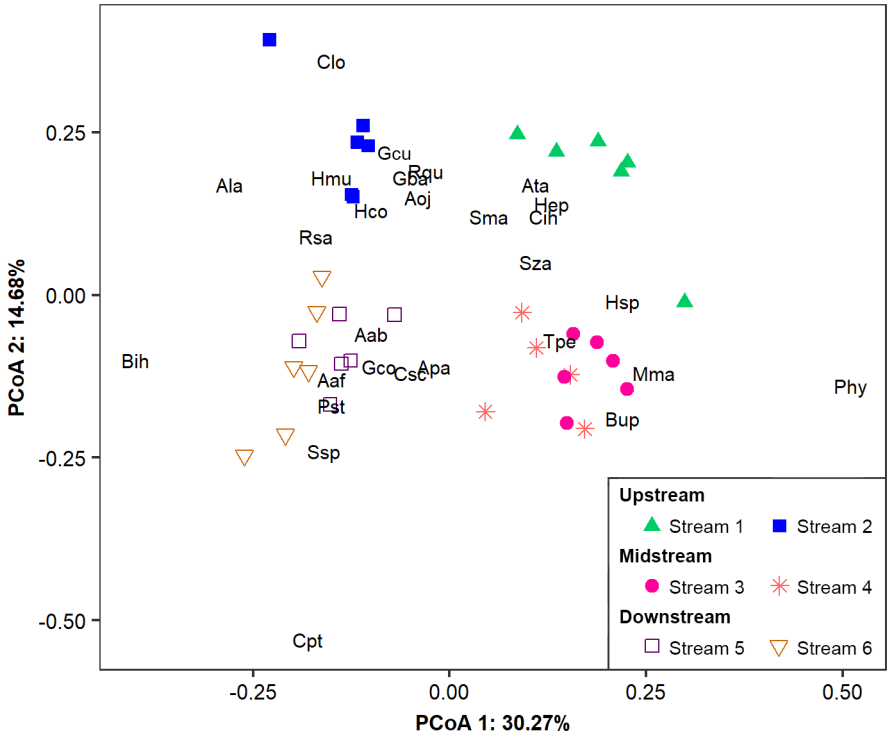


Figure 3. Principal Coordinates Analysis (PCoA) of the composition of species sampled in the upper (streams 1 and 2), mid (streams 3 and 4), and lower portion (streams 5 and 6) of the Ijuí River sub-basin, Brazil. Abbreviations list of species is in Table 2.

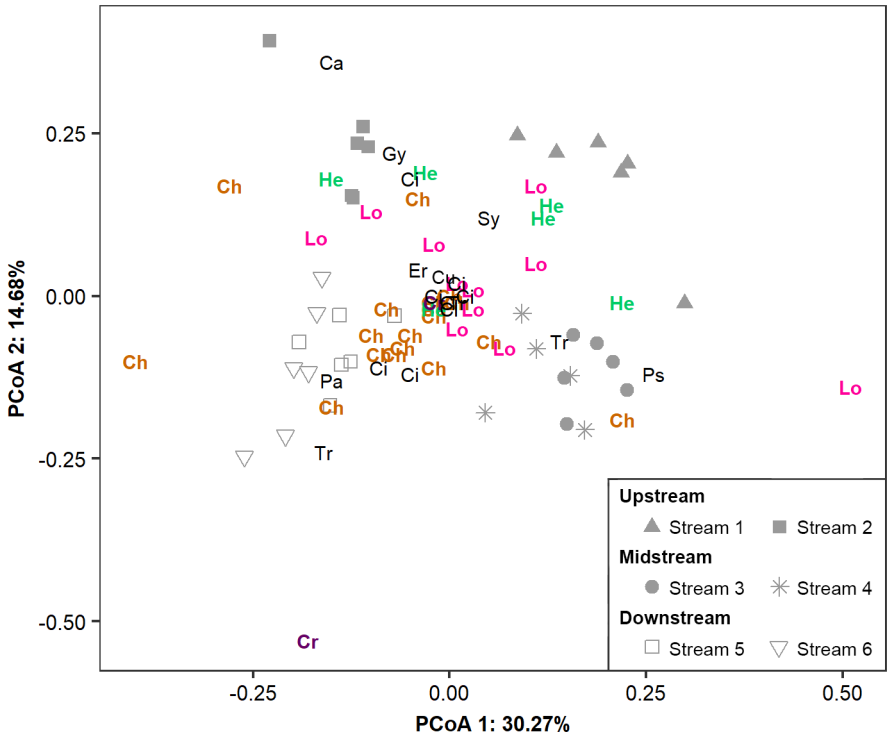


Figure 4. Principal Coordinates Analysis (PCoA) of the composition of species, indicating the representativeness of families, sampled in the upper (streams 1 and 2), mid (streams 3 and 4), and lower portion (streams 5 and 6) of the Ijuí River sub-basin, Brazil. The four most abundant are highlighted by bold typing: Ch: Characidae; Cr: Crenuchidae; Cu: Curimatidae; Er: Erythrinidae; Pa: Parodontidae; Ca: Callichthyidae; He: Heptapteridae; Lo: Loricariidae; Ps: Pseudopimelodidae; Tr: Trichomycteridae; Gy: Gymnotidae; Ci: Cichlidae; Sy: Synbranchidae.

Table 2. Eigenvalues and eigenvectors from the Principal Coordinates Analysis (PCoA) of the composition of species sampled in six streams of the Ijuí River sub-basin, Brazil.

		PCoA 1	PCoA 2
Eigenvalue		1.31	0.63
Proportion Explained		30.27	14.68
Cumulative Proportion		30.27	44.95
Taxa	**Abbreviation**	**PCoA 1**	**PCoA 2**
CHARACIFORMES			
Characidae			
Astyanax abramis (Jenyns 1842)	Aab	-0.10	-0.06
Astyanax aramburui Protogino, Miquelarena & López 2006	Aar	-0.07	-0.09
Astyanax eigenmanniorum (Cope 1894)	Aei	-0.02	-0.02
Astyanax lacustris (Lütken 1875)	Ala	-0.28	0.17
Astyanax laticeps (Cope 1894)	Alat	0.05	-0.07
Astyanax ojiara Azpelicueta & Garcia 2000	Aoj	-0.04	0.15
Astyanax paris Azpelicueta, Almirón & Casciotta 2002	Apa	-0.02	-0.11
Astyanax saguazu Casciotta, Almirón & Azpelicueta 2003	Asa	-0.09	-0.09
Astyanax sp.	Asp	-0.05	-0.06
Astyanax xiru Lucena, Castro & Bertaco 2013	Axi	-0.08	-0.02
Bryconamericus iheringii (Boulenger 1887)	Bih	-0.40	-0.10
Bryconamericus uporas Casciotta, Azpelicueta & Almirón 2002	Bup	0.22	-0.19
Diapoma uruguayense (Messner 1962)	Dur	-0.02	-0.03
Galeocharax humeralis (Valenciennes 1834)	Gum	0.00	0.00
Hyphessobrycon luetkenii (Boulenger 1887)	Hyl	-0.06	-0.08
Hyphessobrycon togoi Miquelarena & López 2006	Hto	0.01	-0.01
Oligosarcus sp.	Osp	-0.02	-0.01
Piabarchus stramineus (Eigenmann 1908)	Pst	-0.15	-0.17
Crenuchidae			
Characidium pterostictum Gomes 1947	Cpt	-0.18	-0.53
Characidium tenue (Cope 1894)	Cte	-0.02	-0.01
Curimatidae			
Steindachnerina biornata (Braga & Azpelicueta 1987)	Sbi	-0.01	0.03
Erythrinidae			
Hoplias malabaricus (Bloch 1794)	Hom	-0.04	0.04
Parodontidae			
Apareiodon affinis (Steindachner 1879)	Aaf	-0.15	-0.13
SILURIFORMES			
Callichthyidae			
Corydoras longipinnis Knaack 2007	Clo	-0.15	0.36
Heptapteridae			
Cetopsorhamdia iheringi Schubart & Gomes 1959	Cih	0.12	0.12
Heptapterus mandimbusu Aguilera, Benitez, Terán, Alonso & Mirande 2017	Hsp	0.22	-0.01
Heptapterus mustelinus (Valenciennes 1835)	Hmu	-0.15	0.18
Heptapterus sp1	Hep	0.13	0.14

Continuation Table 2.

		PCoA 1	PCoA 2
Eigenvalue		1.31	0.63
Proportion Explained		30.27	14.68
Cumulative Proportion		30.27	44.95
Taxa	**Abbreviation**	**PCoA 1**	**PCoA 2**
Rhamdella longiuscula Lucena & da Silva 1991	Rlo	-0.02	-0.02
Rhamdia aff. *quelen* (Quoy & Gaimard 1824)	Rqu	-0.03	0.19
Loricariidae			
Ancistrus taunayi Miranda Ribeiro 1918	Ata	0.11	0.17
Eurycheilichthys pantherinus (Reis & Schaefer 1992)	Epa	0.03	-0.02
Hemiancistrus fuliginosus Cardoso & Malabarba 1999	Hfu	-0.02	0.08
Hisonotus aky (Azpelicueta, Casciotta, Almirón & Koerber 2004)	Hak	0.01	-0.05
Hypostomus commersoni (Valenciennes 1836)	Hco	-0.10	0.13
Pareiorhaphis hystrix (Pereira & Reis 2002)	Phy	0.51	-0.14
Pareiorhaphis sp.	Psp	0.01	0.02
Rineloricaria reisi Ghazzi 2008	Rre	0.03	0.01
Rineloricaria sanga Ghazzi 2008	Rsa	-0.17	0.09
Rineloricaria stellata Ghazzi 2008	Rst	0.07	-0.08
Rineloricaria zaina Ghazzi 2008	Sza	0.11	0.05
Pseudopimelodidae			
Microglanis malabarbai Bertaco & Cardoso 2005	Mma	0.26	-0.12
Trichomycteridae			
Ituglanis sp.	Isp	0.01	-0.01
Scleronema sp.	Ssp	-0.16	-0.24
Trichomycterus perkos Datovo, Carvalho & Ferrer 2012	Tpe	0.14	-0.07
GYMNOTIFORMES			
Gymnotidae			
Gymnotus cuia Craig, Malabarba, Crampton & Albert 2018	Gcu	-0.07	0.22
CICHLIFORMES			
Cichlidae			
Crenicichla hadrostigma Lucena 2007	Cha	0.02	0.00
Crenicichla lepidota Heckel 1840	Cle	0.00	-0.01
Crenicichla missioneira Lucena & Kullander 1992	Cmi	0.00	-0.02
Crenicichla scottii (Eigenmann 1907)	Csc	-0.05	-0.12
Crenicichla sp.	Csp	-0.02	0.00
Crenicichla tendybaguassu Lucena & Kullander 1992	Cten	0.01	0.02
Geophagus brasiliensis (Quoy & Gaimard 1824)	Gba	-0.05	0.18
Gymnogeophagus constellatus Malabarba, Malabarba & Reis 2015	Gco	-0.09	-0.11
SYNBRANCHIFORMES			
Synbranchidae			
Synbranchus marmoratus Bloch 1795	Sma	0.05	0.12

than species of headwaters are lost (Osborne & Lewis, 1992). Therefore, a stream fish community structure changes over time and space, and more changes may occur between different parts of the same stream than between different streams in the same drainage basin, in some cases, such as changes on species richness or diversity of functional groups that change along a headwaters (upstream) toward the mouth (downstream) gradient (Vannote et al. 1980, Araújo-Lima et al. 1995).

Stream 1, upper portion of the sub-basin, presented more species than the streams in the mid portion (streams 3 and 4), becoming an exception to the pattern of longitudinal distribution found for the species richness. We believe this result has been influenced by the size of the stream (wider and with a greater water flow than the others) and by the proximity of the sampling site to the stream discharge into a larger river (about 200 meters), the Ijuí River, the main river of the sub-basin. In addition, information available in the literature indicates size, volume, flow speed and diversity of habitats, among others, as factors known to influence the pattern of ichthyofauna richness distribution (Winemiller 1983, Tejerina-Garro et al. 2005, Ibañez et al. 2009, Bailly et al. 2016). The characteristics of this stream could also be responsible for the association of Siluriformes to the upper portion of the Ijuí River sub-basin, in relation to the representativeness of the families Heptapteridae and Loricariidae.

Regarding the conservation status of the species, *Crenicichla hadrostigma* Lucena 2007, *Microglanis malabarbai* Bertaco & Cardoso 2005 and *Trichomycterus perkos* Datovo, Carvalho & Ferrer 2012 are included in the list of threatened species, officially recognized by the 51.797 act of September 8, 2014, state of Rio Grande do Sul, and classified as "near threatened" (category VI), according to the criteria defined by the International Union for Conservation of Nature (IUCN) (FZB 2014). The other species captured appear as "least concern" (FZB 2014), or there is no information about the status of conservation due to the species description be posterior to the act publishing. Another reason for the lack of information is the existence of possible new species, like *Heptapterus* sp1, *Pareiorhaphis* sp*., Ituglanis* sp. and *Scleronema* sp., identified only to the genre level (Buckup 1988, Malabarba et al. 2013, J. Ferrer 2017, oral communication, Universidade Federal do Rio Grande do Sul). Therefore, we understand that studies like this contribute to the knowledge of the biological diversity of the south of Brazil, bringing complementary information about richness and abundance of endemic, threatened or of large distribution, grounding future research that could contribute to the conservation of fish biodiversity in Neotropical streams.

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Author Contributions

Laísa W. Cavalheiro: Substantial contribution in the concept and design of the study;

Clarice B. Fialho: Substantial contribution in the concept and design of the study.

Conflicts of interest

The author declare that they have no conflict of interest related to the publication of this manuscript.

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Article

Aquatic Oligochaete Communities in Amazonian Streams, Saracá-Taquera National Forest, Pará, Brazil

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Abstract: The aim of this study was to analyze aquatic oligochaete distribution in relation to water column physicochemical variables, structural environmental variation, and predominant substrates in the preserved Amazonian streams of the Saracá-Taquera National Forest (FLONA Saracá-Taquera), northwest Pará, Brazil. Oligochaetes are widely used as bioindicators for monitoring aquatic environments as they are very sensitive to pollution and environmental changes. Physicochemical and structural variables were measured from 100 stream segments in order to understand the distribution of oligochaetes in Amazonian streams. Biotic samples were collected using Surber samplers in three of the most predominant substrate types in each segment. PERMANOVA testing showed that there was a significant difference in the oligochaete community among some substrates, potentially caused by a difference in the abundance of the most common taxa. Canonical Correspondence Analysis showed that physical variables drive the distribution of oligochaetes in preserved Amazonian streams, as they determine the formation of different substrates along the stream, from the source to the mouth; favoring the presence of oligochaetes with more specific ecological needs in low-order streams, and the presence of oligochaetes capable of colonizing various types of substrates and deeper zones in high-order streams. These results suggest that water depth and channel width are the main drivers of aquatic oligochaete distribution along Amazonian streams, determining the formation of unstable and low-quality substrates and, consequently, the low colonization by oligochaetes in high-order streams; and more diverse and stable substrate formation in low-order streams, favoring the colonization by diverse taxa of aquatic oligochaetes in low-order Amazonian streams.

Keywords: *Aquatic macroinvertebrates, biomonitoring, tropical streams, substrates, stream hydrology, mining activities.*

Comunidade de oligoquetos aquáticos em riachos amazônicos, Floresta Nacional Saracá-Taquera, Pará, Brasil

Resumo: O objetivo deste trabalho foi analisar a distribuição da comunidade de oligoquetos em relação às variáveis físico-químicas da coluna da água, variação estrutural do ambiente, e substratos predominantes em riachos amazônicos conservados na FLONA Saracá-Taquera, noroeste do Pará, Brasil. Oligochaetes são amplamente utilizados como bioindicadores para monitoramento de ambientes aquáticos, pois são muito sensíveis à poluição e às mudanças ambientais. Variáveis físico-químicas e estruturais de 100 trechos de riachos foram mensuradas para entender a distribuição de oligoquetos em riachos amazônicos. Amostras bióticas foram coletadas com amostrador Surber em três dos tipos de substratos mais predominantes em cada trecho. A PERMANOVA mostrou que há uma diferença significativa da comunidade de oligoquetos entre alguns substratos, possivelmente baseada nas diferenças no número do táxon mais comum. A Análise de Correspondência Canônica mostrou que as variáveis físicas controlam a distribuição da comunidade de oligoquetos em riachos amazônicos preservados, porque estas variáveis determinam a formação dos diferentes substratos ao longo do riacho, desde a nascente até a foz, favorecendo a presença de

oligoquetos com necessidades ecológicas mais específicas em riachos de baixa ordem, e oligoquetos capazes de colonizar diferentes tipos de substrato e zonas mais profundas em riachos de ordem maior. Os resultados deste trabalho sugerem que a profundidade da água e a largura do canal são as variáveis que controlam a distribuição da comunidade de oligoquetos em riachos amazônicos, determinando a formação de substratos instáveis e de baixa qualidade, e consequentemente baixa colonização de oligoquetos, em riachos de ordem maior; e formação de substratos mais diversificados, mais estáveis e de qualidade em riachos de baixa ordem, favorecendo a colonização de diversos taxa de oligoquetos aquáticos em riachos amazônicos de baixa ordem.

Palavras-chave: *Macroinvertebrados aquáticos, biomonitoramento, riachos tropicais, substratos, hidrologia de riachos, atividades de mineração.*

Introduction

Oligochaetes play important roles in aquatic systems, such as in food webs, as a source of food for other invertebrates, fish, and birds (Ezcurra de Drago et al, 2007); in the organic matter decomposition process; and also fulfilling an important role in the cycling of nutrients, participating in sediment structuring and nutrient exchange in the water/sediment phase (Golterman et al., 1983).

They are good indicators of environmental conditions (Verdonschot, 2001) because they have limited mobility, long life cycles, an intimate relationship with substrates and they are extremely influenced by the habitat characteristics in which they live (Behrend et al., 2009). Different species of oligochaetes are sensitive, moderately tolerant or highly tolerant to physicochemical changes in aquatic ecosystems (Yap et al., 2006, Rodrigues and Reynoldson, 2011, Burdon, et al., 2019). Although many studies evaluate the macroinvertebrate community in tropical streams, oligochaetes are often ignored or identified only as a subclass or family, downplaying the group's role as a bioindicator (Lopes et al., 2011; Couceiro et al., 2009; Alves et al., 2008; Fidelis, 2006; Walker, 2004).

Studies have demonstrated that Oligochaeta species have a wide range of responses to contamination by nutrients, metals, and organic chemicals, showing distribution patterns which are associated with pollution and contaminants (Rodriguez and Reynoldson, 2011). However, there is limited literature about how this group responds to physical factors, such as fine sediment inputs, deforestation and mining activities in lotic environments. Therefore, it is important to know how oligochaetes are distributed and which of this community's structuring variables are present in tropical systems like those found in the Amazon, whereby mineral exploitation is an expanding activity that can impact these environments (Castello and Macedo, 2016).

According to some studies on streams, the main factors that influence aquatic oligochaetes composition and distribution are water flow, waterbody width and depth, and substrate characteristics (Nijboer, 2004, Rosa et al. 2015). However, other factors seem to play a role in shaping oligochaete communities depending on context. Syrovátka (2009) suggested that flow velocity and habitat preference explain the spatial pattern of oligochaete distribution in a small highland stream. Blettler (2008) found a marked relationship between the different substrate types and the oligochaetes associated with them and, according to this author, some physical factors such as water velocity and depth may influence the establishment and availability of the substrates, as well as the composition of their associated fauna. However, other authors such as Prenda and Gallardo (1992) and Schenkova and Helesic (2006) affirm that oligochaetes do not have habitat preferences and show a broad ecological tolerance. More information from tropical streams is needed in order to draw a big picture about the importance of environmental variables in oligochaete distribution.

Central Amazonian streams are low-order heterotrophic environments (Junk, 1983; Lima and Gascon, 1999), and the forest next to the streams supplies them with resources and material to form different kinds of aquatic fauna substrates. The dependence on allochthonous organic matter produces a link between the characteristics of the forest that surrounds the streams and the composition of local aquatic fauna, including some fish and most benthic invertebrates, which is associated with the meso- and micro-habitats structured within them (Nessimian et al., 1998). Thereby faced with different impacts near these kinds of environment the stream bottom can suffer physicochemical and structural transformations, leading to the modification of substrates and their associated fauna (Dedideu et al., 2015). Low-order Amazonian streams are homogeneous in relation to water column physicochemical variables. They are clear, acidic, have low conductivity, constant temperatures and low alkalinity waters, and they are not influenced by the flood pulse of big rivers. Therefore, their periodic flow change is influenced by local daily rainfall, with noticeable changes during different seasons (Junk, 1983). All this information suggests that water column physicochemical factors do not influence t oligochaete community distribution in preserved Amazonian streams; rather, it may be structural and physical factors which influence this distribution.

Considering the homogeneity of the water column physicochemical variables of the Amazonian streams, we hypothesize that oligochaetes distribution in Amazonian streams is determined by physical and structural variables like the flow, depth and substrate material at the bottom of the streams. Therefore, this study aims to analyze oligochaetes distribution in relation to the physicochemical variables of the water column; physical variation; and predominant substrates in preserved Amazonian streams in Brazil. This is a piece of valuable knowledge for the development of biomonitoring tools to assess Amazonian streams; as well as contributing to the body of knowledge about these invertebrates in the region, which is still fragmented and incomplete in all Brazilian freshwater systems (Takeda et al., 2017).

Material and Methods

1. Study area

The study was carried out in the Saracá-Taquera FLONA, in the northwest of the state of Pará (Brazil) (Figure 1). It is located on the right bank of the Trombetas River, between the municipalities of Terra Santa, Oriximiná, and Faro, near the political division of the state of Amazonas.

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The FLONA is responsible for the protection of 441,282.63 hectares of the Amazon Biome (Ministério do Meio Ambiente, 2001). The region is covered by tropical rainforest, with annual rainfall rates ranging between 1,900 and 2,500 mm and a dry season from June to October with less than 100 mm of monthly rainfall (Sioli, 1985). Authorized bauxite extraction occurs within the Saracá-Taquera FLONA, and the streams in this region are impacted in different ways by the products of this activity (such as deforestation, siltation, damming, suppression of riparian forest, etc.), leading to the eventual or permanent modification of the characteristics of these environments.

The entire region is drained by small streams, composed of acidic (pH 4.5-5.4) and low turbidity (clear) waters with low conductivity (7.9-16.7 $\mu S.cm^{-1}$) and average temperatures of 24° C (Mortatti, 2004). These streams do not suffer from significant seasonal variations of physicochemical variables, which is indicative of their great environmental stability instead, local rainfall is responsible for variation of these parameters (Nessimian *et.al.* 2008).

In the Amazon region low-order streams (1st to 3rd order) have, under natural conditions, a full canopy cover that shades them entirely, reducing the primary productivity within them. Larger streams (4th and 5th orders) have lower coverage of surrounding forest, increasing the incidence of light in the stream and favoring the growth of aquatic macrophytes within the channel.

Furthermore, the streams exhibit different channel geomorphologies. Larger streams have well-structured margins, supported by tree roots and riparian vegetation, and the smaller ones generally do not present defined margins. Generally, the bed of the stream is sandy with plant litter accumulation consisting of leaves and wooden materials from surrounding forest in some spots. Branches and trunks act as retention mechanisms in the streams, generating small rapids and pools, favoring the formation of deposition and retention areas which increase environmental heterogeneity (Fidelis, 2006).

2. *Abiotic characterization of the streams*

Overall, 100 stream segment samples from 1st to 5th order, were collected in the months of March (rainy season) and September (dry season), from 2009 to 2011. In each site, the water temperature (electronic thermometer, 0.1 of accuracy), dissolved oxygen in water (YSI Portable Mod. 550A), water depth, channel width, and the substrate types were measured. To evaluate substrate characteristics, a 50 by 50 cm quadrat was used, subdivided into 25 smaller squares. This method consisted of a visual estimate of the percentage of squares filled by the different types of substrate (USEPA, 2004). Water depth was measured with a ruler on two transverse transects in the sampling point, with ten depth measurements being taken from each transect, and the average depth was calculated. Channel width was measured on the same transverse transects as depth, and the average width was calculated. In addition, 1L of water was collected in polyethylene bottles at each point and taken to the laboratory for pH analysis (QUIMIS-Mod. Q400MT benchtop), electrical conductivity measuring (QUIMIS benchtop electronic conductivity meter), and turbidity analysis (Del Lab DL350 portable microprocessor turbidimeter).

3. *Biotic sampling and identification*

In each sampled segment three of the most predominant substrate types were collected, and these were grouped in six categories in accordance with their composition: sand and leaves (SAN+LEA), sand only (SAN), sand with fine organic matter (SAN+MO), macrophytes (MC), gravel (GRA) and roots (ROO). The samples were collected using a "Surber" sampler with an area of 0.09 m² and a 250 µm mesh

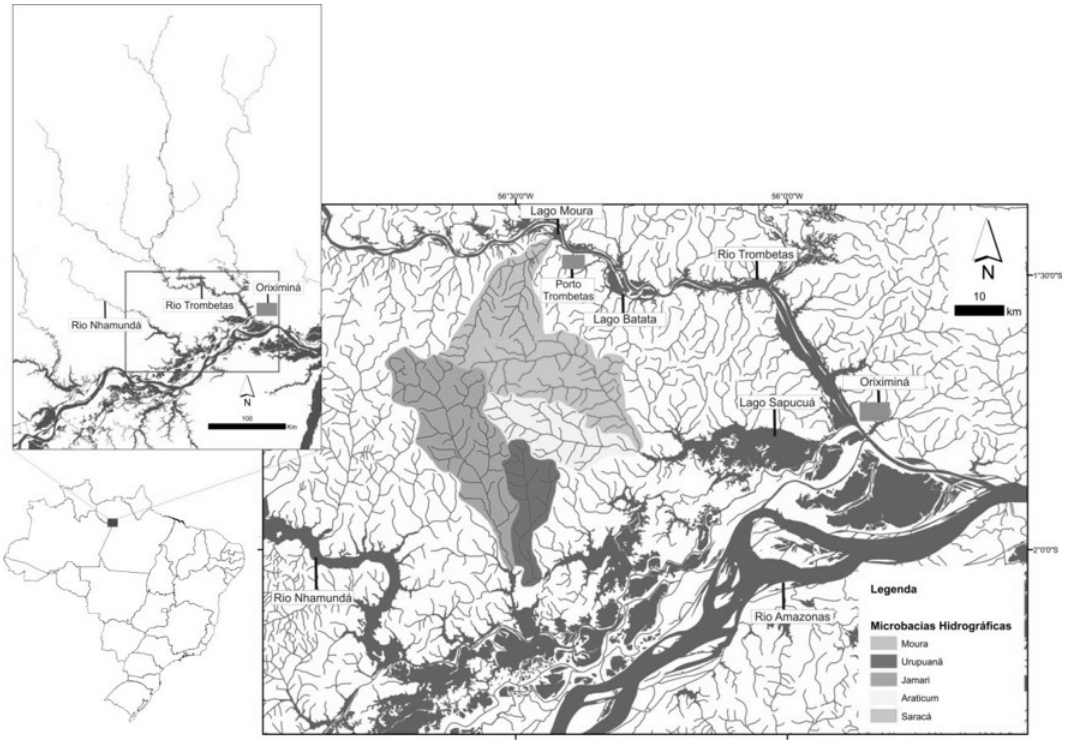


Figure 1. Study Area. Saracá-Taquera National Forest, Municipality of Oriximiná, Pará, Brazil. The micro-basins painted in shades of lighter gray are part of the Trombetas River basin, and the darker grays are part of the Nhamundã River basin.

opening. The samples were stored in plastic bags and transported to the laboratory, where they were washed in a sieve with a 0.5 mm mesh. Subsequently, the organisms were separated and preserved in 70% alcohol for the identification of the lowest possible taxonomic levels (dependent on the taxonomic characteristics required to obtain family, genus and species levels) under an optical microscope with the help of different identification keys (Brinkhurst and Marchese, 1989; Pinder, 2010; Brinkhurst & Jamieson, 1971).

4. Data analysis

Canonical Correspondence Analysis (CCA) was used to explore which variables better explain oligochaete distribution along the streams. A PERMANOVA test was used to evaluate whether there was a significant difference in oligochaete assemblage per substrate, and a SIMPER test was performed in order to identify which taxa most contributed to the differences among the substrates. All analyses were performed using PAST statistical software v3.14.

Results

Sampled streams were similar in physicochemical characteristics: transparent and oxygenated waters [2,02 (±2,70) NTU; 5,92 (±1,12) mg L^{-1}], mean water temperatures of 25 ° C (±0,65), an acidic pH [4,9 (±0,18)] and low conductivity [11,06 (± 4,46) µS/cm] (Table 1). Moreover, these streams do not have significant water nutrient charges due to the soil characteristics found in the Trombetas river watershed (Sioli, 1989).

A total of 780 aquatic oligochaetes were identified in 10 taxa, represented by six families: Naididae, Enchytraeidae, Haplotaxidae, Lumbriculidae, Alluroididae, and Glossoscolecidae. The oligochaetes composition in each substrate can be found in Table 2.

Most taxa were associated with higher organic matter loading substrates. All identified taxa occurred in the SAN+LEA substrate, and *Bratislavia unidentata* (Harman, 1978) and *Aulodrilus pigueti* (Kowalewski, 1914) were found exclusively in this substrate. The taxa Glossoscolecidae n.i, *Haplotaxis* sp. (Hoffmeister, 1843), Tubificinae n.i1 and Lumbriculidae n.i., were recorded in greater abundance in the SAN+LEA substrate. *Nais communis* (Piguet, 1906) was also present in substrates with higher organic matter loading, such as SAN+LEA and SAN+OM, as well as substrates with lower organic matter loading, such as GRA. *Brinkhurstia americana* (Brinkhurst, 1964) occurred in all substrates except for GRA, and showed the highest abundance in SAN + LEA and SAN + OM substrates. The Enchytraeidae family occurred in all sampled substrates, but showed higher abundance in the ROO substrate and the second highest abundance in the MC substrate (Figure 2).

The CCA revealed that the first axis explained 72% of data variability (statistical significance by randomization test p = 0,001) (Figure 3). The first axis was described by the substrate variable to the right of the graph, and by the water depth and channel width to the left. Streams from 1st to 3rd order were distributed to the right of the graph and 4th and 5th orders were distributed to the left of the graph. Oligochaetes taxa were associated with the substrate, water depth, and channel width, which are related to the order of the stream. Tubificinae n.i2, Lumbriculidae, Glososcolecidae, *Nais communis* (Piguet, 1906) were linked to substrate variables in low-order streams (1st to 3rd order); and *Brinkurstia americana* (Brinkhurst, 1964), *Aulodrilus pigueti* (Kowalewski, 1914), Tubificinae n.i1 and Enchytraeidae n.i were associated with wider and deeper streams.

1. Statistical analysis

PERMANOVA (Table 3) showed that there is a significant difference between Oligochaeta communities registered in ROO and in the substrates SAN, SAN+LEA, and GRA, with no significant difference between the communities registered in the ROO, SAN+OM, and MAC substrates. The SIMPER test showed that the taxa which contributed the most to this difference were Enchytraeidae (26.81%), *Brinkhurstia americana* (Brinkhurst, 1964) (23.3%), and Tubificinae n.i1 (19.63%).

Discussion

As expected, this study showed that substrate types, water depth, and channel width are the main drivers of aquatic oligochaetes distribution in Amazonian streams. These variables determine the formation of unstable substrates in high order streams; substrates that cannot be used as refugia and lacking in food sources, which may limit the colonization and establishment of some Oligochaeta species. On the other hand, these physical variables influence the formation of stable substrates in low-order streams, which are good as refugia and can possibly offer enough food sources to create specific microhabitats that enable colonization by more specific oligochaetes taxa.

Our results showed that Oligochaeta species abundance can be partially explained by the type of substrate associated with the order of the streams. The ROO substrate showed significant differences in oligochaete community patterns compared to other substrates, and the taxa that most contributed to this difference were Enchytraeidae, *B. americana* (Brinkhurst, 1964) and Tubificinae ni1. Since these taxa occur in all substrates, the significant difference among the substrates could be related to the abundance levels of such taxa in each substrate. All taxa identified at the present study occurs in the substrates indicated by the bibliography and some aquatic oligochaetes taxa occur in low abundance in specific substrates [*N. communis* (Piguet, 1906), *B.*

Table 1. Abiotic parameters measured with the mean, standard deviation, minimum value and maximum value; pH, Water conductivity (CON); Turbidity (TUR); Water temperature (TEM), Dissolved Oxygen (O2); Channel Depth (PR), Channel Width (LC).

	Channel width (m)	Channel depth (m)	Water Temperature (°C)	pH	Water conductivity (µS/cm)	Turbidity (NTU)	Dissolved oxygen (mg/L)
Mean	3,57	0,54	25,78	4,90	11,06	2,02	5,92
Standard deviation	4,42	0,55	0,65	0,18	4,46	2,70	1,12
Minimum value	0,2	0,05	23	4,58	6,54	0,1	0,23
Maximum value	25,5	3,1	29,2	5,72	38,1	13,2	17,5

Table 2. List of aquatic oligochaetes taxa identified in each sampled substrate. Substrates: Sand (SAN), Sand + Leaves (SAN+LEA), Gravel (GRA), Macrophytes (MAC), Sand + Organic Matter (SAN+OM), and Roots (ROO). The symbol (+) represents the presence and (-) represents the absence of the taxa in each sampled substrate.

Taxa	Substrates					
	SAN	SAN+LEA	GRA	MAC	SAN+OM	ROO
Tubificinae n.i 1	+	+	+	+	+	+
Tubificinae n.i 2	-	+	-	-	+	-
Aulodrilus pigueti	-	+	-	-	-	-
Haplotaxis sp.	+	+	-	-	+	-
Enchytraeidae n.i	+	+	+	+	+	+
Brinkhurstia americana	+	+	-	+	+	+
Lumbriculidae n.i	+	+	+	-	+	+
Glossoscolecidae n.i	+	+	+	-	+	-
Nais communis	-	+	+	-	+	-
Bratislavia unidentata	-	+	-	-	-	-

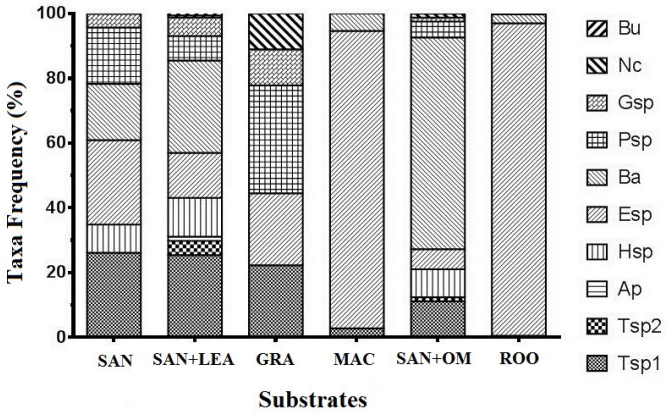


Figure 2. Relationship between the sampled substrates and the occurrence frequency of aquatic oligochaetes. Substrates: Sand (SAN), Sand + Leaves (SAN + LEA), Gravel (GRA), Macrophytes (MAC), Sand + Organic Matter (SAN + OM), and Roots (ROO). Bu - *Bratislavia unidentata*; Nc - *Nais communis*; Gsp - Glossoscolecidae ni1; Psp - Lumbriculidae ni1; Ba - *Brinkhurstia americana*; Esp - Enchytraeidae ni1; Hsp - *Haplotaxis* ni1; Ap - *Aulodrilus pigueti*; Tsp1 - Tubificinae ni1; Tsp2 - Tubificinae ni2.

unidentata (Harman,1978), and *A. pigueti* (Kowalewski, 1914)], which could be understood as a habitat preference when the substrates are available; whereas other taxa seem to have greater plasticity to colonize all types of substrate that could be formed in low- to high-order streams.

In the present study, the SAN+LEA substrate showed the highest richness and diversity of aquatic oligochaetes. This substrate provides food and shelter for different macroinvertebrates and fish species (Passos et al., 2003). *A. pigueti* (Kowalewski, 1914) and the two morphospecies of the Tubificinae subfamily were recorded as having higher abundance in this substrate, which corroborates with what was observed by Alves and Strixino (2000) and Behrend (2009), that where these groups occur is also associated with an abundance in organic matter. Those taxa are abundant in this kind of substrate because, generally, they ingest sediment particles, digesting bacteria and fungi present in them, which accelerates the decomposition of organic matter (Wavre and Brinkhurst, 1971).

The Tubificinae subfamily is characterized by a high abundance in polluted areas and high tolerance to organic pollution caused by the presence of domestic wastewater in aquatic environments (Martins et al., 2008). The present study registered a considerable abundance of tubificids; therefore, the occurrence of this taxon must be carefully analyzed, since the high abundance of this group in preserved Amazonian streams is a natural condition and does not necessarily indicate environmental pollution. As specified by Rodriguez & Reynoldson (2011), not all species respond in the same way to all types of pollutants and impacts, and it is necessary to identify the occurring species in order to stipulate their contaminating or impacting agents, and to analyze their effects on oligochaetes communities through specific studies. The subfamily level identification may lead to misinterpretation of the environmental integrity of the studied streams. A useful tool to assess environmental health conditions would be to identify the individuals of this group at the lowest taxonomic levels in order to understand the different tolerance to pollution of each species. However, in this study, many individuals of Naididae family could not be identified to species level because they were not sexually mature, which could be explained by the fact that the asexual reproduction of Naididae is generally employed during favorable environmental conditions, and sexual reproduction predominates in stressful conditions (Parish, 1981). This could indicate that the abundance of non-reproductive individuals of Tubificinae subfamily could be an important metric to assess the environmental integrity of Amazonian streams.

The genus *Haplotaxis* (Hoffmeister, 1843), deemed predatory because of its well-developed muscular pharynx (Brinkhurst & McKey-Fender 1991), had an abundant presence in the SAN+LEA substrate. The wide variety of benthic invertebrates and availability of food sources that the substrate SAN+LEA provides (Rezende, 2007) could justify the higher abundance of *Haplotaxis* (Hoffmeister, 1843) in this substrate.

In this study, *N. communis* (Piguet, 1906) was registered in the SAN+OM, SAN+LEA, and GRA substrates. According to Dumnicka (1994), these substrates offer protection against predators. He also observed a relationship between *N. communis* (Piguet, 1906) and

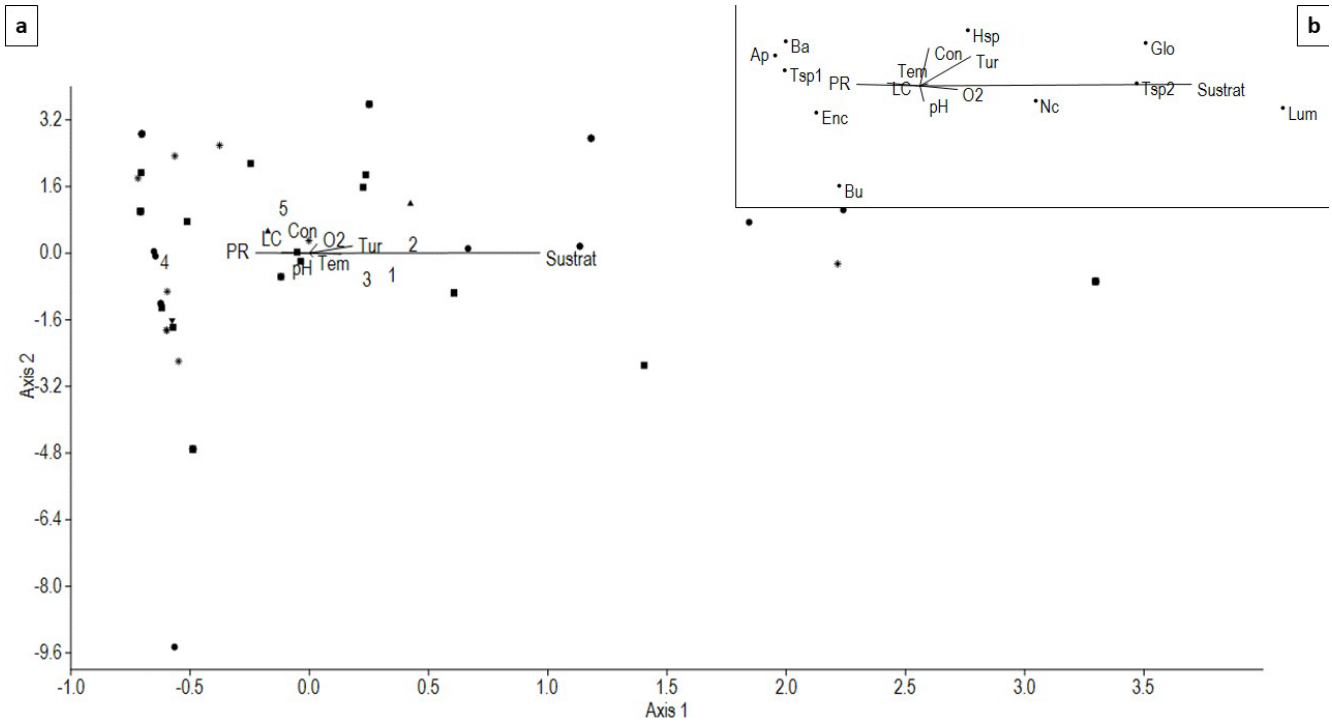


Figure 3. Canonical Correspondence Analysis. To facilitate visualization, the graph was split into two parts. Part "a" shows the streams around abiotic and structural variables. The numbers 1, 2, 3, 4 5, represent the stream order and how these groups are scattered on the graph. The symbols represent: (●) 1st stream order, (*) 2nd stream order, (■) 3rd stream order, (▲) 4th stream order, and (▼) 5th stream order. Part "b" plots the relationship between abiotic and structural variables in accordance with the different taxa of Oligochaeta.

Table 3. One-way PERMANOVA testing of substrates and the aquatic oligochaetes found in each of them. Substrates: Sand (SAN), Sand + Leaves (SAN + LEA), Gravel (GRA), Macrophytes (MAC), Sand + Organic Matter (SAN + OM), and Roots (ROO). (*) indicates a significant difference ($p < 0.05$).

	SAN	SAN+LEA	GRA	MAC	SAN+OM
SAN+LEA	0.5354				
GRA	0.4785	0.2346			
MAC	0.6873	0.7174	0.3489		
SAN+OM	0.9022	0.9915	0.3948	0.7465	
ROO	**0.045***	0.0147*	0.0185*	0.5491	0.096

rocky substrates covered with mud in the rapids of low-order streams. Also, according to Verdonschot (1999) *N. communis* (Piguet, 1906) is generally associated with substrates composed of fine sand and organic sediments, which justifies the occurrence of this species in the SAN+OM substrate. The occurrence of this species in gravel can be justified by the fact that the surface of the gravel would favor the growth of periphytic algae, one of the main food sources of *N. communis* (Piguet, 1906) and a determinant factor in Naidinae distribution.

The Enchytraeidae family was found in all substrates and had its highest abundance in ROO found in first-order, shallow, clear-water pristine streams with moderate concentrations of dissolved oxygen. Such characteristics resemble those described by Rodrigues et al. (2013) for streams in the state of Minas Gerais; and also, data from low-order streams in the state of São Paulo presented by Alves et al. (2008), with very different characteristics to Amazonian streams (low temperature [16 °C], neutral to alkaline pH [7 to 8.5] and water conductivity of 172.6 $\mu S.cm^{-1}$). This underscores the ability of this family to occur in a wide range of environmental conditions, allowing it to colonize a variety of environments: terrestrial, semi-aquatic, and aquatic, with different abiotic characteristics as well as various types of substrate.

The species *B. americana* (Brinkhurst, 1964) was registered in all substrates except gravel. This shows the ecological plasticity of this species, which can colonize several substrates under different conditions. According to Marchese (2010), this species usually occurs in sandy sediments, both of low-order streams and larger rivers. Other authors like Omodeo and Coates (2001) also associate it with lentic environments with profundal zones loaded with organic matter.

Glossoscolecidae is a common terrestrial earthworm family which also has aquatic representatives. In this study, the family occurred frequently in different substrates and was extremely prevalent in low-order streams. The high occurrence of this group in SAN+MO and SAN+LEA substrates and the link of this group to low-order streams and the substrate variable could be explained by ecological earthworm needs. It is common to think that the occurrence of earthworms in low-order streams is an accident derived from adjacent terrestrial populations, since the streams are narrow and shallow, intensifying the interaction

between water and land (Rodrigues, 2013), but earthworms could be found at terrestrial, semi-aquatic and aquatic habitats. Truly aquatic earthworm species can be found in decaying vegetation in marshes and stream banks, in the soils of flooded rice paddies and along river margins and stream banks (James & Brown, 2006) associated with bryophytes (Rodrigues, 2013).

In summary, the results of this work showed that the FLONA Saracá-Taquera streams were homogeneous in relation to physicochemical water parameters. Physical and structural variables such as the substrate, water depth, and channel width, combined with the order of the streams, were the environmental attributes driving oligochaete community distribution in these pristine environments. The results of this work provide an important base for the development of biomonitoring tools for these kinds of environment. Understanding the occurrence and distribution of aquatic oligochaetes in the streams of the FLONA Saracá-Taquera, in which impacts are generally the result of changes in land use, structural modifications due to mineral exploitation and siltation, and not by organic contamination, can add substantial value to the development of tools to evaluate environmental impacts in this region.

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Author Contributions

Maria Silvina Bevilacqua: Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Mercedes Rosa Marchese: Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Rodrigo Weber Felix: Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

João José Fonseca Leal: Contribution to data collection; Contribution to critical revision, adding intellectual content.

Marcos Paulo Figueiredo de Barros: Contribution to manuscript preparation.

Reinaldo Luiz Bozelli: Contribution to critical revision, adding intellectual content.

Francisco de Assis Esteves: Contribution to critical revision, adding intellectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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Drivers of change in biodiversity and ecosystem services in the Cantareira System Protected Area: A prospective analysis of the implementation of public policies

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Abstract: The lack of implementation of well-designed public policies aimed at the conservation of natural ecosystems has resulted, at a global level, in the decline of ecosystem functioning and, consequently, of the contributions they make to people. The poor enforcement of important environmental legislation in Brazil - for instance, the "Atlantic Forest Law" (Law n.11.428/2006) and the "Forest Code" (Law n.12.651/2012) - could compromise the overall maintenance of ecosystems and the services they provide. To explore the implications of different levels of federal laws' enforcement within the Cantareira System Protected Area (PA) - a PA in southeastern Brazil that provides fresh water for 47% of the Sao Paulo Metropolitan Area -, we developed a conceptual framework to identify indirect and direct drives of biodiversity and ecosystem changes. We also projected four land-use scenarios to 2050 to test the effects of deforestation control and forest restoration practices on biodiversity and ecosystem services maintenance: the "business-as-usual" scenario (BAU), which assumes that all trends in land-use cover changes observed in the past will continue in the future, and three alternative exploratory scenarios considering the Atlantic Forest Law implementation, the partial implementation of the Forest Code and the full implementation of the Forest Code. Using the land-use maps generated for each scenario, we assessed the impacts of land-use changes on biodiversity conservation and soil retention. Our results revealed all alternative scenarios could increase biodiversity conservation (by 7%; 12%; and 12%, respectively), reduce soil

loss (by 24.70%; 34.70%; and 38.12%, respectively) and sediment exportation to water (by 27.47%; 55.06%; and 59.28%, respectively), when compared to the BAU scenario. Our findings highlight the importance of restoring and conserving native vegetation for the maintenance and improvement of biodiversity conservation and for the provision of ecosystem services.
Keywords: *Biodiversity, Ecosystem services, Scenarios, Modeling, Cantareira System Protected Area, GLOBIO, InVEST.*

Agentes de mudança na biodiversidade e serviços ecossistêmicos na APA Sistema Cantareira: Uma análise prospectiva da implementação de políticas públicas

Resumo: A falta de implementação de políticas públicas voltadas para a conservação ambiental, tem resultado, em nível global, em impactos sobre a biodiversidade e o funcionamento dos ecossistemas e, consequentemente, na contribuição da natureza para as pessoas. A aplicação inadequada de importantes de leis ambientais no Brasil, como por exemplo, a "Lei da Mata Atlântica" (Lei nº 11.428 / 2006) e o "Código Florestal" (Lei nº 12.651 / 2012), podem comprometer a manutenção dos ecossistemas e dos serviços que eles fornecem. Neste estudo, nós desenvolvemos um mapa conceitual que busca identificar causas diretas e indiretas de mudanças – agentes de mudança – na biodiversidade e na provisão de serviços ecossistêmicos relacionados ao solo e à água, na Área de Proteção Ambiental (APA) Sistema Cantareira. A APA Sistema Cantareira, localizada no sudeste do Brasil, fornece água potável para 47% da Região Metropolitana de São Paulo. Além da abordagem conceitual, nós projetamos quatro cenários de mudança no uso da terra para o ano de 2050, a fim de analisar o impacto de diferentes níveis de aplicação de leis federais: o cenário "*business-as-usual*" (BAU), que pressupõe que as tendências na mudança de uso da terra observadas no passado continuarão no futuro, e três cenários alternativos, considerando a implementação da Lei da Mata Atlântica, a implementação parcial do Código Florestal e a implementação completa do Código Florestal. A partir dos mapas de uso da terra gerados, avaliamos os impactos de cada cenário na conservação da biodiversidade, na retenção de solos e na exportação de sedimentos para os corpos d'água. Nossos resultados mostraram que os três cenários alternativos podem aumentar a conservação da biodiversidade (em 7%; 12%; e 12%, respectivamente), reduzir a perda de solo (em 24,70%; 34,70%; e 38,12%, respectivamente) e reduzir a exportação de sedimentos para a água (em 27,47 %; 55,06%; e 59,28%, respectivamente), quando comparados ao cenário BAU. Este estudo destaca a importância da restauração e conservação da vegetação nativa para a manutenção da biodiversidade e melhoria na provisão de serviços ecossistêmicos relacionados ao solo e à água, em uma região estratégica para o abastecimento de água no Brasil.
Palavras-chave: *Biodiversidade, Serviços ecossistêmicos, Modelagem, Área de Proteção Ambiental Sistema Cantareira, GLOBIO, InVEST.*

Introduction

Human well-being depends directly and indirectly on nature, and the complexity of these interactions is very difficult to map or measure. Despite these difficulties, there is abundant evidence worldwide that overall improvement in human well-being and economic development have resulted in negative impacts on biodiversity and ecosystem services (hereafter BES) (MEA 2005, IPBES 2018, 2019). According to these estimates, human activities have modified about half of the land and diverted half of the freshwater around the planet (MEA 2005, McGill 2015), triggering severe negative consequences for terrestrial and aquatic biodiversity and for their related ecosystem services, and affecting the long-term provision, regulation and maintenance of water, food, climate, soil and nutrient cycling. To reverse the consequences of ecosystem degradation for BES, the Millennium Ecosystem Assessment (MEA) was the first to compile, back in 2005, the scientific basis of the conditions and trends in the world's ecosystems and the services they provide (such as clean water, food, forest products, flood control, and natural resources); as well as the options to restore, conserve or enhance their sustainable use. Reinforced by the information of other international assessments, such as the Intergovernmental Panel on Climate Change (IPCC), it was clear that the science-policy interface had to grow stronger to foster sustainable development. With that purpose, the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES 2018) was established in 2012, aiming to assess and update current knowledge, stimulate new advances and support policy formulation and implementation (Díaz et al. 2015). Modeling the influence of human-driven changes on BES is of vital importance in the global context of the environmental crisis described above. Model-based analysis can inform decision-making, by enabling the understanding of the implications of different scenarios for biodiversity conservation and ecosystem functioning (Pereira 2010).

Human activity is having a significant impact on water resources and in some places it is actually constraining freshwater availability (Ceola et al. 2015). Freshwater bodies (e.g. rivers, lakes and groundwater) are subject to a wide variety of habitat transformation and degradation, including hydrological manipulations (dams and reservoirs), pollution by sewage waste, contamination by toxic substances and introduction of exotic species, amongst others (Hoekstra & Wiedmann 2014, Martin-

Ortega et al. 2015). Water provides key ecosystem services of all sorts - support, regulation, provision or cultural services - with complex inter-linkages with ecosystems functioning: it maintains terrestrial and aquatic species and habitats, regulates micro and local climate, provides drinking water for human consumption, but also for fish, agricultural and industrial production, affecting different components of human well-being (Grizzetti et al. 2016, IUFRO 2018). For these reasons, the conservation of freshwater ecosystems and their biodiversity has been receiving much attention in recent years and is now considered a priority issue at the global level (MEA 2005, Hoestra & Wiedmann 2014, Schiermeier 2014, IUFRO 2018, IPBES 2018). It is estimated that, at the global level, we consume from 22 to 150% of the annual freshwater supply (1,000 to 1,700 billion m^3/year) (Hoekstra & Wiedmann 2014), and official reports for the Americas revealed a declining water supply per capita and unsustainable use of surface and groundwater (IPBES 2018). For instance, Brazil has abundant aboveground water (Pires et al. 2019) and yet water shortage events are getting quite common, especially within regions with a long history of land use conversion, reduced vegetation cover and increased human population (Schiermeier 2014, IPBES 2018). That is precisely the situation for the state of São Paulo, southeastern Brazil, which has experienced severe water scarcity episodes during the past few years (Loyola & Bini 2015).

The destruction and degradation of natural ecosystems is the major cause of biodiversity loss on the planet (Haddad et al. 2015, McGill 2015, Newbold et al. 2015) and it is particularly threatening for the tropical region, which supports over half of the world's terrestrial biodiversity (Malhi et al. 2014). Several studies showed that ecosystems functions and services depend upon local biodiversity (Isbell et al. 2011, Cardinale et al. 2012, Tilman et al. 2014), highlighting the direct and indirect benefits of biodiversity conservation to ecosystem productivity, stability, invasibility and nutrient dynamics (Tilman et al. 2014, Isbell et al. 2017). It is also known that different types of land-use change and land-use intensity have different effects on biodiversity loss, from moderate negative impacts (i.e. little species loss) when land is converted to tree plantations or secondary vegetation, to heavy impacts, when converted to pasture, cropland or urban areas (Newbold et al. 2015). The designation of Protected Areas (PAs) is currently the main conservation strategy to preserve natural ecosystems and protect biodiversity from land-use change, but despite the worldwide overall increase in the percentage of PAs over the last decades, they still fail to adequately address conservation needs in the Anthropocene and under changing climatic conditions (Jenkins & Joppa 2009, Oliveira et al. 2017). For that reason, other complementary policies are essential to foster the conservation and restoration of BES.

Until very recently, Brazil was setting an example for the rest of the world with its commitments to achieve the sustainable development goals (SDGs) through the reduction of deforestation rates, designation of protected areas and implementation of environmental laws (Loyola 2014, Brancalion et al. 2016, Oliveira et al. 2017). Despite the numerous recent decisions that oppose the global policies and commitments previously ratified by Brazil (Loyola 2014, Vieira et al. 2017), there remain in place a few key pieces of environmental legislation that aim to protect and regulate native vegetation both within public and private properties. For instance, the Atlantic Forest, a global hotspot (Myers et al. 2000), is protected since 2006 by the Atlantic Forest Law (Law n.11.428/2006) (Brasil 2006), which restricts deforestation to very specific situations under a strict licensing process. Another example is the Native Vegetation Protection Law (Law n.12.651/2012) (Brasil 2012, Brancalion et al. 2016), popularly known as the Forest Code. First created in 1934, the Forest Code has gone through changes and the different versions have served varying purposes (Brancalion et al. 2016). It is the main environmental legislation to regulate the maintenance and restoration of native vegetation in private properties (Loyola 2014, Brancalion et al. 2016, Vieira et al. 2017), which encompasses 53% of the remaining native vegetation in Brazil (Soares-Filho et al. 2014) and up to 70% of the Atlantic Forest according to recent estimates (Rezende et al. 2018). The Forest Code specifies that every property, apart from the productive areas (i.e. agriculture, silviculture or pasturelands), has to set aside native vegetation in environmentally sensitive areas for biodiversity, soil and water conservation, known as Permanent Protection Areas (PPAs), and a portion of vegetation to ensure the sustainable economic use and conservation of natural resources, known as Legal Reserves (LRs). The PPAs are delimited based on predefined specific rules for several situations such as water springs, rivers, ponds, reservoirs, steep slopes and hilltops. The LRs are defined according to the region in which a private property is located, with varying proportions within different regions in Brazil: in the Amazon, LRs must cover 80% of forest or 20-35% of savannas, while in other regions the LRs must reach 20% of the property, including the PPAs (Brancalion et al. 2016). Nonetheless, the constitutionality of the most recent version of the Forest Code, published in 2012, has been increasingly challenged by the agribusiness in recent years (Loyola 2014, Brancalion et al. 2016, Metzger et al. 2019) and new initiatives have emerged to extinguish the LRs obligation (Metzger et al. 2019). In this critical situation, policy makers could benefit from the support of scientific evidence evaluating the benefits of enforcing the environmental legislation (Loyola 2014, Metzger et al. 2019).

How might different levels of compliance with the legislation affect biodiversity and the provision of ecosystem services in the Cantareira System Protected Area? To address this question, we used various methods – developing a conceptual framework, scenarios and modeling biodiversity and ecosystem services – to illustrate and emphasize key relationships and feedbacks in the complex social-ecological system in our study area. In particular, we investigated how different scenarios of implementation of the Atlantic Forest Law (Law n.11.428/2006) and of the Forest Code (Law 12.651/2012) could affect biodiversity and soil conservation in the Cantareira System Protected Area, composed both of public and private properties, and important for the provision of water for over 9 million people who live in the metropolitan area of the city of São Paulo. Apart from its importance for the provision of water, the area is a biodiversity hotspot (Myers et al. 2000). We expected that a higher level of implementation of the Forest Code and the Atlantic Forest Law would have positive impacts on biodiversity and soil conservation and the related provision of water. In general, we aimed to provide a scientific basis for policy and decision-makers who are responsible for the implementation of these laws.

Material and Methods

1. Methodological approach

The approach we developed had three steps: (1) the development of a conceptual framework indicating the main pressures and components

in the system, the relations between them, the current status of the different components, and the delivery of some ecosystem services; (2) the projection of different scenarios of land-use/land-cover (LULC), based on the implementation of the Atlantic Forest Law and the partial or full implementation of the Forest Code; and (3) the assessment of biodiversity conservation and ecosystem services (soil loss and sediment exportation to water bodies, as *proxies* for soil retention) - delivered in each scenario.

2. *Study area*

The Cantareira System Protected Area (PA) located in southeastern Brazil (hereafter 'Cantareira System PA'), is a sustainable use protected area (IUCN category VI) established by the Sao Paulo State Law 10.111/1998 (Estado de São Paulo 1998). The Cantareira System PA encompasses both public (13.2%) and private (86.8%) properties in seven municipalities of São Paulo. We also included in the analysis the municipality of *Bom Jesus dos Perdões*, which is not within the Cantareira System PA boundaries, but it is in the middle of that geographical range (Figure 1). The Cantareira System PA was created mainly for water security purposes, aiming to maintain and improve water quality in the Cantareira Supply System - a large complex of reservoirs that provides freshwater to the metropolitan area of São Paulo city, with over 9 million people (IBGE 2014). The Cantareira System PA consists of four sub-watersheds of the *Piracicaba* river (*Jaguari, Jacareí, Cachoeira and Atibainha*) and one of the *Alto Tietê* river (*Juqueri*). It comprises five reservoirs and a 2,300 km² catchment drainage area, with a total water demand of 33 m³/s (Water National Agency 2019), providing 46 % of the water supply for the metropolitan area of São Paulo. According to the Köppen classification, the climate is Cwa - humid subtropical: mild and dry winter, and moderately warm with a rainy summer. The Cantareira System PA is located in the Atlantic Forest region, a biodiversity hotspot that has only 26% of its original vegetation cover remaining (Myers et al. 2000, Rezende et al. 2018). According to the latest assessment, our study area has 35% forest cover, and 74% of this vegetation is secondary Atlantic Forest in an intermediate stage of succession (Instituto Florestal 2010).

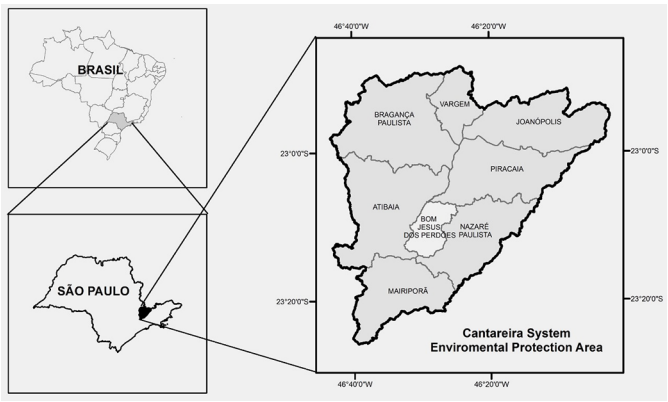


Figure 1. Study area located in the Atlantic Forest of the State of São Paulo, Brazil, including the Cantareira System PA and the municipality of Bom Jesus dos Perdões.

3. *Development of a conceptual framework*

To develop a conceptual framework, we first identified the focal BES elements to target within the study area given the current state of the system, related conjunctures regarding the implementation of public policies, and data availability. Based on these criteria, we selected soil retention together with biodiversity conservation as the elements of most interest for our case study. Secondly, we applied the Driver-Pressure-State-Impact-Response (DPSIR) causal framework (Martins et al. 2012, Tscherning et al. 2012) to identify the various components and dimensions of BES in our study case, including the major driving forces and pressures affecting BES outputs, their relationships, the state of the system at different scales, and the potential impacts of the implementation of public policies. Third, we used the IPBES Nature Futures Framework (NFF, *sensu* PBL 2018) to classify selected components of the Cantareira System PA related to BES into three different dimensions reflecting how people relate to nature: (i) nature for society, addressing the utilitarian benefits of nature for people; (ii) nature for nature, addressing the intrinsic value of nature functioning and diversity; and (iii) nature for culture, addressing the spiritual and other non-material benefits for people living in harmony with nature. Fourth, we added the direct and indirect drivers and conceptualized how they are connected and how their changes impact biodiversity and the provision of these services. As a last step, we included the social-ecological feedbacks in the system. Given the high complexity of the system and of our conceptual model, we focused primarily on some key-components that we believe are representative of the overall relationships between people and nature within this system (public policies, forest ecosystems, water and land-use).

4. *Land-use change scenarios*

We projected four land-use scenarios to test the effects of deforestation control and forest restoration practices on BES maintenance. We used land-use and cover maps from 1997 and 2017 (Mapbiomas v.4 2017) to analyze land-use cover changes trends and project these to 2050. At one extreme, is the "business-as-usual" scenario (BAU), which assumes that all trends of land-use and cover change observed in the past 20 years will continue until 2050. Then, we built three alternative scenarios: (i) Atlantic Forest Only (AFO) - considering only the implementation of the Atlantic Forest Law, that is, no further deforestation on the current land-use and cover map for 2017; (ii) Partial implementation of the Forest Code (PFC): considering the Atlantic Forest Law implementation and the restoration of Permanent Protected Areas; and (iii) Full implementation of the Forest Code (FFC) - considering the Atlantic Forest Law implementation, and the restoration of both Permanent Protected Areas and Legal Reserves. We built the BAU and the AFO scenarios using the Dinamica EGO software (Soares-Filho et al. 2002). The difference between BAU and AFO scenarios is that AFO assumes no deforestation from 2017 onwards. To build the PFC and FFC scenarios we used AFO scenario as a baseline and then we simulated native vegetation recovery in Permanent Protected Areas (PPA) related to water bodies (riparian areas along rivers and around springs, reservoirs, lakes and lagoons) and in Legal Reserves (LR). The PPA were defined using a 1:50,000 scale hydrographic network (IBGE - Brazilian Institute of Geography and Statistics, topographic maps). For the perennial rivers, lakes and lagoons (with surface smaller than 20 hectares), we used a buffer of 30 m; for the springs, we used a buffer of 50 m; for the large reservoirs (surface

larger than 20 hectares), a buffer of 100 meters; following what is established by the Forest Code (Brasil 2012). For the LR areas, we employed the map available in the Rural Environmental Registry System (SICAR), which is based on the self-declaratory status of rural properties done by the landowners (see details in Brancalion et al. 2016), and therefore could have underestimated the extent of these areas.

5. *Assessment of biodiversity*

To estimate the current biodiversity conservation value of the areas and assess the impacts of LULC change on biodiversity, we used the approach developed for the GLOBIO3 framework (Alkemade et al. 2009). For this purpose, we considered the LULC categories and the remaining mean species abundance values (MSA_{LU}) detailed in **Table 1**. The MSA_{LU} represents a measure of the species abundance in the different LULCs relative to the pristine or primary vegetation proposed by Alkemade et al. (2009). We attributed an MSA_{LU} of 0.7 to the forest remnants in the region, as these are mainly secondary forests intensively exploited in the past, which have been regenerating over many years, but remain different in structure and composition from well preserved forests in the region (Instituto Florestal, 2010). Using the same reasoning, restored forests may take longer than 30 years (our time frame for this study) to have the same MSA as that of today's secondary forests; so, we defined an MSA of 0.5 for restored forests. For all the other categories, we used the MSA_{LU} values suggested by Alkemade et al. (2009).

6. *Assessment of ecosystem services*

For the ES assessment, we compared the potential soil loss and sediment exportation into streams among the scenarios. To calculate the soil loss on a 30x30 m spatial resolution, we used the Sediment Delivery Ratio (SDR) module from InVEST 3.7.0, which is a spatially explicit model that calculates the average annual amount of soil loss for each pixel. As a result, the SDR estimated the sediment yield into streams and the annual loss of soils in tons. The SDR is based on the Universal Soil Loss Equation (Wischmeier & Smith 1978).

$$A = R * K * LS * C * P \quad (1)$$

In which: A is the average loss of soil per unit area (t ha^{-1} $year^{-1}$); R is the rainfall erosivity factor (MJ mm ha^{-1} h^{-1} $year^{-1}$); K is the soil erodibility factor (t h MJ^{-1} mm^{-1}); LS is the topographic factor (dimensionless); C is the soil use and management factor (dimensionless) and P is the conservation dimension factor (dimensionless). To calculate the LS-factor, we used a 30-m digital elevation model (DEM) obtained from EMBRAPA - Brazilian Agricultural Research Company/Satellite Monitoring. The R-factor was obtained from Neto (1995). The K factor was estimated using global data (Harmonized World Soil Database -HWSD – FAO 2012) and values obtained from the literature (Saad et al. 2016, Mannigel et al. 2002, Miteva et al. 2014) (**Table 2**). The soil types were obtained from Rossi (2017). The C-factor was also estimated from the literature, including studies in the same biome (**Table 3**) (Ruhof et al. 2006, Machado et al. 2009, Silva et al. 2010, Barbosa 2012, Gomez 2012, Silva et al. 2012, Thompson & Fidalgo 2013, Xavier et al. 2013, Ribeiro 2015, Saad et al. 2016). The P-factor is related to the conservation practices used in the region for each use and land cover class, and since the region does not currently include conservation practices, we attributed the value 1 to all land-uses.

Results

1. *Conceptual framework*

Based on our DPSIR and the Nature's Future Frameworks we developed the conceptual framework presented in Figure 2.

2. *Land-use scenarios*

Pastureland is the predominant land-use class in the Current situation (48% of total area), but its extent tended to decrease under the forest conservation (AFO) and restoration (PFC and FFC) scenarios, reducing to 30.2% in the most optimistic simulation. Natural forests were the second largest land-use type (35.4% of total area) and may

Table 1. Land-use / land-cover (LULC) categories and Mean Species Abundance values considered for modeling biodiversity in the different scenarios. Adapted from Alkemade et al. (2009).

Land-use category	Description	Mean Species Abundance per land-use value (MSALU)
Natural forest	Secondary patches of Atlantic Forest that are either remnants heavily exploited in the past but never cleared, or second-growth forests	0.7
Restored forest	Atlantic Forest patches in different stages of secondary succession growing on former farmland as a result of active restoration or natural regeneration in areas set aside after legal requirement	0.5
Agriculture	Predominantly small-scale agriculture comprising several different crops	0.3
Silviculture	Pure stands of *Eucalyptus* spp. or *Corymbia* spp. planted for commercial exploitation in areas originally covered by Atlantic Forest	0.2
Pastureland	Artificial grasslands maintained for livestock in areas originally covered by Atlantic Forest	0.1
Urban area	Areas built up in more than 80% of the surface	0.05

Table 2. Soil Types and *K*-Factor values considered for modeling soil loss and sediment exportation to water in the different scenarios.

Soil Type	*K*-Factor
Dystrophic red-yellow argisol	0.036
Dystrophic red-yellow latosol	0.015
Dystrophic yellow latosol	0.03
Eutrophic red-yellow argisol	0.03
Haplic Cambisol	0.03
Humic Cambisol	0.035
Melanic gleysol	0.026

Table 3. Land-use / land-cover categories and *C*-Factor values considered for modeling soil loss and sediment exportation to water in the different scenarios.

LULC class	*C*-Factor
Natural forest	0.0001
Pastureland	0.052
Restored forest	0.0001
Silviculture	0.0007
Urban area	0.0375
Agriculture	0.26

increase to 43.1%, under the scenario of Full implementation of the Forest Code. These tendencies were accompanied by a decrease in silviculture and an increase in forest restoration, as well as a slight increase in agricultural areas (**Table 4**). The native forest of the Cantareira System PA might be reduced from 35.4% (its current area) to 34.5% (BAU scenario) by 2050 if the current trends continue (Table 4). Most of these trends are visually distinguishable on the land-use maps presented in Figure 3 and Figure 4.

3. Consequences for BES

Overall native forest cover (natural forest remnants and restored forests) increased consistently, and markedly, as we shifted from the BAU scenario (34.5% of total area) to the scenario of Full Implementation of the Forest Code (52.5% of total area) (Figure 5-A). The same pattern was observed for Mean Species Abundance (MSA), that ranged from 0.29 (BAU) to 0.40 (FFC) (Figure 5-B). The potential soil loss decreased from the Business as usual scenario (16.32 million tons/yr) to the scenario of Full Implementation of the Forest Code (11.73 million tons/yr), as did the amount of sediment exported into water bodies (1.98 to 1.00 million tons/yr) (Figure 5 - C and D).

Our results suggested an MSA decrease under the BAU scenario relative to the Current situation. On the other hand, the MSA increased from 29% (BAU) to 35% (AFO) with the implementation of the Atlantic Forest Law (AFO scenario) and to 40% with the partial

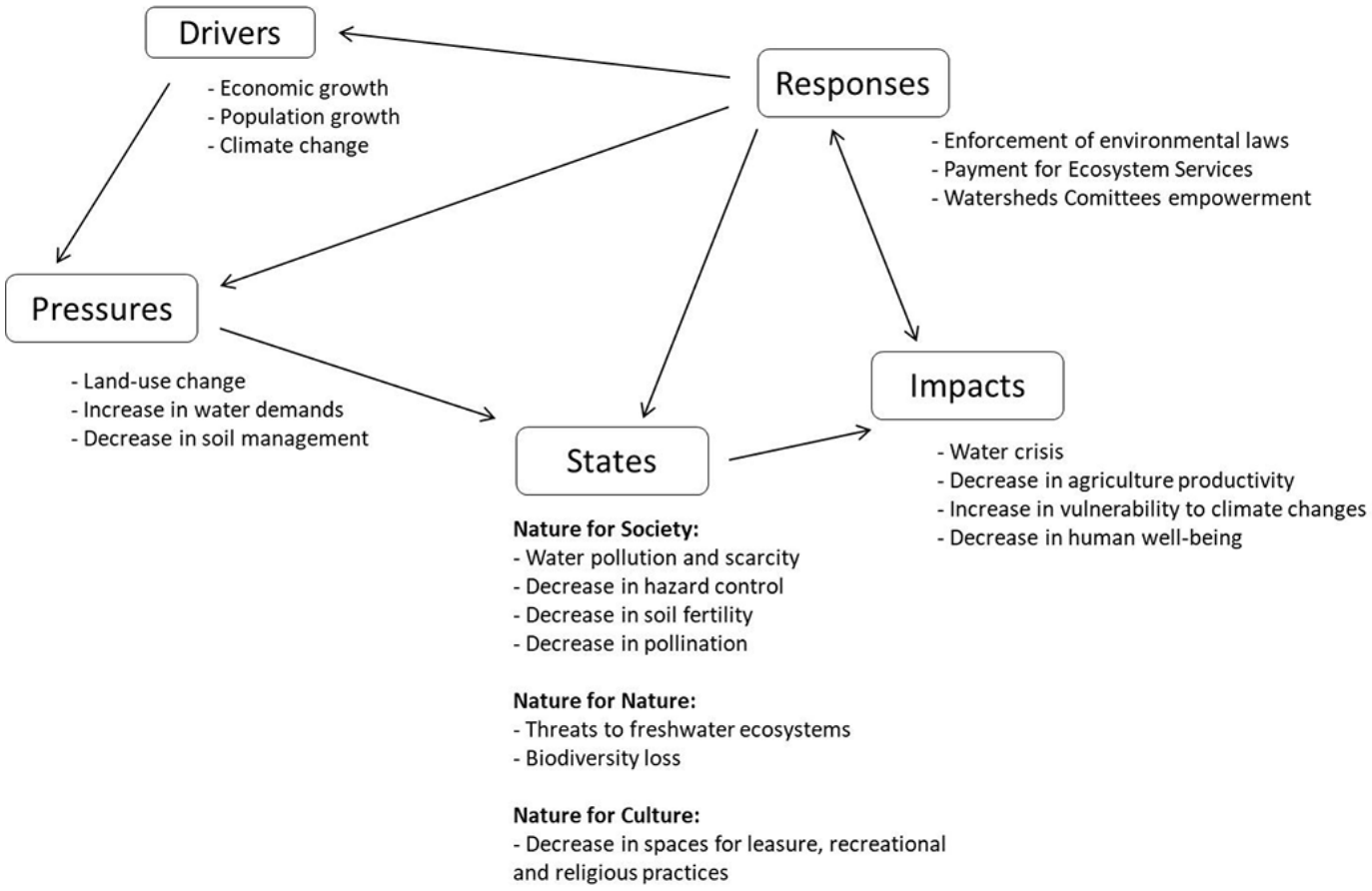


Figure 2. Application of DSPIR framework to the Cantareira System Protected Area, São Paulo, Brazil.

Table 4. Land-use and land-cover (LULC) of the current situation (2017) and future scenarios (2050) in the Cantareira System Protected Area, São Paulo, Brazil.

LULC class	2017 (CUR)		2050 (BAU)		2050 (AFO)		2050 (PFC)		2050 (FFC)	
	(ha)	(%)	(ha)	(%)	(ha)	(%)	(ha)	(%)	(ha)	(%)
Natural forest	93,869	35.4	91,3	34.5	93,87	35.4	114,23	43.1	114,23	43.1
Pastureland	127,22	48.0	110,7	41.8	98,22	37.1	83,037	31.4	80,06	30.2
Restored forest	0	0.0	0	0.0	20,36	7.7	20,509	7.7	24,938	9.4
Silviculture	20,449	7.7	31,53	11.9	21,99	8.3	19,431	7.3	18,329	6.9
Urban area	10,501	4.0	16,43	6.2	16,03	6.1	14,291	5.4	14,188	5.4
Agriculture	5,759	2.2	8,592	3.2	8,146	3.1	7,684	2.9	7,446	2.8

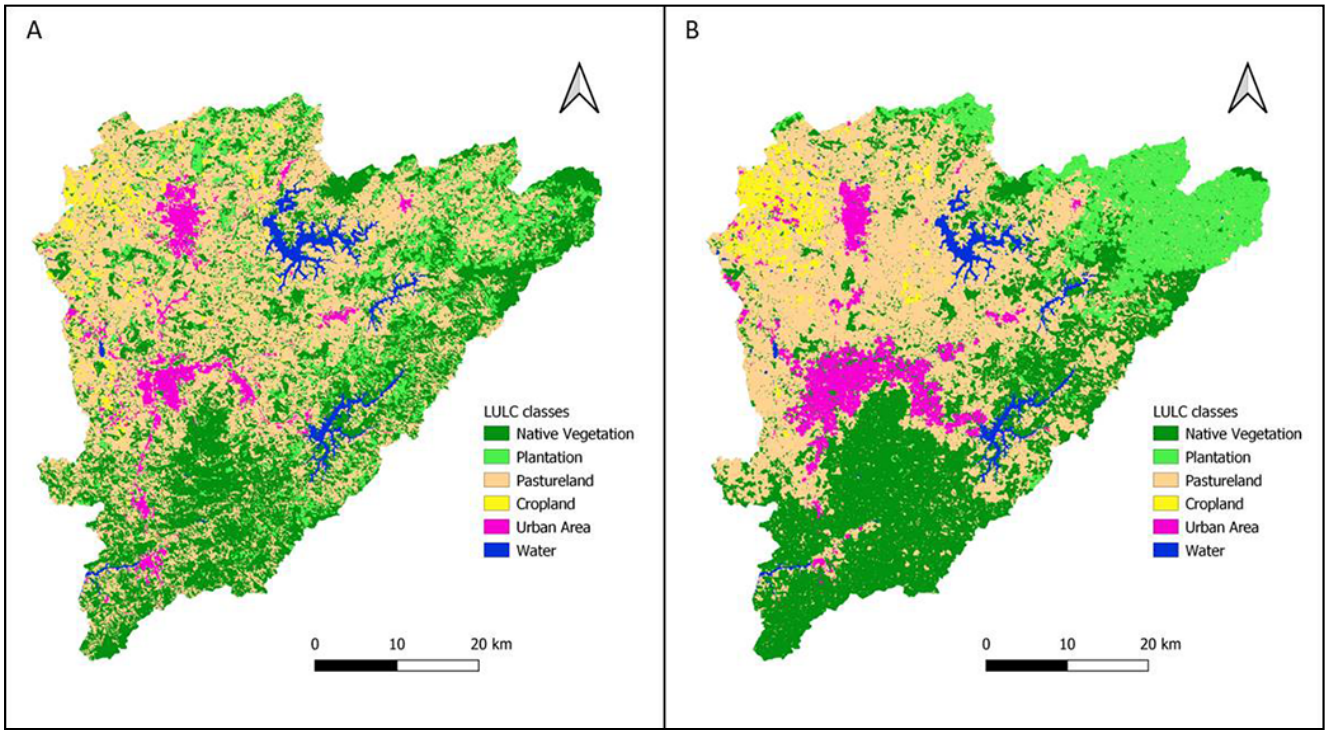


Figure 3. Cantareira System PA maps representing Land Use and Land Cover in (A) the Current situation (Mapbiomas v.4 2017) and (B) the Business as Usual scenario (projection for 2050).

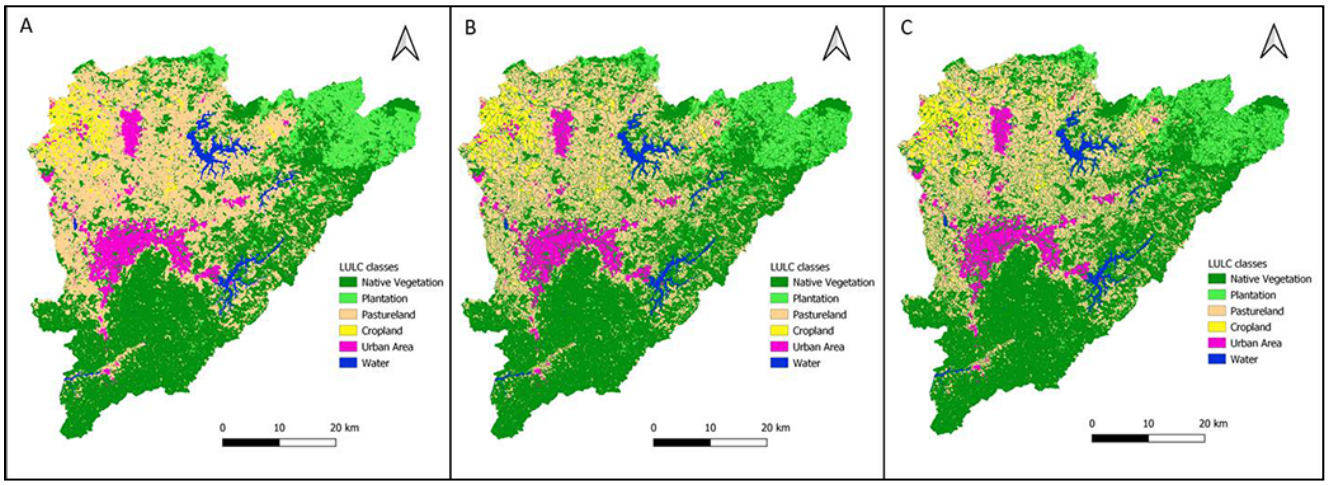


Figure 4. Cantareira System PA maps representing Land-use and Land Cover alternative scenario projections for 2050: (A) AFO - Atlantic Forest Only; (B) PFC - Partial Forest Code; and (C) FFC - Full Forest Code implementation (restoration of Permanent Protection Areas and Legal Reserves).

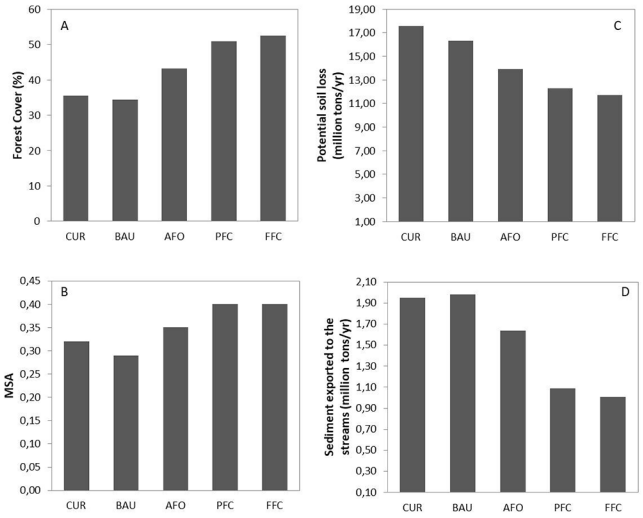


Figure 5. Trends of change in forest cover, biodiversity and soil conservation for the current situation and for future scenarios in the Cantareira System PA. (A) Forest cover percentage (native and restored forests); (B) Mean Species Abundance-MSA; (C) Potential soil loss; (D) Amount of sediment exported to water bodies. CUR = Current situation; BAU = Business As Usual; AFO = Atlantic Forest protection law Only; PFC = Partial Forest Code implementation (restoration of Permanent Protection Areas); FFC = Full Forest Code implementation (restoration of Permanent Protection Areas and Legal Reserves).

or full implementation of the Forest Code. We did not observe marked differences in MSA when comparing PFC an FFC scenarios (Figure 5-B). Considering the soil retention assessment, our results showed a tendency of decrease in soil loss and increase in sediment exportation to water, comparing BAU to the Current situation. Also, our projections showed a decrease of soil loss in all alternative scenarios in relation to the BAU (AFO: reduction of 24.70%; PFC: reduction of 34.70%; FFC: reduction of 38.12%). The results for sediment exported into water bodies exhibited the same pattern. However, the reduction was even more marked in the restored scenarios (AFO: reduction of 27.47%; PFC: reduction of 55.06%; FFC: reduction of 59.28%). This suggested that the sediment retention service provided by the landscape was more efficient under scenarios in which PPA and RL were restored.

Discussion

The development and the evaluation of possible scenarios suggested that we can expect an overall increase of BES under higher levels of compliance to Brazilian environmental legislation, reinforcing their importance for accomplishing Brazil's national commitments to achieve the SDGs (Loyola 2014). Our study predicted that forest cover will increase up to 48% when comparing the Business as usual (BAU) with the most optimistic scenario (FFC), with a resulting improvement in values of Mean Species Abundance and the reduction in potential soil loss and exportation of sediments into streams, with likely positive impacts on water quality.

Based on the DPSIR framework, our conceptual model included, in a broad way, the current trends of the economic system and human population growth as the main indirect drivers affecting large-scale water quantity and quality, as well as the maintenance of biodiversity within our study area. According to this perspective, these indirect drivers influence the dynamics of other more direct drivers such as the demand for this resource (total and *per capita*) by the inhabitants both within the Cantareira System Protected Area and in the city of Sao Paulo. In the same direction, it is likely that a greater proportion of the native vegetation within our study area will be susceptible to conversion to other uses, such as urban, agricultural or silvopastoral, affecting both LULC proportions and soil management. Considering that, in recent years, trends in precipitation and temperature have shown significant anomalies (Nobre et al. 2016), climate change is likely to be another factor of great importance in the Cantareira System PA. All these factors, both direct and indirect, were established as the main potential drivers of change in the state of nature, encompassing different dimensions of our interest: the availability of good quality water for human consumption, agricultural and industrial use (nature for society dimension); the maintenance of stable hydrological cycles and healthy freshwater ecosystems (nature for nature dimension); and the recreation, education, leisure, and religious associated aspects (nature for culture dimension). In parallel, these drivers are also seen as the main causes of loss of biodiversity in our study area, affecting both the abundance of species of different taxa, and the services that emerge from them in all the dimensions (Nature for Society, for Nature, and for Culture). We identified the Forest Code and the Atlantic Forest Law as external factors (i.e., public policies) whose application in the near future can play an important role in regulating direct and indirect drivers of change, and helping to conserve the system, through their influence on the maintenance of native vegetation cover.

Apart from the restoration outputs resulting from the partial or full implementation of the Forest Code, our results also highlighted the potential contribution of natural regeneration within our study region, revealed by the increased percentage of natural forest cover in all scenarios except for the BAU. Studies evaluating the potential of tropical secondary forests state that international conservation and restoration commitments depend on the regeneration of forests on abandoned areas (Brancalion et al. 2019, Crouzeilles et al. 2019). Despite the limited habitat quality and provision of ecosystem services, there is consistent evidence demonstrating the value of secondary forests (Rozendaal et al. 2019). Putting together all types of forests, even the Business as Usual scenario shows a small increase compared to the Current situation, in that case, related to an increase in silviculture. The more optimistic scenarios showed an overall large increase in forested area, characterized by a slight decrease in silviculture outweighed by significant increases in restored areas necessary to comply with the Forest Code and also by significant increases in natural forest remnants regenerating outside of the areas required to be restored by the Forest Code, probably resulting from the abandonment of marginal agricultural areas of low productivity.

The land that needs to be restored within the Cantareira System Protected Area corresponds to 20,509 ha of riparian forests and 4,429 ha outside of riparian forests; a total of

24,938 ha currently being used irregularly for the production of livestock, crops and wood. Besides the irregular aspect of this current land-use, it also negatively affects the price of the land (which is lower when a landowner does not comply with the law), threatens biodiversity conservation, and compromises the provision of ecosystem services, including water to a large human population. The average cost of forest restoration in the Atlantic Forest ranges from R$ 0.2 to 21.3 thousand Brazilian reais per hectare (Benini & Adeodato, 2017, Tymus et al. 2018), depending on the conditions of the site and the characteristics of the landscape. Considering that the area has a large natural forest cover, it may have an overall high natural regeneration potential. For this reason, it is reasonable to assume that the average cost for restoring a hectare is around R$ 10k, summing to nearly R$ 250 million Brazilian reais. There are recent developments towards cost-effective restoration of the Legal Reserves in degraded areas of the Atlantic Forest that provide financial return to offset at least part of the costs of converting degraded lands back into natural forests (Amazonas et al. 2018a, Brancalion et al. 2019). In protected areas important to water production such as our study site, these mixed forests could be even used as an alternative to traditional silviculture since they result in less drying of soils (Amazonas et al. 2018b).

We observed a small decrease in native forest cover in the BAU scenario, compared to the Current situation, coupled with some conversion of pastureland into silviculture. Therefore, the resulting overall forest cover increase was predominantly due to silviculture expansion, and it resulted in soil loss reduction. Despite that, the amount of sediment exported into water bodies was greater in the BAU scenario, which may be explained by a loss of riparian vegetation. When we compared the BAU with the more optimistic scenarios of increasingly higher forest cover, we observed an increase in sediment retention coupled with higher forest cover. Moreover, in the scenarios in which the riparian forests are restored, the sediment retention ecosystem service is further improved since less sediment is exported to the water. The scenario of Partial implementation of the Forest Code, for example, where riparian forests are restored, soil loss is reduced in 34% and sediment exportation is reduced in 55%. The major sources of sediment pollution in the Cantareira System PA are the pasturelands and croplands (Richards et al. 2017), especially in those areas with insufficient or absent sustainable management practices. Forest conservation and restoration can substantially reduce erosion effects (Zaimes et al. 2008). Also, it is expected that this vegetation reduces siltation and pollution, by trapping a large fraction of the soil particles and runoff originating from arable land (Dosskey et al. 2010, Zhang et al. 2010). These benefits reduce costs associated with water treatment and dredging.

The higher soil retention and lower sediment exportation to streams in the optimistic scenarios compared to the Current situation and to the BAU scenario were probably related to the capacity of forests to counteract the detrimental effects of soil erosion downslope of the areas of sediment production as well as to act as a buffer to water bodies, protecting against stream bank erosion (McKergow et al., 2003; Zaimes et al., 2008; Zaimes and Schultz, 2015) and against pollution. Furthermore, the Atlantic Forest areas always maintain litterfall over the soil and the Leaf Area Index is constant, which means that the soil is covered during the entire year. The higher the Leaf Area Index, the greater the interception of water by leaves, preventing further increases in runoff and preventing soil detachment by raindrop impact. Another important point is that forested areas generally have larger water infiltration rate than cropped areas due soil compaction and surface crust formation as a result of heavy machinery use in cropland and the lack of sustainable practices for soil management (Gomes et al. 2019). These results thus strongly suggest that the full implementation of the Forest Code could improve water quality and availability in the Cantareira System Protected Area.

Reaching a future in which the land-use in the Cantareira System Protected Area resembles our most optimistic scenario requires efforts and resources, including setting aside areas and restoring native vegetation, to promote the land-use changes necessary to comply with the Forest Code. Investing in the implementation of the Forest Code may translate in avoided costs of water treatment and dredging. Also, these changes are likely to result in significant biodiversity gains (MSA increase). Moreover, the value of land may increase once landowners comply with the Forest Code (Pires et al. 2019). By modeling the impacts of land-use change in each scenario on biodiversity and ecosystem services provision, our aim was to inform relevant stakeholders about the consequences of an incomplete implementation of the land-use changes necessary to comply with the Forest Code. We hope this information convinces and mobilizes society for the implementation of land-use changes that clearly improve biodiversity conservation, the functioning of ecosystems and the related provisioning of ecosystem services important for human well-being. Our results emphasize the urgent need to implement/enforce the two major regulating instruments in the Atlantic Forest biome: the Forest Code and the Atlantic Forest Law.

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Authors' Contributions

Viviane Dib: Substantial contribution in the concept and design of the study; Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis

and interpretation; Contribution to critical revision, adding intelectual content.

Marco Aurélio Nalon: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Nino Tavares Amazonas: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intelectual content.

Cristina Yuri Vidal: Substantial contribution in the concept and design of the study; Contribution to manuscript preparation; Contribution to critical revision, adding intelectual content.

Iván A. Ortiz-Rodríguez: Substantial contribution in the concept and design of the study; Contribution to manuscript preparation; Contribution to critical revision, adding intelectual content.

Jan Daněk: Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intelectual content.

Maíra Formis de Oliveira: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intelectual content.

Paola Alberti: Substantial contribution in the concept and design of the study; Contribution to manuscript preparation.

Rafaela Aparecida da Silva: Substantial contribution in the concept and design of the study; Contribution to manuscript preparation.

Taciana Figueiredo Gomes: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intelectual content.

Raíza Salomão Precinoto: Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

The authors declare that they have complied with the guidelines established by the ethics committees of their respective research institutions.

Data availability

Additional data regarding the mathematical models used will be archived in the in public data repository “Sistema de Informação Ambiental do Programa Biota/Fapesp/SinBiota”.

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Inventory

Checklist of dragonflies and damselflies (Insecta: Odonata) of the Amazonas state, Brazil

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Abstract: Here we provide a checklist of the odonates from Amazonas state, Brazil. We registered 324 species and 101 genera, making Amazonas the Brazilian state with the most Odonata species recorded. The families with the highest number of species were Coenagrionidae with 32 genera and 101 species, followed by Libellulidae with 28 genera and 100 species and Gomphidae with 12 genera and 45 species. Some regions of Amazonas state remain poorly explored, such as the southern area, and large municipalities, such as São Gabriel da Cachoeira. This work underlines the importance of the biological diversity from Amazonas state and the Amazonian Biome for Odonata species richness in Brazil and shows that many areas in the world's largest tropical forest have not yet been sampled.
Keywords: *Aquatic insects, List of species, Anisoptera, Zygoptera, Amazon, Neotropical region.*

Checklist das libélulas (Insecta: Odonata) do estado do Amazonas, Brasil

Resumo: Aqui nós apresentamos a lista de espécies de libélulas presentes no estado do Amazonas, Brasil. Nós registramos 324 espécies e 101 gêneros, tornando o estado com o maior número de espécies de libélulas registradas no país. As famílias com maior número de espécies foram Coenagrionidae, com 32 gêneros e 101 espécies, seguido por Libellulidae, com 28 gêneros e 100 espécies e Gomphidae com 12 gêneros e 45 espécies. Regiões do estado do Amazonas permanecem pouco exploradas, como a parte sul e os municípios com grande extensão territorial, como São Gabriel da Cachoeira. Este trabalho reconhece a importância da diversidade biológica do estado do Amazonas e do bioma Amazônico para a riqueza de espécies de Odonata no Brasil e mostra que ainda existem muitas áreas não amostradas na maior floresta tropical do mundo.
Palavras-chave: *Insetos aquáticos, lista de espécies, Anisoptera, Zygoptera, Amazônia, região Neotropical.*

Introduction

Considered one of the most diverse regions for Odonata, the Neotropical region has more than 1,700 species, and in Brazil 749 species are registered (Olaya 2019). Dragonflies and damselflies (Insecta: Odonata) constitute an important group of aquatic insects characterized by their extensive predation, with larvae being important links for fish and other aquatic vertebrates in food webs. Besides their ecological importance, odonates have great artistic appeal, and have been used in environmental quality assessments using several environmental quality metrics (Abbott 2015).

Even with such importance, the taxonomic knowledge about Odonata in Brazil is still heterogeneous. As evidenced by Dalzochio et al. (2018), Brazilian studies concerning Odonata fauna are mainly concentrated in the south-center of Brazil, with species lists registered for the states of São Paulo (Costa et al. 2000), Rio de Janeiro (Costa & Santos 2000), Mato Grosso do Sul (Koroiva et al. 2017; Rodrigues et al. 2018), Rio Grande do Sul (Dalzochio et al. 2018; Pires et al. 2019), Espírito Santo (Costa & Oldrini 2005), Goiás and the Federal District (Nóbrega & De Marco 2011). Despite the increasing number of new species descriptions, the lack of species lists in other regions and states make the analysis of current sampling distributions and knowledge about Odonata species distribution inviable, which directly affects large-scale conservation assessments (Silveira et al. 2010).

The Amazonas state located in the northern region of Brazil, presents the largest territorial extension and stands out (IBGE 2019) as it encompasses Amazonian and Cerrado biomes (Parédio 2012). In recent years, political issues and increased deforestation rates in both biomes have raised concerns for the maintenance of their forested areas and associated fauna (Rochedo et al. 2018, Fearnside 2019). Regarding Odonata, several studies have been dedicated to increasing knowledge about its fauna in Amazonas state in the last 120 years, however, almost all of them are restricted to taxonomic descriptions and ecological analysis and do not provide information about the total number of species. In the most recent estimate, Neiss & Hamada (2014) indicated about 262 Odonata species in Amazonas, representing 35% of the known species from Brazil. Considering this information gap in Amazonas, the main objective of this work was to present the diversity of Odonata species in this state, as well as their known locations in the municipalities.

Materials and Methods

1. Study area

The state of Amazonas has an area of 1,559,168 km² (IBGE 2019) and stands out due to the predominant presence of the Amazonian Biome. The state shares borders with Pará, Mato Grosso, Rondônia, Acre and Roraima states and with the countries of Venezuela, Peru and Colombia (Figure 1). The geographical relief of Amazonas state is constituted by depressions (Western Amazon Depression, Northern Amazonian Depression and Southern Amazon Depression), plains, and plateaus (North-Amazonian Residual Plateau and Plateau of the Eastern Amazon). Its hydrology is formed mainly by the eastern basin of the Amazon River and is composed of most of the rivers from this hydrographic basin, whose tributaries are the rivers Negro, Japurá, Solimões, Juruá, Purus and Madeira. The northern and eastern regions of the state are located in the northern Amazonian plateau, which contain the highest altitudes (above 2,950 m) in Brazil: "Pico da Neblina" and "31 de Março" mountains (Parédio 2012). The vegetation types vary from Ombrophylous Forest to "Campinarana" and Savana in the Amazon and Cerrado biomes. According to Köppen's climatic classification, the predominant climate is Af type, tropical without dry season, except in the southern part of the state, which is considered Am, tropical monsoon. The average annual precipitation varies between 1,900 mm in the extreme southwest and above 3,000 mm in other areas and average temperatures are above 23° C (Alvares et al. 2013).

2. Elaboration of the list

To prepare the list, we gathered information from the Invertebrates Collection at the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil. Additional data were collected from 102 publications, published between 1897 and 2019, the sites SpeciesLink (http://splink.cria.org.br/) and "Catálogo Taxonômico da Fauna do Brasil" (http://fauna.jbrj.gov.br ; "Brazilian Fauna Taxonomic Catalog" in English; Pinto 2019) (see Table 1). We also gathered information about the municipalities where the species were collected (Table 1). For systematic classification, we followed Dijkstra et al. (2014, 2013) and Fleck (2018).

Results

The total number of Odonata species recorded in Amazonas is 324 (Table 2). Some species recorded in this study are shown in Figure 2. The total number of genera recorded for the state is 101, distributed in 16 families; this number include one genus from the Calopterygoidea "*Incertae sedis* group 3" and one genus from the Libelluloidea "*incertae sedis*". Coenagrionidae is the family with the highest number of records, with 32 genera and 101 species, followed by Libellulidae with 28 genera and 100 species, Gomphidae with 12 genera and 45 species, and Aeshnidae with eight genera and 27 species. The other families are: Calopterygidae (two genera, 12 species), Corduliidae (two genera, four species), Dicteriadidae (two genera, two species), Heteragrionidae (two genera, seven species), Lestidae (one genus, one species), Megapodagrionidae (one genus, one species), Perilestidae (two genera, seven species), Philogeniidae (one genus, two species), Platystictidae (one genus, one species), Polythoridae (three genera, 10 species), Rimanellidae (one genus, one species) and Oxygastridae *sensu* Fleck (2018) (one genus, one species). Calopterygoidea "*incertae sedis* group 3" was represented by one genus and one species and Libelluloidea *incertae sedis* was also represented by one genus and one species.

Considering the territorial divisions of the state, Manaus (code number 1) municipality has the most species registered, 163 species, followed by Presidente Figueiredo (code number 2), 100 species, and Barcelos (code number 4), 71 species. In addition, only 33 of the 62 municipalities in Amazonas have published Odonata records.

Discussion

The 324 species listed from Amazonas state represent about 43% of the known species in Brazil (749 species). This number increases the species records for the state by 23% (Neiss & Hamada 2014). With the results presented in this study, Amazonas state is the Brazilian state with the highest number of Odonata species recorded, followed by

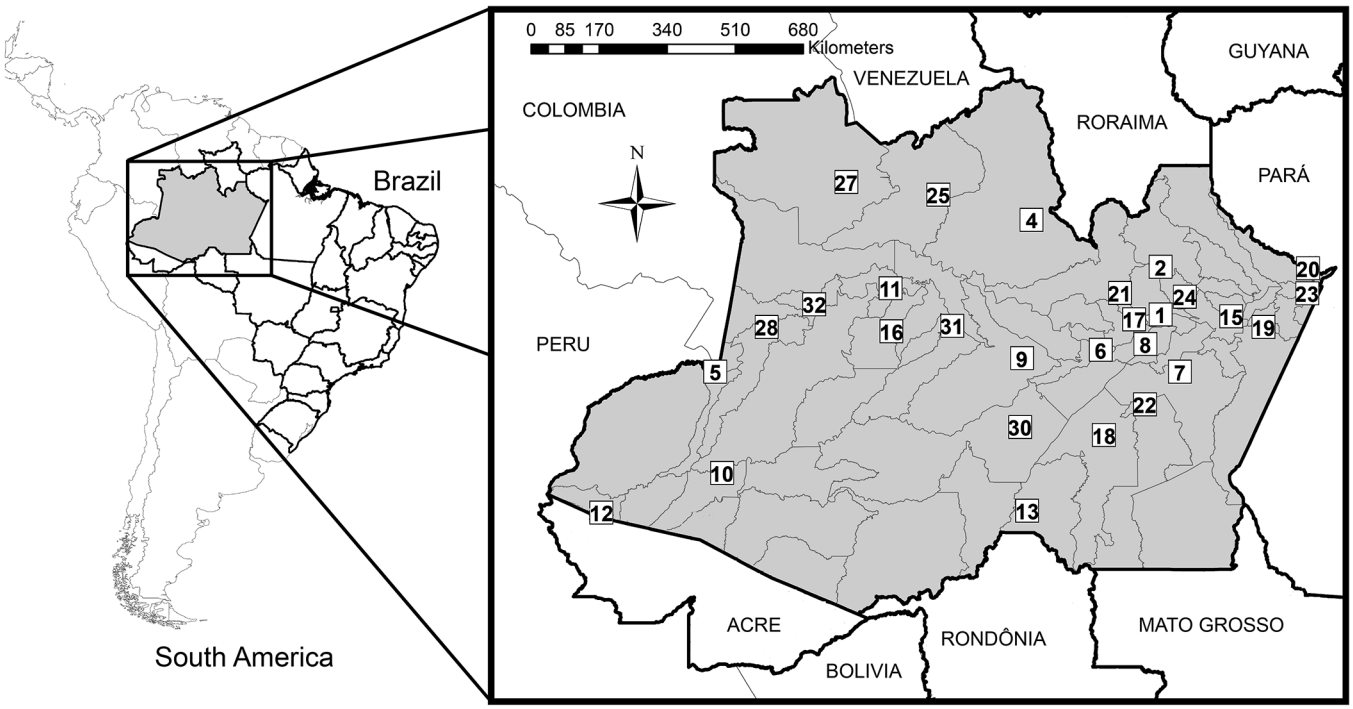


Figure 1. Left, Map of South America highlighting the geopolitical division of Brazil and Amazonas State (grey) (Datum: WGS 84); Right, Municipalities with Odonata recorded in Amazonas State. For code numbers see Table 1.

Table 1. Numbers and codes for municipalities and references used in the list of Odonata species from Amazonas state, Brazil. Where the municipality is unknown, only the state is provided.

Municipalities	Code	Number	References	Number
State of Amazonas (municipality not informed)	AMZ	-	Heckman 2006	1
Manaus	MAO	1	Pinto 2019	2
Presidente Figueiredo	PRF	2	Neiss 2012	3
Atalaia do Norte	ATA	3	Belle 1973	4
Barcelos	BAR	4	Belle 1983	5
Benjamin Constant	BEC	5	Belle 1984	6
Beruri	BER	6	Belle 1989	7
Borba	BOR	7	Belle 1994	8
Careiro/Careiro da Várzea	CAR	8	Belle 1998	9
Coari	COA	9	Bick & Bick 1985	10
Eirunepé	EIR	10	Bick & Bick 1986	11
Fonte Boa	FOB	11	Bick & Bick 1988	12
Guajará	GJR	12	Borror 1931	13
Humaitá	HMT	13	Borror 1942	14
Iranduba	IRN	14		
Itacoatiara	ITA	15	Calvert 1908	15
Juruá	JUR	16	Costa & Oldrini 2003	16
Manacapuru	MPU	17	Costa & Santos 1997	17
Manicoré	MNE	18	Costa 1990	18
Maués	MAU	19	Costa et al. 2002	19
Nhamundá	NHA	20	Lencioni 2005	20
Novo Airão	NAI	21	De Marco 1998	21

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Continuation...

Municipalities	Code	Number	References	Number
Novo Aripuanã	NRP	22	De Marmels & Rácenis 1982	22
Parintins	PAR	23	De Marmels 1987	23
Rio Preto da Eva	RPE	24	De Marmels 1989	24
Santa Isabel do Rio Negro	SIR	25	De Marmels 2001	25
Santo Antônio do Içá	SAI	26	De Marmels & Neiss 2011	26
São Gabriel da Cachoeira	SGC	27	De Marmels & Neiss 2013	27
São Paulo de Olivença	SPO	28	Dunkle 1991	28
Tabatinga	TAB	29	Fleck & Neiss 2012	29
Tapauá	TAP	30	Fulan et al. 2015	30
Tefé	TEF	31	Garrison & Ellenrieder 2006	31
Tonantins	TON	32	Garrison & Ellenrieder 2009	32
			Garrison & Ellenrieder 2015	33
			Garrison 1990	34
			Garrison 1999	35
			Garrison 2004	36
			Garrison 2006	37
			Garrison 2009	38
			Garrison 2014	39
			Geijskes 1963	40
			Geijskes 1970	41
			Geijskes 1984	42
			Guillermo-Ferreira et al. 2014	43
			Hamada & Oliveira 2003	44
			Kirby 1897	45
			Lencioni 2006	46
			Lencioni 2013	47
			Leonard 1977	48
			Machado & Lacerda 2017	49
			Machado 2002	50
			Machado 2007	51
			Machado 2009a	52
			Machado 2009b	53
			Machado 2012	54
			Machet 1990	55
			May 1991	56
			Monteiro-Júnior et al. 2013	57
			Montgomery 1940	58
			Neiss & Hamada 2010	59
			Neiss & Hamada 2016	60
			Neiss et al. 2008	61
			Neiss et al. 2013	62
			Pessacq 2014	63
			Pessacq et al. 2012	64
			Pinto & Carvalho 2010	65
			Pinto & Lamas 2010	66

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Municipalities	Code	Number	References	Number
			Pinto & Lamas 2011	67
			Pinto 2013	68
			Pujol-Luz & Fonseca 1997	69
			Ris 1911	70
			Ris 1930	71
			Rodrigues et al. 2016	72
			Rodríguez et al. 2015	73
			Santos & Machado 1960	74
			Santos 1954	75
			Santos 1961	76
			Santos 1967	77
			Santos 1970a	78
			Santos 1970b	79
			Schmidt 1952	80
			Spindola et al. 2001	81
			St. Quentin 1973	82
			Tennessen 2015	83
			Torreias et al. 2008	84
			von Ellenrieder & Garrison 2003	85
			von Ellenrieder & Garrison 2008	86
			Vilela et al. 2018	87
			von Ellenrieder 2008	88
			von Ellenrieder 2009	89
			von Ellenrieder 2013	90
			Walker 2009	91
			Williamson & Williamson 1924b	92
			Williamson & Williamson 1924a	93
			Williamson 1923	94
			Species Link website	95
			Neiss & Hamada 2012	96
			Juen & De Marco 2011	97
			Juen 2011	98
			Vilaça 2017	99
			Heckman 2008	100
			De Marco-Júnior et al. 2015	101
			Ris 1910	102
			Invertebrates Collection (INPA)	103
			Neiss & De Marmels 2017	104
			Vilela et al. 2019	105

Rio de Janeiro, 280 species (Costa & Santos 2000), Minas Gerais, 269 species (Vilela et al. 2020), São Paulo, 251 species (Costa et al. 2000), Mato Grosso do Sul, 209 species (Koroiva et al. 2017; Rodrigues et al. 2018), Rio Grande do Sul, 183 species (Pires et al. 2019), Espírito Santo, 180 species (Costa & Oldrini 2005), and Goiás and the Federal District, 152 species (Nóbrega & De Marco 2011).

We highlight that five species were not included in the results due to imprecise information. Despite being cited for Amazonas state in Heckman (2008), in the original description of *Planiplax machadoi* Santos, 1949, Santos (1949) states that the species is present in "Amazonas", but in the text the author explains that specimens came from Pará state. Similar problem occurs with *Erythrodiplax juliana* Ris, 1911 and *Erythrodiplax latimaculata* Ris, 1911. Borror (1942) states that these species are present in Amazonas state; however, the specimens were collected in Monte Roraima and Uraricoera, respectively, which currently belong to Roraima state. Finally,

Table 2. Odonata species recorded for Amazonas State, Brazil. For references and municipalities codes, please check Table 1.

Species	Municipalities	References
ZYGOPTERA		
Dicteriadidae		
Dicterias atrosanguinea Selys, 1853	MPU; MAO; PRF; NAI; RPE	3; 95; 1; 57; 87; 97; 103
Heliocharis amazona Selys, 1853	PRF; TEF	3; 28; 103
Calopterygidae		
Hetaerina amazonica Sjöstedt, 1918	ITA; BAR; MPU; MAO; PRF; NRP; RPE; NAI	3; 95; 1; 57; 97; 103
Hetaerina auripennis (Burmeister, 1839*)*	AMZ	100
Hetaerina caja (Drury, 1773*)*	BAR	3; 103
Hetaerina laesa Hagen in Selys, 1853	BAR	3; 103
Hetaerina medinai Rácenis, 1968	BAR	3; 100; 103
Hetaerina moribunda Hagen in Selys, 1853	MAO; NAI; PRF; RPE; MPU	3; 100; 57; 34; 97
Hetaerina sanguinea Selys, 1853	MAO	3; 95; 100; 57; 103
Hetaerina westfalli Rácenis, 1968	BAR; MPU; MAO; RPE; NAI	3; 100; 34; 103
Mnesarete aenea (Selys, 1853*)*	BER	37; 100
Mnesarete astrape De Marmels, 1989	MPU; MAO; PRF; RPE; BAR; NAI	3; 95; 100; 37; 103
*Mnesarete cupraea (*Selys, 1853*)*	BAR; PRF; RPE; SPO; MAO	3; 95; 100; 37; 103
Mnesarete loutoni Garrison, 2006	SPO	1; 37; 46
Polythoridae		
*Chalcopteryx rutilans (*Rambur 1842*)*	NRP	3
Chalcopteryx scintillans McLachlan, 1870	BAR; ITA; MPU; MAO; PRF; RPE; NAI; BEC; SGC; SPO	3; 95; 1; 98; 43; 74; 57; 103
Chalcopteryx seabrai Santos & Machado, 1961	PRF	3; 103
Euthore fasciata (Hagen in Selys, 1853)	AMZ	100
Polythore aurora (Selys, 1879)	TEF	100; 11; 20
Polythore batesi (Selys, 1879)	SPO	100; 11; 20
Polythore beata (McLachlan, 1869)	FOB	100; 11; 20
Polythore picta (Rambur, 1842)	TEF	100; 10; 20
Polythore procera (Selys, 1869)	AMZ	100; 20
Polythore vittata (Selys, 1869)	CAR; PRF; BOR; FOB; MNE; SPO; TEF	3; 100; 11; 20
Philogeniidae		
Philogenia margarita Selys, 1862	TEF	12; 100
Philogenia silvarum Ris, 1918	AMZ	100
Rimanellidae		
Rimanella arcana (Needham, 1933)	PRF	3; 100; 20; 44; 103
Calopterygoidea ***incertae sedis group 3***		
Dimeragrion percubitale Calvert, 1913	BAR	3; 103
Heteragrionidae		
Heteragrion angustipenne Selys, 1886	TAP	100; 105
Heteragrion bariai De Marmels, 1989	PRF; MAO	3; 95; 103
Heteragrion ictericum Williamson, 1919	MAO; RPE; MPU	95; 100; 47; 57
Heteragrion icterops Selys, 1862	MAO; NAI; RPE	3; 100; 23; 103
Heteragrion silvarum Sjöstedt, 1918	MAO	95; 100; 23; 47; 97
Oxystigma cyanofrons Williamson, 1919	NAI; PRF; RPE; MAO	3; 95; 39; 103
Oxystigma petiolatum (Selys, 1862)	BAR; ITA; MPU; NAI; PRF; RPE; MAO	95; 3; 39; 57; 97

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Megapodagrionidae		
Megapodagrion megalopus (Selys, 1862)	BAR; TAP; SGC; COA	3; 100; 99; 25; 103
Lestidae		
Lestes falcifer Sjöstedt, 1918	BAR	3; 100; 103
Perilestidae		
Perilestes attenuatus Selys, 1886	BAR; MAO; NAI; PRF	3; 95; 100; 59; 92; 57; 103
Perilestes bispinus Kimmins, 1958	AMZ	100; 20
Perilestes fragilis Hagen in Selys, 1862	AMZ	100
Perilestes gracillimus Kennedy, 1941	MAO	95; 100
Perissolestes cornutus (Selys, 1886)	TEF; SPO	100; 20; 80
Perissolestes flinti De Marmels, 1988	BAR	3; 103
Perissolestes paprzyckii Kennedy, 1941	AMZ	100; 20
Platystictidae		
Palaemnema brasiliensis Machado, 2009	BAR; PRF	3; 60; 103
Coenagrionidae		
Acanthagrion adustum Williamson, 1916	MAO; SIR	95; 100; 48; 57; 46
Acanthagrion amazonicum Sjöstedt, 1918	MAO	95; 100; 48; 46
Acanthagrion apicale Selys, 1876	BAR; HMT; MAO	3; 30; 54; 103
Acanthagrion chararum Calvert, 1909	BAR	3; 103
Acanthagrion chicomendesi Machado, 2012	SIR; BEC; BAR; TEF; SPO	54
Acanthagrion cuyabae Calvert, 1909	MAO	3; 103
Acanthagrion flaviae Machado, 2012	ATA	54
Acanthagrion kaori Machado, 2012	MAO	54
Acanthagrion minutum Leonard, 1977	SGC	3; 103
Acanthagrion phallicorne Leonard, 1977	MAO	3; 103
Acanthagrion rubrifrons Leonard, 1977	MAO	100; 48; 46
Acanthallagma caeruleum Williamson & Williamson, 1924	TAP	100; 99; 93; 46
Aeolagrion dorsale (Burmeister, 1839)	MAO	2; 100; 57; 46
Aeolagrion inca (Selys, 1876)	AMZ	2; 100; 46
Amazoneura ephippigera (Selys, 1886)	TEF	100; 64
Argia bicellulata (Calvert, 1909)	MAO	3; 57; 103
Argia botacudo Calvert, 1909	MAO	95
Argia collata Selys, 1865	AMZ	100
Argia cuneifera Garrison & von Ellenrieder, 2015	BAR	2; 33
Argia euphorbia Fraser, 1946	BAR; NAI; MPU; TAP	2; 100; 33; 46
Argia fumigata Hagen in Selys, 1865	MAO; MPU; RPE; BAR; PRF	95; 2; 100; 33; 46
Argia gemella Garrison & von Ellenrieder, 2015	MAO; BAR; PRF; RPE	95; 2; 33
Argia hasemani Calvert, 1909	MAO	100; 46; 97
Argia impura Rambur, 1842	AMZ	100
Argia indicatrix Calvert, 1902	MAO; RPE; PRF	3; 95; 2; 100; 33; 57; 46; 97; 103
Argia infumata Selys, 1865	MPU; TEF; SPO; MNE; TON; NAI	3; 2; 100; 33; 46; 103
Argia insipida Hagen in Selys, 1865	MPU; MAO; PRF; BAR	3; 2; 100; 33; 46; 103
Argia loutoni Garrison & von Ellenrieder, 2015	TAP; BAR; MAU	2; 33
Argia meioura Garrison & von Ellenrieder, 2015	MAO; MPU; PRF	2; 33

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Argia mollis Hagen in Selys, 1865	AMZ	100; 46
Argia oculata Hagen in Selys, 1865	BAR; PRF; NAI; MAO	2; 100; 33; 46; 97
Argia palmata Garrison & von Ellenrieder, 2015	MAO	2; 33
Argia pulla Hagen in Selys, 1865	MAO	2; 33
Argia reclusa Selys, 1865	AMZ	100; 46
Argia subapicalis Calvert, 1909	MAO	97
Argia thespis Hagen in Selys, 1865	MAO	97; 46
Argia tinctipennis Selys, 1865	AMZ	100; 46
Argia translata Hagen in Selys, 1865	AMZ	2;
Bromeliagrion rehni Garrison, 2005	MAO	3; 95; 100; 84; 46; 103
Calvertagrion charis Tennessen, 2015	AMZ	2; 83;
Calvertagrion minutissimum (Selys, 1876)	AMZ	2; 100; 46
Denticulobasis ariken Machado, 2009	MAO	3; 103
Dolonagrion fulvellum (Selys, 1876)	AMZ	46
Drepanoneura muzoni von Ellenrieder & Garrison, 2008	BAR	3; 103
Epipleoneura capilliformis (Selys, 1886)	MPU; MAO; NAI; PRF; RPE	3; 95; 63; 57; 103
Epipleoneura fuscaenea Williamson, 1915	NRP	3; 103
Epipleoneura haroldoi Santos, 1964	MPU; MAO; NAI; PRF	3; 100; 63; 103
Epipleoneura humeralis (Selys, 1886)	COA	3; 99; 63; 103
Epipleoneura kaxuriana Machado, 1985	MPU; MAO; NRP; PRF; RPE; NAI	3; 100; 63; 103
Epipleoneura lamina Williamson, 1915	BOR	63
Epipleoneura manauensis Santos, 1964	BAR; MPU; MAO; RPE; NAI	3; 95; 100; 98; 63; 57; 96; 103
Epipleoneura metallica Rácenis, 1955	MAO	97
Epipleoneura spatulata Rácenis, 1960	BAR	3; 103
Epipleoneura tariana Machado, 1985	BAR	3; 100; 98; 63; 103
Epipleoneura uncinata De Marmels, 1989	BAR	3; 103
Epipotoneura nehalennia Williamson, 1915	MAO	3; 95; 64; 86; 103
Forcepsioneura itatiaiae (Santos, 1970)	AMZ	99; 98
Homeoura nepos (Selys, 1876)	MAO	100; 88; 46
Homeoura obrieni von Ellenrieder, 2008	MAO	88
Hylaeonympha magoi Rácenis, 1968	AMZ	2
Inpabasis machadoi Santos, 1961	MPU; MAO; NAI	3; 2; 100; 76; 46; 103
Inpabasis rosea (Selys, 1877)	MPU; MAO	3; 95; 2; 100; 76; 46; 103
Ischnura capreolus (Hagen, 1861)	MPU; MAO; SGC	3; 95; 57; 97; 103
Ischnura fluviatilis Selys, 1876	MAO; PRF	3; 91; 103
Leucobasis candicans Rácenis, 1959	AMZ	2
Mecistogaster linearis (Fabricius, 1777)	BAR; MAO; NAI; PRF	3; 72; 103
Mecistogaster lucretia (Drury, 1773)	MAO; PRF	3; 100; 97; 103
Mesoleptobasis acuminata Santos, 1961	IRN; CAR	95; 100; 46
Mesoleptobasis cantralli Santos, 1961	BAR; SGC	3; 2; 100; 98; 32; 103
Mesoleptobasis elongata Garrison & von Ellenrieder, 2009	CAR	2; 32
Mesoleptobasis incus Sjöstedt, 1918	MPU; NAI; BOR; TEF	3; 2; 100; 98; 99; 32; 46; 103
Metaleptobasis amazonica Sjöstedt, 1918	MAO	1; 32; 46
Metaleptobasis brysonima Williamson, 1915	PRF	2; 90

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Metaleptobasis paludicola von Ellenrieder, 2013	MAO	95; 2; 90
Metaleptobasis tridentigera von Ellenrieder, 2013	NAI; MPU	2; 90
Microstigma anomalum Rambur, 1842	MAO	95; 100; 97
Microstigma maculatum Hagen in Selys, 1860	MAO; PRF	3; 100; 61; 103
Microstigma rotundatum Selys, 1860	BAR; MPU; MAO; PRF; SGC; TEF; SPO; NAI	3; 95; 100; 80; 103
Neoneura bilinearis Selys, 1860	BAR	3; 103
Neoneura desana Machado, 1989	COA	3; 100; 98; 103
Neoneura luzmarina De Marmels, 1989	BAR; NRP; PRF; RPE; SGC; MAO	3; 100; 35; 103
Neoneura mariana Williamson, 1917	MAO	95
Neoneura rufithorax Selys, 1886	COA; ATA	3; 100; 35; 50; 103
Neoneura sylvatica Hagen in Selys, 1886	AMZ	51
Oxyagrion terminale Selys, 1876	AMZ	2; 100; 4
Phasmoneura exigua (Selys, 1886)	ITA; MPU; MAO; NAI; PRF; RPE	3; 95; 100; 98; 57; 103
Phoenicagrion flammeum (Selys, 1876)	MAO; NAI	3; 95; 2; 100; 98; 103
Platystigma buckleyi (McLachlan, 1881)	AMZ	100; 49
Protoneura scintilla Gloyd, 1939	BAR	3; 103
Protoneura tenuis Selys, 1860	MAO; PRF	3; 103
Psaironeura bifurcata (Sjöstedt, 1918)	MPU; MAO; PRF; NAI	3; 100; 36; 97; 103
Psaironeura tenuissima (Selys, 1886)	MPU; MAO; PRF; RPE	3; 95; 100; 99; 103
Telebasis abuna Bick & Bick, 1995	IRN	95
Telebasis dunklei Bick & Bick, 1995	IRN; CAR	95
Telebasis griffinii (Martin, 1896)	IRN	95; 2
Telebasis inalata (Calvert, 1961)	AMZ	2
Telebasis obsoleta (Selys, 1876)	IRN; CAR	95; 2; 38; 46
Telebasis sanguinalis Calvert, 1909	AMZ	100; 46
Telebasis simulata Tennessen, 2002	PRF; MAO	3; 95; 2; 100; 38; 46; 103
Tuberculobasis inversa (Selys, 1876)	TEF	2; 99; 52
Tukanobasis corbeti Machado, 2009	SGC	2; 53
ANISOPTERA		
Aeshnidae		
Anax amazili (Burmeister, 1839)	AMZ	2
Anax concolor Brauer, 1865	BAR; RPE	3; 1; 103
Castoraeschna tepuica De Marmels, 1989	BAR	3; 103
Coryphaeschna adnexa (Hagen, 1861)	BEC	1; 78
Coryphaeschna amazonica De Marmels, 1989	PRF	3; 2; 103
Coryphaeschna viriditas Calvert, 1952	MAO	95
Gynacantha auricularis Martin, 1909	BAR; MAO; PRF	3; 26; 103
Gynacantha dryadula Neiss & De Marmels, 2017	BAR; MAO	104
Gynacantha gracilis (Burmeister, 1839)	BAR; MAO	3; 1; 103
Gynacantha klagesi Williamson, 1923	MPU	3; 103
Gynacantha litoralis Williamson, 1923	MAO; SGC	3; 1; 103
Gynacantha membranalis Karsch, 1891	MAO; PRF	3; 103
Gynacantha mexicana Selys, 1868	MAO	3; 103
Gynacantha nervosa Rambur, 1842	MAO	95
Gynacantha tenuis Martin, 1909	PRF	3; 103

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Neuraeschna calverti Kimmins, 1951	PRF; MAO	3; 1; 7; 103
Neuraeschna capillata Machet, 1990	MAO	55
Neuraeschna claviforcipata Martin, 1909	BAR; MAO	1; 27; 7
Neuraeschna costalis (Burmeister, 1839)	AMZ	1
Neuraeschna harpya Martin, 1909	AMZ	1; 98
Rhionaeschna planaltica (Calvert, 1952)	BAR	3; 103
Staurophlebia gigantula Martin, 1909	AMZ	1
Staurophlebia wayana Geijskes, 1959	PRF	3; 103
Triacanthagyna dentata (Geijskes, 1943)	AMZ	85
Triacanthagyna ditzleri Williamson, 1923	MAO; SGC	3; 103
Triacanthagyna satyrus (Martin, 1909)	MAO	3; 103
Triacanthagyna septima (Selys in Sagra, 1857)	MAO	95; 85
Gomphidae		
Agriogomphus sylvicola Selys, 1869	PRF; TEF	3; 99; 82; 103
Aphylla barbata Belle, 1994	AMZ	1
Aphylla brasiliensis Belle, 1970	AMZ	2; 1
Aphylla dentata Selys, 1859	AMZ	2
Aphylla edentata Selys, 1869	AMZ	2; 99
Aphylla molossus Selys, 1869	AMZ	2
Cacoides latro (Erichson in Schomburgk, 1848)	PRF	3; 103
Desmogomphus tigrivensis Williamson, 1920	PRF; RPE; MAO	3; 82; 103
Diaphlebia angustipennis Selys, 1854	MAO; PRF	3; 95; 2; 1; 57; 97; 103
Epigomphus hylaeus Ris, 1918	MAO; PRF; NAI	3; 1; 82; 103
Gomphoides infumata (Rambur, 1842)	MAO	82
Peruviogomphus bellei Machado, 2005	AMZ	1; 99
Phyllocycla armata Belle, 1977	MAO; RPE; PRF	3; 103
Phyllocycla diphylla (Selys, 1854)	AMZ	1
Phyllocycla modesta Belle, 1970	MAO	95
Phyllocycla neotropica Belle, 1970	PRF	3; 103
Phyllocycla ophis (Selys, 1869)	AMZ	1
Phyllocycla pegasus (Selys, 1869)	AMZ	1
Phyllocycla volsella (Calvert, 1905)	MAO	95
Phyllogomphoides andromeda (Selys, 1869)	AMZ	98
Phyllogomphoides angularis Belle, 1982	AMZ	1
Phyllogomphoides atlanticus (Belle, 1970)	PRF	3; 103
Phyllogomphoides major Belle, 1984	SGC	3; 103
Phyllogomphoides pedunculus Belle, 1984	AMZ	2; 1
Phyllogomphoides pseudangularis Belle, 1994	COA	2; 1; 99; 8
Phyllogomphoides selysi (Navás, 1924)	AMZ	95; 2; 1; 6
Phyllogomphoides undulatus (Needham, 1944)	MAO; PRF; SGC	3; 103
Progomphus amazonicus Belle, 1973	MPU	2; 1; 4
Progomphus angeloi Belle, 1994	AMZ	2; 1; 99
Progomphus approximatus Belle, 1966	MAO; PRF	3; 103
Progomphus cf. boliviensis Belle, 1973	RPE	3; 103
Progomphus cf. phyllochromus Ris, 1918	PRF	3; 103
Progomphus cf. tibialis Belle, 1973	SGC	3; 103

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Progomphus delicatus Belle, 1973	NAI; PRF	3; 103
Progomphus fassli Belle, 1973	AMZ	1
Progomphus guyanensis Belle, 1966	MAO; PRF	3; 103
Progomphus intricatus Hagen in Selys, 1858	AMZ	2
Progomphus maculatus Belle, 1984	MAO	3; 103
Progomphus perpusillus Ris, 1918	AMZ	2; 1; 4
*Progomphus pijpers*i Belle, 1966	AMZ	2
Zonophora batesi Selys, 1869	AMZ	2; 1; 99
Zonophora calippus Selys, 1869	TEF	2; 1; 99; 5
Zonophora nobilis Belle, 1983	SGC	2; 1; 5
Zonophora supratriangularis Schmidt, 1941	MAO; TEF	95; 2; 1; 99; 5
Zonophora wucherpfennigi Schmidt, 1941	MAO; PRF; RPE	3; 2; 1; 99; 103
Oxygastridae		
Neocordulia batesi (Selys, 1871)	SPO	56; 66
Corduliidae		
Aeschnosoma auripennis Geijskes, 1970	MPU; MAO; PRF; NAI; BAR	66; 3; 2; 62; 21; 103
Aeschnosoma forcipula Hagen in Selys, 1871	BAR; MPU; MAO; NAI; PRF	3; 95; 2; 1; 41; 103
Aeschnosoma hamadae Fleck & Neiss, 2012	MAO; PRF; NAI	3; 2; 29; 103
Paracordulia sericea (Selys, 1871)	BAR	2; 29; 3; 103
Libelluloidea *incertae sedis*		
Lauromacromia cf. dubitalis (Fraser, 1939)	MAO	65
Libellulidae		
Anatya guttata (Hoffmansegg in Schomburgk, 1848)	COA	70
Argyrothemis argentea Ris, 1911	MAO; MPU; NAI	3; 16
Brachymesia herbida (Gundlach, 1889)	MAO; PRF	95; 98; 91; 21; 15
Brechmorhoga nubecula (Rambur, 1842)	BAR; MAO; PRF	3; 103
Brechmorhoga praedatrix Calvert, 1909	PRF	3; 103
Dasythemis esmeralda Ris, 1910	PRF; RPE; MAO	3; 95; 57; 103
Dasythemis essequiba Ris, 1919	AMZ	1
Diastatops estherae Montgomery, 1940	BAR; MAO; MAU; SGC; TON	3; 1; 45; 58; 101; 103
Diastatops maxima Montgomery, 1940	PRF; TEF	1; 99; 58; 101
Diastatops nigra Montgomery, 1940	BAR; MAO; MAU; PAR; PRF; SGC	3; 1; 98; 58; 101; 103
Diastatops obscura (Fabricius, 1775)	MAO	102
Diastatops pullata (Burmeister, 1839)	BAR; PRF; MAU; MAO; MPU; SPO	3; 1; 98; 99; 58; 103
Elasmothemis williamsoni (Ris, 1919)	MAO; PRF	3; 103
Elga leptostyla Ris, 1911	NAI; MAO; NRP; PRF	3; 103
Erythemis attala (Selys in Sagra, 1857)	NAI; PRF; MAO; BEC; PAR; SPO	3; 95; 2; 99; 73; 15; 68; 97; 103
Erythemis carmelita Williamson, 1923	BEC; TEF	1; 94; 68
Erythemis haematogastra (Burmeister, 1839)	MAO; BAR; PRF; PAR; MNE; BEC	3; 95; 21; 91; 73; 15; 68; 103
Erythemis mithroides (Brauer, 1900)	PAR	73
Erythemis peruviana (Rambur, 1842)	IRN; NRP; MAO; PAR; ITA	3; 95; 98; 45; 73; 15; 68; 103
Erythemis plebeja (Burmeister, 1839)	MAO	73
Erythemis vesiculosa (Fabricius, 1775)	IRN; MAO; NAI; PRF; MNE	3; 21; 91; 73; 15; 68; 103
Erythrodiplax amazonica Sjöstedt, 1918	BAR; PRF; MAO; MAO	3; 95; 2; 1; 14; 103
Erythrodiplax anatoidea Borror, 1942	MAO; PRF	3; 103

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Erythrodiplax attenuata (Kirby, 1889)	MAO; MNE	1; 98; 99; 14; 70
Erythrodiplax basalis (Kirby, 1897)	COA; MPU; MAO; RPE; NRP	3; 95; 1; 57; 14; 103
Erythrodiplax castanea (Burmeister, 1839)	MAO; MPU; PRF; NAI; RPE	3; 95; 1; 57; 103
Erythrodiplax famula (Erichson in Schomburgk, 1848)	BAR; MAO; PRF; RPE	3; 57; 14; 103
Erythrodiplax fusca (Rambur, 1842)	MPU; MAO; PRF; NRP; RPE; ITA; NAI	3; 95; 1; 99; 57; 103
Erythrodiplax lativittata Borror, 1942	MPU; MAO; PRF; RPE; SGC; NAI; NRP	3; 98; 99; 21; 103
Erythrodiplax laurentia Borror, 1942	PRF	3; 103
Erythrodiplax longitudinalis (Ris, 1919)	AMZ	1
Erythrodiplax solimaea Ris, 1911	TEF	1; 99; 14
Erythrodiplax umbrata (Linnaeus, 1758)	MPU; MAO; PRF; SPO; COA	3; 95; 1; 99; 21; 14; 103
Erythrodiplax unimaculata (de Geer, 1773)	MAO; ITA; MNE; TEF; SPO	95; 1; 99; 14
Erythrodiplax venusta (Kirby, 1897)	RPE; MAO	3; 95; 1; 14; 103
Fylgia amazonica Kirby, 1889	MAO; NAI; PRF	3; 95; 97; 103
Gynothemis pumila (Karsch, 1890)	BAR; MPU; MAO; NRP; PRF; RPE; NAI	3; 57; 31; 95; 103
Idiataphe amazonica (Kirby, 1889)	AMZ	1
Idiataphe cubensis (Scudder, 1866)	PRF	3; 103
Libellula herculea Karsch, 1889	BAR; PRF; MAO	3; 95; 103
Macrothemis brevidens Belle, 1983	MPU; PRF	3; 103
Macrothemis idalia Ris, 1919	BAR; PRF; MPU	3; 103
Macrothemis newtoni Costa, 1990	MAO	1; 18
Macrothemis nobilis Rácenis, 1957	AMZ	1
Macrothemis rupicola Rácenis, 1957	BAR	3; 103
Macrothemis taurepan De Marmels, 2008	BAR	3; 103
Miathyria marcella (Selys in Sagra, 1857)	MPU; IRN; MAO	3; 98; 21; 15; 102; 103
Miathyria simplex (Rambur, 1842)	PRF	3; 21; 103
Micrathyria artemis Ris, 1911	MAO	1; 19
Micrathyria atra (Martin, 1897)	PRF; MAO; ITA	3; 95; 1; 19; 68; 103
Micrathyria cambridgei Kirby, 1897	AMZ	1
Micrathyria catenata Calvert, 1909	NHA; MAO	1; 19; 24
Micrathyria hippolyte Ris, 1911	MAO	3; 103
Micrathyria laevigata Calvert, 1909	MNE	99; 75
Micrathyria pseudeximia Westfall, 1992	MAO	1; 19
Micrathyria romani Sjöstedt, 1918	MAO	1; 40
Micrathyria spinifera Calvert, 1909	MAO	3; 1; 103
Micrathyria venezuelae De Marmels, 1989	BAR	3; 103
Misagria calverti Geijskes, 1951	NAI	3; 103
Misagria divergens De Marmels, 1981	BAR	3; 103
Misagria parana Kirby, 1889	MAO	3; 95; 1; 103
Oligoclada abbreviata (Rambur, 1842)	BAR; MAO	3; 95; 1; 98; 13; 103
Oligoclada amphinome Ris, 1919	NRP; MAO	3; 95; 1; 13; 103
Oligoclada monosticha Borror, 1931	NRP; BAR	3; 103
Oligoclada pachystigma Karsch, 1890	BAR; COA	3; 42; 103
Oligoclada risi Geijskes, 1984	PRF; MAO	3; 103
Oligoclada sylvia (Kirby, 1889)	BAR; PRF	3; 1; 98; 99; 13; 67; 103
Oligoclada walkeri Geijskes, 1931	PRF; BAR	3; 98; 99; 13; 103
Oligoclada xanthopleura Borror, 1931	MAO	1; 13

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Orthemis aequilibris Calvert, 1909	MPU; MAO	3; 89; 103
Orthemis attenuata (Erichson in Schomburgk, 1848)	RPE	3; 103
Orthemis biolleyi Calvert, 1906	MAO; NRP; PRF; RPE	3; 57; 102; 103
Orthemis cultriformis Calvert, 1899	SPO	1; 77
Orthemis discolor (Burmeister, 1839)	MPU; MAO; RPE; NAI	3; 103
Orthemis ferruginea (Fabricius, 1775)	MAO	15; 57
Pantala flavescens (Fabricius, 1798)	MPU; MAO; PRF	3; 2; 21; 57; 103
Perithemis bella Kirby, 1889	MAO; SPO	3; 1; 102; 103
Perithemis cornelia Ris, 1910	TEF	1; 99; 71
Perithemis electra Ris, 1930	BEC	79
Perithemis lais (Perty, 1834)	BAR; MAO; SGC	3; 2; 1; 98; 99; 91; 71; 103
Perithemis mooma Kirby, 1889	MAO	3; 103
Perithemis thais Kirby, 1889	BAR; PRF; BEC	3; 1; 81; 103
Rhodopygia cardinalis (Erichson in Schomburgk, 1848)	MAO	1; 68;
Rhodopygia geijskesi Belle, 1964	MAO; SAI	9; 68
Rhodopygia hollandi Calvert, 1907	AMZ	1
Tauriphila australis (Hagen, 1867)	MAO	3; 98; 103
Tholymis citrina Hagen, 1867	BAR; ITA; MAO; NRP; PRF; MNE	3; 95; 103
Tramea binotata (Rambur, 1842)	BAR	3; 103
Tramea calverti Muttkowski, 1910	RPE; ITA; PRF; MAO; TEF	3; 95; 2; 1; 99; 21; 22; 103
Tramea minuta De Marmels & Rácenis, 1982	BAR; SPO	3; 2; 1; 22; 103
Tramea rustica De Marmels & Rácenis, 1982	MAO	2; 22
Uracis fastigiata (Burmeister, 1839)	PRF; SPO; MAO; MNE; JUR; GJR; EIR; BEC; TAB	3; 1; 98; 99; 70; 17; 103
Uracis imbuta (Burmeister, 1839)	MAO; NRP; CAR; ATA; MNE; SPO; BEC; TAB; SGC	3; 95; 1; 98; 99; 57; 70; 17; 103
Uracis infumata (Rambur, 1842)	PRF; MAO; SPO; EIR	3; 1; 17; 103
Uracis ovipositrix Calvert, 1909	NAI; MAO; SPO; MNE; SGC	3; 95; 1; 98; 99; 70; 17; 103
Uracis siemensi Kirby, 1897	PRF; BAR; MAO; NRP; PAR; MNE; EIR; SPO	3; 95; 1; 99; 17; 103
Zenithoptera anceps Pujol-Luz, 1993	MAO; ITA	2; 69
Zenithoptera fasciata (Linnaeus, 1758)	MPU; PRF; MAO; BOR; ITA; PAR	3; 2; 57; 95; 69; 102; 103
Zenithoptera lanei Santos, 1941	NAI; PRF; ITA; MAO; TAB	3; 2; 98; 69; 103
Zenithoptera viola Ris, 1910	ITA	95; 2

Diastatops intensa Montgomery, 1940 and *Diastatops dimidiata* Montgomery, 1940 were registered for the floodplains of the Solimões-Amazonas rivers by Nessimian et al. (2008). Although most of their sampled sites were in the Amazonas state, there are some sites in Pará state as well, and authors do not present a detailed list of where each species was found.

Despite the significant increase in the number of species known from Amazonas, some regions remain poorly explored, such as municipalities in the southwest region of the state. Besides Guajará (code number 10) and Eirunepé (code number 12), there are no published species records from municipalities located on the border with Acre state. In addition, large municipalities also appear to be under-sampled. For example, São Gabriel da Cachoeira, the third largest municipality in Brazil (109,181 km²; IBGE 2019) with an area larger than Portugal, only has 20 recorded species. In this way, we suggest that new field expeditions should focus on such large municipalities and the 29 municipalities that presented no specimen records in our survey.

In general, knowledge about the Odonata order in Amazonas state has improved, especially in the last two decades. However, limitations on sampling still underestimate the number of odonates species, both for new species and new records. Therefore, this work recognizes the importance of the biological diversity in Amazonas state and the Amazonian Biome for species richness of Brazil and shows that we still do not entirely know the odonatofauna in the world's largest tropical forest.

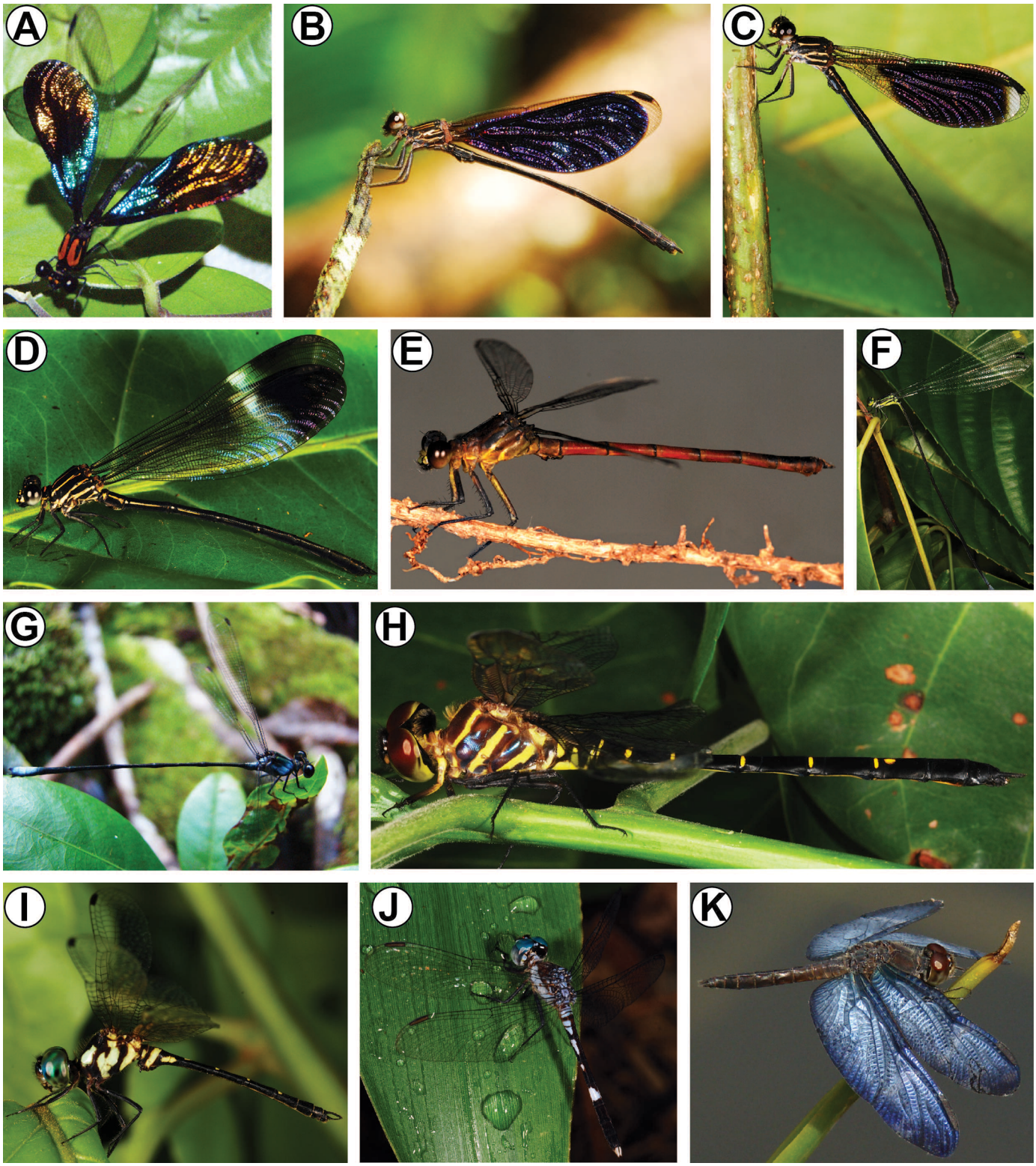


Figure 2. Some Odonata species recorded in Amazonas State, Brazil. A, *Chalcopteryx rutilans* (Rambur 1842); B, *Chalcopteryx scintillans* McLachlan, 1870; C, *Chalcopteryx seabrai* Santos & Machado, 1961; D, *Polythore vittata* (Selys, 1869); E, *Rimanella arcana* (Needham, 1933); F, *Mecistogaster linearis (*Fabricius, 1777); G, *Dimeragrion percubitale* Calvert, 1913; H, *Aeschnosoma hamadae* Fleck & Neiss, 2012; I, *Elga leptostyla* Ris, 1911; J, *Erythrodiplax anatoidea* Borror, 1942; K, *Zenithoptera lanei* Santos, 1941.

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Author Contributions

Ricardo Koroiva: Contribution to data collection and manuscript preparation; Substantial contribution in the concept and design of the study; Contribution to critical revision, adding intellectual content.

Ulisses Gaspar Neiss: Contribution to data collection and manuscript preparation; Substantial contribution in the concept and design of the study; Contribution to critical revision, adding intellectual content.

Günther Fleck: Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Neusa Hamada: Contribution to data collection and manuscript preparation; Contribution to critical revision, adding intellectual content.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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