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Inventory

Dragonflies and Damselflies in a region of the Triângulo Mineiro, Minas Gerais: checklist and taxonomic additions

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Abstract: Remaining freshwater systems are historically under threat mainly due to human activities such as agriculture and urbanization. The consequences of such activities are innumerous, and among them there is a decrease of suitable habitats for threatened fauna. In the Brazilian Cerrado, the odonatofauna of palm swamps and riparian forests are still poorly explored, a fact that difficult conservation efforts of the group. Thus, we performed an inventory in several urban and rural sites containing these phytophysiognomies in Uberlândia, Triângulo Mineiro region, western Minas Gerais state. In total, we found 101 Odonata species, seven families and 46 genera in the municipality, with 76 and 66 species, respectively, belonging to palm swamp and forest sites. From this diversity, eight species were first records in the state of Minas Gerais: *Neuraeschna claviforcipata* Martin, 1909, *Phyllocycla* cf. *medusa* Belle, 1988, *Diastatops intensa* Montgomery, 1940, *Oligoclada pachystigma* Karsch, 1890, *O. xanthopleura* Borror, 1931, *Angelagrion nathaliae* Lencioni, 2008, *Telebasis sanguinalis* Calvert, 1909 and *Telebasis simulacrum* (Calvert, 1909). We also sampled *Erythrodiplax ana* Guillermo-Ferreira & Vilela 2016, a species listed as endangered (EN) by the IUCN red list. Additionally, we include some taxonomic notes of Forcepsioneura machadorum females, a newly discovered species in the region. Our results contribute to the Odonata database in Brazil and highlights the importance inventories in poorly explored aquatic ecosystems.

Keywords: *Odonata; Cerrado; Brazil; inventory; female description.*

Libélulas de uma região do Triângulo Mineiro, Minas Gerais: lista de espécies e adições taxonômicas

Resumo: Os sistemas remanescentes de água doce estão historicamente ameaçados, principalmente devido às atividades humanas, como agricultura e urbanização. As consequências de tais atividades são inúmeras, e entre elas há a diminuição de habitats adequados para a fauna ameaçada. No cerrado brasileiro, a odonatofauna de veredas e matas ripárias ainda são pouco exploradas, fato que dificulta os esforços de conservação do grupo. Assim, realizamos um inventário em diversos pontos urbanos e rurais com essas fitofisionomias em Uberlândia, na região do Triângulo Mineiro, oeste de Minas Gerais. No total, foram encontradas 101 espécies de Odonata, sete famílias e 46 gêneros no município, com 76 e 66 espécies, respectivamente, pertencentes a pontos de veredas e de matas. Dessa diversidade, oito espécies foram os primeiros registros no estado de Minas Gerais: *Neuraeschna claviforcipata* Martin, 1909, *Phyllocycla* cf. medusa Belle, 1988, *Diastatops intensa* Montgomery, 1940, *Oligoclada pachystigma* Karsch, 1890, *O. xanthopleura* Borror, 1931, *Angelagrion nathaliae* Lencioni, 2008, T*elebasis sanguinalis* Calvert, 1909 e *Telebasis simulacrum* (Calvert, 1909). Nós também coletamos *Erythrodiplax ana* Guillermo-Ferreira & Vilela 2016, uma espécie listada como em perigo (EN) pela lista vermelha da IUCN. Além disso, incluímos algumas notas taxonômicas de fêmeas de *Forcepsioneura machadorum*, uma espécie recém-descoberta na região. Nossos resultados contribuem para o banco de dados Odonata no Brasil e destacam a importância dos inventários em ecossistemas aquáticos pouco explorados.

Palavras-chave: *Odonata; Cerrado; Brasil; inventário; descrição de fêmea.*

Introduction

Freshwater systems comprise a large part of the planet's biodiversity, although being also some of the most vulnerable ecosystems in the current global biodiversity crisis (Albert et al. 2020). The anthropic effects (e.g., deforestation, waste deposit and exotic species) in these environments modify aquatic and terrestrial integrity, endangering future populational stability of several species (Calvão et al. 2016, Reid et al. 2019, Araújo et al. 2020). Thus, to mitigate these impacts, it is important to fill biodiversity gaps as an initial step for determining conservationist actions in aquatic ecosystems. Surveys have helped to fill gaps for many freshwater organisms (Troia & McManamay 2017, Bolpagni et al. 2018, Guerra et al. 2020) as species distribution and cataloging (Wallacean and Linnean shortfalls, respectively) (Hórtal et al. 2015). However, these shortfalls are still predominant for some threatened and little-known groups, such as aquatic insects (Sánchez-Bayo & Wyckhuys 2019).

Odonata compose a small portion of aquatic insect, totalizing 6,300 species (Paulson & Schorr 2020) that occupies freshwater habitats associated to different vegetation types in almost all continents (Corbet 1980). Brazil holds circa of 30% of this diversity, with approximately 900 described species, being more than 20% of this number in endemism (Pinto 2020). Many odonate species are known to be endangered with the overexploitation in many regions of the country (ICMBio 2018, Araújo et al. 2020). This situation has encouraged great effort in preservation measures in the last years, including inventories in priority regions (e.g., Cerrado) and species conservation categorizations (De Marco & Viana 2005, Koroiva et al. 2017, Rodrigues & Roque 2017, Dalzochio et al. 2018a, Bastos et al. 2019, Garcia Junior et al. 2021, Koroiva et al. 2020, Vilela et al. 2020a). Despite this progress, distribution and taxonomic gaps are still frequently reported problems in the literature, even in explored regions. For example, more than one third of odonate fauna from Serra da Bodoquena and some regions of southeast and west of Minas Gerais could not be classified in an IUCN red list category due to data deficiency (Koroiva et al. 2017, Ávila Júnior et al. 2020, Vilela et al. 2020a).

The majority of odonate studies are concentrated in the Cerrado, one of the Brazilian hotspots (Myers et al. 2000, Miguel et al. 2017). Nonetheless, new recent taxonomic and distribution discoveries have been indicating gaps in little explored and endangered phytophysiognomies of this biome, such as riparian forest (including gallery forest) and veredas (i.e., palm swamps) (Rodrigues et al. 2018, Barbosa et al. 2019, Palacio et al. 2020, Lozano & Rodrigues 2018). Both formations are associated with important water courses to local and regional biodiversity and hydrographic maintenance (Ribeiro & Walter 1998, Latrubesse et al. 2019). Despite this similarity, these environments differ in aquatic and terrestrial characteristics, including plant community composition (Oliveira-Filho & Ratter 2002). Water bodies of palm swamps are mainly composed by a variety of macrophytes species surrounded by terrestrial grassy-shrubby plants, generally associated to "buriti" palms [Mauritia flexuosa L.f. (Arecaceae)], while large canopy trees cover riparian zones in forests (Ribeiro & Walter 1998, Araújo et al. 2002, Oliveira-Filho & Ratter 2002). These characteristics, including aquatic types (i.e., lotic and lentic systems), are determinant for the diversity of dragonflies of the Cerrado. For example, the low solar radiation in extensive areas of closed canopy riparian forests is essential for adults of small size Zygoptera (De Marco et al. 2015), while open palm swamps favor the presence of endemic macrophytes (Araújo et al. 2002), which are sites for oviposition and development of some heliothermic dragonflies (Vilela et al. 2016, Brito et al. 2020). In relation to types of aquatic systems, lotic and lentic environments have unique physical-chemical, biotic and geographic distribution characteristics that have resulted in distinct dragonfly diversifications of these habitats during the evolutionary history of the group (Letsch et al. 2016). Consequently, the composition of species between lotic and lentic bodies of water are distinct, differing at broader taxonomic levels, such as family (Vilela et al. 2020a, Pires et al. 2019). Such habitat heterogeneity is known to harbor different Odonata communities (Dutra & De Marco 2015), reflecting in great species diversity and endemism (Calvert 1909, Guillermo-Ferreira et al. 2016, Vilela et al. 2016, 2018).

Despite the habitat heterogeneity, the diversity of palm swamps and riparian forests are highly threatened by human activities (Sano et al. 2010, Colli et al. 2020). Modifications generated by land use, such as monoculture, livestock and urban areas, replace native vegetation by exotic species and impermeable surfaces (i.e., buildings), resulting in local microclimate change and other aquatic and terrestrial physicochemical characteristics of riparian zones (McKinney 2002, Wen et al. 2017, Brasil et al. 2021). These effects convert natural environments into areas with homogeneous biotic and abiotic characteristics that also affect the diversity and composition of odonates (Calvão et al. 2018, Renner et al. 2018, Borges et al. 2021, Sganzerla et al. 2021). In anthropic areas, sensitive species (e.g., some Zygoptera) are substituted by generalist groups with tolerant traits (e.g., multivoltine, r-strategist and heliothermic), often simplifying odonate communities (De Marco et al. 2015, Dalzochio et al. 2018b, Oliveira-Júnior & Juen 2019). Considering the vulnerability of many odonates species to environmental degradation, more inventories are needed to fill gaps about the diversity in these phytophysiognomies, even in anthropized areas.

Minas Gerais state present a great area composed by riparian forests and palm swamps, which are constantly decreasing with the intensification of urbanization and agriculture (Ratter et al. 1997, Velazco et al. 2019). The state has currently over 304 dragonfly species inventoried (Vilela 2020), with more than 20 new records and new species recently reported (Ávila Júnior et al. 2020, Vilela et al. 2020a, Vilela et al. 2020b). Mostly of these new data were obtained in poorly explored areas, such as Uberlândia, in Triângulo Mineiro region, western of the Minas Gerais state. Three inventories in this municipally found more than 60 species of adult dragonflies in just two palm swamp areas and in a degraded riparian forest (Vilela et al. 2016, Barbosa et al. 2019, Vilela et al. 2020a). Then, it is expected that a robust checklist can record a greater diversity of local dragonflies, since previous inventories explored few portions of the municipality territory. Moreover, some new species were also discovered in region, opening new opportunities for taxonomic studies. This is the case of *Forcepsioneura machadorum* Vilela, Venâncio and Santos, 2020, which was recently discovered, but species description was based only on males (Vilela et al. 2020b), remaining a taxonomic description of the female.

Thus, the main objective of this study is to conduct an inventory of dragonfly fauna in riparian forests and palm swamps of Uberlândia. As aquatic environments of the municipality are mainly represented by these types of vegetation, we will also indirectly perform a general inventory of the municipality. In addition, we also present some taxonomic notes on the females of *F. machadorum*. Our study aims to complement the state's Odonata record and distribution, contributing to reduce Linnean and Wallacean shortfalls.

Material and Methods

1. Study area

The territory of Uberlândia (18º55'23" S, 48º17'19" W) is approximately 4,115 km² (IBGE 2020), consisting of typical Cerrado biome vegetation and areas with agricultural (mainly livestock farming and monocultures) and urban activities. Local remnants of riparian vegetation consist of riparian forests, palm swamps and humid fields are located in areas with some type of protection (Cardoso & Schiavini 2002, Maywald & Marçal-Júnior 2013). The hydrography is represented by sub-basins and microbasins of the Paranaíba River, such as the Araguari and Uberabinha basins (Rosa et al. 2019). Part of this water is used for urban supply and agricultural activities in the municipality, which causes the pollution of some courses (Netto et al. 2011). Climate of region is AW type, according to the Köppen classification, characterized by hot and rainy summers (October-March) and dry and cold winters (April-September) (Alvares et al. 2013). The local mean annual temperature and rainfall are approximately 22ºC and 1,500 mm, respectively.

2. Sampling

We performed the samplings in 111 water bodies in the municipality (Figure 1). These localities consisted in lentic (ponds and lakes; n = 50) and lotic habitats up to third order (springs, streams and rivers; n = 61), located in or next to palm swamps (n = 54) and riparian forests (n = 56) in urban and rural areas (Figure 2; Table1). Site 57 was located in a highly urbanized area and the nearest riparian vegetation was more than 1.5 Km away from this point. Therefore, we did not classify this site with a phytophysiognomy type and we excluded it from the phytophysiognomy analyses (see below). The urbanization class was determined according to urban limits of municipality. Two ponds (sites 3 and 57) and a small lotic section (site 89) were temporary and the others were permanent.

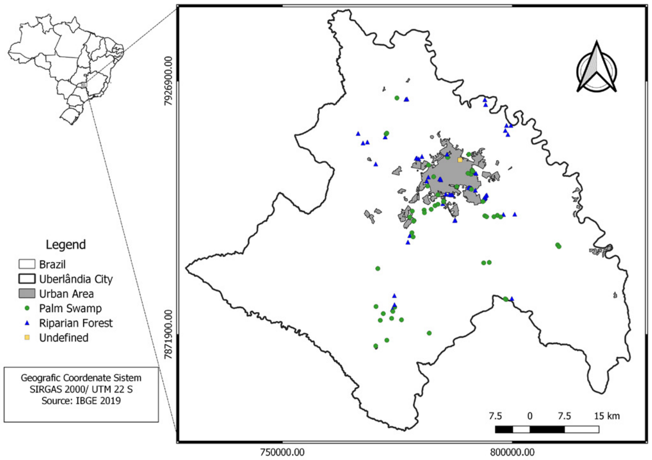

Figure 1. Sampled sites in Uberlândia, Minas Gerais, Brazil. Detailed information about the sites is presented in Table 1.

Collections in urban area were performed in parks with remnants of native vegetation and private lands. In rural area, seven localities were sampled in Conservation Units (sites 86-89, 90 and 92), and remaining areas in private farms with agricultural activities (fish farming, livestock and monoculture). Aquatic habitats and riparian vegetation in some degraded urban and rural areas have been intensively modified, losing their original characteristics. In some sites, there was a change in the type of habitat, usually due to damming or deviation of water from lotic courses to artificial ponds used for urban landscaping, animal drinking or fish tanks. The native vegetation in altered sites were partially or entirely replaced by exotic species (e.g., *Brachiaria* spp., *Hyparrhenia* spp. and *Saccharum* sp.). Despite these changes, we decided to maintain the original local phytophysiognomy classification, following other studies in the region (Borges et al. 2019, Barbosa et al. 2019).

We sampled most adult dragonflies with entomological nets, but light traps and larvae rearing were also used in some sites in order to sample species that are not so easily captured through traditional methods (Almeida et al. 2013, Pinto 2019). Active samplings were performed by one or two people during often one hour in a 100 m transect of each water body, from December 2018 to November 2020, during dry and rainy seasons. We sampled the dragonflies on hot, sunny days with few clouds between 9:00 am and 3:00 pm, conditions and period of greatest diversity and activity of the group (Calvão et al. 2018). Each site was sampled once, totaling an effort of approximately 110 hours. Collections with light trap (type "Luiz de Queiroz") were performed only at site 93 in October 2018. The trap was placed 3 m above the ground, with illumination effectuated by two black ultraviolet light that were activated for 12 hours (18:00 - 6:00 h) during seven days, totaling 84 sampling hours. We did not perform any other type of sampling method at this site. Finally, larvae specimens were sampled during two expeditions in August 2018 and May 2020 at site 10. The larvae were collected through D-network (250 µm) scans close to emerged macrophytes. All F1-F0 larvae were reared in aquariums until adult emergence. Entomological nets were also used to sample adults at this site. Only larvae species not previously collected were reared.

Collected adults were stored in glassine envelopes (Cezário et al. 2020), kept in pure acetone during 12 hours and dried for 30 minutes under direct solar irradiation. The identification occurred at species level following the keys of Lencioni (2017), Garrison et al. (2006, 2010), Needham et al. (2000), and genus specific literature (e.g., revisions, synopses and species description). Collections were carried out under the authorization of ICMBio (SISBIO: 28398-1 and 28398-3) and IEF (064/2018). The material is deposited in the collection of the Laboratory of Ecology and Biodiversity of the Federal University of Sergipe.

3. Statistical analysis

Interpolation and extrapolation curves were performed for palm swamp and riparian forest, and from the combination of both to evaluate the effectiveness of odonate sampled for phytophysiognomies and municipality, respectively. Specimens of the site 57 were included only in overall municipality curve estimation due to absence of a defined phytophysiognomy. The curves (Hill number q = 0) were based on specimen abundance, and confidence intervals (95%) were determined from 1,000 bootstraps, with the extrapolation estimated to the triple of sampled specimens (Chao et al. 2014). The rarefaction curves were generated using the iNEXT (Hsieh et al. 2020) in software R version

Figure 2. Environment characteristics of some sampled sites in Uberlândia, Minas Gerais, Brazil: (a) urban lotic palm swamp (site 53); (b) urban lotic palm swamp (site 8); (c) urban lentic palm swamp (site 25); (d) riparian forest located in public urban green area (site 26); (e) urban riparian forest located at urban park (site 41);(f) lentic urban pond near riparian forest; (g) rural palm swamp stream (site 94); (h) preserved rural lentic palm swamp (site 66); (i) rural riparian forest stream (site 103); (j) stream in a rural gallery forest (site 99); (k) lentic section surrounded by riparian forest (site 92); (l) rural pond in riparian forest segment (site 80).

4.0.2 (R Core Team 2020). Image editions were performed in Gimp version 2 (The GIMP Development Team 2019).

4. *Taxonomic notes*

To perform the female description, lateral views of habitus were scanned with an Epson V600 Perfection at colored 1,200 dpi with 200% magnification. Structure images were made from multiple photographs focused at different levels, using Canon EOS T5 digital camera coupled to Tecnival stereomicroscope. Free hand illustrations were made using trace paper and scanned with Epson V600 Perfection at black and white 1,200 dpi with 100% magnification. Morphological terminology follows Lencioni (1999) and Garrison et al. (2010). All measurements are in millimeters (mm).

Abbreviations: AB: abdomen length; Fw: fore wings; Hw: hind wings; MP: media posterior vein; Px: postnodal crossvein; Pt: pterostigma; RP2: radius posterior, second branch; S1–10: abdominal segments; TL: total length.

Results

1. *Odonata diversity*

We collected 2,154 individuals belonging to seven families, 46 genera and 101 species in the municipality (Table 2). Of this total, Anisoptera and Zygoptera presented 61% and 50%, respectively, of species richness. Among the families, Libellulidae was the most specious group, comprising more than half of the species (51%), followed by Coenagrionidae (36%), Aeshnidae (5%), Gomphidae (4%), Calopterygidae, Dicteriadidae and Lestidae (4%). Libellulidae and Coenagrionidae also presented the two richest genera (*Erythrodiplax*: 12% spp. and *Telebasis*: 8% spp.), and abundant [*Erythrodiplax*: 556 (~ 25%); *Argia*: 424 (~ 20%)], while *Dicteriadidae* and *Lestidae* were the less rich families (1% each).

In general, sampled sites presented a mean richness of 6.43 (SD: ± 3.18) species, varying from 1 to 18 species per water body. Urban sites presented 77 (mean ± SD: 6.74 ± 3.39) and rural 81 (6.98 ± 2.92) of the richness of this study, with 20 species occurring exclusively in the

Table 1. Detailed information of the sampled sites in Uberlândia, Minas Gerais, Brazil. Legends: Liv: Livestock farming; Urb: Urbanization; Mono: Monoculture; Pisc: Pisciculture; Preserv: Preserved.

Site	Coordinates	Sampling date	Sampling method	Area	Habitat	Vegetation	Environmental change in the channel	Land Use beyond riparian zone
1	18°58’11”S-48°17’42”W	Mar/2019	EN	Urban	Lotic	RF	Yes	Liv/Urb
2	18°53’03”S-48°20’48”W	Mar/2020	EN	Urban	Lentic	RF	Yes	Liv/Urb
3	18°52’53”S-48°21’03”W	Mar/2020	EN	Urban	Lentic	RF	Yes	Liv/Urb
4	18°52’53”S-48°20’58”W	Mar/2020	EN	Urban	Lotic	RF	No	Liv/Urb
5	18°58’18”S-48°18’17”W	Out/2019	EN	Urban	Lentic	PS	Yes	Liv/Urb
6	18°52’45”S-48°17’08”W	Mar/2019	EN	Urban	Lotic	PS	Yes	Urb
7	18°55’03”S-48°18’50”W	Jul/2019	EN	Urban	Lotic	PS	Yes	Urb
8	18°53’40”S-48°19’31”W	Jul/2019	EN	Urban	Lotic	PS	Yes	Urb
9	18°56’34”S-48°13’41”W	Jul/2019	EN	Urban	Lotic	PS	Yes	Liv/Urb
10	18°57’42”S-48°12’38”W	May/2019 Jul/2020	EN DN	Urban	Lentic	RF	Yes	Pisc/Urb
11	18°57’32”S-48°12’34”W	May/2019	EN	Urban	Lotic	RF	Yes	Pisc/Urb
12	18°57’26”S-48°12’28”W	May/2019	EN	Urban	Lentic	RF	Yes	Liv/Urb
13	18°57’29”S-48°12’29”W	Out/2019	EN	Urban	Lotic	RF	Yes	Liv/Urb
14	18°57’21”S-48°12’21”W	Jul/2020	EN	Urban	Lotic	RF	Yes	Liv/Urb
15	18°57’38”S-48°12’40”W	Dez/2019	EN	Urban	Lotic	RF	No	Liv/Urb
16	18°57’51”S-48°12’43”W	Dez/2019	EN	Urban	Lentic	PS	Yes	Pisc/Urb
17	18°57’26”S-48°12’33”W	Nov/2019	EN	Rural	Lotic	RF	No	Liv
18	18°57’08”S-48°12’13”W	Out/2019	EN	Urban	Lotic	RF	No	Liv
19	18°57’13”S-48°12’23”W	Out/2019	EN	Urban	Lotic	RF	No	Liv
20	18°59’08”S-48°21’31”W	Mar/2019	EN	Urban	Lentic	PS	Yes	Urb/Liv
21	18°58’02”S-48°17’36”W	Dez/2019	EN	Urban	Lentic	PS	Yes	Urb
22	18°57’54”S-48°17’35”W	Dez/2019	EN	Urban	Lentic	PS	Yes	Urb
23	18°52’22”S-48°14’32”W	Jul/2019	EN	Urban	Lotic	PS	Yes	Urb
24	18°56’11”S-48°19’35”W	Jul/2019	EN	Urban	Lentic	PS	Yes	Urb
25	18°57’09”S-48°18’18”W	Mar/2019	EN	Urban	Lentic	PS	Yes	Urb
26	18°55’37”S-48°19’44”W	Mar/2019	EN	Urban	Lotic	RF	Yes	Urb
27	18°57’10”S-48°16’32”W	Feb/2019	EN	Urban	Lentic	RF	Yes	Urb
28	18°57’09”S-48°16’35”W	Feb/2019	EN	Urban	Lotic	RF	Yes	Urb
29	18°57’09”S-48°16’43”W	Feb/2019	EN	Urban	Lotic	RF	Yes	Urb
30	18°57’06”S-48°16’51”W	Feb/2019	EN	Urban	Lotic	RF	Yes	Urb
31	18°55’03”S-48°19’32”W	Mar/2019	EN	Urban	Lentic	RF	Yes	Urb
32	18°56’10”S-48°15’59”W	Mar/2019	EN	Urban	Lotic	PS	Yes	Urb
33	18°54’23”S-48°13’56”W	Feb/2019	EN	Urban	Lentic	RF	Yes	Urb
34	18°54’29”S-48°13’53”W	Feb/2019	EN	Urban	Lotic	RF	Yes	Urb
35	18°54’31”S-48°13’41”W	Feb/2019	EN	Urban	Lotic	RF	No	Urb
36	18°54’13”S-48°14’07”W	Feb/2019	EN	Urban	Lentic	PS	Yes	Urb
37	18°54’40”S-48°14’15”W	Feb/2019	EN	Urban	Lentic	PS	Yes	Urb
38	18°54’35”S-48°14’37”W	Feb/2019	EN	Urban	Lentic	PS	Yes	Urb
39	18°54’23”S-48°14’02”W	Jan/2019	EN	Urban	Lentic	PS	Yes	Urb
40	18°54’19”S-48°14’04”W	Feb/2019	EN	Urban	Lentic	PS	Yes	Urb
41	18°56’16”S-48°14’19”W	Mar/2019	EN	Urban	Lotic	RF	Yes	Urb
42	18°56’17”S-48°14’12”W	Mar/2019	EN	Urban	Lotic	RF	Yes	Urb
43	18°56’20”S-48°14’10”W	Mar/2019	EN	Urban	Lotic	RF	Yes	Urb
44	18°56’15”S-48°14’24”W	Mar/2019	EN	Urban	Lotic	RF	Yes	Urb
45	18°56’23”S-48°14’13”W	Mar/2019	EN	Urban	Lotic	RF	Yes	Urb
46	18°56’16”S-48°14’31”W	Mar/2019	EN	Urban	Lotic	RF	Yes	Urb
47	18°56’26”S-48°14’10”W	Mar/2019	EN	Urban	Lentic	PS	Yes	Urb

Continue...

Continuation..

48	18°52’23”S-48°17’14”W	Jan/2019	EN	Urban	Lotic	RF	Yes	Urb
49	18°57’04”S-48°17’19”W	Jul/2019	EN	Urban	Lentic	RF	Yes	Urb
50	18°55’24”S-48°17’57”W	Feb/2019	EN	Urban	Lentic	RF	Yes	Urb
51	18°55’17”S-48°17’59”W	Feb/2019	EN	Urban	Lotic	RF	Yes	Urb
52	18°55’18”S-48°18’09”W	Feb/2019	EN	Urban	Lentic	RF	Yes	Urb
53	18°58’28”S-48°18’43”W	Out/2019	EN	Urban	Lotic	PS	Yes	Urb/Liv
54	19°00’15”S-48°21’13”W	Jan/2019	EN	Urban	Lentic	PS	Yes	Liv
55	19°00’19”S-48°21’15”W	Jan/2019	EN	Urban	Lentic	PS	Yes	Liv/Pisc
56	19°00’15”S-48°21’09”W	Feb/2019	EN	Urban	Lotic	PS	No	Liv
57	18°53’02”S-48°15’38”W	Out/2019	EN	Urban	Lentic	-	Yes	Urb
58	18°59’17”S-48°08’45”W	Jan/2019	EN	Rural	Lentic	RF	Yes	Liv/Mono
59	19°00’02”S-48°16’07”W	Jan/2019	EN	Rural	Lotic	RF	Yes	Liv
60	19°00’08”S-48°16’10”W	Jan/2019	EN	Rural	Lotic	RF	Yes	Liv
61	19°13’26”S-48°19’03”W	Mar/2020	EN	Rural	Lotic	PS	Yes	Mon
62	18°59’34”S-48°12’26”W	Apr/2020	EN	Rural	Lotic	PS	No	Liv/Mono
63	18°52’27”S-48°20’29”W	Fev/2019	EN	Urban	Lotic	RF	Yes	Liv
64	18°59’20”S-48°10’10”W	Apr/2020	EN	Rural	Lotic	RF	No	Mon
65	19°04’59”S-48°11’49”W	Mar/2020	EN	Rural	Lentic	PS	Yes	Liv/Mon
66	19°05’05”S-48°12’30”W	Mar/2020	EN	Rural	Lentic	PS	No	Mon
67	19°02’02”S-48°21’55”W	Apr/2019	EN	Rural	Lotic	PS	Yes	Liv
68	19°01’40”S-48°21’26”W	Apr/2019	EN	Rural	Lentic	PS	Yes	Mon
69	19°02’08”S-48°21’18”W	Nov/2019	EN	Rural	Lentic	PS	Yes	Liv
70	19°14’20”S-48°24’23”W	Mar/2020	EN	Rural	Lentic	PS	Yes	Mon
71	18°58’39”S-48°18’54”W	Out/2019	EN	Urban	Lentic	PS	Yes	Liv
72	19°11’44”S-48°23’46”W	Mar/2020	EN	Rural	Lentic	PS	Yes	Mon
73	19°11’14”S-48°24’48”W	Mar/2020	EN	Rural	Lentic	PS	Yes	Mon
74	19°12’03”S-48°25’11”W	Mar/2020	EN	Rural	Lentic	PS	Yes	Mon
75	19°09’06”S-48°23’26”W	Mar/2020	EN	Rural	Lentic	RF	Yes	Liv/Mono
76	19°11’53”S-48°22’36”W	Apr/2020	EN	Rural	Lentic	PS	Yes	Mon
77	18°59’14”S-48°19’56”W	Dez/2019	EN	Rural	Lentic	PS	Yes	Liv
78	18°58’59”S-48°19’22”W	Dez/2019	EN	Urban	Lotic	PS	Yes	Liv/Urb
79	18°45’55”S-48°22’20”W	May/2020	EN	Rural	Lotic	RF	Yes	Liv
80	18°45’59”S-48°22’25”W	May/2020	EN	Rural	Lentic	RF	Yes	Liv
81	18°59’28”S-48°10’53”W	Fev/2020	EN	Rural	Lotic	PS	Yes	Liv/Mono
82	18°59’38”S-48°11’19”W	Apr/2020	EN	Rural	Lotic	PS	Yes	Liv
83	19°09’16”S-48°09’45”W	Fev/2020	EN	Rural	Lentic	PS	Yes	Liv
84	19°09’23”S-48°09’35”W	Fev/2020	EN	Rural	Lotic	PS	Yes	Liv
85	19°09’11”S-48°08’58”W	Fev/2020	EN	Rural	Lotic	RF	Yes	Liv
86	19°10’57”S-48°23’39”W	Feb/2019	EN	Rural	Lentic	PS	No	Preserv
87	19°10’36”S-48°23’40”W	Jan/2020	EN	Rural	Lotic	RF	No	Preserv
88	19°10’10”S-48°23’27”W	Jan/2020	EN	Rural	Lotic	RF	No	Preserv
89	19°09’39”S-48°23’13”W	Jan/2020	EN	Rural	Lotic	PS	Yes	Liv
90	18°49’30”S-48°10’03”W	Dez/2018	EN	Rural	Lotic	RF	No	Preserv
91	18°49’56”S-48°09’46”W	Mar/2019	EN	Rural	Lotic	RF	Yes	Liv
92	18°48’52”S-48°09’24”W	Apr/2019	EN	Rural	Lentic	RF	Yes	Liv
93	18°49’04”S-48°09’48”W	Oct/2018	LT	Rural	Lotic	RF	No	Preserv
94	19°02’39”S-48°21’57”W	Jul/2019	EN	Rural	Lotic	PS	Yes	Liv
95	19°05’55”S-48°25’37”W	Mar/2020	EN	Rural	Lotic	PS	Yes	Liv
96	18°45’50”S-48°23’29”W	Mar/2020	EN	Rural	Lotic	RF	Yes	Liv
97	19°15’04”S-48°25’43”W	Mar/2020	EN	Rural	Lotic	PS	Yes	Mono
98	19°10’22”S-48°25’40”W	Mar/2020	EN	Rural	Lotic	PS	Yes	Liv
99	18°53’39”S-48°26’03”W	Mar/2020	EN	Rural	Lotic	RF	No	Liv
100	18°46’27”S-48°12’33”W	May/2020	EN	Rural	Lotic	RF	Yes	Liv

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101	18°50’06”S-48°28’16”W	Apr/2020	EN	Rural	Lotic	RF	Yes	Liv
102	18°51’07”S-48°27’09”W	Apr/2020	EN	Rural	Lentic	RF	Yes	Liv
103	18°51’12”S-48°27’40”W	Apr/2020	EN	Rural	Lotic	RF	Yes	Liv/Mono
104	18°59’34”S-48°10’25”W	Fev/2020	EN	Rural	Lentic	PS	Yes	Liv
105	18°45’38”S-48°12’31”W	May/2020	EN	Rural	Lentic	RF	Yes	Pisc
106	18°59’39”S-48°12’15”W	Apr/2020	EN	Rural	Lotic	PS	Yes	Liv/Mono
107	18°50’06”S-48°24’49”W	Mar/2020	EN	Rural	Lentic	PS	Yes	Mon
108	18°50’01”S-48°24’40”W	Mar/2020	EN	Rural	Lentic	PS	Yes	Mon
109	18°50’33”S-48°24’55”W	Mar/2020	EN	Rural	Lotic	RF	No	Mon
110	19°02’50”S-48°03’16”W	Feb/2019	EN	Rural	Lentic	PS	Yes	Liv
111	19°02’57”S-48°03’17”W	Feb/2019	EN	Rural	Lentic	PS	No	Liv

first class, 24 in the second and 57 in both areas. Lentic habitats were richer than lotic (lentic: 79 species, 7.47 ± 3.56; lotic: 61 species, 6.35 ± 2.77) and also presented more exclusively species (lentic: 40; lotic: 21; both: 39). Considering the phytophysiognomies, palm swamps and forests presented, respectively, a richness of 76 (7.79 ± 3.15) and 66 (6.02 ± 2.93) of the sampled species; and approximately 36 species were exclusive to palm swamps, 25 to forests and 41 were common to both habitats. Lestidae was the only family with all species common to all classes, while Dicteriadidae was specific to lotic forested sites.

Four specimens of four species (*Aphylla distinguenda* Campion, 1920, *Phyllocycla* cf. *medusa* Belle, 1988, *Miathyria marcella* Selys in Sagra, 1857, *Tholymis citrina* Hagen, 1867) were captured through light trap. One individual of *Anax amazili* Burmeister, 1839, several of *Acanthagrion truncatum* Selys, 1876 and three of *Angelagrion nathaliae* Lencioni, 2008 emerged in the laboratory. Some *A. truncatum* and all other species were sampled using entomological net.

Almost 50% of the sampled species are not included in any of the IUCN conservation categories; one species (*Oligoclada xanthopleura* Borror, 1931) was classified as Data Deficient (DD) and ~45% were listed as (LC) least concern. However, *Erythrodiplax ana* Guillermo-Ferreira & Vilela 2016 is considered endangered (EN).

The rarefaction and extrapolation curves suggested that samples were satisfactory, although the sampling of more specimens indicate a diversity increment in all cases (Figure 3). Considering the triple of estimated richness was approximately 93 for palm swamps, 72 for riparian forest and 126 for all habitats, we sampled more than 80% of the richness of dragonflies in each phytophysiognomy and in the municipality.

2. *New records for the State*

We found eight new species records for Minas Gerais: one Aeshnidae, one Gomphidae, three Libellulidae and three Coenagrionidae. Below, we present the distribution in the Brazilian states and a brief description of occurrence sites. Brazilian states are represented by respective acronyms: Acre (AC), Amapá (AP), Amazonas (AM), Bahia (BA), Espírito Santo (ES), Goiás (GO), Maranhão (MA), Mato Grosso (MT), Mato Grosso do Sul (MS), Pará (PA), Pernambuco (PE), Rio de Janeiro (RJ), Rio Grande do Sul (RS), Roraima (RO) and São Paulo (SP).

2.1 *Neuraeschna claviforcipata* Martin, 1909 - 1♂; 1♀ (Figure 4a). Distribution: AM (Koroiva et al., 2020). The two individuals were flying next to a spring of preserved riparian forest at site 35 (urban park). Due to low solar incidence in the course, both specimens had low flight speed during sampling.

2.2 *Phyllocycla* cf. *medusa* Belle, 1988 - 1♀ (Figure 4b). Distribution: PA (Belle 1988). The specimen was collected in light trap at a riparian forest of the site 93, a conservation unit. The stream bed received direct sunlight and margins were completely shaded by tree vegetation.

2.3 *Diastatops intensa* Montgomery, 1940 - 4♂; 2♀ (Figure 4c). Distribution: PA, AP, RS, MT, MS, SP, PE and RJ (Ferreira-Peruquetti & Fonseca-Gessner 2003, Silveira 2003, Costa et al. 2004, Garrison et al. 2006, Heckman 2006, Calvão et al. 2014, Dalzochio et al. 2018a, Rodrigues & Roque 2017). All specimens were collected at site 92, in a lentic stretch of a riparian forest of a conservation unit. Despite the predominance of grasses in the area, there was a preserved forest nearby and some macrophytes near the sampled transect, where specimens often were perching.

2.4. *Oligoclada pachystigma* Karsch, 1890 - 3♂ (Figure 4d). Distribution: AM, MS, MT, PA, SP (Costa et al. 2000, Pinto & Lamas 2011, Carvalho et al. 2013, Rodrigues & Roque 2017, Koroiva et al. 2020). All males were collected during mid-flight. The first specimen was found in the edge of a closed canopy palm swamp (site 62) and the other in a small pond in the same phytophysiognomy (site 65). Both areas were small fragments surrounded by livestock farming and corn crops (*Zea mays* L.).

2.5. *Oligoclada xanthopleura* Borror, 1931 - 1♂ (Figure 4e). Distribution: AM, PA, MT, MA (Pinto & Lamas 2011, Carvalho et al. 2013, Calvão et al. 2014, Côrrea et al. 2014, Veras 2017, Koroiva et al. 2020). The specimen was collected in a palm swamp (site 5) with margins predominantly composed by *Brachiaria* sp. and exotic herbaceous species. Although the site was inserted in urban area, the nearest impervious structure was ~500 m from the pond.

2.6. *Angelagrion nathaliae* Lencioni, 2008 - 2♂; 1♀ (Figure 4f). Distribution: SP (Lencioni 2008). The immature individuals were collected on *Eichhornia crassipes* Mart. in fish farming tanks near an urban gallery forest (site 10). The adults were reared during approximately one month until emergence at the laboratory. The larva and the male of this species are currently being described by Frederico Lencioni (pers. comm.).

2.7. *Telebasis sanguinalis* Calvert, 1909 - 1♂ (Figure 4g). Distribution: MT, MS, AM, MA (Pinto & Carvalho 2012, Koroiva et al. 2017, Rodrigues & Roque 2017, Veras 2017, Koroiva et al. 2020). An individual was collected at a small palm swamp at 86, a different conservation unit from previous new records. The adjacent vegetation was composed of grasses and shrubs native to the Cerrado, near some *M. flexuosa* L.

Table 2. List of dragonfly species sampled in Uberlândia, Minas Gerais, Brazil, indicating aquatic habitat type, vegetation type, area type, sampled season, abundance (N) and occurrence sites. Le: Lentic; Lo: Lotic; R: Riparian Forest; P: Palm Swamp; Ru: Rural, U: Urban, D: Dry, R: Rainy. IUCN Red List Status: EN: Endangered, LC: Least Concern, DD: Data Deficient, "-": Not categorized in the UCN list. New records for Minas Gerais are marked with an asterisk (*); "r" indicate larvae reared up to adults; l indicate species collected by light trap. Conservation status of the species were extracted from IUCN database (IUCN 2020).

Taxon	Habitat	Vegetation	Area	Season	N	IUCN Status	Collection sites
Anisoptera							
Aeshnidae							
Anax amazili (Burmeister, 1839)[r]	Le	R	U	D	1	LC	10
Anax concolor Brauer 1865	Le	P	Ru	R	1	LC	86
Gynacantha nervosa Rambur,1842	Le	-	U	R	1	LC	57
Coryphaeschna adnexa (Hagen, 1861)	Lo	R	U	R	1	LC	35
Neuraeschna claviforcipata Martin. 1909*	Lo	R	U	R	2	-	35
Gomphidae							
Aphyla distinguenda (Campion, 1920)[l]	Lo	R	Ru	R	1	-	93
Gomphoides perdita (Förster, 1914)	Le	P	Ru	R	3	-	73, 104
Phyllocycla cf. *medusa* Belle, 1988*[l]	Lo	R	Ru	R	1	-	93
Progomphus intricatus Hagen in Selys, 1858	Le, Lo	P, R	Ru, U	D, R	7	LC	30, 67, 68, 85, 106
Libellulidae							
Brachymesia herbida (Gundlach, 1889)	Le, Lo	P, R	Ru, U	R	2	LC	5, 88
Dasythemis venosa (Burmeister, 1839)	Lo	P	Ru	D, R	2	-	89, 106
Diastatops intensa Montgomery, 1940*	Le	R	Ru	D	6	-	92
Diastatops obscura (Fabricius, 1775)	Le	R	Ru	D	1	-	102
Elasmothemis cannacrioides Calvert, 1906	Le, Lo	R	Ru, U	D, R	11	-	15, 26, 41, 62, 90, 111
Elasmothemis constricta (Calvert, 1898)	Le	P	Ru	R	1	-	5
Erythemis credula (Hagen, 1861)	Le	P	Ru, U	R	4	-	16, 73, 86
Erythemis peruviana (Rambur, 1842)	Le	P	Ru	R	7	LC	25
Erythemis vesiculosa (Fabricius, 1775)	Le	P	Ru	R	2	LC	21
Erythrodiplax ana Guillermo-Ferreira & Vilela 2016	Le, Lo	P	Ru, U	D, R	3	EN	37, 40, 94
Erythrodiplax castanea (Burmeister, 1839)	Le, Lo	P, R	Ru, U	D, R	79	-	6-8, 14, 22, 23, 36-38, 49, 54, 60, 61, 63, 68, 73, 74, 82, 84, 92, 94, 101, 102, 105,108, 110
Erythrodiplax fusca (Rambur, 1842)	Le, Lo	P, R	Ru, U	D, R	193	LC	2, 3, 5, 8, 10-12, 14, 16, 20, 23-25, 28, 29, 31-33, 42, 43, 46, 47, 49, 50, 52, 55, 56, 61, 62, 64, 65, 67, 68, 70, 72, 73, 75, 77, 78, 80-82, 89, 92, 94, 100, 101, 104, 106, 107, 108, 109
Erythrodiplax juliana Ris, 1911	Le, Lo	P, R	Ru, U	D, R	43	LC	9, 36, 40, 49, 66, 68, 69, 74, 78, 80-82, 85, 86, 100, 105
Erythrodiplax lygaea Ris, 1911	Le	P	U	R	1	LC	71
Erythrodiplax latimaculata Ris, 1911	Le, Lo	P, R	Ru, U	D, R	62		5, 11, 19, 21, 22, 25, 40, 53, 54, 61, 65, 66, 69, 70-73, 75, 78, 80, 83, 85, 86, 102, 104, 107, 110, 111
Erythrodiplax maculosa (Hagen, 1861)	Le	P	Ru, U	R	8	LC	40, 70, 71, 78
Erythrodiplax media Borror, 1942	Le, Lo	P, R	Ru, U	D, R	104	-	5, 8, 10, 21, 22, 24, 25, 27, 29, 31-33, 36-38, 40, 45-47, 49-52, 65, 66, 72, 77, 78, 83, 86, 92, 94, 101, 102, 104, 111
Erythrodiplax ochracea (Burmeister, 1839)	Le	R	Ru	R	2	LC	58
Erythrodiplax paraguayensis (Förster, 1904)	Le, Lo	P, R	Ru, U	D, R	34	LC	5, 9, 10, 16, 21, 22, 31, 32, 40, 49, 53, 65, 66, 68, 70, 76, 77, 104, 111
Erythrodiplax umbrata (Linnaeus, 1758)	Le, Lo	P, R	Ru, U	D, R	21	LC	6, 3, 10, 21, 31, 40, 77, 78, 54, 111
Erythrodiplax venusta (Kirby, 1897)	Le	P	Ru, U	R	6	-	21, 110
Gynothemis venipunctata Calvert. 1909	Le, Lo	P	Ru, U	D, R	7	-	5, 53, 82, 106
Idiataphe amazonica (Kirby, 1889)	Le	P	Ru	D, R	3	-	73, 76

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Idiataphe longipes (Hagen, 1861)	Le	P	Ru, U	R	2	-	65, 71
Macrothemis heteronycha (Calvert, 1909)	Lo	P	Ru	D, R	4	LC	53, 85, 106
Macrothemis imitans Karsch, 1890	Le, Lo	P, R	Ru, U	D, R	6	LC	9, 61, 88, 98
Miathyria marcella (Selys in Sagra, 1857)[1]	Lo	R	Ru	R	1	LC	93
Miathyria simplex (Rambur, 1842)	Le	R	Ru	D	1	-	92
Micrathyria catenata Calvert. 1909	Le	P	Ru, U	R	11	LC	16, 25, 72, 74
Micrathyria cf. *hypodidyma* Calvert, 1906	Lo	R	Ru	R	1	-	87
Micrathyria hesperis Ris, 1911	Le	P	Ru, U	R	9	-	25, 27, 47, 52, 72, 75
Micrathyria ocellata Martin, 1897	Le	P	U	R	9	-	21, 25, 50, 54
Micrathyria pirassunungae Santos, 1953	Le	P	Ru, U	R	7	-	20, 55, 66, 73
Micrathyria pseudeximia Westfall, 1992	Le, Lo	P, R	Ru, U	D, R	20	-	16, 25, 29, 45, 46, 52, 69, 71, 73, 86, 87, 102
Micrathyria spuria (Selys, 1900)	Le	P	Ru, U	D, R	6	LC	5, 102, 110
Nephepeltia berlai Santos, 1950	Le	P	U	R	3	-	5, 21, 22
Oligoclada laetitia Ris, 1911	Le	P	Ru, U	R	4	LC	40, 110
Oligoclada pachystigma Karsch, 1890*	Le, Lo	P	Ru	D, R	3	-	62, 65
Oligoclada xanthopleura Borror, 1931*	Le	P	U	R	1	DD	5
Orthemis aequilibris Calvert, 1909	Le, Lo	P	Ru, U	D, R	3	-	24, 32, 104
Orthemis cultriformis Calvert, 1899	Lo	R	Ru, U	R	3	-	43, 87
Orthemis discolor (Burmeister, 1839)	Le, Lo	P, R	Ru, U	D, R	18	LC	2, 10, 19, 23, 46-48, 55, 69, 73, 85, 102, 108
Pantala flavescens (Fabricius, 1798)	Le, Lo	P, R	Ru, U	D, R	6		7, 10, 26, 67, 68, 91
Perithemis icteroptera (Selys in Sagra, 1857)	Le	P	U	R	6	LC	47
Perithemis lais (Perty, 1834)	Le	P, R	Ru, U	R	14	LC	22, 39, 52, 54, 55, 75
Perithemis tenera (Say, 1840)	Le, Lo	P, R	U	D, R	13	LC	5, 8, 24, 25, 27, 54, 55
Tauriphila argo (Hagen, 1869)	Le	P	U	R	1	LC	5
Tholymis citrina Hagen, 1867[1]	Lo	R	Ru	R	1	LC	93
Tramea abdominalis (Rambur, 1842)	Le	P	U	R	3	LC	16
Tramea binotata (Rambur, 1842)	Le	P	Ru, U	R	3	LC	39, 72, 110
Uracis siemensi Kirby, 1897	Lo	P	U	R	1	-	17
Zenithoptera lanei Santos, 1941	Le, Lo	P	Ru, U	R	10	-	5, 22, 53, 66, 71
Zygoptera							
Calopterygidae							
Hetaerina rosea Selys, 1853	Le, Lo	P, R	Ru, U	D, R	90	-	1, 4, 6, 7, 11, 13, 15, 19, 26, 30, 32, 41, 42, 45, 46, 51, 58, 67, 88, 90, 94-98, 103, 109
Mnesarete guttifera (Selys,1873)	Lo	R	Ru	R	1	LC	90
Coenagrionidae							
Acanthagrion aepiolum Tennessen, 2004	Le, Lo	P, R	Ru, U	D, R	79	LC	9, 21, 24, 31, 33, 39, 41, 43, 45, 46, 54, 55, 58, 59, 64, 75, 103, 105
Acanthagrion gracile (Rambur, 1842)	Le, Lo	P, R	Ru, U	D, R	110	-	2, 3, 5-8, 10-12, 14, 20-23, 27-29, 33, 38, 39, 47, 49, 52, 54, 55, 59, 61, 64, 70, 72, 74, 75, 79, 80, 83, 94, 100, 102, 105
Acanthagrion lancea Selys, 1876	Le	R	U	R	2	LC	5, 31
Acanthagrion minutum Leonard, 1977	Le	P	Ru, U	D, R	5	LC	5, 73, 77, 102
Acanthagrion temporale Selys, 1876	Le	P, R	Ru, U	D, R	16	-	5, 10, 16, 24, 65, 69, 71, 72, 80, 102
Acanthagrion truncatum Selys, 1876[r]	Le, Lo	P, R	Ru, U	D, R	201	LC	2, 3, 5, 10, 16, 24, 25, 28, 36, 37, 40, 47, 49, 53, 54, 60, 61, 65, 69, 71, 72, 80, 89, 94, 101, 102, 104, 106, 107, 108, 110, 111
Angelagrion nathaliae Lencioni, 2008[r]*	Le	R	U	D	3	-	10
Argia lilacina Selys, 1865	Le, Lo	P, R	Ru, U	D, R	82	-	8, 9, 10, 14, 17, 33, 53, 54, 61, 62, 67, 68, 78, 81, 83, 84, 85, 89, 100, 109
Argia mollis Hagen in Selys, 1865	Lo	P, R	Ru, U	D, R	56	LC	6, 17, 18, 35, 41, 42, 44, 46, 56, 60, 62, 79, 87, 89, 96, 100
Argia reclusa Selys, 1865	Lo	P, R	R, U	D, R	275		1, 4, 8, 9, 11, 13, 15, 18, 19, 26-30, 32, 34, 35, 41-46, 56, 59, 60, 64, 83, 89, 90, 91, 94, 95, 96-99, 103, 109

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Argia tamoyo Calvert, 1909	Lo	R	Ru, U	D, R	8	LC	51, 59, 60, 63
Argia sp.	Lo	R	U	R	3	-	17,18
Cyanallagma nigrinuchale (Selys, 1876)	Le, Lo	R	Ru	D, R	4	-	84, 102
Epipleoneura venezuelensis Rácenis, 1955	Le, Lo	P, R	Ru, U	D, R	27	-	2, 4, 33, 34, 53, 88, 90, 91, 95, 98, 103
Epipleoneura williamsoni Santos, 1957	Le, Lo	P, R	Ru, U	D, R	20	LC	11, 12, 17, 18, 55, 64, 103
Forcepsioneura machadorum Vilela, Venâncio & Santos, 2020	Lo	R	U	R	5	-	17-19
Homeoura chelifera (Selys, 1876)	Le, Lo	P, R	Ru, U	D, R	20	-	17, 24, 36, 58, 68, 104, 110, 111
Homeoura lindneri (Ris, 1928)	Le	P, R	Ru, U	D, R	16	-	10, 21, 31, 65, 92, 110
Ischnura capreolus (Hagen, 1861)	Le, Lo	P, R	Ru, U	D, R	23	-	8, 10, 49, 71, 72, 77, 83, 92, 101, 102, 104, 108
Ischnura fluviatilis Selys, 1876	Le, Lo	P, R	Ru, U	D, R	10	LC	10, 25, 40, 47, 51, 63, 85
Nehalennia minuta (Selys in Sagra, 1857)	Le	P	Ru	R	1	-	86
Neoneura sylvatica Hagen in Selys, 1886	Le, Lo	P, R	Ru, U	D, R	14	-	4, 11, 12, 30, 64, 67, 92, 95, 101, 103, 105
Oxyagrion basale Selys, 1876	Lo	R	U	R	8	-	29, 42, 43
Oxyagrion chapadense Costa, 1978	Le, Lo	P, R	Ru, U	D, R	56	-	6, 8, 13, 14, 19, 26- 28, 30, 32, 41, 42, 48, 51, 64, 79, 87, 89, 98, 103
Oxyagrion microstigma (Selys, 1876)	Le, Lo	P, R	Ru	D, R	7	-	62, 71, 72, 80, 82
Oxyagrion terminale Selys, 1876	Le, Lo	P, R	Ru, U	D, R	31	-	6, 17, 23, 28, 29, 36, 38, 42, 43, 51, 79
Protoneura tenuis Selys, 1860	Lo	R	U	R	2	LC	18, 19
Telebasis carmesina Calvert, 1909	Le	P, R	Ru, U	D, R	51	LC	10, 16, 36, 37, 66, 69, 70, 72, 74, 77, 80, 86, 108
Telebasis coccinea (Selys, 1876)	Lo	P, R	Ru, U	D, R	31	-	20, 22, 39, 66, 70, 71, 73, 77, 80, 86, 102, 104
Telebasis corallina (Selys, 1876)	Lo	P	Ru	D	1	LC	80
Telebasis filiola (Perty, 1834)	Le, Lo	P, R	U	R	20	-	25, 28, 50
Telebasis griffinii (Martin, 1896)	Le, Lo	R	Ru, U	D, R	20	LC	38, 51, 92
Telebasis sanguinalis Calvert, 1909*	Le	P	Ru	R	1	LC	86
Telebasis simulacrum (Calvert, 1909)*	Le	P	Ru, U	R	8	LC	22, 111
Telebasis willinki Fraser, 1948	Le	P, R	Ru, U	D, R	9	LC	2, 27, 92
Tigriagrion aurantinigrum Calvert, 1909	Le, Lo	P, R	Ru, U	D, R	22	-	7, 11, 12, 17, 22, 58, 64, 75, 87, 94, 101
Dicteriadidae							
Heliocharis amazona Selys, 1853	Lo	R	Ru, U	R	10	-	15, 88, 90
Lestidae							
Lestes forficula Rambur, 1842	Le, Lo	P, R	Ru, U	R	15	LC	3, 16, 21, 59, 72, 74, 77, 111

2.8. *Telebasis simulacrum* (Calvert, 1909) - 7♂; 1♀ (Figure 4h). Distribution: RO, MT, MS, (Garrison 2009, Juen & De Marco 2012, Rodrigues & Roque 2017). We recorded these specimens at a degraded urban palm swamp adjacent to some small forest fragments (site 22), and at a rural palm swamp with a predominance of native grasses (site 111). All specimens were perching in emerged macrophytes at the time of sampling.

3. *Taxonomy*

Few months after the publication of *F. machadorum*, we collected three females in the type locality, including a tandem pair. Thus, here we describe the female of *F. machadorum* (Figure 5).

Head (Figure 5a). Labium, mandible and genae pale colored; anteclypeus dark brown with a brown spot at the center; remainder of the head black, except for a longitudinal pale dorsal stripe covering along postocular spots and occipital bar areas; antennifer pale colored with a pale ring at the apex; antenna dark brown, except for pale coloration on the posterior surface of pedicel; rear of the head pale colored.

Thorax (Figures 5a–d). Anterior lobe of prothorax dark brown dorsally, pale laterally; medial lobe dark brown except for pale areas in the propleuron, with two lateral tubercles; hind lobe rectangular with a slightly concave medial depression, laterally blunt with posterolateral corners forming rounded angles. Pterothorax with a thick black/metallic green stripe dorsally, except for a brown stripe on the interpleural suture; metepisternum and metepimeron pale colored except for a darker stripe

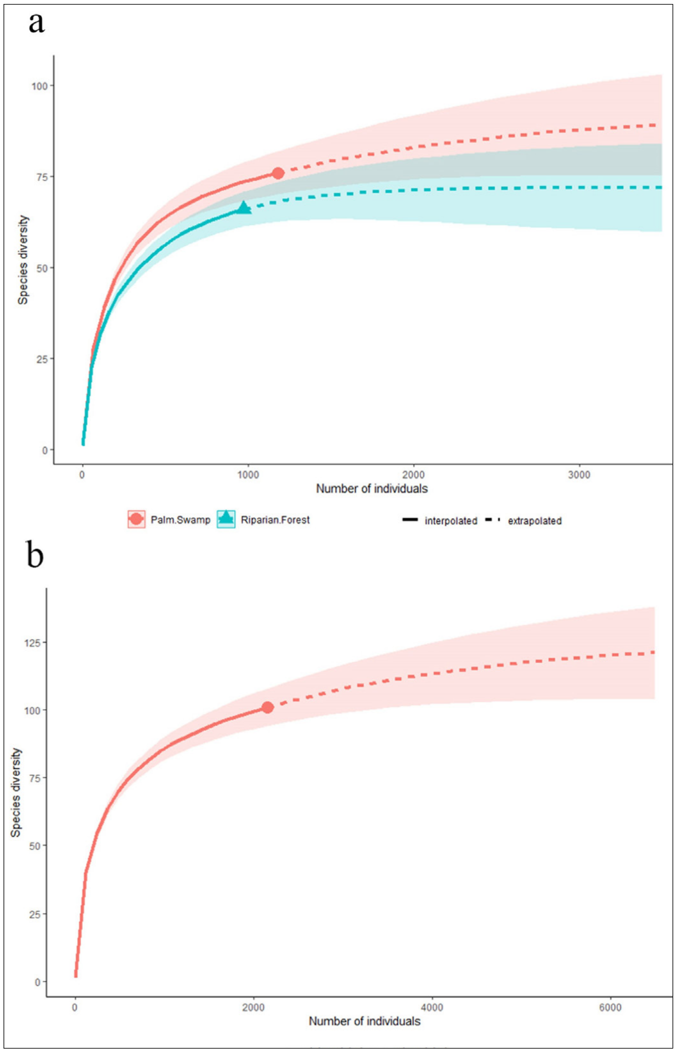

Figure 3. Accumulation curve (solid curve) and extrapolation (hatched curve) with 95% confidence interval (shaded area) of dragonflies sampled in (a) palm swamps and riparian forests and (b) general samples of Uberlândia, Minas Gerais, Brazil.

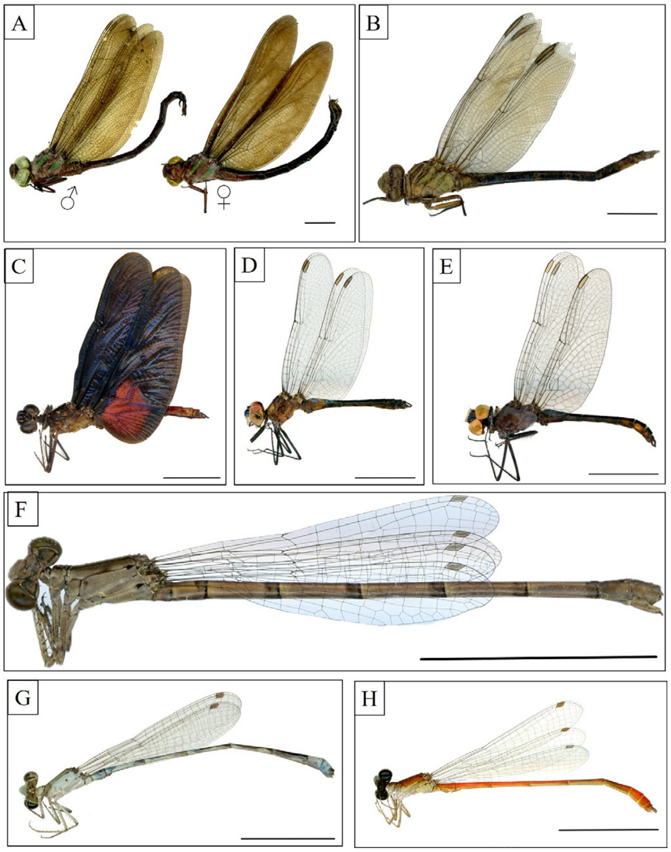

Figure 4. New species records for the state of Minas Gerais found in Uberlândia: a) male and female of *Neuraeschna claviforcipata* (Aeshnidae); b) female of *Phyllocycla* cf. *medusa* (Gomphidae); c) male of *Diastatops intensa* (Libellulidae); d) juvenile male of *Oligoclada pachystigma* (Libellulidae); e) male of *Oligoclada xanthopleura* (Libellulidae); f) female of *Angelagrion nathaliae* (Coenagrionidae); g) male of *Telebasis simulacrum* (Coenagrionidae); h) male of *Telebasis sanguinalis* (Coenagrionidae). Specimens were scanned at 1.200 dpi with the scanner Epson® V600 Perfection. Scale = 1 cm.

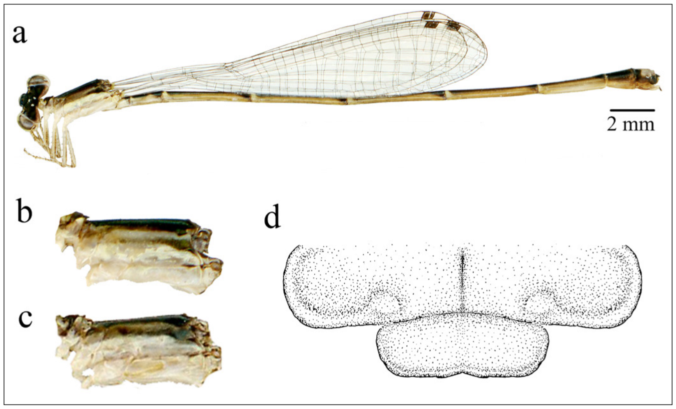

Figure 5. The female of *Forcepsioneura machadorum* Vilela, Venâncio & Santos, 2020: (a) lateral view of habitus; (b–c) lateral close-up of thorax; (d) dorsal view of prothoracic hind lobe.

on the upper posterior portion of metepimeron and a small dark spot on the posterior metepisternum/metepimeron suture; venter pale.

Legs (Figure 5a). Overall coloration pale, femoral-tibial and tarsal articulations brown; spurs light brown.

Wings (Figure 5a). Hyaline; venation dark brown; Pt dark brown with pale contours; MP reaches anal margin 0.5 cell distal to the vein descending from subnodus; RP2 originating at Px 5 in Fw, at Px 4 in Hw; 11 Px in Fw, 10 Px in Hw.

Abdomen (Figure 5a). S1−8 dark brown dorsally, pale laterally, with pale apical rings, black color broadly extending on dorsal and lateral S8; S9 black/dark brown with a pale spot on its posterior dorsal 1/2; S10 pale dorsally, black laterally; cerci black; ovipositor valves pale, surpassing posterior margin of S10.

Measurements. TL: 32.3; AB: 27.3; head width: 3; FW: 19.2; HW: 17.9; Pt: 0.6; metathoracic femur 2.3; metathoracic tibia 1.9.

Diagnosis. Similarly to the male, the female of *F. machadorum* can be easily separated from the other female congeners by the morphology of the prothoracic hind lobe. It presents a roughly squared hind prothoracic lobe (Figure 5d), whereas in *F. sancta* (Hagen in Selys, 1860), its closely related species, the hind lobe is rounded. Among the examined females, the morphology is identical, although some coloration variation could be observed, as seen in Figure 4.

Discussion

Considering the knowledge gaps of Odonata in the Cerrado, we conducted an inventory in palm swamps and riparian forests of

Uberlândia, Minas Gerais, in addition to the taxonomic description of the female of *Forcepsioneura machadorum*, and the description of the larvae of *Acanthagrion truncatum* (Vilela et al. 2020c). Altogether, we found 101 odonate species in the municipality, representing approximately 32% and 11% of the total richness in Minas Gerais and Brazil, respectively. Our study also added eight new records for the state, which now has 312 recorded species (Vilela 2020). This number represents the second highest Odonata richness reported to a Brazilian state, being only surpassed by Amazonas, with 335 species (Koroiva et al. 2020).

The number of species in palm swamp, riparian forest and both habitats, are greater in relation to standard diversity found in others inventories in the Cerrado, which, on average, are close to 50 species (Vilela et al. 2016, Barbosa et al. 2019, Borges et al. 2019). Possibly the heterogeneity of sampled sites can justify this difference. Other inventories with this pattern presented similar diversity to ours, even with fewer sampling effort. For example, in Minas Gerais, Bedê et al. (2015), Vilela et al. (2020a) and Amorim et al. (2018) sampled 128, 90 and 71 species, respectively, in more than 13 lotic and lentic sites. In other states, with less than 12 water bodies, Ferreira-Peruquetti & Fonseca-Gessner (2003) registered 85 species in lotic and lentic sites of riparian forests of São Paulo, and Juen et al. (2014) found more than 2,000 specimens and 79 species in streams of three Cerrado phytophysiognomies in Mato Grosso. In addition, some extensive inventories of heterogeneous habitats in Cerrado and Atlantic Forest presented great numbers of new records for Minas Gerais (Bedê et al. 2015, Souza et al. 2017), which may also explain the novelties found in this study. Regardless of the comparisons, all surveys of dragonflies in the country are of great importance, since it contributes to Odonata database, ecology and taxonomy, even with small sampling effort.

The abundance and number of new records in our study were concentrated mainly on Libellulidae and Coenagrionidae. This result was expected, since these groups are represented by a great diversity of species present in numerous aquatic habitats in worldwide (Garrison et al. 2006, Garrison et al. 2010), and are commonly representative in Brazilian inventories (Souza et al. 2013, Calvão et al. 2014, Pires et al. 2019, Garcia Junior et al. 2021). Nevertheless, Aeshnidae and Gomphidae were slightly diverse in our study compared to other Cerrado inventories. This representativity may be justified due to larvae rearing and use of light traps methods, which, only in two sites, sampled almost 30% of the group diversity. Our results reinforce the adoption of alternative methods to sample these families, since adults of aeshnids and gomphids are strongfliers, cryptic and some species are crepuscular (Ferreira-Peruquetti & Fonseca-Gessner 2003, Garrison et al. 2006, Almeida et al. 2013). Other families, such as Cordullidae and Megapodagrionidae were not recorded in our study. Despite nearly 50 or more species of these groups are known to occur in the neotropics (von Ellenrieder 2009), there are few inventoried species in Minas Gerais, with approximately 10 records in the Cerrado or ecotone zones of this biome and Atlantic Forest (Vilela 2020).

The riparian vegetation of many sampled sites were open with native grasses in palm swamp or, almost always, exotic grasses in disturbed forests. This may explain the great diversity of some libellulids, such as *Erythrodiplax* and *Micrathyria*. These groups are predominantly habitat generalists, abundant in open areas and some species are indicators of degraded sites, such as *Erythrodiplax fusca* Rambur, 1842 (Dutra & De Marco 2015, Dalzochio et al. 2018b), the most abundant libellulid in our study. However, even if anthropized areas are diverse in generalist dragonflies, they may contain not reported species with restricted distribution (Barbosa et al. 2019, Santos et al. 2020). In this context, we found *Oligoclada xanthopleura* and *Angelagrion nathaliae* in degraded ponds. The first species was not yet reported for the southeastern region, and the second occurred only in São Paulo state.

Despite the prevalence of generalist groups, few inventoried species and often restricted to integer habitats, such as *Neuraeschna claviforcipata*, *Mnesarete guttifera* Selys, 1873, *Perithemis icteroptera* Selys in Sagra, 1857 and *Telebasis willinki* Fraser, 1948 were found in the municipality. These records occurred mainly in urban green areas and conservation units, that even representing a small portion of the sampled locations, also held for approximately 50% of the novelties of this study. These results show that vegetation remnants hold a great richness of Odonata species, even being near or at urban areas. New species for science and states are often reported in protected urban or rural areas (e.g., Bedê et al. 2015, Pinto 2019), even if adjacent matrixes are unfavorable for odonates. For example, *Erythrodiplax ana* and *F. machadorum* were first discovered, respectively, at a preserved palm swamp and forest fragment adjacent to urban and cattle areas (Guillermo-Ferreira et al. 2016, Vilela et al. 2020b). Moreover, *Acanthagrion marinae* Lozano & Rodrigues, 2018, a recent discovered coenagrionid, was also recorded in preserved urban palm swamps in Brazil (Lozano & Rodrigues 2018, Rodrigues et al. 2019). In addition to provide suitable habitats to sensitive and low dispersion populations, most part of regional dragonfly community can also be benefited in conserved fragments, since these areas hold resources and microhabitats absent in degraded matrices (Ferreira-Peruquetti & Fonseca-Gessner 2003, Paulson et al. 2006, Araújo et al. 2020). These benefits can extend to surrounding zones of low degradation level that contain some environmental characteristics of preserved fragments, being also favorable to sensitive species and different communities (Monteiro-Júnior et al. 2016, Rodrigues et al. 2019). This highlights the importance of preserving and increase the number of such preserved areas and surrounding low disturbed zones to maintain riverine species (Oliveira et al. 2017, Azevedo-Santos et al. 2019). Despite this importance, the number of protected areas with incorporated aquatic environments is scarce in the Brazil, not ideally protecting most of aquatic taxa, including Odonata (Nóbrega & De Marco 2011, Azevedo-Santos et al. 2019).

The IUCN red list is an important indicator of the conservation of global species for communities within and outside the scientific and conservation ambits (IUCN 2020). Considering some population characteristics, such as size, dynamics and geographic distribution (Rodrigues et al. 2006), several species are categorized under some conservation status (IUCN 2020). Nonetheless, data of some threatened groups, such as dragonflies, are still incomplete (Clausnitzer et al. 2009, Koroiva et al. 2017, Ávila Júnior et al. 2021). Our results showed that more than half of the species sampled in this study (including not evaluated species) do not present enough data to be listed in a threaten category, confirming the knowledge gap of Odonata for Brazil (Vilela et al. 2020b). With the increment of inventories and updates of vulnerability statuses in the future, many species restricted to a single habitat or that have been recently discovered will be included in some risk of extinction. For example, *E. ana*, a species restricted to preserved palm swamps (Guillermo-Ferreira et al. 2016, Vilela et al. 2020b), is listed at risk of extinction due to the low number of individuals, low geographic coverage and to the vulnerability of this phytophysiognomy. Thus, we believe that our present data will contribute to fill the gaps about the vulnerability of odonates. However, we emphasize again the need for more surveys of the group in palms swamps, riparian forests and other phytophysiognomies of Brazil.

All phytophysiognomies present unique species occurrence. Forest habitats had a higher diversity of exclusive damselflies, mainly composed by shade demand species (ex., *Oxyagrion basale* Selys, 1876 and *Protoneura tenuis* Selys, 1860), while palm swamps were diverse in open habitat dragonflies (ex., *Micrathyria* spp. and *Erythemis* spp.). This result indicates bank vegetation as an important regulator of local species for each habitat due to thermoregulatory demands of many Zygoptera and Anisoptera, as presented by many studies (De Marco et al. 2015, Carvalho et al. 2013, Oliveira-Júnior & Juen 2019). Moreover, aquatic vegetation and abiotic factors are also related to Odonata structure of these habitats (Juen et al. 2007, Borges et al. 2021). For example, palm swamp and open habitats, such as degraded areas (Fares et al. 2020), are diverse in macrophytes, which are used as oviposition site or substrate during larvae development of some dependent libellulids and coenagrionids species (Vilela et al. 2016, Brito et al. 2020). Notably, degradation level, biased sample methods and time effort between phytophysiognomies must also be considered in our results, since some species found in a specific habitat in our study were present or absent in other palm swamp and forest studies (Rodrigues et al. 2018, Barbosa et al. 2019, Vilela et al. 2020a).

Here we demonstrated that inventories and taxonomic studies in poorly explored phytophysiognomies are important to overcome knowledge gaps of Brazilian odonatofauna. In addition to contributing to the knowledge of the diversity of dragonflies, new species reports, with other groups that inhabit palm swamps and forests, reinforce the importance of conserving these habitats, since many endemic species are at risk of extinction with land use expansion in these habitats. Therefore, we recommend more inventories of such phytophysiognomies in other regions.

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Author Contributions

Henrique Venâncio: 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.

Diogo Silva Vilela: 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.

Marcela Silva Barbosa: Contribution to data collection. Contribution to critical revision, adding intellectual content.

Jean Carlos Santos: 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.

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Aquatic oligochaetes (Annelida: Clitellata) in reservoirs in São Paulo State: list of occurrence and ecological observations on the species

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Abstract: This work sought the survey of species and information about the distribution of the Class Oligochaeta in reservoirs sampled in the Sediment Quality Monitoring Network of CETESB (Environmental Company of the State of São Paulo). As such, this study aimed to inventory the limnic oligochaetes fauna to expand knowledge of the ecology and distribution of this group in reservoirs in the state of São Paulo. Ninety replicates were performed in 12 reservoirs in the state of São Paulo between 2014 and 2016, using van Veen or Ponar samplers in the sublittoral region, and Ekman-Birge in the deep region. Twenty-eight taxa were inventoried, belonging to the families Naididae and Opistocystidae. The species *Dero righii* and *Pristina longisoma* were recorded for the first time in São Paulo State, *Nais magnaseta* and *Spirosperma velutina* were first recorded in Brazil. The results presented here make this inventory extremely important for understanding the distribution of aquatic oligochaetes throughout the Brazilian territory.

Keywords: *distribution; bioindicators; diversity; reservoir; inventory.*

Oligoquetos aquáticos (Annelida: Clitellata) em reservatórios no Estado de São Paulo: lista de ocorrência e observações ecológicas das espécies

Resumo: Este trabalho buscou o levantamento de espécies e informações sobre a distribuição da Classe Oligochaeta em reservatórios amostrados na Rede de Monitoramento da Qualidade de Sedimentos da CETESB (Companhia Ambiental do Estado de São Paulo). Sendo assim, este estudo objetivou inventariar a fauna de oligoquetos para expandir o conhecimento de ecologia e distribuição deste grupo em reservatórios no Estado de São Paulo. Foram realizadas 90 réplicas em 12 reservatórios no estado de São Paulo entre os anos de 2014 a 2016, utilizando amostradores van Veen ou Ponar na região sublitoral, e Ekman-Birge na região profunda. Foram inventariados 28 táxons, pertencentes às famílias Naididae e Opistocystidae. As espécies *Dero righii* e *Pristina longisoma*, foram registradas pela primeira vez no Estado de São Paulo, *Nais magnaseta* e *Spirosperma velutina* foram identificadas pela primeira vez no Brasil. Os resultados apresentados aqui tornam este inventário de suma importância para o conhecimento da distribuição dos oligoquetos aquáticos em todo o território brasileiro.

Palavras-chave: *distribuição; bioindicadores; diversidade; reservatório; inventário.*

Introduction

Species surveying is essential for understanding the biota of a given environment, specifically in Brazilian aquatic ecosystems where species diversity is poorly known due to the small number of taxonomists (ROCHA, 2003; AGOSTINHO et al., 2005). Although oligochaetes are among the most abundant species in sediments of Neotropical lakes and reservoirs, there is relatively poor ecological information, especially in comparison to the knowledge generated in temperate-zone habitats where these species are used to monitor water quality (BRINKHURST; GELDER 1991, MARTIN et al., 2008, CHRISTOFFERSEN, 2010, TIMM; MARTIN 2015, RODRIGUES; ALVES 2018). The community composition and structure of the Class Oligochaeta provides important information for the assessment of water and sediment quality, and has therefore proved to be a great tool for aquatic biomonitoring (LAFONT, 1989; ROSSO, 1995; PRYGIEL et al., 2000; VIVIEN et al., 2014). Despite their representativeness in aquatic macroinvertebrate fauna, oligochaetes are poorly studied compared to other benthic groups (GORNI, 2007), however, several authors have been collecting information about the diversity and ecology of the Oligochaeta assemblage in São Paulo State (MARCUS DU BOIS-REYMOND MARCUS, 1949; RIGHI, 1984; CORBI et al., 2004; PAMPLIN et al., 2005; DORNFELD et al., 2006; ALVES; GORNI, 2007; SURIANI et al., 2007; GORNI; ALVES, 2007; GORNI; ALVES, 2008b; GORNI; ALVES, 2006; GORNI, 2007; GORNI et al., 2015; GIROLLI et al., 2018).

Given this, gathering information about the assemblages of oligochaetes is essential for knowledge of limnic biodiversity, assessment and water management. To provide information to environmental management bodies and facilitate decision-making on recovery and / or preservation of Brazilian aquatic ecosystems.

Thus, this article aims to inventory the diversity of Class Oligochaeta species in lentic environments of São Paulo State monitored by CETESB, as well as contribute to the knowledge of distribution and ecological observations in the State of São Paulo.

Material and Methods

1. *Area of study*

The Oligochaeta fauna samples were granted for the purpose of this research by the Aquatic Communities Sector (ELHC) and are part of the Sediment Quality Monitoring Network of CETESB. Twelve reservoirs were studied in the state of São Paulo between 2014 and 2016, where a total of 90 replicates were collected. Reservoir identification is described in Table 1, and the location of the points is illustrated in Figure 1.

Physical and Chemical Variables

The physical and chemical variables were collected in two groups, water and sediment. The variables collected in the water were: total surface phosphorus (P), bottom dissolved oxygen (DO), bottom electrical conductivity (EC), chlorophyll a (C), and depth (Dep). The variables collected in the sediment were: sediment organic matter (OM), total organic carbon (TOC), total Kjeldahl nitrogen (NKj), total phosphorus (Ptot) and granulometry were performed and determined by CETESB. The bibliography and analytical methods used to collect and determine the variables are available in Annex E of the Relatório da Qualidade das Águas Interiores no Estado de São Paulo (CETESB, 2017). The values of the environmental variables measured were tested using multivariate variance analysis (MANOVA) to identify possible significant differences between the collected points.

The Trophic State Index (IET) was used to classify the water quality of the reservoirs for nutrient enrichment. The IET is composed of the indices of the Trophic State for phosphorus - IET (PT), and for

Table 1. Identification of sampling points of the Sediment Quality Monitoring Network of São Paulo State reservoirs, conducted by CETESB from 2014 to 2016. Ugrhi - Water Resources Management Unit; N - sampling effort.

Site	Reservoirs	Coordinate	Ugrhi	*N*	
				Sublittoral	Deep
BILL	Billings – Central body	23°47'11"S / 46°38'49"W	6	3	3
BIRP	Billings - Rio pequeno	23°47'28"S / 46°28'14"W	6	6	6
BITQ	Billings - Taquacetuba	23°50'26"S / 46°39'31"W	6	-	3
CAFR	França	23°56'01"S / 47°09'28"W	11	3	3
GRAM	Graminha	21°35'06"S / 46°37'04"W	4	3	6
IUNA	Paraibuna	23°25'06"S / 45°34'17"W	2	3	3
JQJU	Paiva Castro	23°21'13"S / 46°39'56"W	6	6	6
JURU	Jurumirim	23°16'28"S / 49°04'05"W	14	3	3
NOVA	Ponte Nova	23°34'46"S / 45°57'02"W	6	3	3
PEBA	Taiaçupeba	23°34'45"S / 46°17'30"W	6	-	3
RGDE	Rio grande	23°44'30"S / 46°24'59"W	6	-	3
SANT	Santa Branca	23°22'15"S / 45°51'35"W	2	3	3
SOIT	Ituparaaranga	23°37'08"S / 47°23'22"W	10	3	3
TIPR	Promissão	21°18'49"S / 49°45'49"W	16	3	3

Fount: Adapted from the São Paulo State Inland Water Quality Report (CETESB, 2015, 2016 and 2017).

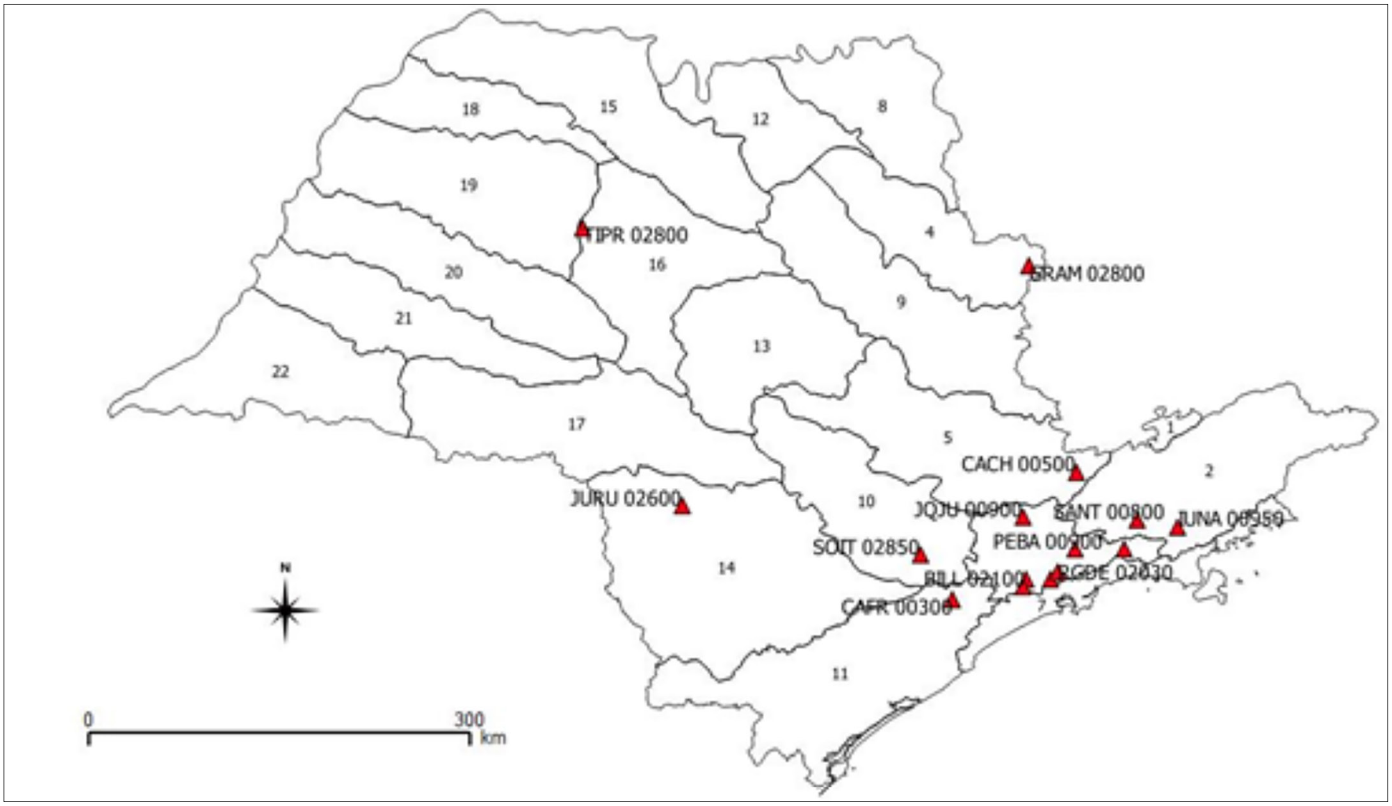

Figure 1. Spatial distribution of the sampling points of the Sediment Quality Monitoring Network of São Paulo State reservoirs, conducted by CETESB from 2014 to 2016.

chlorophyll a - IET (CL). Thus, the result of the IET is the arithmetic mean between the IET (PT) and IET (CL) indices, with their respective equations:

$$IET(PT)=10\{6-[1{,}77-0{,}42.(InPTIn2)]\} \tag{1}$$

$$IET(CL)=10\{6-[0{,}92-0{,}34.(InCLIn2)]\} \tag{2}$$

$$IET=[IET(PT)+IET(CL)]2 \tag{3}$$

where: PT = total phosphorus concentration measured at the water surface, expressed in µg/L; CL = chlorophyll concentration at total measured at the water surface, expressed in µg/L; and ln = natural logarithm.

Oligochaeta Collection and Identification

The sediment samples for analysis of Oligochaeta assemblage were collected by CETESB with van Veen or Ponar sewers in the sublittoral region and Ekman-Birge in the deep region. The fixation and sample preparation followed the CETESB Technical Standard L5.309 (CETESB, 2003). For the identification of the organisms the taxonomic criteria adopted by Brinkhurst and Jamieson (1971), Righi (1984), Brinkhurst and Marchese (1989) and Timm (2009) were used.

To evaluate the efficiency of the samples collected in the reservoirs, species richness estimators (Jackknife 1 and 2, Bootstrap) and randomized species accumulation curves (collector curve) were used. Species accumulation curves were constructed using 100 curves generated by the random addition of the samples, using the software “R” version 3.1.1 (R CORE TEAM, 2017).

We applied a Boxplot chart and selected the most abundant species (upper quartile) to perform a descriptive analysis of the reservoirs in which these species were found.

Results and Discussion

The means of environmental variables (depth, sand, silt, clay, organic matter, dissolved oxygen, total surface phosphorus, total sediment phosphorus, electrical conductivity, chlorophyll a, total organic carbon, total Kjeldahl nitrogen, and trophic state index), as well as the standard deviation, are exposed in Table 2. The same variables were submitted to a Multivariate Variance Analysis (MANOVA), in which a significant difference was identified between the points ($p<0.05$), which means that the reservoirs are statistically different from the environmental variables presented above.

As for the Trophic State Index, the highest values were recorded in two regions of the Billings reservoir. The first was in the central body (72.9) and in the Taquacetuba arm (70.8), they were classified as Hypereutrophic, followed by the Rio Grande (65.6) and PEBA (63.4) reservoirs, which were classified as Supereutrophic. However, all other reservoirs showed a degree of nutrient enrichment, since the lowest IET class recorded was Mesotrophic. None of the reservoirs were classified as Ultraoligotrophic or Oligotrophic.

The highest values of the variables OM (20.2%), EC (204), P (0.15 mg / L), Ptot (5,573 mg / Kg) and C (93.56 µg / L) and the lowest value of DO (3.1 mg / L) were recorded in the central body of the Billings reservoir. Other reservoirs, such as SANT and JURU, had opposite values for the same variables.

The assemblage of oligochaetes inventoried in this study was composed of two families (Naididae and Opistocystidae) distributed in 28 species. The sample design adopted in the present study can be considered adequate for species survey, since the accumulation curve stabilized in 70 samples. Figure 2 illustrates the species accumulation curve and richness estimators.

The Naididae family presented 96% of the found taxa (n=27), being represented by the subfamilies Naidinae, Pristininae, Rhyacodrilinae

Table 2. Environmental variables of the reservoirs sampled by the Sediment Quality Monitoring Network of the State of São Paulo, carried out by CETESB in the period from 2014 to 2016. ***BILL*** (central body) - Billings, ***SOIT*** - Itupararanga, ***TIPR*** - Promissão, ***NOVA*** - Ponte Nova, ***SANT*** - Santa Branca, ***CAFR*** - França, ***IUNA*** – Paraibuna, ***JURU*** - Jurumirim, ***GRAM*** – Graminha, ***BIRP*** - Billings (Rio pequeno), ***JQJU*** - Paiva Castro, ***BITQ*** - Billings (Taquacetuba), ***PEBA*** - Taiaçupeba, ***RGDE*** - Rio grande. ***Dep***. – Depth (m), ***OM*** - Sediment organic matter (%), ***DO*** - Bottom dissolved oxygen (mg/L), ***P*** - Total surface phosphorus (mg/L), ***TOC*** - Total organic sediment carbon (%), ***NKj*** - Total Kjeldahl sediment nitrogen (mg/g), ***Ptot*** - Total sediment phosphorus (mg/Kg), ***EC***- Bottom electrical conductivity, ***C*** - Chlorophyll a (µg/L), ***IET*** - Trophic State Index, and - Environmental variable not measured.

Ponto	Dep	SAND	SILT	CLAY	OM	DO	P	TOC	NKj	Ptot	EC	C	IET (Classes)	
BILL	9,2 (4,2)	11,7 (7,6)	27,8 (5,7)	60,53 (13,2)	20,2 (1,6)	3,1 (0,4)	0,15 (0)	5,36 (0)	6979 (0)	5573 (0)	204 (2,8)	93,56 (0)	72,9	Hypereutrophic
BIRP	6,5 (2,1)	42,8 (35,4)	24,9 (10,1)	32,2 (28,4)	9,9 (6,2)	7,7 (0,3)	0,02 (0)	4,16 (0)	4139 (0)	389,5 (0)	84,8 (19,4)	14,3 (7,7)	62,1	Eutrophic
TIPR	14,1 (10,3)	37,7 (30,1)	23,9 (9,7)	38,4 (20,9)	10,3 (4,7)	4,1 (5,3)	<0,02 (0)	1,76 (0)	1824 (0)	519 (0)	203,5 (14,8)	2,14 (0)	56	Mesotrophic
NOVA	8,5 (4,1)	35,1 (24,1)	26,6 (12,5)	38,4 (12,5)	16,2 (3,4)	4,9 (1,8)	0,01 (0)	3,66 (0)	4502 (0)	681 (0)	32 (9,9)	1,34 (0)	54,2	Mesotrophic
SANT	19,5 (17,0)	36,6 (34,8)	19,9 (3,8)	43,5 (33,9)	9,3 (5,9)	6,8 (0)	0,01 (0)	1,82 (0)	2600 (0)	740 (0)	-	<0,01 (0)	56,3	Mesotrophic
IUNA	4,8 (0,76)	9,1 (1,6)	23,1 (1,2)	67,7 (2,1)	15,7 (0,6)	6,9 (0)	<0,02 (0)	4,28 (0)	3331 (0)	691 (0)	54 (25,5)	<1 (0)	55,63	Mesotrophic
CAFR	8,9 (5,0)	28,8 (27,7)	15,1 (5,9)	56,1 (31,7)	10,8 (6,4)	8,6 (1,1)	0,01 (0)	2,64 (0)	2960 (0)	978 (0)	26,5 (0,7)	1,92 (0)	55,1	Mesotrophic
JURU	16,9 (12,7)	42,4 (30,6)	14,4 (7,8)	43,1 (26,1)	7,2 (3,7)	6,8 (0)	0,01 (0)	1,3 (0)	866 (0)	476 (0)	136 (0)	1,13 (0)	53,8	Mesotrophic
GRAM	23,3 (15,6)	15,3 (22,3)	13,2 (3,7)	71,5 (22,5)	14,3 (6,1)	4,2 (4,1)	0,04 (0,04)	3,18 (0)	1340,33 (0)	1479 (0)	62,3 (15,6)	2,05 (0,16)	59,6	Eutrophic
JQJU	10,0 (5,5)	14,1 (15,0)	24,0 (18,4)	61,9 (31,9)	10,1 (4,1)	4,1 (3,1)	0,015 (0,01)	2,3 (0)	2481,5 (0)	868 (0)	61 (22,9)	2,11 (0,03)	56,4	Mesotrophic
PEBA	9,4 (0,3)	8,1 (4,9)	23,8 (1,3)	68,1 (5,6)	19,3 (3,5)	7,0 (0)	0,08 (0)	10,3 (0)	6910 (0)	978 (0)	171 (0)	87,32 (0)	63,4	Supereutrophic
RGDE	2,6 (0,7)	17,5 (3,1)	35,9 (1,8)	46,6 (4,9)	13,7 (0,6)	10,3 (0)	0,06 (0)	4,1 (0)	2583 (0)	1328 (0)	91 (0)	14,97 (0)	65,6	Supereutrophic
BITQ	9,4 (0,1)	8,1 (2,7)	23,8 (1,0)	68,1 (2,3)	19,3 (9,0)	7,0 (0)	0,08 (0)	8,7 (0)	7467 (0)	2516 (0)	171 (0)	87,32 (0)	70,8	Hypereutrophic
SOIT	8,8 (5,8)	11,0 (9,7)	26,3 (4,2)	62,7 (12,7)	12 (3,6)	7,3 (1,1)	0,03 (0)	1,86 (0)	2534 (0)	598 (0)	86 (0)	0 (0)	62,9	Eutrophic

and Tubificinae. Among the Naidids, the subfamily Naidinae, which represented 59% of the species (n=16), was composed by the genera *Aulophorus, Chaetogaster, Dero, Nais, Slavina* and *Stephensoniana.* The subfamily Pristininae presented 22% of species (n=6), represented by its only genus (Pristina). The subfamily Rhyacodrilinae was represented by the taxa, *Bothrioneurum* sp. and *Branchiura sowerbyi*, corresponding to 7% of the identified species. Finally, the subfamily Tubificinae was represented by the genera *Aulodrilus, Limnodrilus* and *Spirosperma* making up 11% of the identified species (n=3). The Opistocystidae family was represented by only one species, *Opistocysta funiculus*, corresponding to 4% of the identified species.

Among the 28 species identified in this study, *Dero righii* and *Pristina longisoma* had not been registered in the state of São Paulo, occurring only in the states of Mato Grosso do Sul, Minas Gerais and Paraná, and Mato Grosso do Sul and Paraná, respectively. Two other species had not been recorded in Brazil, *Nais magnaseta* whose knowledge of their distribution was restricted to Texas, USA (Harman, 1973); and *Spirosperma velutina*, whose distribution was registered in Venezuela and Europe (CHRISTOFFERSEN, 2007).

The species identified in this study, as well as the record of their ecological observations in the State of São Paulo, are presented below distributed in family, genus and species, following alphabetical order. The synonym list was based on the catalog proposed by Christoffersen (2007).

The species recorded with the highest abundances recorded in the upper quartile of the boxplot were *Aulodrilus pigueti* (40.4%); *Bothrioneurum* sp. (13,7%); *Limnodrilus hoffmeisteri* (11.9%); *Opistocysta funiculus* (8.9%); *Pristina osborni* (4.4%) and *Pristina synclites* (4.3%). Table 3 shows the reservoirs where these species were found.

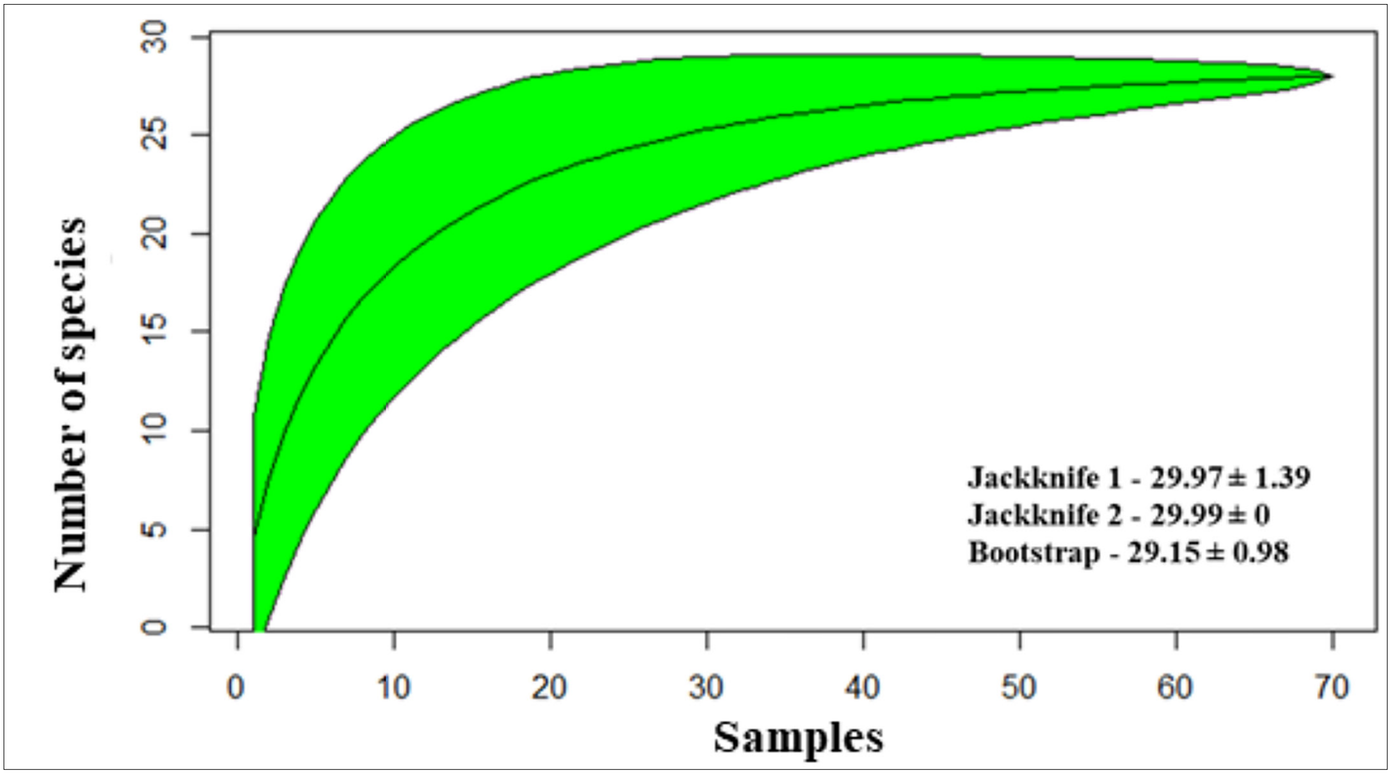

Figure 2. Species accumulation curve and richness estimators for oligochaetes collected at the sampling points of the Sediment Quality Monitoring Network of São Paulo State reservoirs, conducted by CETESB from 2014 to 2016.

Table 3. Occurrence of the most abundant species of Oligochaeta in reservoirs in the State of São Paulo. ***BILL*** - Billings, ***SOIT*** - Itupararanga, ***TIPR*** - Promissão, ***NOVA*** - Ponte Nova, ***SANT*** - Santa Branca, ***IUNA*** – Paraibuna, ***CAFR*** - França, ***JURU*** - Jurumirim, ***GRAM*** - Graminha, ***BIRP*** - Billings (Rio pequeno), ***JQJU*** - Paiva Castro, ***BITQ*** - Billings (Taquacetuba), ***PEBA*** - Taiaçupeba, ***RGDE*** - Rio grande. Presence (X).

Species	BILL	SOIT	TIPR	NOVA	SANT	CAFR	JURU	IUNA	GRAM	BIRP	JQJU	BITQ	PEBA	RGDE
Aulodrilus pigueti	X	X	X	X	X	X	X		X	X	X			X
Bothrioneurum sp	X	X	X	X	X	X	X	X		X	X	X	X	X
Limnodrilus hoffmeisteri	X	X	X	X		X	X			X	X	X	X	X
Opistocysta funiculus	X		X	X	X	X	X				X			X
Pristina osborni	X		X	X	X		X				X			X
Pristina synclites	X	X	X	X		X	X		X	X	X	X		

List and species considerations

NAIDIDAE FAMILY Ehrenberg, 1828

NAIDINAE SUBFAMILY

Aulophorus borelli Michaelsen, 1900.

Synonyms: *Dero* sp. Cognetti, 1900; *Dero borelli* Michaelsen, 1900; *Aulophorus borellii* Michaelsen, 1900; *Dero (Aulophorus) borellii* Michaelsen, 1900.

Record and ecological observations: Found associated with sediment in Araraquara, Santa Clara stream (ALVES; LUCCA, 2000); associated with *Scirpus cubensis* (Cyperaceae), Luiz Antônio, Infernão Lake (CORREIA; TRIVINHO-STRIXINO, 1998; TRIVINHO-STRIXINO et al., 2000); Associated with *Salvinia* (Salviniaceae) and *Egeria* (Hydrocharitaceae), Américo Brasiliense, Anhumas stream dam (SANCHES; GORNI, 2014). We found it in Promissão and Billings reservoirs.

Aulophorus costatus Du Bois-Reymond Marcus, 1944.

Synonyms: *Aulophorus schmardai f. costata* Du Bois-Reymond Marcus, 1944; *Dero (Aulophorus) costatus* Du Bois-Reymond Marcus, 1944; *Dero (Aulophorus) schmardai*, Harman, 1974.

Record and ecological observations: Found in São Paulo, in the Pinheiros river (DU BOIS-REYMOND MARCUS, 1944; MARCUS, 1942; 1943); associated with submerged macrophytes in Brotas, at Lagoa Dourada dam (ALVES; GORNI, 2007), and with *Salvinia* (Salviniaceae) and *Egeria* (Hydrocharitaceae) in Américo Brasiliense, at Anhumas stream dam (ALVES; GORNI, 2007; SANCHES; GORNI, 2014); associated with *Metania spinata* (Metaniidae) in Itirapina, in the Dourada Lake dam (GORNI; ALVES, 2008a). We found it in Paiva Castro, Jurumirim and Graminha reservoirs.

Aulophorus furcatus O. F. Müller, 1774.

Synonyms: *Nais furcata* O. F. Müller, 1774. *Dero (Aulophorus) furcatus* O. F. Muller, 1774; *Dero* sp. Stephenson, 1910; *Aulophorus stephensoni* Michaelsen, 1912; Dero roseola Nicholls, 1921.

Record and ecological observations: Found in Bariri, in the Ponte Nova reservoir (PAMPLIN et al., 2005), in São Paulo in the Tietê, Pinheiros, São Lourenço rivers in Jardim Europa sewage (MARCUS, 1943), and in a stream of Bocaina (SANCHES et al., 2016). Associated with *Pomacea bridgesii* (Ampullaridae) in Araraquara (GORNI; ALVES, 2006); and the sediment in Barra Bonita (SURIANI et al., 2007). We found it in the Graminha and Billings reservoirs.

Chaetogaster diaphanus Gruithuisen, 1828.

Synonyms: *Nais diaphana* Gruithuisen, 1828.

Record and ecological observation: Found associated with the *Pomacea bridgesii* (Ampullaridae) in Araraquara (GORNI; ALVES, 2006); associated with *Salvinia* (Salviniaceae) and *Egeria* (Hydrocharitaceae) in the Anhumas stream dam, in Américo Brasiliense (SANCHES; GORNI, 2014). We found it in the Cachoeira do França, Rio Grande and Graminha reservoirs.

Dero digitata O. F. Müller, 1773.

Synonyms: *Nais digitata* O. F. Müller, 1773; *Dero (Dero) digitata* O. F. Müller, 1773; *Nais (Proto) digitata* O. F. Müller, 1773; *Uronais digitata* O. F. Müller, 1773; *Proto digitata* O. F. Müller, 1773; *Xantho hexapoda* Dutrochet, 1819; *Dero limosa* Leidy, 1852; *Dero acuta* Bousfield, 1886; *Dero michaelseni* Svetlov, 1924; *D. bonariensis* Michaelsen, 1933; D. *kawamurai* Kondô, 1936; *Dero tanimotoi Kondô*, 1936; *Dero quadribranchiata* Cernosvitov, 1937.

Record and ecological observations: Found in Bariri, in the Ponte Nova reservoir (PAMPLIN et al., 2005), and in São Paulo, in the São Lourenço river (ROSA et al., 2015). Associated with sediment in Bariri, in the Ponte Nova reservoir (SURIANI et al., 2007); associated with submerged macrophytes in Brotas, at Lagoa Dourada Dam, and in Américo Brasiliense, at Anhumas stream dam (ALVES; GORNI, 2007); in *Salvinia* (Salviniaceae) and *Egeria* (Hydrocharitaceae) (SANCHES; GORNI, 2014). In Araraquara, was found associated with sediment in Santa Clara stream (ALVES; LUCCA, 2000); and *Pomacea bridgesii* (Ampullaridae) (GORNI; ALVES, 2006). We found it in the reservoirs Graminha, Promissão and Billings.

Dero evelinae Marcus, 1943.

Synonyms: *Dero (Dero) evelinae* Marcus, 1943.

Record and ecological observations: Found in São Paulo (MARCUS, 1942, 1943, 1944). Associated with sediment in the Bariri reservoir (SURIANI et al., 2007) and in São Carlos, in the Fazzari dam (FUSARI; FONSECA-GESSNER, 2006); associated with submerged macrophytes in Brotas, at Lagoa Dourada Dam, and in Américo Brasiliense, at Anhumas stream dam (ALVES; GORNI, 2007); and associated with *Scirpus cubensis* (Cyparaceae) (CORREIA; TRIVINHO-STRIXINO, 1998; TRIVINHO-STRIXINO et al., 2000). We found it in the Promission reservoir and in the central body of the Billings reservoir.

Dero multibranchiata Stieren, 1892.

Synonyms: *Dero florifera* Oken, 1815.

Record and ecological observations: Found associated with sediment in Bariri (SURIANI et al., 2007), at Ponte Nova reservoir (PAMPLIN et al., 2005), in Américo Brasiliense, at Anhumas stream dam (CORBI; TRIVINHO- STRIXINHO, 2002). We found it in the Billings reservoir, and in the arm of Taquacetuba.

Dero righii Varela, 1990.

Synonyms: *Dero (Dero) righi* Varela, 1990.

Record and ecological observation: This species was first registered in the state of São Paulo. The reservoirs where *D. righii* occurred were Billings - Rio Pequeno, Graminha, Taiaçupeba, Rio Grande, Itupararanga, Ponte Nova, and Paiva Castro. In previous studies, this species occurred in the states of Mato Grosso do Sul (TAKEDA et al., 2000); Minas Gerais (MARTINS; ALVES, 2008); and Paraná (RAGONHA; TAKEDA, 2014).

Dero Sawayai Marcus, 1943.

Synonyms: *Dero heterobranchiata* Michaelsen, 1933; *Dero (Dero) sawayai* Marcus, 1943.

Record and ecological observations: Found associated with the Pinheiros River sediment (MARCUS, 1943); in Araraquara was found associated with *Pomacea bridgesii* (Ampullaridae) (GORNI; ALVES, 2006); associated with submerged macrophytes at Lagoa Dourada dam in Brotas, and at Anhumas stream dam in Américo Brasiliense (ALVES; GORNI, 2007); and associated with *Metania spinata* (Metaniidae) in Itirapina in Dourada Lake (GORNI; ALVES, 2008a). We found it in the Itupararanga, Paiva Castro, Rio Grande, Graminha, Promissão and Billings - Rio Pequeno reservoirs.

Nais communis Piguet, 1906.

Synonyms: *Nais heterochaeta* Benham, 1893; *Nais* Walton, 1906; *Nais parviseta* Walton, 1906; *Nais variabilis* var. *punjabensis* Stephenson, 1909; *Nais* communis var. *punjabensis* Stephenson, 1909; *Nais communis* var. *caeca* Stephenson, 1910; *Pterochaeta astronensis* Pierantoni, 1911; *Nais communis* var. acuta Pointner, 1914; *Nais communis f. magenta* Marcus, 1943.

Record and ecological observations: Found in Rio Claro (MARCUS, 1943), in Monjolinho (ALVES et al., 2006), São Lourenço river (ROSA et al., 2014), in streams of Intervales State Park, Bocaina, Carmo, Lageado and Água Comprida (ALVES et al., 2008) and Bocaina in the Himalaia stream (SANCHES et al., 2016). Associated with sediment in Araraquara in the Santa Clara (ALVES; LUCA, 2000) and Pinheirinho stream (ALVES et al., 2006); in Campos do Jordão in the Campo Meio stream associated with sediment and substrate of erosional and depositional areas (GORNI; ALVES, 2008b). Associated with the sponge *Ephydatia crateriformis* (Spongillidae), in the Ribeira de Iguape river and the Tietê river (MARCUS, 1943), in São Carlos in the Espraiado stream associated with *Radiospongilla amazonenses* (Spongillidae) (CORBI et al., 2005; PAMPLIM et al., 2005); *Metania spinata* (Metaniidae) in Itirapina in the Lagoa Dourada dam (GORNI; ALVES, 2008a); and associated with *Pomacea bridgesii* (Ampullaridae) (GORNI; ALVES, 2006). Associated to submerged macrophytes in Brotas in Lagoa Dourada (ALVES; GORNI, 2007), to aquatic macrophytes in Luiz Antônio in Infernão Lake (TRIVINHO-STRIXINO et al., 2000), associated to bryophytes in Jacaré-Pepira river (GORNI; ALVES, 2007); in Campos do Jordão, associated with leaflets, in the Galharada streams (GORNI; ALVES, 2012). We found it in the Itupararanga, Paiva Castro, Rio Grande, Promissão and Billings reservoirs.

Nais magnaseta Harman, 1973.

Record and ecological observations: This species was registered in the Promissão reservoir, however, to date this species had not been registered in Brazil, its distribution was limited only to Texas, USA (HARMAN, 1973).

Nais pardalis Piguet, 1906.

Synonyms: *Nais bretscheri* var. *Piguet pardalis*, 1906; *Nais lastockini* Sokolskaya, 1958.

Record and ecological observations: Found in São Paulo in Pinheiros river (MARCUS, 1943), in Araraquara in Pinheirinhos stream (ALVES; LUCCA, 2000; ALVES et al., 2006); association with *Pomacea bridgesii* (Ampullaridae) (GORNI; ALVES, 2006). We found it in the central body of the Billings and Paiva Castro reservoir.

Nais schubarti Marcus, 1944.

Record and ecological observations: Found in the Paiva Castro reservoir, in the municipality of Franco da Rocha (GIROLLI *et al*., 2018). We found it in the Itupararanga, Paiva Castro, França and Ponte Nova reservoirs.

Nais variabilis Piguet, 1906.

Record and ecological observations: Found in a stream in Bocaina (SANCHES *et al*., 2016) and in the Paranapanema river (CESAR; HENRY, 2017); associated with submerged macrophytes in Américo Brasiliense and Brotas, in Anhumas stream and Dourada Lake dams (ALVES; GORNI, 2007); associated with larvae of organisms of the order Odonata in Ipeúna, in the Cantagalo and Lapa streams (CORBI et al., 2004); and Campos do Jordão, in the Galharada stream (GORNI; ALVES, 2015) associated with the leaflets (GORNI; ALVES, 2012) and in substrate of erosional and depositional areas (GORNI; ALVES, 2008b). We found it in the Itupararanga, Paiva Castro, Graminha, Promissão, Ponte Nova reservoirs, and in the Billings reservoir in the central body and in the Rio Pequeno arm.

Slavina evelinae Marcus, 1942.

Synonyms: Peloscolex evelinae Marcus, 1942.

Record and ecological observations: Found in São Paulo on the Pinheiros River (DU BOIS-REYMOND MARCUS, 1944; MARCUS, 1942; 1943); in the Ponte Nova (PAMPLIN et al., 2005) and Bariri reservoirs (PAMPLIN et al., 2005; SURIANI et al., 2007); in Bocaina, in the Himalaia stream (SANCHES et al., 2016). Associated with submerged macrophytes in the municipalities of Américo Brasiliense, at Anhumas stream dam, and Brotas, at Dourada Lake Dam, (ALVES; GORNI, 2007); and *Salvinia* (Salviniaceae) and *Egeria* (Hydrocharitaceae) (SANCHES; GORNI, 2014); in Luiz Antônio in the Infernão Lake associated with *Scirpus cubensis* (Cyperaceae) (CORREIA; TRIVINHO-STRIXINO, 1998); and to aquatic macrophytes (TRIVINHO-STRIXINO et al., 2000); associated with the decaying leaves of *Ficus elastic* (Rosales: Moraceae) (MARCUS, 1942); Found associated with sediment in Américo Brasiliense, at Anhumas stream dam (CORBI; TRIVINHO-STRIXINO, 2002). We found it in the Paiva Castro and Santa Branca reservoirs.

Stephensoniana trivandrana Aiyer, 1926.

Synonyms: *Naidium trivandranum* Aiyer, 1926; *Stephensonia trivandrana* (Aiyer, 1926); *Slavinia trivandrana* (Aiyer, 1926).

Record and ecological observations: Found in the deep region (± 21m) of the Promissão reservoir, in the municipality of Promissão (GIROLLI et al., 2019). We found it in the Paiva Castro, Santa Branca, Jurumirim, Promissão and Billings - Rio Pequeno reservoirs.

PRISTININAE SUBFAMILY

Pristina americana Černosvitov, 1937.

Synonyms: *Pristina americana f. typica* Cernosvitov, 1937; *Pristina americana* var. *loretana* Cernosvitov, 1937; *Pristina peruviana* Černosvitov, 1939; *Pristina longidentata* Harman, 1965; Pristinella longidentata Harman, 1965; *Pristina orghidani* Botea, 1983.

Record and ecological observations: Found in São Paulo on the Pinheiros river (DU BOIS-REYMOND MARCUS 1944; MARCUS 1942; 1943), and on the Tietê River (DU BOIS REYMOND MARCUS 1949; MARCUS 1942; 1943); in the Ponte Nova reservoir (PAMPLIN et al., 2005); in the Monjolinho river (ALVES et al., 2006); in the Bariri reservoir (PAMPLIN et al., 2005; SURIANI et al., 2007). Associated with sediment in Ibitinga, Nova Avanhandava, Três Irmãos, Promissão and Barra Bonita (SURIANI et al., 2007), in Araraquara, in the Pinheirinho streams (ALVES; LUCCA, 2000; ALVES et al., 2006); Santa Clara, in Luiz Antônio, in Diogo Lake (ALVES; STRIXINO, 2000); in Campos do Jordão, in the Galharada stream (GORNI; ALVES, 2015), associated with leaflets (GORNI; ALVES, 2012), and the substrate of erosional and depositional areas (GORNI; ALVES, 2008b). We found it in Santa Branca, França, Jurumirim, Graminha and Promissão reservoirs.

Pristina longisoma Harman, 1977.

Synonyms: *Pristinella longisoma* Haran, 1977.

Record and ecological observations: This species was first registered in the state of São Paulo. The reservoirs where *P. longisoma* occurred were central body Billings, Promissão and Rio Grande. A previous study reports its occurrence in Paraná, in the coastal region of Paranapanema, in the Iguaçú River (MORETTO et al., 2013).

Pristina osborni Walton, 1906 (Figure 3).

Synonyms: *Naidium osborni* Walton, 1906; *Pristinella osborni* Walton, 1906; *Naidium minutum* Stephenson, 1914; *Pristinella minuta* Stephenson, 1914; *Pristina minuta* Stephenson, 1914.

Record and ecological observations: Found in São Paulo, associated with aquatic macrophytes of the Bromeliaceae family (Lamiales), in a stream in Jardim Europa and Jardim Paulista (MARCUS, 1943); at Ribeira de Iguape, the Araquá River (MARCUS, 1943; 1944), and the Guareí River (CESAR; HENRY, 2017), and at the Intervales State Park (ALVES et al., 2008). It was also registered in Américo Brasiliense, at Anhumas stream dam, and in Brotas, at Lagoa Dourada Dam, associated with submerged macrophytes (ALVES; GORNI, 2007); in Campos do Jordão, in the Galharada stream, associated with sediments (GORNI; ALVES, 2012) and in substrates of erosional and depositional areas (GORNI; ALVES, 2008b). We found it in the reservoirs Paiva Castro, Santa Branca, Jurumirim, Promissão, Ponte Nova (Mesotrophic), Rio Grande (Supereutrophic) and Billings (Hypereutrophic), according to Table 3. In fact, a wide range was observed between the variables OM, DO, P, TOC, NKj, Ptot, EC and C, as shown in Table 2.

Pristina probocidea Beddard, 1896.

Synonyms: *Pristina proboscidea f. typica* (Beddard, 1896); *Pristina proboscidea* var. *paraguayensis* Michaelsen, 1905.

Record and ecological observations: Occurred in Araraquara, in Água Branca stream (ALVES et al., 2006); in São Carlos, associated

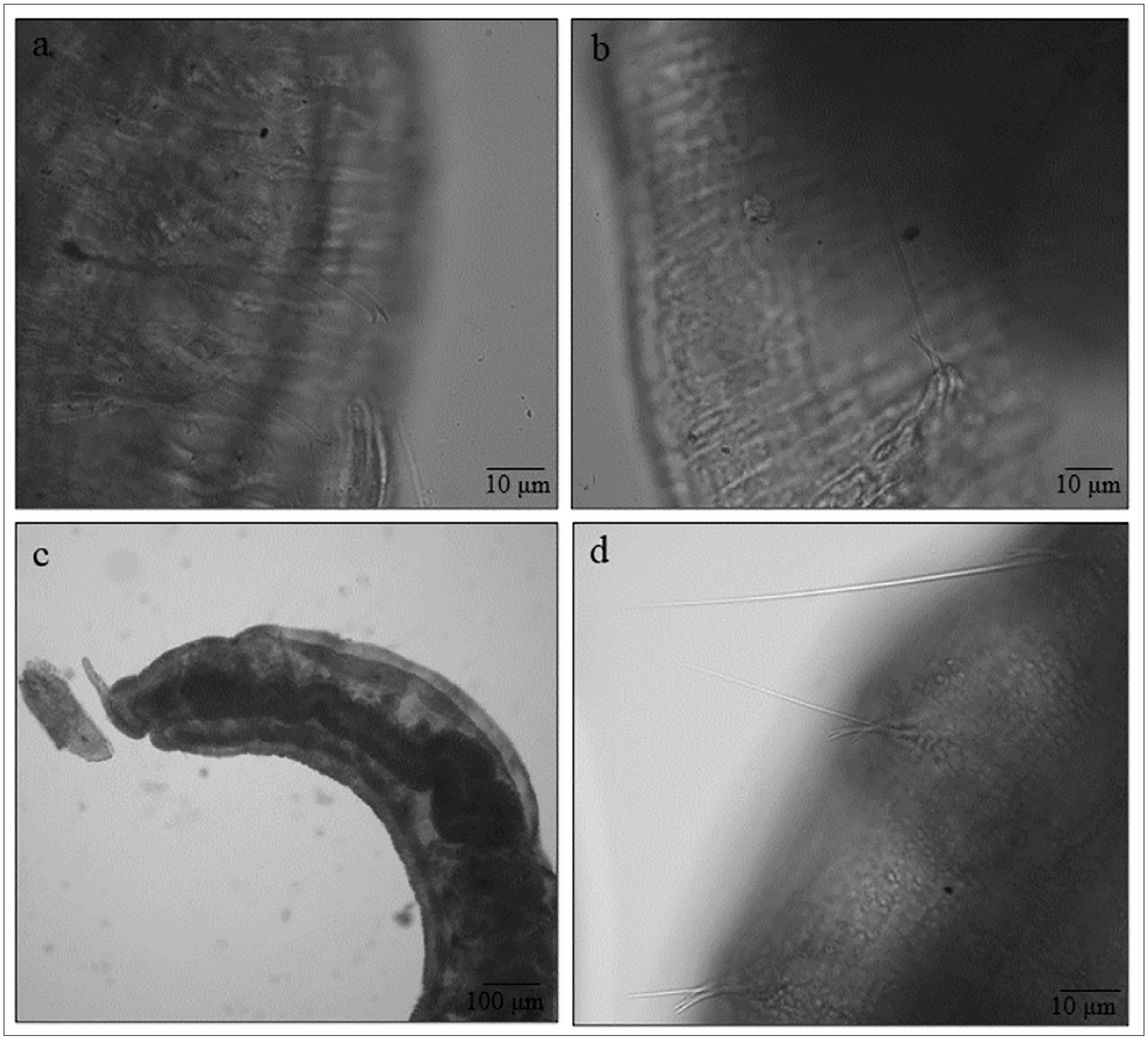

Figure 3. a) Ventral setae of *Pristina osborni*; b) dorsal setae (hair and needle) of *Pristina osborni*; c) prostomium with proboscis of *Pristina synclites*; d) dorsal setae (hair and needle) of *Pristina synclites*.

with *Radiospongilla amazonensis* (Spongillidae) (PAMPLIN et al., 2005), and in the Jacaré-Guaçu River associated with the same organism (CORBI et al., 2005); associated with submerged macrophytes in Américo Brasiliense and Brotas, in Anhumas stream and Dourada Lake dams, respectively (ALVES; GORNI, 2007); associated *Salvinia* (Salviniaceae) and *Egeria* (Hydrocharitaceae) (SANCHES; GORNI, 2014); and Campos do Jordão, in the Galharada stream (GORNI; ALVES, 2015), associated with substrates of erosional and depositional areas (GORNI; ALVES, 2008b), and sediments (GORNI; ALVES, 2012). We found it in the Paiva Castro and Ponte Nova reservoirs.

Pristina rosea Piguet, 1906.

Synonyms: *Naidium roseum* Piguet, 1906; *Naidium jenkinae* Stephenson, 1931; *Pristinella jenkinae* Stephenson, 1931; *Naidium roseum f. jenkinae* Stephenson, 1931; *Pristina jenkinae* Stephenson, 1931; *Naidium roseum,* Marcus, 1943 (non Piguet); *Pristina idrensis* Sperber, 1948; *Pristinella idrensis* Sperber, 1948; *Pristina taita* Stout, 1956; *Pristina nothophagi* Stout, 1958.

Record and ecological observations: Found in São Paulo, in the Pinheiros river (DU BOIS-REYMOND MARCUS, 1944; MARCUS, 1942; 1943) and in the municipality of Bocaina, in the Himalaia and Bocaina streams (SANCHES et al., 2016), in Araraquara, in Água Branca, Gouveia and Pinheirinho streams (ALVES et al., 2006); associated with sediments in São Carlos (ALVES; LUCCA, 2000), in the Monjolinho dam also associated with sediment (FUSARI; FONSECA-GESSNER, 2006); in Campos do Jordão, in the Galharada streams (GORNI; ALVES, 2015) associated with sediments (GORNI; ALVES, 2012); and Campo Meio and Serrote associated with substrates of erosional and depositional areas (GORNI; ALVES, 2008b). Associated with *Egeria* (Hydrocharitaceae) in Américo Brasiliense, Anhumas stream dam (SANCHES; GORNI, 2014), and in Brotas in the Jacaré-Pepira River, associated with bryophytes (GORNI; ALVES, 2007). We found it in the reservoirs Paiva Castro, França, Graminha and Billings.

Pristina synclites Stephenson, 1925 (Figure 3).

Record and ecological observations: Found in São Paulo, on the São Lourenço river (ROSA et al., 2014), and in Bocaina, in the Himalaia and Bocaina streams (SANCHES et al., 2016); associated with sediment in Araraquara, in the Pinheirinho stream (ALVES; LUCCA, 2000; ALVES et al., 2006), and in São Carlos, in the Monjolinho river (ALVES et al., 2006; FUSARI; FONSECA-GESSNER, 2006); associated with *Egeria* (Hydrocharitaceae) in Américo Brasiliense, at Anhumas stream dam (SANCHES; GORNI, 2014). We found it in the Itupararanga reservoirs, Graminha (Eutrophic) Paiva Castro, França, Jurumirim, Promissão, Ponte Nova (Mesotrophic); and the Billings reservoir in Rio Pequeno (Eutrophic), Taquacetuba and central body (Hypereutrophic). A wide amplitude was observed in these reservoirs between the variables OM, DO, P, TOC, NKj, Ptot, EC and C, as shown in Table 2.

RHYACODRILINAE SUBFAMILY

Bothrioneurum sp. Stolc, 1886 (Figure 4).

Record and ecological observations: This genus has 3 species distributed in the state of São Paulo, namely: *B. americanum* Beddard, 1894, found in Ponte Nova and Bariri reservoirs (PAMPLIN et al., 2005); *B. iris* Beddard, 1901 found in Sao Paulo: (MARCUS, 1942; 1943; 1944); and *B. vejdovskyanum* Stolc, 1886 found in the Tietê rivers (DU BOIS-REYMOND MARCUS, 1949; MARCUS, 1942; 1943), Pinheiros (MARCUS, 1943), in a stream in Jardim Europa (MARCUS, 1942; 1943). We found it in all the reservoirs Itupararanga (Eutrophic), Promissão, Ponte Nova, Santa Branca, França, Jurumirim, Paraibuna, Paiva Castro (Mesotrophic), Taiçupeba, Rio Grande (Seupereutrophic), and in the points of the Billings reservoir in Rio Pequeno (Eutrophic), Taquacetuba and central body (Hypereutrophic); except in Graminha. Some biogeographic characteristic, not studied here, may be influencing the non-distribution of this species in this reservoir, because none of the variables measured were in a discrepant way. In other studies, *Bothrioneurum* sp., it was also identified as a species tolerant to organically enriched environments (BEHREND et al., 2012; GIROLLI, 2019).

Figure 4. Sensory pit of *Bothrioneurum* sp.

Branchiura sowerbyi Beddard, 1892.

Record and ecological observations: Occurred in the Guareí River (CESAR; HENRY, 2017); in the Ponte Nova reservoir (PAMPLIN et al., 2005); on the Tietê River (DU BOIS-REYMOND MARCUS 1949; MARCUS 1942; 1943); and in the municipalities of Barra Bonita, Ibitinga, Nova Avanhandava, Três Irmãos, Promissão (SURIANI et al., 2007); in Americana, in the Salto Grande reservoir (PAMPLIN et al., 2006; DORNFELD et al., 2006); in São Carlos, at the Monjolinho Dam (FUSARI; FONSESA-GESSNER, 2006); in Mogi-Guaçu, on Diogo Lake (ALVES; STRIXINO, 2000; 2003); and in Bariri (PAMPLIN et al., 2005; SURIANI et al., 2007), all associated with sediment. We found it in the Itupararanga, Paiva Castro, Santa Branca, Rio Grande, Promissão, Ponte Nova reservoirs; and the Billings reservoir in the arms of Rio Pequeno and Taquacetuba.

TUBIFICINAE SUBFAMILY

Aulodrilus pigueti Kowalewski, 1914 (Figure 5).

Record and ecological observations: Found in the Guareí River (CESAR; HENRY, 2017); associated with *Egeria* (Hydrocharitaceae) in Américo Brasiliense, at Anhumas stream dam (SANCHES; GORNI, 2014); and in Mogi-Guaçu, in Diogo Lake, associated with sediment (ALVES; STRIXINO, 2000; 2003). We found it in the reservoirs Billings central body (Hipereutrophic) and Rio Pequeno, Graminha (Eutrophic), Itupararanga, Promissão, Ponte Nova, Santa Branca, França, Jurumirim, Paraibuna, Paiva Castro (Mesotrophic) and Rio Grande (Supereutrophic). It was verified in the central body of billings reservoir high organic enrichment and low level of DO, according to Table 2. This may have favored the development of *A. pigueti* as dominant species (55.4% of the total organisms identified at this point). Other authors such as Prygiel et al., (2000), Ragonha et al. (2013) and Sales et al. (2014), corroborate that *A. pigueti* reaches high densities in environments with great intake of organic matter.

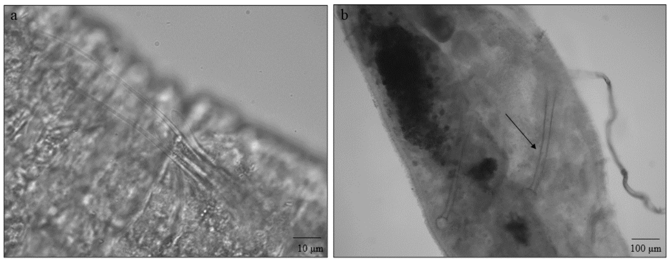

Figure 5. a) Dorsal setae (hair and needle) of *Aulodrilus pigueti*; b) Penial sheath of *Limnodrilus hoffmeisteri*.

Limnodrilus hoffmeisteri Claparède, 1862 (Figure 5).

Synonyms: *Limnodrilus hoffmeisteri f. typica* Claparede, 1862; *Clitellio hoffmeisteri* Claparède, 1862; *Clitellio (Limnodrilus) hoffmeisteri* Claparede, 1862; *Tubifex hoffmeisteri* Claparède, 1862; *Camptodrilus spiralis* Eisén, 1879; *Limnodrilus spiralis* Eisén, 1879; *Camptodrilus californicus* Eisén, 1879; *Limnodrilus californicus* Eisén, 1879; *Clitellio (Limnodrilus) californicus* Eisén, 1879; *Camptodrilus corallinus* Eisén, 1879; *Clitellio (Limnodrilus) corallinus* Eisén, 1879; *Limnodrilus corallinus* Eisen, 1879; *Limnodrilus dugesi* Rybka, 1898; *Limnodrilus hoffmeisteri f. dugesi* Rybka, 1898; *Limnodrilus gotoi* (part) Hatai, 1899; *Limnodrilus lucasi* Benham, 1903; *Limnodrilus vejdovskyanus* Benham, 1903; *Limnodrilus subsalsus* (part) Moore, 1905; *Limnodrilus aurostriatus* Southern, 1909; *Limnodrilus aurantiacus* Friend, 1911; Limnodrilus hoffmeisteri var. *tenellulus* Friend, 1912; *Limnodrilus socialis* Stephenson, 1912; *Limnodrilus hoffmeisteri f. socialis* Stephenson, 1912; *Limnodrilus parvus* var. *biannulatus* Lastockin, 1927; *Limnodrilus pacificus* Chen, 1940; *Limnodrilus hoffmeisteri f. divergences* Marcus, 1942; *Limnodrilus subsalus*, Marcus, 1944; *Limnodrilus parvus*, Du Bois-Reymond Marcus, 1947, Gavrilov & Tomsic Peace, 1950; *Limnodrilus hoffmeisteri f. silly* Marcus 1942.

Record and ecological observations: This species was found in the Ponte Nova reservoirs (PAMPLIN et al., 2005), Lomoeiro (MARCUS, 1943), in São Paulo (MARCUS, 1942; 1943; 1944); in the São Lourenço river (ROSA et al., 2014); in Bariri (Pamplin et al., 2005; SURIANI et al., 2007); in Americana, on the Atibaia river, in the Salto Grande reservoir (DORNFELD et al., 2006; PAMPLIN et al., 2006); and in a stream in Bocaina (SANCHES et al., 2016). Associated with sediment at all of the following sites, such as Intervales State Park in the Bocaina, Lageado, Rio das Mortes, Roda d'Água, Três Córregos streams (ALVES et al., 2008); in the municipality of Araraquara, in the Pinheirinho streams (ALVES; LUCCA, 2000; ALVES et al., 2006), Água Branca (ALVES et al., 2006) and Santa Clara (ALVES; LUCCA, 2000); in Pirituba (MENDES et al., 1951); in Mogi-Guaçu on the Diogo Lake (ALVES; STRIXINO, 2000; 2003); in São Carlos on the Monjolinho River (ALVES et al., 2006; FUSARI; FONSECA-GESSNER, 2006); in Ribeirão Preto on the Monte Alegre lake (CLETO-FILHO; ARCIFA, 2006); in Campos do Jordão in the Serrote streams, associated with substrate of erosional and depositional areas (GORNI; ALVES, 2008b); and Galharada (GORNI; ALVES, 2015), associated with sediments and sediments (GORNI; ALVES, 2012); also registered in Barra Bonita, Ibitinga, Nova Avanhandava, Três Irmãos and Promissão reservoirs (SURIANI et al., 2007). We found it in the Itupararanga (Eutrophic) reservoirs, Promissão, Ponte Nova, França, Jurumirim, Paraibuna, Paiva Castro (Mesotrophic), Taiçupeba, Rio Grande (Supereutrophic); and in the Billings reservoir in the central body, and in the arms of Taquacetuba (Hypereutrophic) and Rio Pequeno (Eutrophic).

The *L. hoffmeisteri species* has hemoglobin, which enables them to support low oxygen concentrations (ESTEVES, 1998), and is therefore characterized as an indicator of organically polluted environments (VERDONSCHOT, 1989; PASTERIS et al., 1999; SURIANI et al., 2007; BEHREND et al., 2012; ZHAO; LIU, 2012; ZEYBEK et al., 2018; GORNI et al., 2018; GIROLLI, 2019).

Spirosperma velutina Grube, 1879.

Synonyms: *Saenuris velutina* Grube, 1879; *Peloscolex velutinus* Grube, 1879; P*eloscolex velutinus velutinus* Grube, 1879; *Embolocephalus velutinu*s Grube, 1879; *Spirosperma (Embolocephalus) velutinus* Grube, 1879; *Psammoryctes velutinus* Grube, 1879; *Tubifex velutinus* Grube, 1879; *Tubifex (Peloscolex) velutinus* Grube, 1879; *Tubifex sarnensis* Pierantoni, 1904; *Peloscolex velutinus sarnensi*s Pierantoni, 1904; *Peloscolex cernosvitovi* Arabic, 1958; *Peloscolex fontinali*s Arabic, 1964.

Record and ecological observations: Until now there was no record of occurrence of this species in Brazil, its occurrence was recorded only in Venezuela and Europe (CHRISTOFFERSEN, 2007). In this study *S. velutina* occurred in Taiaçupeba reservoirs, Rio Grande, Promissão; and the Billings reservoir in the central body and arms of Rio Pequeno and Taquacetuba.

OPISTOCYSTIDAE FAMILY Černosvitov, 1936

Opistocysta funiculus Cordero, 1948 (Figure 6).

Synonyms: *Pristina flagellum*, Cernosvitov, 1936 (non Leidy, 1880); *Opistocysta flagellum*, Marcus, 1944, Du Bois-Reymond Marcus, 1947 (non Leidy, 1880).

Record and ecological observations: Found in Mogi-Guaçu (ALVES; STRIXINO, 2000; 2003), Luiz Antônio (ALVES; STRIXINO, 2000), in Bariri and Ponte Nova reservoirs (PAMPLIN et al., 2005), Americana, at the Atibaia river and Salto Grande reservoir (DORNFELD et al., 2006), Paranapanema river (CESAR; HENRY,

2017) and Bocaina, in the Himalaia stream (SANCHES et al., 2016). Associated with Egeria (Hydrocharitaceae) (SANCHES; GORNI, 2014) and; associated with sediment in the municipalities of Americana, the Atibaia river and Salto Grande reservoir (DORNFELD et al., 2006; PAMPLIN et al., 2006), Américo Brasiliense, at the Anhumas stream dam (CORBI; TRIVINHO-STRIXINO, 2002), Barra Bonita, Ibitinga, Nova Avanhandava, Três Irmãos (SURIANI et al., 2007), São Paulo on Diogo Lake (MARCUS, 1942; 1943; 1944). We found it in the Paiva Castro, Santa Branca, França, Jurumirim, Promissão, Ponte Nova (Mesotrophic), Rio Grande (Supereutrophic) and Billings reservoirs (Hypereutrophic). *O. funiculus*, is abundant in organically enriched environments (DORNFELD et al., 2006; GIROLLI, 2019).

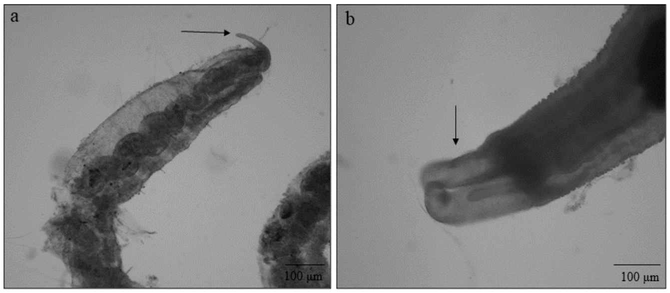

Figure 6. a) Prostomium with proboscis and b) caudal appendages of *Opistocysta funiculus.*

Finals considerations

The results presented above make this inventory extremely important for the knowledge of the distribution of aquatic oligochaetes, not only for the State of São Paulo, but throughout the Brazilian territory. Moreover, using the methodology of species accumulation curves and richness estimators, it was found that the sample number of this research was sufficient to obtain a reliable result, since the number of identified species corroborated the richness estimators.

The number of taxa identified (total of 28) in this research was higher than other studies performed in lentic environments in Brazil, such as Suriani et al. (2007) who identified 17 species in São Paulo; in Paraná, Behrend et al. (2012) identified 25 species; Gomes et al. (2017) identified 12 species in Rondônia; and Gorni et al. (2018) who identified 22 species in Mato Grosso. In addition, the identified species represented 36.4% of the 77 previously recorded species in the State of São Paulo (GORNI et al., 2015; GIROLLI et al., 2018; GIROLLI et al., 2020).

In relation to South America, Christoffersen (2010) claims that the cataloged Oligochaeta represent only a fraction of their true diversity, which emphasizes the need for more studies that contemplate the species inventory in the Neotropical regions. However, it is noteworthy that over the past few years the number of surveys with freshwater Oligochaeta has been growing, especially in Brazil, and there are more than 2,300 surveys between the years 1985 and 2015 (Rodrigues; Alves, 2018).

In this research, the three most abundant species were found in organically enriched reservoirs with low dissolved oxygen levels. This factor favors the development of dominant species, such as *Aulodrilus pigueti* (55.4%), *Limnodrilus hoffmeisteri* (16.4%) and *Bothrioneurum* sp. (7.9%). Generally, these species are found in sediments with abundant organic matter (Marchese, 1987; Montanholi-Martins; Takeda, 1999; Behrend et al., 2009; Lafont et al., 2012). Other studies (Rosenberg; Resh, 1993; Popp; Hoagland, 1995; Suriani et al., 2007) show that when one or a few species have high percentages of individuals in the community or assembly, it may be a sign of an environment with a high level of eutrophication or organically enriched. The Billings reservoir showed significant concentrations of nutrients, which can influence the colonization of tolerant taxa (Esteves, 2011).

The *Bothrioneurum* sp. it is a Tubificinae commonly found in impacted waters, presenting high numerical density, often occurring together with *Limnodrilus hoffmeisteri*, in organically enriched places, with high conductivity and low oxygenation (Alves; Lucca, 2000). Its tolerance to eutrophication and organic pollution has already been stated by Timm (2009) and Dumnicka (2007). Timm (1997) goes so far as to report that a high level of organic pollution is a limiting factor for the occurrence of the genus. Similarly, *L. hoffmeisteri* is commonly known as an indicator of eutrophic environments, which explains its frequency in places more intensely influenced by this condition.

Aulodrilus pigueti, which was the most abundant species in this study, is a cosmopolitan organism found in greater density in environments with high conductivity, low to moderate current speed and mud and clay sediments with abundant organic matter. The authors Schenková et al. (2010) collected the species on the bottom substrate of a fish pond and in the submerged coastal vegetation. In addition, *Aulodrilus pigueti* has the habit of digging the sediment and forming tubes from detritus (Timm; Veldhijzen Van Zanten, 2002). Although the species occurs in lentic or lotic freshwater environments (Finogenova; Arkhipova, 1994; Schloesser et al., 1995; Šporka, 1996), but it demonstrates having preference for environments in which the quality of the water and the substrate present characteristics of oligo to mesotrophic trophic level (Šporka, 2003), and is able to tolerate smaller amounts of dissolved oxygen and acidification (Orciari; Hummon, 1975). These characteristics reinforce the expressive occurrence of the species in intensely eutrophic reservoirs, showing its possible preference for lentic waters, rich in nutrients and with high conductivity.

The high trophic level can provide a series of microhabitats for Oligochaeta, such as surface macrophytes and sediments with abundant availability of organic matter. Notably, for Naidinae, microorganisms associated with macrophytes, such as epiphytic algae, bacteria and protozoa, are important sources of food (Brinkhurst; Jamieson, 1971; Alves; Gorni, 2007; Timm; Martin, 2015). On the other hand, tubificinae reach high abundances in the superficial layers of the sediment with a high concentration of total organic carbon, nitrogen and organic matter (Brinkhurst; Jamieson, 1971). Lin and Yo (2008), studying the effect of organic pollution on the distribution of Oligochaeta found the highest values for species richness, abundance and diversity in the sites with the greatest organic enrichment. Several other authors point out that high numbers of the total of Oligochaeta occur when the environment is highly polluted (Chapman et al., 1980; Rosenberg; Resh, 1993; Suriani et al., 2007).

The enriched reservoirs showed high metabolic potentials, where the organic load present in the sediment favored diversity of species and abundance of the Oligochaeta. However, they have low ecological quality, as they do not present the expressive occurrence of sensitive species. In general, sensitive species occurred in a low percentage in all reservoirs. However, it should be noted that the list of sensitive species was based on Lafont et al. (2012) for temperate environments, with the need for a functional survey for neotropical taxa, aiming at the biomonitoring of water and sediment quality.

In this context, inventories of oligochaete fauna and ecological relationships between species and the environment are very important for the formulation of biodiversity conservation policies, especially in tropical environments (Christoffersen, 2010; Rodrigues; Alves, 2018). Studies of oligochaete assemblage patterns can be useful to predict changes along environmental gradients, as well for standardized methods for testing organisms in ecotoxicological studies (Castro et al., 2020; Suriani et al., 2007; Behrend et al., 2012). However, oligochaete species surveryed and systematics studies still are scarce in Brazilian environments, probably due to the lack of specialists in the taxonomic identification of these worms.

Finally, further research using the Oligochaeta class is necessary due to its importance as bioindicators of water quality and sediment associated with the unique characteristics of Brazilian continental ecosystems.

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Author Contributions

Douglas Aparecido Girolli: 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.

Mariana Futenma de Lima: Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Nathalie Aparecida de Oliveira Sanches: Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Vanessa Colombo-Corbi: Contribution to manuscript preparation.

Juliano José Corbi: Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Guilherme Rossi Gorni: 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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Nematodes of *Proceratophrys ararype* (Anura: Odontophrynidae), an endemic frog from the Araripe Plateau, northeastern Brazil

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Abstract: Parasites are an important component of the global biomass, having significant roles in several regulatory mechanisms in the ecosystem. Parasitism is one of the most common ecological interactions on the planet. Studies have shown that the helminth fauna of only 8% of amphibian species in Brazil have been studied, and this percentage is lower for the Odontophrynidae family, with only four of the 50 species kown to occur in Brazil having been investigated. Here, we present the helminth fauna of *Proceratophrys ararype*, an anuran endemic to the "Brejo de Altitude" Chapada do Araripe (Araripe Plateau), northeastern Brazil. The infection parameters analyzed were prevalence, mean intensity of infection and mean abundance of parasites. We used the Pearson's linear correlation coefficient to check the correlations between the abundance of the parasites with the snout-vent length (SVL) of hosts. To verify the degree of aggregation of parasites in hosts, we used the dispersion index. Out of 40 specimens examined, 19 specimens were infected with at least one parasite. The overall prevalence was 47.5% with a mean infection intensity of 18.93 ± 10.77. The endoparasitic community associated with *P. ararype* consisted of six species of parasites, with *Falcaustra mascula* having the highest prevalence (25%). Most parasites had a uniform dispersion index in the hosts and their abundance was unrelated to host size. Here, we also present a compilation of all parasites associated with host species of the genus *Proceratophrys* from South America. Overall, we found 23 species of parasites associated with five host species (*P. ararype, P. appendiculata, P. boiei, P. cristiceps, P. mantiqueira*). Of these, two species of parasites (*Oswaldocruzia mazzai* and *Strongyloides* sp.) represent new records for the genus *Proceratophrys*. Our results demonstrate the lack of studies on amphibian helminth fauna and fill an important knowledge gap on the diversity of parasites of *Proceratophrys ararype*, an endemic frog from the Araripe Plateau, northeastern Brazil.

Keywords: *Parasitism; Nematoda; Anuran.*

Nematódeos de *Proceratophrys ararype* (Anura: Odontophrynidae), um sapo endêmico do Planalto do Araripe, nordeste do Brasil

Resumo: Os parasitas são um componente importante da biomassa global, tendo papel significativo em vários mecanismos reguladores no ecossistema. O parasitismo é uma das interações ecológicas mais comuns no planeta. Estudos demonstraram que somente 8% da fauna de helmintos das espécies de anfíbios que ocorrem no Brasil foi estudada, sendo esta porcentagem mais baixa para a família Odontophrynidae, tendo sido investigadas apenas quatro das 50 espécies com ocorrência conhecida para o Brasil. Aqui, apresentamos a helmintofauna de *Proceratophrys ararype*, um anuro endêmico do "Brejo de Altitude" Chapada do Araripe, nordeste do Brasil. Os parâmetros de infecção analisados foram prevalência, intensidade média de infecção e abundância média de parasitas. Utilizamos o coeficiente de correlação linear de Pearson para verificar as correlações entre a abundância dos parasitas com o comprimento rostro-cloacal dos hospedeiros. Para verificar o grau de agregação dos parasitas nos hospedeiros, utilizamos o índice de dispersão. Dos 40 espécimes examinados, 19 estavam infectados com pelo menos um parasita. A prevalência geral foi de 47.5% com intensidade média de infecção de 18.93 ± 10.77. A comunidade endoparasitária associada a *P. ararype* constituiu de seis espécies de parasitas, com *Falcaustra mascula* tendo a maior prevalência (25%). A maioria dos parasitas apresentaram índice de dispersão uniforme nos hospedeiros e sua abundância não esteve relacionada ao tamanho do hospedeiro. Aqui, nós também apresentamos uma compilação de todos os parasitas associados as espécies de hospedeiros do gênero *Proceratophrys* na América do Sul. No geral, nós encontramos 23 espécies de parasitas associadas a cinco espécies de hospedeiros (*P. ararype, P. appendiculata, P. boiei, P. cristiceps, P. mantiqueira*). Destas, duas espécies de parasitas (*Oswaldocruzia mazzai* e *Strongyloides* sp.) representam novos registros para o gênero *Proceratophrys*. Nossos resultados demonstram a carência de estudos sobre a helmintofauna de anfíbios e preenchem uma importante lacuna de conhecimento sobre a diversidade de parasitas de *Proceratophrys ararype*, um sapo endêmico do Planalto do Araripe, nordeste do Brasil.

Palavras-chave: *Parasitismo; Nematoda; Anuros.*

Introduction

Currently, 50 species of the Odontophrynidae family have been identified, with the genus Miranda-Ribeiro, 1920 making up 40 species registered in Brazil, Argentina, and Paraguay (Segalla et al. 2019, Mângia et al. 2020, Frost 2021). Species of the genus *Proceratophry* can be clumped into four species groups, based on the morphological similarities of adult individuals (Cruz et al. 2005, Prado & Pombal 2008, Mângia et al. 2018): *P. appendiculata*, *P. bigibbosa*, *P. boiei* and *P. cristiceps* species groups. The *P. cristiceps* group comprises 14 species including *P. ararype* Mângia, Koroiva, Nunes, Roberto, Ávila, Sant'Anna, Santana & Garda, 2018 (Ávila et al. 2011, Brandão et al. 2013, Mângia et al. 2018). This species was identified from specimens collected at the slope of Chapada do Araripe, a humid forest in the municipality of Crato, state of Ceará, northeastern Brazil. The distribution of this species is very restricted and limited to the slope of Chapada do Araripe (Mângia et al. 2018), a climate exception area in the Caatinga biome (Tabarelli & Silva 2003), where local climatic conditions shape isolated systems (Vanzolini 1981, Borges-Nojosa & Caramaschi 2003). Currently, information on the associated parasitic fauna of *P. ararype* is lacking.

The parasites are integral components of the global biomass, and one of the most common life forms on the planet (Kuris 2008, Poulin 2014, Oliveira et al. 2019). Among these parasites, the helminth fauna associated with amphibians is rich and diverse, despite being hidden within known biodiversity (Poulin 2014, Campião et al. 2014). The study of parasitic fauna is extremely important due to the roles they have in several regulatory mechanisms within the ecosystem, including the negative effects they have on their hosts such as anaemia, anorexia, reduced survival and fertility, and competition (Vitt & Caldwell 2009, Matias et al. 2018). The study of these organisms not only contributes to our knowledge of animal diversity, but also clarifies the parasite dynamics of the host (Brooks & Hoberg 2001, Galli et al. 2001, Poulin 2014), because the richness of parasite species can be assumed as a characteristic of the host, where rates of parasite colonization vary according to biology of hosts (Poulin 2014, Campião et al. 2015).

The latest checklist of helminths in South America stated that only about 8% of all amphibian species in Brazil have had their helminth fauna studied (Campião et al. 2014). Of the *Proceratophrys* genus, the helminth fauna of only four species has been studied: *P. tupinamba* Prado & Pombal, 2008 (Boquimpani-Freitas et al. 2001), *P. cristiceps* Müller, 1883 (Teles et al. 2017, Silva et al. 2019, Sampaio et al. 2020), *P. boiei* Wied-Neuwied, 1824 (Toledo et al. 2018), and *P. mantiqueira* Mângia, Santana, Cruz & Feio, 2014 (Almeida-Santos et al. 2017). As such, studies on parasitism are of fundamental importance for the conservation of hosts, especially those with a restricted distribution, in addition to filling knowledge gaps in host-parasite interactions, since hosts, in general, are more susceptible to local extinctions (Pontes & Rocha 2011). Here we describe the composition and patterns of parasitic infection of helminths associated with *P. ararype*, an endemic frog from Chapada do Araripe, northeastern Brazil, and also present a compilation of all parasites associated with host species of the genus *Proceratophrys* from South America.

Material and Methods

This study was conducted on the slope of Chapada do Araripe in the state of Ceará, Brazil, within the limits of the Environmental Protection Area of Chapada do Araripe (APA Araripe). The owerall landscape is characterized of different vegetation types, with cut-outs of humid forest (sampled area), dry forest, Cerrado and Cerradão (Ferreira-Silva et al. 2019). Specimens of *P. ararype* were collected at night from the following locations: (i) Clube Recreativo Grangeiro (7°16'47"S, 39°26'18"W, 706 m asl, WGS84) and Nascente (7°15'21"S, 39°28'08"W, 739 m asl, WGS84), both in the municipality of Crato; (ii) Sítio Farias (7°20'17"S, 39°23'43"W, 600 m asl, WGS84), in the municipality of Barbalha; and (iii) Sítio Aleixo (7°26'25"S, 39°05'27"W, 946 m asl, WGS84) and Sítio Riachão (7°27'05"S, 39°06'38"W, 931 m asl, WGS84), both in the municipality of Missão Velha. The sampling period extended from November 7, 2018 to February 22, 2019.

A total of 40 *Proceratophrys* specimens were collected using the active search method (visual and auditory) (Bernarde 2012). Specimens were kept in individualized plastic containers and later euthanized by lethal injection of Lidocaine Hydrochloride (CFMV 2013). We measured the snout-vent lengths (SVL, in mm) of hosts using a digital caliper Mitutoyo® (precision 0.01 mm). Hosts were fixed according to Calleffo (2002) and deposited in the Herpetological Collection of the Regional University of Cariri, (URCA-H 15.579-15.616), Crato municipality and in the Herpetological Collection of the Federal University of Cariri (CHERP-UFCA 01-02), Brejo Santo municipality, both in the Ceará state, Brazil.

Specimens were necropsied and the organs (gastrointestinal tract, lungs, liver, kidneys and internal cavity) were harvested for analyses. Helminths were collected and fixed according to Amato et al. (1991) and Andrade (2000), the remaining food items were also accounted. For the identification of nematodes, we followed Vicente et al. (1991), in addition to recent studies on species descriptions. Analysed infection parameters include prevalence (P%), mean infection intensity (MII), and mean parasite abundance (MA), as previously described by Bush et al. (1997). All the parasites were deposited in the Parasitology Collection of Universidade Federal do Cariri (CHERP-P-UFCA 01-29), Brejo Santo municipality, Ceará state, Brazil.

We used the Pearson's linear correlation coefficient (r) to assess correlation between parasite abundance with host snout-vent length (SLV, in mm). The Mantel test was used to evaluate spatial autocorrelation between parasitic richness and sampled areas to verify if use the data as one or several parasite communities. The variance / mean ratio ($s2/\overline{x}$), also known as the dispersion index (ID), and the k parameter of the negative binomial distribution, were used to determine the degree of parasite aggregation within the hosts. The higher the $s2/\overline{x}$ ratio, and the lower the value of parameter k (closer to zero), the higher the level of aggregation (Pielou 1977).

To compile literature data on parasites associated with host species of the genus *Proceratophrys* from South America, we conducted a wide search in different databases (e.g., Google Academic, Scielo, Scopus) and in bibliographic reviews on the topic (e.g., Campião et al. 2014).

Ethical Standards

The authors assert that all procedures contributing to this study comply with the ethical standards of the relevant national and institutional guides on the care and use of laboratory animals. The study was approved by the Ethical Committee of Universidade Regional do Cariri (CEUA/URCA, process number 00260/2016.1) and Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/SISBIO, number 66099-2).

Results

We examined 40 *P. ararype* specimens, of these 19 (five females and 14 males) were parasitized by 511 helminths, with a total prevalence of 47.5% and mean infection intensity of 18.93 ± 10.77. The *P. ararype* endoparasitic community was comprised of six parasite species: *Aplectana membranosa* Schneider, 1866, *Falcaustra mascula* Rudolphi, 1819, *Oswaldocruzia mazzai* Travassos, 1935, *Physaloptera* sp., *Raillietnema spectans* Gomes, 1964 and *Strongyloides* sp. *Falcaustra mascula* had the highest prevalence (25%) and *R. spectans* had the lowest prevalence (2.5%), the highest abundance rate (6.5), and a mean intensity of (260.0) (Table 1).

There was no correlation between parasite general abundance and host snout-vent length ($R^2 = 0.01$, $p = 0.43$), when analyzing the most prevalent parasite species individually, we also found no significant correlation between parasite abundance and SVL: *A. membranosa* ($R^2 = 0.13$, $p = 0.79$), *Physaloptera* sp. ($R^2 = 0.34$, $p = 0.56$), and *F. mascula* ($R^2 = 0.18$, $p = 0.61$). Additionally, spatial autocorrelation was not observed between sample areas and parasitized individuals ($R^2 = 0.3545$, $p = 0.11667$). Examination of pattern dispersion revealed that most helminth species had a uniform distribution among hosts (Table 2), that is, the growth in the number of infected individuals is directly proportional to the prevalence of infection.

In our literature data compilation, we found, in general, five host species (*P. ararype*, *P. appendiculata*, *P. boiei*, *P. cristiceps*, *P. mantiqueira*) being parasitized by 23 helminth species. *Proceratophrys cristiceps* was the host species with the highest number of associated parasitic helminths (n = 10 spp.). *Physaloptera* sp. was the only helminth common to all studied *Proceratophrys* species (Table 3). In this study we identified two additional species (*O. mazzai* and *Strongyloides* sp.) (Figure 1A, B) registered for the genus *Proceratophrys*.

Discussion

The genus *Proceratophrys* has 23 species of registered parasites (Campião et al. 2014, Almeida-Santos et al. 2017, Teles et al. 2017, Toledo et al. 2018, Silva et al. 2019, Sampaio et al. 2020, this study). Like observations made in previous studies, we observed a particular parasitic community per host species, with *Physaloptera* sp. being the only helminth common to all studied *Proceratophrys* species (Table 3). This result could be due to the geographical locations of each species, which have different environmental conditions, and thereby affecting the composition and richness of biotic factors (Poulin & Krasnov 2010). On the other hand, *P. cristiceps*, which has a wide geographical distribution (Mângia et al. 2020), was the best studied species (Teles et al. 2017, Müller et al. 2018, Silva et al. 2019, Sampaio et al. 2020) and with the highest number of associated parasitic helminths (n = 10 spp.). This result emphasizes that habitat, along with the biology, life history of the host and study effort, can influence parasitic composition (Campião et al. 2015).

Species of the genus *Aplectana* are usually found infecting the large intestine of reptiles and amphibians, have a direct life cycle, and actively infect their hosts (Travassos 1931, Anderson 2000, Campião et al. 2014, Lins et al. 2017). This genus has been observed in four species of the Odontophrynidae family: *Proceratophrys tupinamba* and *P. boiei*, infected by *A. delirae* Fabio, 1971 (Boquimpani-Freitas et al. 2001, Klaion et al. 2011), and *P. cristiceps* (Silva et al. 2019, Sampaio et al. 2020) and *Odontophrynus americanus* Duméril & Bibron, 1841, infected by *A. membranosa* (Lent & Freitas 1948). In this

Table 1. Prevalence (P), mean intensity of infection (MII) with standard error (SD), mean abundance (MA), and site of infection (SI) of nematodes found in *Proceratophrys ararype*, Chapada do Araripe, northeastern Brazil.

Parasite	P (%)	MII ± EP	MA ± EP	SI
Aplectana membranosa	15	31.3 ± 26.8	4.7±7.9	large intestine
Falcaustra mascula	25	1.7 ± 0.3	0.43±0.9	large intestine, small intestine
Oswaldocruzia mazzai	7.5	1.3 ± 0.3	0.1±0.6	small intestine
Physaloptera sp.	12.5	3.4 ± 0.6	0.43±1.5	stomach
Raillietnema spectans	2.5	260.0	6.5	large intestine
Strongyloides sp.	7.5	8.3 ± 4.4	0.63±9.2	small intestine

Table 2. Dispersion index (ID) values, k exponent of the negative binomial distribution (k), and parasite distribution in *Proceratophrys ararype*, Chapada do Araripe, northeastern Brazil.

Parasite	ID	k	Distribution
Aplectana membranosa	164.89	0.19	Aggregate
Falcaustra mascula	0.56	–3.55	Uniform
Oswaldocruzia mazzai	0.25	–1.77	Uniform
Physaloptera sp.	0.67	–10.50	Uniform
Raillietnema spectans	0.00	–261.00	Uniform
Strongyloides sp.	10.24	0.90	Aggregate

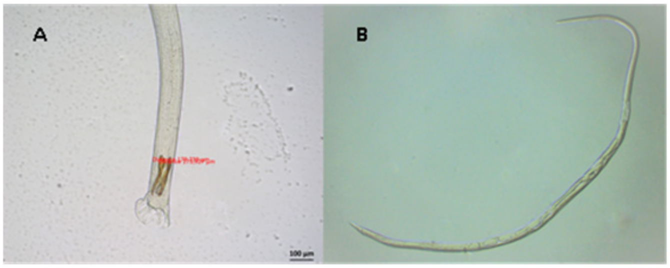

Figure 1. New parasite records for *Proceratophrys ararype*. (A) *Oswaldocruzia mazzai*, posterior view with taxonomic diagnostic characteristics (spicula and copulating bag; in red, measure of the spicula). (B) *Strongyloides* sp., total view with taxonomic diagnostic characteristics (prolonged esophagus and ovary disposition).

study, *A. membranosa* has also been registered for *P. ararype*, and it is the parasite with the second highest prevalence, abundance, and overall mean intensity. High indices were also found for *Leptodactylus syphax* (MII= 250.4) (Lins et al. 2017) and *P. cristiceps* (MII= 65.5; cited as *P. aridus* by Silva et al. 2019). High infection values can be explained by the low host vagility that contributes to increased parasite transmission (Mcalpine 1997). Additionally, *A. membranosa* females produce large amounts of infective larvae in the environment, increasing infection rates (Lins et al. 2017).

Falcaustra mascula has been shown to infect the small and large intestine of several amphibians (e.g., Campião et al. 2014, Toledo et al. 2015, Toledo et al. 2018, Silva et al. 2019). Little is known about its modes of transmission. Anderson (2000) suggested that the larvae reach its third development stage and then infect an intermediate invertebrate host, which in turn is ingested by amphibians. Toledo et al. (2018) found that among all host parasites *F. mascula* had the highest prevalence rate in *Boana faber* (Wied-Neuwied, 1821) (P = 9.1%), *Leptodactylus latrans* (Steffen, 1815) (P = 13.9%), and *Rhinella icterica* (Spix, 1824) (P = 33.3%). Therefore, our result for prevalence rate (P = 25%) is consistent with the literature data. One plausible explanation for the high infection rates observed for this parasite is that the intermediate host is an arthropod, which is a type of prey that is extensively consumed by anurans.

Oswaldocruzia mazzai have been shown to infect a variety of anuran hosts (e.g., Campião et al. 2014, Teles et al. 2015, Alcantara et al. 2018, Oliveira et al. 2019) but our study is the first to record a species of the genus *Proceratophrys* as a host of *O. mazzai*. The low host specificity is usual for some groups of helminths (Campião et al. 2015, Oliveira et al. 2019). The great diversity of hosts registered for *O. mazzai* is related to the direct life cycle, and the simple mode of transmission that can occur by ingesting eggs or larval penetration into the host's skin (Anderson 2000).

Nematodes of the *Physaloptera* genus have a worldwide geographical distribution and have been recorded in several classes of terrestrial vertebrates, including felines (Ogassawara 1986), rodents (Tung et al. 2009), lizards (Da Silva et al. 2008, Cabral et al. 2018) and anurans (Da Graça et al. 2017). This parasite was usual for all studied *Proceratophrys* species (see Table 3). In amphibians, this parasite is usually found in larval stage, making it difficult to identify at the species level, and is suggestive that these amphibians are not definitive hosts. Although there is not enough data about its life cycle, nematodes of this genus are known to use insects during their intermediate phase (Anderson 2000). Additionally, the acquisition of *Physaloptera* by anuran hosts occurs through the ingestion of infected insects, mainly Orthoptera (Klaion et al. 2011).

The *Strongyloides* genus has a low specificity, with records for several classes, including mammals (occasionally humans), birds, reptiles, and amphibians (Little 1966, Urquhart et al. 1998). Although there is a lack of detailed biology on this parasite, it is known to have a direct or indirect life cycle, with the former being the most usual (Santos et al. 2010). The infection occurs on land through skin penetration or ingestion of infected preys (Mati & Melo 2014, Sulieman et al. 2015). Even though this nematode infects several amphibian species (Campião et al. 2014, Sulieman et al. 2015), this is the first record of the genus *Strongyloides* acting as a parasite for species of the Odontophrynidae family.

The parasite *Raillietnema spectans* was initially described in the large intestine of leptodactylids and bufonids (Alcântara et al. 2018), and it has been registered for several other species: *Rhinella crucifer* (Wied-Neuwied, 1821), *R. icterica* and *Leptodactylus latrans* (Campião et al. 2014), *Pleurodema diplolister* (Peters, 1870) (Teles et al. 2015), *Physalaemus albifrons* (Spix, 1824), *P. cicada* Bokermann, 1966 *P. cuvieri* Fitzinger, 1826 (Oliveira et al. 2019), and *Dermatonotus muelleri* (Boettger, 1885) (Alcantara et al. 2018). This parasite is known to presents a direct life cycle and transmission that occurs via ingestion or penetration of larvae in the skin (Anderson 2000). In this study, *R. spectans* had the lowest prevalence, contrary to the results from Alcântara et al. (2018) and Oliveira et al. (2019). This low prevalence may be related to host phylogeny, which is reflected in the structuring of parasitic interactions (Krasnov et al. 2012), or geographical, biological, and life history effects on the host, which can influence parasitic composition (Campião et al. 2015).

Helminths registered for the genus *Proceratophrys* are usually found in other taxa of amphibians, and therefore can be considered generalists (Campião et al. 2014, Müller et al. 2018, Silva et al. 2019). Nevertheless, studies on *Procetatophrys cristiceps* (Teles et al. 2017, Müller et al. 2018, Silva et al. 2019), and P. ararype (this study), in northeastern Brazil, and on *P. boiei*, *P. mantiqueira* and *P. tupinamba*, in humid forests of southeastern Brazil (Boquimpani-Freitas et al. 2001, Klaion et al. 2011, Almeida-Santos et al. 2017, Toledo et al. 2018), show a greater similarity between helminth communities in locally close hosts. These results suggest that geographic distribution of the host, and the different local conditions, could influence the composition of helminth fauna.

We did not find correlation between parasitism and host size. This result contrasts with those found for the genus *Leptodactylus*, where body size accounted for 17% of the variation in species composition, compared to the 3% accounted for the host's habitat (Campião et al. 2016a). However, our results were similar to those described by Oliveira et al. (2019) for *Physalaemus* species. This similarity between the results may be due to the smaller size variation, when species are analysed

Table 3. Helminths associated with the genus Proceratophrys Miranda-Ribeiro, 1920 from South America.

Host	Parasite	Reference
P. tupinamba Prado & Pombal, 2008	*Aplectana delirae*	Boquimpani-Freitas et al. (2001)
	Cosmocerca brasiliense	Boquimpani-Freitas et al. (2001)
	Schulzia travassIosi	Boquimpani-Freitas et al. (2001)
	Physaloptera sp.	Boquimpani-Freitas et al. (2001)
	Rhabdias androgyna	Boquimpani-Freitas et al. (2001)
	Cestoda unidentified	Boquimpani-Freitas et al. (2001)
P. boiei (Wied-Neuwied, 1824)	*Aplectana delirae*	Klaion et al. (2011)
	Cosmocerca parva	Klaion et al. (2011)
	Cosmocercidae unidentified	Toledo et al. (2018)
	Oxyascaris oxyascaris	Klaion et al. (2011)
	Oswaldocruzia subauricularis	Toledo et al. (2018)
	Physaloptera sp.	Klaion et al. (2011)
	Rhabdias sp.	Toledo et al. (2018)
P. cristiceps (Müller, 1883)	*Aplectana membranosa*	Teles et al. (2017); Silva et al. (2019); Sampaio et al. (2020)
	Cosmocercidae unidentified	Teles et al. (2017); Silva et al. (2019)
	Cystacanth	Silva et al. (2019)
	Falcaustra mascula	Silva et al. (2019)
	Oswaldocruzia sp.	Silva et al. (2019)
	Physaloptera sp.	Teles et al. (2017); Silva et al. (2019)
	Raillietnema spectans	Teles et al. (2017)
	Rhabdias breviensis	Müller et al. (2018); Silva et al. (2019)
	Rhabdias sp.	Teles et al. (2017); Müller et al. (2018)
	Trematoda unidentified	Silva et al. (2019)
P. mantiqueira Mângia, Santana, Cruz & Feio, 2014	Cosmocercidae unidentified	Almeida-Santos et al. (2017)
	Physaloptera sp.	Almeida-Santos et al. (2017)
	Oswaldocruzia lopesi	Almeida-Santos et al. (2017)
	Oxyascaris sp.	Almeida-Santos et al. (2017)
	Rhabdias sp.	Almeida-Santos et al. (2017)
P. ararype Mângia, Koroiva, Nunes, Roberto, Ávila, Sant'Anna, Santana & Garda, 2018	*Aplectana membranosa*	This study
	Falcaustra mascula	This study
	Oswaldocruzia mazzai	This study
	Physaloptera sp.	This study
	Raillietnema spectans	This study
	Strongyloides sp.	This study

separately, as observed for *Physalaemus* by Oliveira et al. (2019) and for *Proceratophrys* in this study, different from that observed in the genus *Leptodactylus* by Campião et al. (2016a). Thus, the diversity of parasites in *Proceratophrys ararype* does not appear to be influenced by the size of the hosts.

The dispersion of parasites in *Procetatophrys ararype* was uniform for most species (Table 2). One of the most usual characteristics of parasitic infections in populations of vertebrate hosts is aggregation, because these infections rarely happen or are due to the high lethality in infected hosts, which cannot survive for long periods (Von Zuben 1997). Therefore, the uniform dispersion model, predominant in the helminth species of this study, may be due to parasite mortality, a process dependent on the density and mortality of the host induced by the parasite. Additionally, regular or uniform distribution is also observed if there is strict competition between individuals, or if there is positive antagonism, causing a constant minimum distance between individuals (Odum & Barrett 2008).

Anurans have the supracommunity pattern of diversified generalist helminth parasites with low host specificity and wide distribution (Campião et al. 2014). Due to the increase in studies conducted on this topic (e.g., Campião et al. 2016a, b, Lins et al. 2017, Teles et al. 2017, Leivas et al. 2018, Alcantara et al. 2018, Oliveira et al. 2019), it is quite common to find new records of hosts containing parasites that have not previously been described for the species (e.g., Aguiar et al. 2014, Silva et al. 2019). In this study, we present new records on species of parasites (*O. mazzai* and *Strongyloides* sp.) for the genus *Proceratophrys*, increasing the total number to 21 helminths. Additionally, all helminth species found represent their first records for *Procetatophrys ararype*, a frog endemic to the Brejo de Altitude Chapada do Araripe, Northeastern Brazil.

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Author Contributions

Wilmara Mascarenhas: Contribution to data collection; contribution to identification of parasites and amphibians; contribution to data analysis and interpretation; contribution to manuscript preparation and critical revision

Cicero R. Oliveira: Contribution to data collection; contribution to identification of parasites and amphibians; contribution to data analysis and interpretation; contribution to manuscript preparation and critical revision.

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Samuel C. Ribeiro: Contribution to data collection; contribution to data analysis and interpretation; contribution to manuscript preparation and 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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Article

Insect (Hexapoda) diversity in the Oceanic Archipelago of Fernando de Noronha, Brazil: Seasonality and Populational Density of Tabanidae (Diptera)

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Abstract: The seasonal population density is informed for two epidemiologically important species of bloodsucking Tabanidae, *Tabanus occidentalis* Linnaeus and *T. pungens* Wiedemann, recorded at the Fernando de Noronha archipelago that was never connected to the continent. The two species are widespread in the Neotropical Region, have not been recorded from any other oceanic island, and have most likely been introduced accidentally in the archipelago. *Tabanus occidentalis* dominated the samples, encompassing 99.6% of the specimens collected in the two local seasons, rainy and dry. *Tabanus pungens* was rarer, encompassing 0.4% of the specimens collected mainly in the dry season. The tabanids of Fernando de Noronha are able to transmit blood pathogens, bringing risks to the health of the livestock. They also pester the tourists, which brings losses to the local tourist industry. Larvae of both species were already collected in the water lettuce *Pistia stratiotes* Linnaeus and it is highly recommend that this introduced aquatic plant be removed from the ponds of Fernando de Noronha to control tabanid populations.
Keywords: *Fernando de Noronha archipelago; horse flies; neotropics; oceanic islands fauna; Tabanus.*

Diversidade de insetos (Hexapoda) no Arquipélago Oceânico de Fernando de Noronha, Brasil: Sazonalidade e Densidade Populacional de Tabanidae (Diptera)

Resumo: A densidade populacional e a sazonalidade é informada para duas espécies epidemiologicamente importantes de Tabanidae, *Tabanus occidentalis* Linnaeus e *T. pungens* Wiedemann, registradas no arquipélago de Fernando de Noronha, o qual nunca foi conectado ao continente. As duas espécies estão amplamente distribuídas na Região Neotropical, não foram registradas em nenhuma outra ilha oceânica e provavelmente foram introduzidas acidentalmente no arquipélago. *Tabanus occidentalis* dominou as amostras, englobando 99,6% dos exemplares coletados nas duas estações locais, chuvosa e seca. *Tabanus pungens* foi mais rara, abrangendo 0,4% dos espécimes coletados principalmente na estação seca. Os tabanídeos de Fernando de Noronha são capazes de transmitir patógenos do sangue, trazendo riscos à saúde do gado. Eles também incomodam os turistas, o que traz prejuízos para a indústria turística local. Larvas de ambas as espécies já foram coletadas na alface d'água *Pistia stratiotes* Linnaeus e é altamente recomendável que esta planta aquática, introduzida no arquipélago, seja removida das lagoas de Fernando de Noronha para o controle de populações de tabanídeos.
Palavras-chave: *mutucas; Neotrópico; fauna de ilhas oceânicas; Tabanus.*

Introduction

The Brazilian oceanic archipelago of Fernando de Noronha is located at the equatorial South Atlantic region (Figure 1). It is under the jurisdiction of the state of Pernambuco, but it is also a federal preservation area (i.e., National Park) managed by Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio (agency of the Brazilian Ministry of Environment) (Rafael et al. 2020). Fernando de Noronha is located c. 360 km from the nearest continental Brazilian coast in the state of Rio Grande do Norte (Figure 1). The archipelago represents the top of a volcanic cone belonging to an underwater mountain. This mountain is estimated at 12.0 to 1.5 million years old and has never been connected to the mainland (Barcellos et al. 2015). In total, the archipelago has 21 islands, encompassing 18.4 km^2. The only island inhabited by humans is the main island, Fernando de Noronha, encompassing 16.9 km^2 (Teixeira et al. 2003, Rafael et al. 2020).

Fernando de Noronha is the most intensively studied Brazilian oceanic island. Its marine biota, terrestrial vertebrates and plants have received especial attention. The archipelago's biota has suffered major ecological perturbations from several invasive animal and plant species that have been introduced to the islands (Teixeira et al. 2003). Tourism is now a major economic activity and the archipelago faces challenges to minimize anthropogenic impacts on its biota, prompting the need for inventories.

There are only a few studies on the insects of the Fernando de Noronha archipelago and the publication records for all groups of insects occurring there were summarized by Rafael et al. (2020). The first flies recorded from the archipelago were one species each in Dolichopodidae, Sarcophagidae and Syrphidae (Kirby 1890). Seventy-two years later, Alvarenga (1962) recorded two species in Culicidae and one in Calliphoridae, followed by Couri et al. (2008), who recorded three species in Sarcophagidae, two in Calliphoridae, one in Fanniidae, six in Muscidae and four morphospecies based on unidentified specimens of Sepsidae, Stratiomyidae, Tabanidae and Ulidiidae, the last as Otitidae. Over the last 12 years the largest amount of information was generated. Cordeiro et al. (2008) added one species of Culicidae; Oliveira et al. (2009, 2010) added seven species of Drosophilidae and Carmo & Vasconcelos (2014) added one species of Calliphoridae, totaling 31 species of Diptera. The last paper was published recently treating all groups of insects and increasing the number of Diptera to 134 species/morphospecies (Rafael et al. 2020).

The first record of Tabanidae in Fernando de Noronha was made by Couri et al. (2008) based on one unidentified specimen. Only recently two species were identified, *Tabanus occidentalis* Linnaeus, 1758 and *T. pungens* Wiedemann, 1828 (Rafael et al. 2020) based on a large series of specimens collected during nine months using interception traps and animal bait.

The presence of tabanids pests poses an important problem to livestock, local residents and the tourist industry, particularly when the tourists are attacked by tabanids when they are trying to enjoy the beach. This study aims to gain a better understanding of the seasonality, density, and habitat of this epidemiologically important group of insects.

Materials and Methods

The Fernando de Noronha archipelago (latitude 3°45’S to 3°57’S; longitude 32°19’W to 32°41’W) (Figure 1) is of volcanic origin and was never connected to the continent. It has a tropical oceanic climate (Awi - Köppen classification). The temperature ranges from 23.5°C

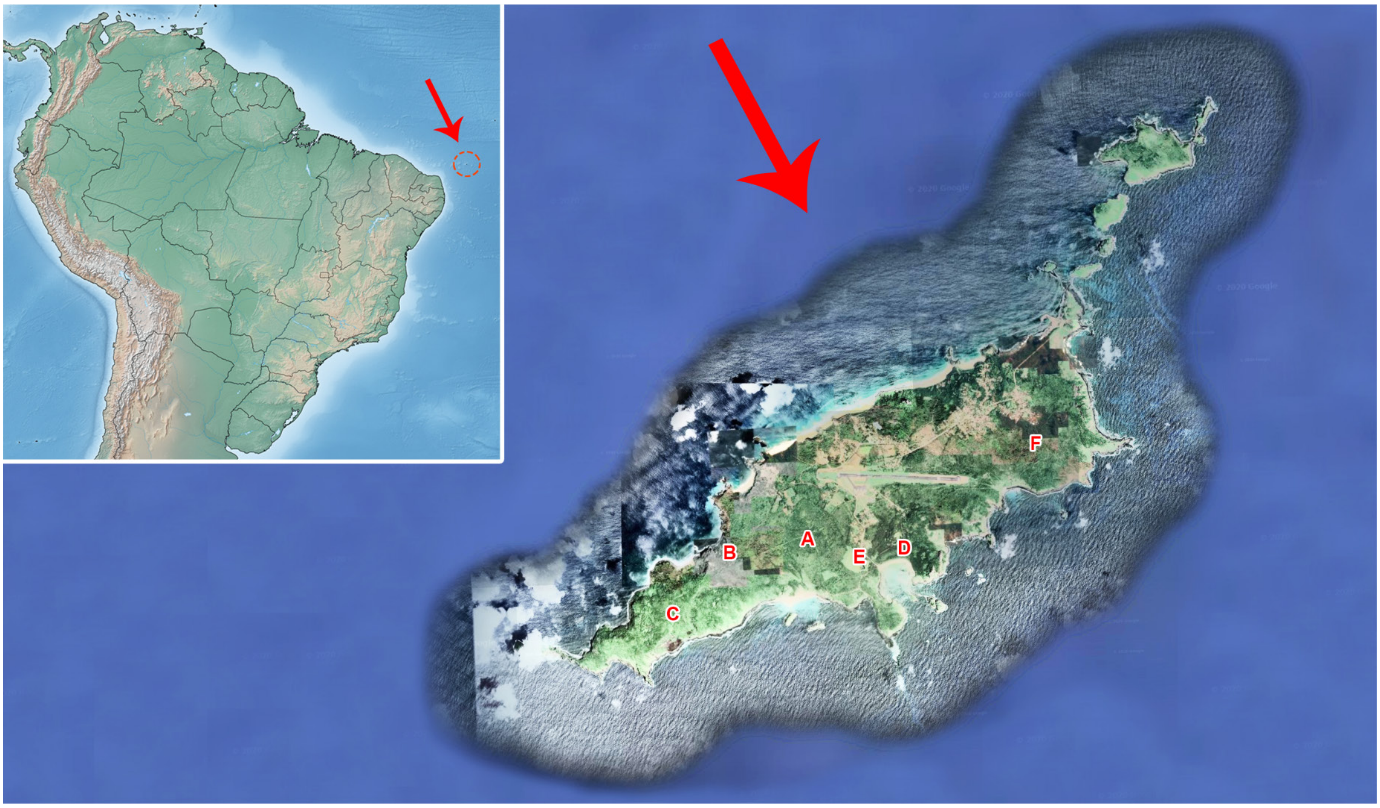

Figure 1. Location of the Archipelago Fernando de Noronha and points of Tabanidae collections: A) Sancho-Dolphins bay trail; B) Dolphins bay lookout; C) Capim-Açú trail; D) Mangrove; E) Xaréu pond; F) Atalaia trail.

to 31.5ºC, with an annual mean of 28ºC (IBAMA 2006) and annual precipitation of 1,400 mm, but with large interannual variability. It is characterized by a dry season, with a mean precipitation of 27.2 mm/month (August–January), and a rainy season, with a mean precipitation of 211.7 mm/month (March–July). The climatic regimes of Fernando de Noronha are similar to the semi-arid region of the Brazilian Northeast. There, most of the rain is concentrated in a period of three to four months. The archipelago has a harsh environment, lacking a permanent source of freshwater, with low vegetation diversity and a shallow soil that has little capacity for water retention (Freitas et al. 2013, Rafael et al. 2020).

The specimens collected during this survey will be distributed among main Brazilian collections, namely: **INPA**, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas; **CZMA**, Coleção Zoológica do Maranhão, Caxias, Maranhão; **DZUP**, Coleção Entomológica Padre Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná; **MNRJ**, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro; **MPEG**, Museu Paraense Emílio Goeldi, Belém, Pará and **MZUSP**, Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo.

The collecting license number for this project is 62.821, issued by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

Three sites on the main island Fernando de Noronha (Figure 1) were selected for continuous collecting (from June 9, 2019 to February 27, 2020) using Malaise interception traps based on the following criteria: accessibility, diversity of vegetation, low degree of exposure to human activities, and geographical position inside the National Park area. Human impact on the collecting sites was categorized as minor since the three areas are only open to guided tourism, scientific and management activities. The three sites are: 1) Sancho-Dolphins bay trail, near the information and control desk (Figure 1a): two interception traps, model Townes (Townes 1972) (Figure 2a), placed 100 meters from each other; 2) next to the lookout at dolphins bay (Figure 1b): one interception trap, model Gressitt & Gressitt (1962) (Figure 2b) and; 3) on the Capim-Açu trail (Figure 1c): one interception trap, model Gressitt & Gressitt. The collecting activities were interrupted on March 15, as a result of the covid-19 pandemic.

Additionally, insects were sampled using Malaise interception traps from 2 to 9 June 2019 and from 20 to 27 February 2020, with additional points of collection in the following locations of the main island:

Figure 2. Collection methods: A) Malaise trap, Townes model (Atalaia trail); B) Malaise trap, Gressitt & Gressitt model (Capim-Açú trail); C) Net sweeping over dunes (area around the Fernando de Noronha harbor); D) Light trap, UV and mercury lamps (Golfinhos trail).

Mangrove (Figure 1d); Xaréu pond (Figure 1e) and Atalaia trail (Figure 1f). Active collecting was conducted during June and February with entomological nets (Figure 2c), light trapping using a white sheet lit by a 250-watt mercury vapor and 40-watt UV lamps (Figure 2d) and animal bait (i.e. horse) to attract hematophagous horse flies and mosquitoes.

Specimens were labelled, preserved in small containers with commercial ethanol (94°), and temporarily stored in the ICMBio laboratory in the main island. The collected material was later transported to the INPA and CZMA, where each sample was sorted, labelled, identified and quantified.

We used the software R program (R Core Team 2020) to calculate the Pearson correlation between populational density versus precipitation and temperature only for continuous collecting (from June 9, 2019 to February 27, 2020). The precipitation data was obtained from https://pt.climate-data.org/america-do-sul/brasil/pernambuco/fernando-de-noronha-1006098/ and refers to the mean monthly precipitation during 40 years (1982 to 2012) and the monthly data on tabanids refers to the two combined biweekly collections.

The distribution map was generated on the website www.simplemappr.net (Shorthouse 2010).

Results

A total of 1,653 adult horse fly specimens, distributed in two species, were collected during nine months using interception traps: 1,648 specimens were *Tabanus occidentalis* (99.6%), and six were *T. pungens* (0.4%).

Tabanus occidentalis (Figures 3a–e)

This species belongs to a complex of species that have been treated as "varieties" or subspecies, but presently all "varieties" or subespecies are under *T. occidentalis* according to the Neotropical catalogue (Coscarón & Papavero 2009).

It is characterized by the following combination of characters: 10 mm from head (excluded antennae) to apex of abdomen; eye in live or relaxed specimens with green and blue iridescent bands (Figure 3c); frons (Figure 3b) slightly converging toward basal callus, about 6X higher than basal width (measured at ventral level of basal callus to the vertex); basal callus subrectangular, narrower than frons; antenna (Figure 3d) with basal plate produced dorsally, 1.5X longer than maximum height and distinctly longer than stylus (the darker terminal segments); fore leg (Figure 3e) with femur black and tibia distinctly bicolored white and black on distal half; wing (Figure 3a) hyaline with pterostigma dark brown; abdomen (Figure 3a) with both midlongitudinal and sublateral stripes of contiguous pale triangles, the mid one whitish and more conspicuous.

This species is widely spread in the Neotropical Region, from Mexico to Argentina (Entre Ríos, Buenos Aires) and in Trinidad (Coscarón & Papavero 2009). It was recorded only recently from the Fernando de Noronha island (Rafael et al. 2020) and this is the only oceanic island where it has been recorded.

Tabanus occidentalis is the most abundant horse fly in Fernando de Noronha, representing 99.6% of the specimens collected throughout the nine months using interception traps, from June 2019 to February 2010, in both rainy and dry seasons (Figure 4).

In the six months of the dry season, from August to January (Figure 4), 968 specimens were collected using interception traps, against 685 specimens in only three months of collections during the rainy season (June, July/2019 and February/2020). The fewest number of specimens

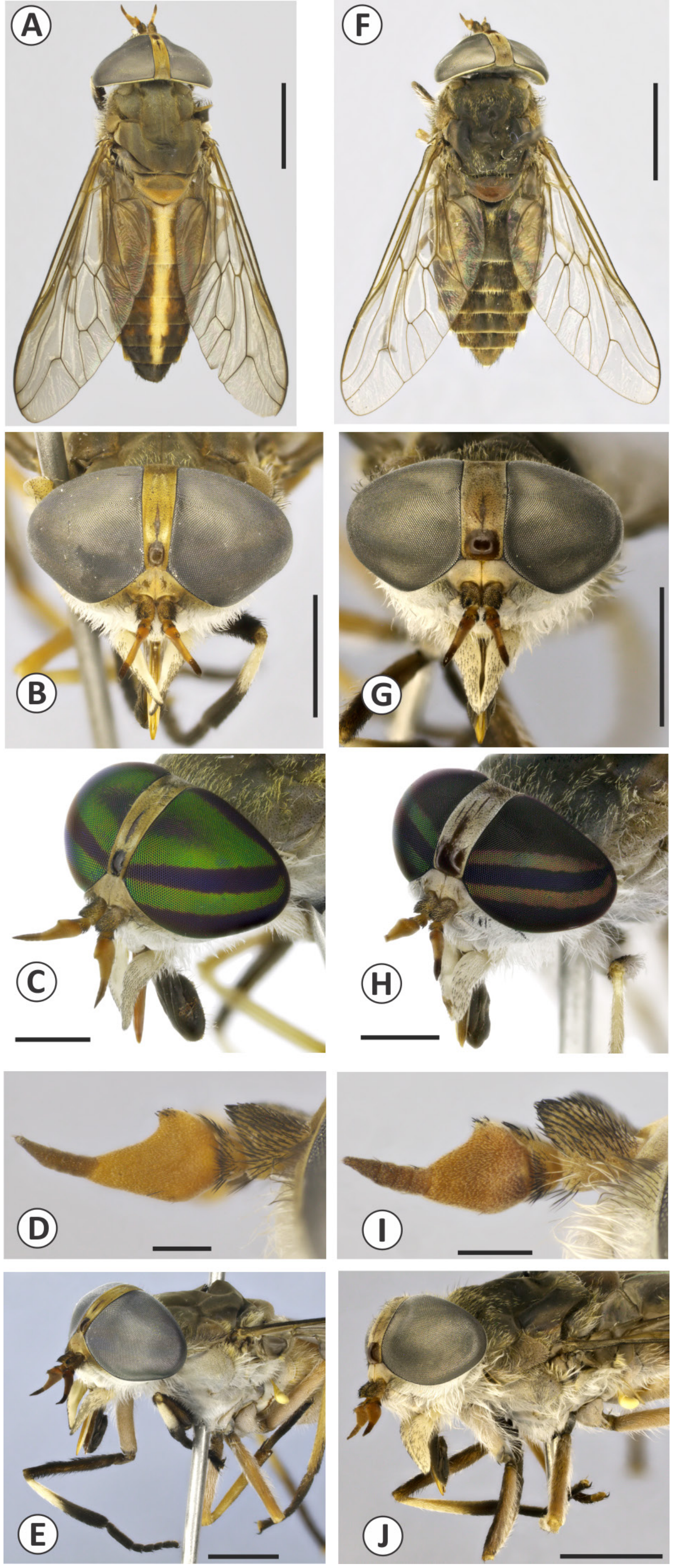

Figure 3. Morphology of *Tabanus* species: A–E) *Tabanus occidentalis*; F–J) *Tabanus pungens*; A and F), Habitus, dorsal view; B and G) Frons, frontal view; C and H) Head, frontolateral view; D and I) Antenna, lateral view; E and J) Head, thorax and legs, lateral view.

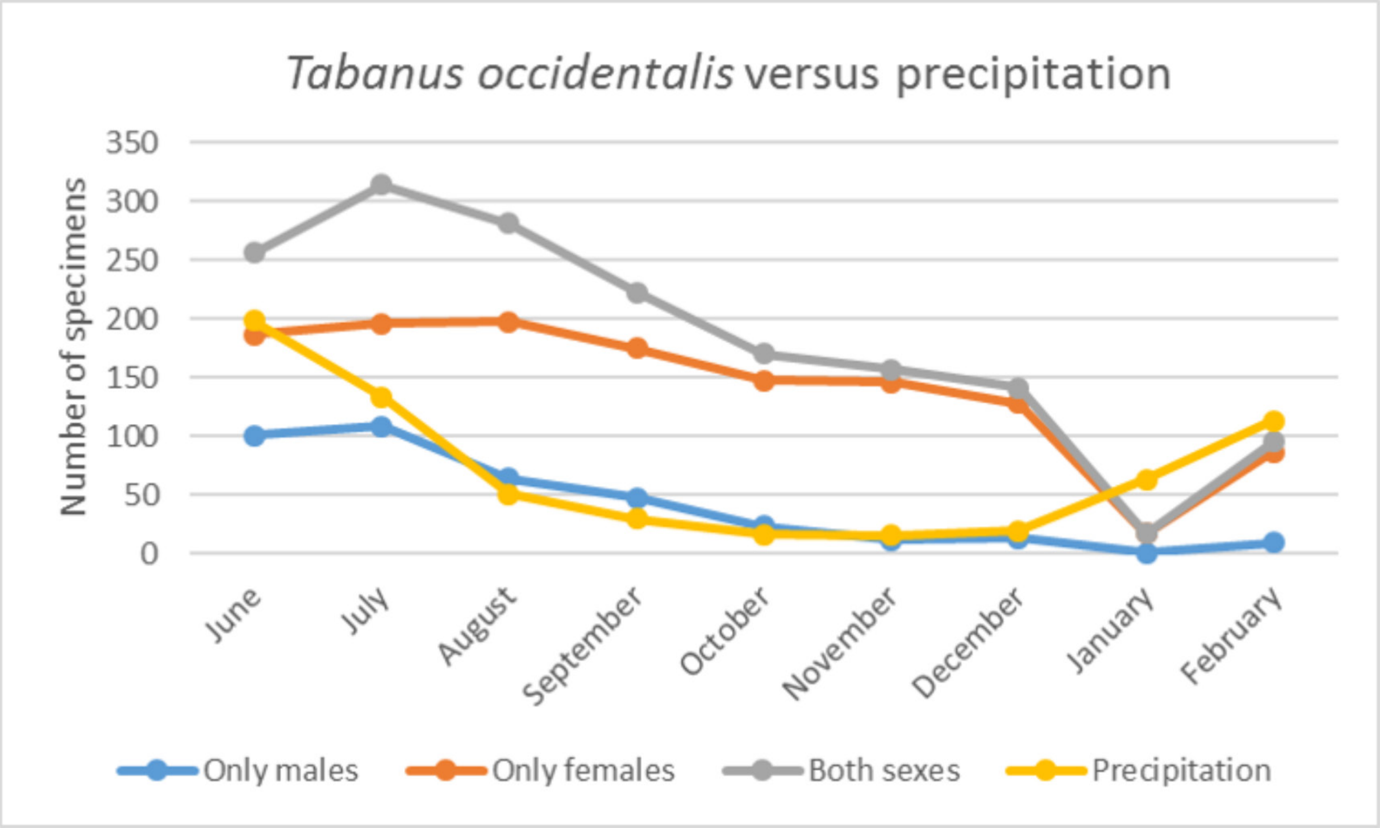

Figure 4. *Tabanus occidentalis*: Seasonal ocurrence of males, females and both together using interception traps in Fernando de Noronha and average of precipitation.

were collected in January, the last month of the dry season (Figure 4). Over the next month, February, first month of the rainy season, the number of tabanids specimens increased (Figure 4). The prediction is that we would find many more specimens in the following three months (March, April, May), reflecting the moderate to high positive linear relationship with precipitation. To analyze the linear relationship we considered only males, then only females, followed by males and females together.

The results for *T. occidentalis* failed to find a positive relationship between density and precipitation when considering male and female specimens together (Pearson r = 0.360, p>0.05, non significative) or when considering only female specimens (Pearson r = 0.097, p>0.05). However, when considering only male specimens, a positive linear relationship with precipitation was revealed (Pearson r = 0.683, p<0.05).

Concerning the temperature, there was a negative linear relationship with density for *T. occidentalis* (Pearson r = -0.882, p<0.01) when male and females specimens were pooled together. When both sexes are analyzed individually, a negative linear relationship with temperature was found (Pearson r = - 0.987, p<0.001) when considering only male specimens and a non significative relationship with temperature (Pearson r = 0.097, p>0.05) when considering only female specimens.

The average monthly temperature did not vary much during the year, maintaining an average of 27ºC, varying around one degree above and below.

Tabannus occidentalis was found in all three sites throughout the nine months using continuous interception traps and surprisingly with a high proportion of male specimens, 375 specimens (22.7%). Both sexes were more abundant at Capim-Açú trail, with 1,402 specimens (84,8%). Capim-Açu is a more preserved area and the trap was mounted crossing a wide trail.

Tabanus pungens (Figures 3f–j)

Tabanus pungens is characterized by the following combination of characters: 10 mm from head (excluded antennae) to apex of abdomen; eye in life or relaxed specimens with green and blue iridescent bands (Figure 3h); frons (Figure 3g) subparallel, about 2.5 to 3.0X higher than wide (measured at ventral level of basal callus to the vertex); basal callus subquadrate, slightly narrower than frons; antenna (Figure 3i) with basal plate produced dorsally, as long as maximum high and slightly longer than stylus (the darker terminal segments); fore leg (Figure 3j) with femur yellow to light brown and tibia bicolored light yellow and black at distal third; wing (Figure 3f) hyaline with pterostigma light brown; abdomen (Figure 3f) with black mid-longitudinal stripe wider than sublateral stripes of contiguous pale triangles, smaller posteriorly.

A widely distributed species occurring from Texas (USA) to entire Neotropical Region (except West Indies and Chile) and in Trinidad (Coscarón & Papavero 2009). As the first species, it also was recorded only recently in Fernando de Noronha (Rafael et al. 2020) and this is the only oceanic island from which it has been recorded.

Tabanus pungens was collected in low density, only six specimens collected throughout the nine months using continuous interception traps. This species was collected at two sites: at Dolphins bay lookout (2 specimens in August 2019) and at Capim-Açu trail (4 specimens in July, August, September, October and November 2019).

Despite the few specimens (six), the results suggest that the relationship between the density of *T. pungens* with precipitation is linear negative (Pearson r = -0.748, p<0.05) and no significant correlation was found with temperature (Pearson r = 0.207, p>0.05).

Tabanus pungens specimens were collected while biting humans, cows and horses and were more frequently found on humans. No male specimens were collected.

During a short period, eight days, one small interception trap, Townes model, was mounted at one side of the Xaréu pond and there it collected 40 female specimens of *T. pungens*, more than in all other traps together during nine months.

Additionally, horse bait was used trying to find more species of tabanid species in Fernando de Noronha, but only *T. occidentalis* and *T. pungens* were collected. Both species, but *T. pungens* in higher numbers, were also collected attacking humans.

Discussion

We consider that the survey techniques employed in this work, using extensive sampling based on light traps, animal bait, and Malaise interception traps for nine months (interrupted after Covid-19 pandemy), were sufficient to ascertain the total diversity of tabanids living in Fernando de Noronha: only two common species.

Tabanus occidentalis is the most common species in the Neotropical Region, where it can be found all year long (Henriques & Rafael 1999). In the continental mainland it is more abundant in the rainy season, as verified by Rafael & Charlwood (1980) in the Occidental Amazon Basin and by Gorayeb (1993) in the Oriental Amazon Basin. One possible explanation for the positive relationship of *T. occidentalis* with precipitation is that humidity provides more viable habitats for oviposition, for instance moist soil. This species was more abundant at the Capim-Açú trail, a more preserved area. However, we have to consider that small bodies of water can be used as substrate for oviposition, considering that larvae have been found in water lettuce, *Pistia stratiotes* Linnaeus (Araceae) (Goodwin & Murdoch 1974). This Araceae is common on the surface of the small ponds in Fernando de Noronha (Teixeira et al. 2003).

The density of *T. pungens* also correlated with precipitation, but negatively, in the continental mainland, where the specimens can be found throughout the year (Henriques & Rafael 1999), they are more frequently collected in the drier months, and in open area as verified by Rafael (1982) in the Occidental Amazon Basin; and by Gorayeb (1993) in the Oriental Amazon Basin.

Despite the few numbers of *T. pungens* collected (six specimens) using interception traps, we collected 40 specimens (more than all other traps together during nine months that collected) near the Xaréu pond, with one small interception trap left in the field for only eight days. A possible explanation for this is the great density of water lettuce on the pond, one of the substrates already recorded for the larvae of this species (Goodwin & Murdoch 1974). This shows that horse fly collecting must include as many different habitats as possible.

We collected some smaller specimens of *T. occidentalis* with some color variation, the smaller specimens being paler. The paler, smaller specimens have been treated by taxonomists as a "variety" of *T. occidentalis*. However, because of the similar morphology, we consider all specimens conspecific and follow the classification of Coscarón & Papavero (2009), who considered all varieties as synonyms of *T. occidentalis.*

The tabanid fauna of the Fernando de Noronha is entirely derived from South America. It is opportune to consider that these two species are morphologically identical with mainland specimens, suggesting they are conspecific. Both species occur in the Brazilian Northeast, from which they most likely colonized Fernando de Noronha.

It is uncertain whether these species have been brought to Fernando de Noronha by man or wheather it was a natural dispersal. Although natural dispersion seems less likely, it should not be discarded. Tabanids are good fliers and movement through air is one probable means of dispersion. However, no *Tabanus* species has been documented breaking a distance of 360 km from the continent. Furthermore, these species are not found in the Greater Antilles island, which is much closer to the continent. A passive dispersion via rafting on the vegetation or other flotsam appears unlikely. To disperse this way, these flies would have to tolerate salt very well. This is not the case of either species since their larvae have been found in moist soil and roots of the aquatic plant water lettuce on the continent. Another argument against the natural dispersion hypothesis is that the predominant oceanic and wind currents from the occidental african coast, which can facilite dispersal on the sea surface and air, are counterclockwise, carrying marine floating debris from coastal Africa (Ivar do Sul et al. 2009). We think that the tabanid fauna of Fernando de Noronha has most likely been imported by humans and is now widespread. There has been active commerce between the continent and Fernando de Noronha over the years, which most likely has facilitated the transport of both species as immatures (eggs, larvae or pupae) or as adults. It is possible that larvae were transported in ships or planes in roots or leaves of plants, or adult female specimens were trapped in one or both these means of transport. About 300 plant species have been introduced to Fernando de Noronha (Teixeira et al. 2003). Cargo ships are not inspected to control the introduction of exotic species.

Larvae of *T. occidentalis* and *T. pungens* were taken from moist soil, usually in the vicinity of the roots of grasses and from water lettuce (Goodwin & Murdoch 1974) and these could be the substrate where both species were transported when introduced in the archipelago. Water lettuce, *Pistia stratiotes* L. (Araceae) is dense on surface of the Xaréu pond and in other smaller ponds of the main island. The large numbers of *T. pungens* collected in the Xaréu pond, in only eight days, in the end of the rainy season, using small Malaise interception trap, is indicative that larvae are growing in the roots of this aquatic plant. No effort was made to find the larvae in Fernando de Noronha.

Tabanids are nuisance because of their painful and irritating persistent biting behavior, and blood ingestion. Cattle and horses suffer the most from constant annoyance and most animals react, as cow and horses, to the biting of the females by trying to dislodge them using the head, the tail, shaking the muscles or stamping the feet. Even when dislodged, the flies usually persist on the same animal or go on to a neighbor. The interrupted biting is likely a cause of direct transfer of blood-inhabiting pathogenic organisms among animals. According to Baldacchino et al. (2014) tabanids are 20-20,000 times more efficient mechanical vectors than other biting insects because the females can retain a large amount of blood (7-15 nL) in their mouthparts. For this reason they are implicated as vectors of the following diseases around the world: anaplasmosis, anthrax, equine encephalitis, equine infectious anemia, loiasis, mansonelosis, surra and tularemia (Rafael & Henriques 2011, Baldacchino et al. 2014).

The high populational density of tabanids have an economic impact on tourism activities in the main island. They pester the tourists and their bite is quite painful. Additionally, cows and horses may suffer severely from heavy attacks of tabanids lowering milk production and impairing weight gain. Furthermore, during the rainy season when tabanid population densities are high, transmission of pathogens is facilitated.

Little is known about the potential transmission of pathogenic agents and parity by *T. occidentalis* and *T. pungens*. Unfortunately we did not collect during the three wetter months (March, April and May), which may hold more epidemiological importance because the density of tabanids is predicted to be higher.

If proved that both species are growing in the water lettuce, removal of this introduced aquatic plant from the ponds in Fernando de Noronha may be sufficient to control the density of the tabanid population in the archipelago.

Recently a horse fly species was detected attacking a lizard in Pará (Gorayeb & Campos 2018). This record deserves attention because lizards are a reservoir of *Salmonella*, a bacterium with zoonotic potential that may represent a risk to children, elders and immunosuppressed people (Michelleti et al. 2020). The introduced teju lizard, *Salvator merianae* Duméril & Bibron is abundant in Fernando de Noronha and a potential tabanid host.

Fernando de Noronha's native species have been impacted by the arrival of several exotic and invasive species, for instance domestic cats, dogs, brown and black rats, teju lizards, cattle egret (Michelleti et al. 2020), cows, horses and goats. Moreover, several zoonotic diseases, like salmonellosis and toxoplasmosis, have been linked to some of these invasive species (Michelleti et al. 2020) and this pathogens can be transmitted by *T. occidentalis,* as shown by Luz-Alves et al. (2007) in the North of Pará.

Our analysis focused mainly on elucidating the seasonality, density and population dynamics of *T. occidentalis* and *T. pungens*. These tabanids are hematophagous species harming the tourist industry, the main economic activity of Fernando de Noronha.

The tabanids of Fernando de Noronha might be able to transmit blood pathogens, thereby bringing health risks. Adult emergence of *T. occidentalis* occurs throughout the year with predictable peaks of abundance in the rainy season, mainly March to June; this leads to short but extremely high periods of tabanid activity and as a result tabanids can have drastic impacts. Tabanid density must be monitored throughout the year since they are also mechanical vectors of pathogenic agents.

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Author Contributions

José Albertino Rafael: Contribution in the concept of the study; data collection; identification of the species; data analysis and interpretation; manuscript preparation.

Dayse Willkenia Almeida Marques: Contribution in the concept and design of the study; contribution to critical revision; manuscript preparation; preparation of the figures.

Alberto Moreira Silva-Neto: Contribution to data analysis and interpretation; manuscript preparation; contribution to critical revision, adding intellectual content.

Francisco Limeira-de-Oliveira: Contribution in the concept of the study; data collection; identification of the species; 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

Effect of land-use types on the ecomorphological structure of fish assemblage in distinct mesohabitats of neotropical streams

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Abstract: The use and occupation of land by human population substantially influence environmental variables and fish assemblage in streams. However, there is little knowledge on how these changes affect the ecomorphological structure of fish assemblage in mesohabitats. Therefore, we aim to assess whether the land-use types affect the ecomorphological structure of fish assemblage in distinct mesohabitats. Environmental and ichthyofaunistic data were collected in three mesohabitats (rifles, runs, and pools) of five rural and five urban streams. Twenty-one ecomorphological indices were obtained from the mean of linear morphological measurements and areas of the fishes. Subsequently, the Euclidean distance was calculated, based on the ecomorphological indices, between each pair of species, to measure the ecomorphological distances for the mesohabitats of the rural and urban streams. The results show that the urban environment is more harmful to streams than the rural one, due to changes in the environmental variables and decrease in species richness. The main environmental changes found in urban streams were the decrease in canopy cover by riparian vegetation and dissolved oxygen, and the increase in electrical conductivity and bed silting. Also, there was a significant decrease in the morphological similarity between fish species in the mesohabitats of urban streams compared to rural ones. Therefore, we can conclude that the urban environment leads to the loss of morphologically similar fish species in the mesohabitats, with only a few functionally distinct species remaining.

Keywords: *urban ecosystem; headwater streams; ecomorphological distances; fauna homogenization.*

Efeito dos tipos de uso do solo na estrutura ecomorfológica da assembleia de peixes em distintos mesohábitats de riachos neotropicais

Resumo: O uso e ocupação do solo pela população humana influencia substancialmente as variáveis ambientais e a assembleia de peixes em riachos. No entanto, há pouco conhecimento de como estas alterações afeta a estrutura ecomorfológica da assembleia de peixes em mesohábitats. Portanto, objetiva-se avaliar se o tipo do uso do solo afeta a estrutura ecomorfológica da assembleia de peixes nos distintos mesohábitats. Dados ambientais e ictiofaunísticos foram coletados em três mesohabitats (corredeiras, rápidos e remansos) de cinco riachos rurais e cinco urbanos. Vinte e um índices ecomorfológicos foram obtidos a partir das médias das medidas morfológicas lineares e áreas dos peixes. Posteriormente, a distância Euclidiana foi calculada, baseada nos índices ecomorfológicos, entre cada par de espécies, afim de mensurar as distâncias ecomorfológicas para os mesohábitats dos riachos rurais e urbanos. Os resultados mostram que o ambiente urbano é mais danoso aos riachos do que o rural, devido a diminuição da riqueza de espécies e as alterações nas variáveis ambientais. As principais mudanças ambientais encontradas em riachos urbanos foram a diminuição da cobertura do dossel pela vegetação ripária e do oxigênio dissolvido e o aumento da condutividade elétrica e do assoreamento do leito. Além disso, houve uma diminuição significativa da similaridade morfológica entre as espécies de peixes nos mesohábitats de riachos urbanos em comparação com os rurais. Portanto, podemos concluir que o ambiente urbano leva à perda de espécies de peixes morfologicamente similares nos mesohábitats, restando apenas algumas espécies funcionalmente distintas.

Palavras-chave: *ecossistema urbano; riachos de cabeceira; distâncias ecomorfológicas; homogeneização da fauna.*

Introduction

The alteration of natural landscapes caused by anthropogenic activities is one of the greatest threats to biodiversity worldwide (Sala et al. 2000, Foley et al. 2005). The use and occupation of land by the human population, such as rural and urban landscapes, are responsible for influencing several environmental factors of streams, such as hydrology, channel morphology, and water quality and toxicity (Allan 2004, Walsh et al. 2005, Cunico et al. 2012). Although both rural and urban landscapes cause environmental damage to streams (Tóth et al. 2019), comparative studies have shown that the urban environment is generally more harmful to stream fish assemblages than the rural one (Cunico et al. 2006, 2012, Alexandre et al. 2010, Cruz & Pompeu, 2020). This difference in the preservation condition of the streams have been associated with the presence of an impermeable surface in the drainage basin (Wang et al. 2001, Cunico et al. 2012), which increases the strength of the runoff, causing more drastic changes in the hydrological and geomorphological variables of these ecosystems, such as increased flow velocity, erosion of the margin, and sedimentation of the channel (Wood & Armitage 1997, Hancock 2002, Booth et al. 2004, Hasenmueller et al. 2017). A common response of the fish assemblage to urbanization is the decrease in the diversity of native species and the dominance by few exotic ones (Walters et al. 2003, Perkin et al. 2019). However, the effects of the land use on fish assemblages are still largely evaluated only by metrics that consider the number of species (species richness) and their abundance (Weaver & Garman 1994, Wang et al. 2001, Walsh et al. 2005, Cunico et al. 2006, 2012, Tóth et al. 2019). Such metrics, based on taxonomic identity, provides an incomplete response to changes in biodiversity, as they assume that all species contribute equally to the functioning of the ecosystem and sometimes fail to detect changes caused by anthropogenic activities (Rabeni & Smale 1995, Villéger et al. 2010, Teresa & Casatti 2012, Casatti et al. 2015). Therefore, it is necessary to use the functional characteristics of the species as a complementary approach to assess the impact of land use on the fish assemblage, instead of only taxonomic identity (Brown et al. 2009, Cunico et al. 2011, Kern & Langerhans 2018).

Morphological traits have been widely used to qualify the functions that species develop in a given ecosystem (Moreno et al. 2006, Villéger et al. 2010, Inward et al. 2011, Toussaint et al. 2016), with a premise that adaptive changes in the phenotype are capable of producing differences in species performance, which consequently generates changes in the use of resources (Wikramanayake 1990, Casatti & Castro 2006, Oliveira et al. 2010, Pagotto et al. 2011). The interaction between morphology and ecological aspects of species is the basis of ecomorphology (Peres-Neto 1999) and provides support for the use of morphology as a tool to determine the functional characteristics of species (Pease et al. 2012). In this approach, the ordering of morphological traits in multivariate analysis is used to evaluate the diversification of niches and ecological functions existing in a given ecosystem (Winemiller 1991, Villéger et al. 2010). Consequently, from the calculation of interspecific ecomorphological distances, it becomes possible to estimate the niche space occupied by the assemblages and describe the pattern of functional similarity existing among its members (Winemiller 1991; Montaña et al. 2014).

Streams are considered complex ecosystems, and their communities are influenced by several factors operating at multiple scales (Cunico et al. 2012, Barbosa et al. 2019). On a local scale, streams can be understood as a mosaic of mesohabitats (rifles, runs, and pools) that are delimited by different combinations of current velocity, depth, and substrate composition (Rincón 1999). Riffles are characterized as areas of high gradient, with fast and turbulent waters and rocky substrate; runs also have relatively fast waters, but are generally deeper than riffles, with a smaller gradient and non-turbulent waters; pools are deep areas with low current velocity, and the presence of fine substrate is common. These hydrological and geomorphological differences among the mesohabitats act as environmental filters for the fish assemblage, selecting the species mainly by the body shape (Wikramanayake 1990, Leal et al. 2011, Kano et al. 2013). For example, the high current velocity of the riffles favors species with a dorsoventrally depressed body, while the low velocity of the pools is associated to species with a laterally compressed body (Gaston et al. 2012). Therefore, we can expect that the fish assemblage in the mesohabitats would show high morphological similarity between species. However, there is little knowledge on how changes in the environmental variables of streams caused by land-use types (*e.g.* rural and urban environment) affect the ecomorphological structure of fish assemblage in the mesohabitats.

Previous studies have shown that environmental changes in streams caused by land use affect the availability of micro and mesohabitats (Zeni et al. 2019), influencing the distribution of fish species along the channel (Berkman & Rabeni 1987, Teresa & Casatti 2012). For example, the silting of streams usually buries the coarse substrate (Walters et al., 2003), leading to a decrease of species that inhabit the riffles (i.e. species with a dorsoventrally depressed body) and can create microhabitats for species adapted to pools (i.e. species with a laterally compressed body) (Berkman & Rabeni 1987). This reorganization of the assemblage along the stream results in the homogenization of species composition among mesohabitats (Berkman & Rabeni 1987, Teresa & Casatti 2012). Therefore, it is expected that this homogenization of species would decrease the morphological similarity between species and increase the volume of ecomorphological space in mesohabitats.

In this context, we conducted the study in three mesohabitats (riffles, runs, and pools) of streams inserted in the rural and urban environment to assess whether the land-use type influences the ecomorphological structure of the fish assemblage in the mesohabitats. We hypothesized that (i) urban streams would have less preserved environmental conditions and less species richness compared to rural ones, (ii) mesohabitats of urban streams would present fish assemblage with less morphological similarity between species, and (iii) greater volume of ecomorphological space than rural mesohabitats.

Materials and methods

1. *Study Area*

This study was carried out in ten low-order streams (1st to 3rd order) belonging to the Pirapó River Basin, close to and inserted in the metropolitan region of Maringá, southern Brazil. The Pirapó River Basin is located in the northern region of the state of Paraná, specifically in the polygon bounded by latitudes of 22º30 'and 23º30'S and longitudes of 51º15' and 52º15'W (Figure 1). With a drainage area of approximately 5,000 km^2 and an extension of 168 km, the Pirapó River is one of the main tributaries of the Paranapanema River, in the upper Paraná River Basin (Maak 2002). The climate of the region is subtropical, being classified, according to Köppen, as a hot humid climatic zone, Cfa (h)

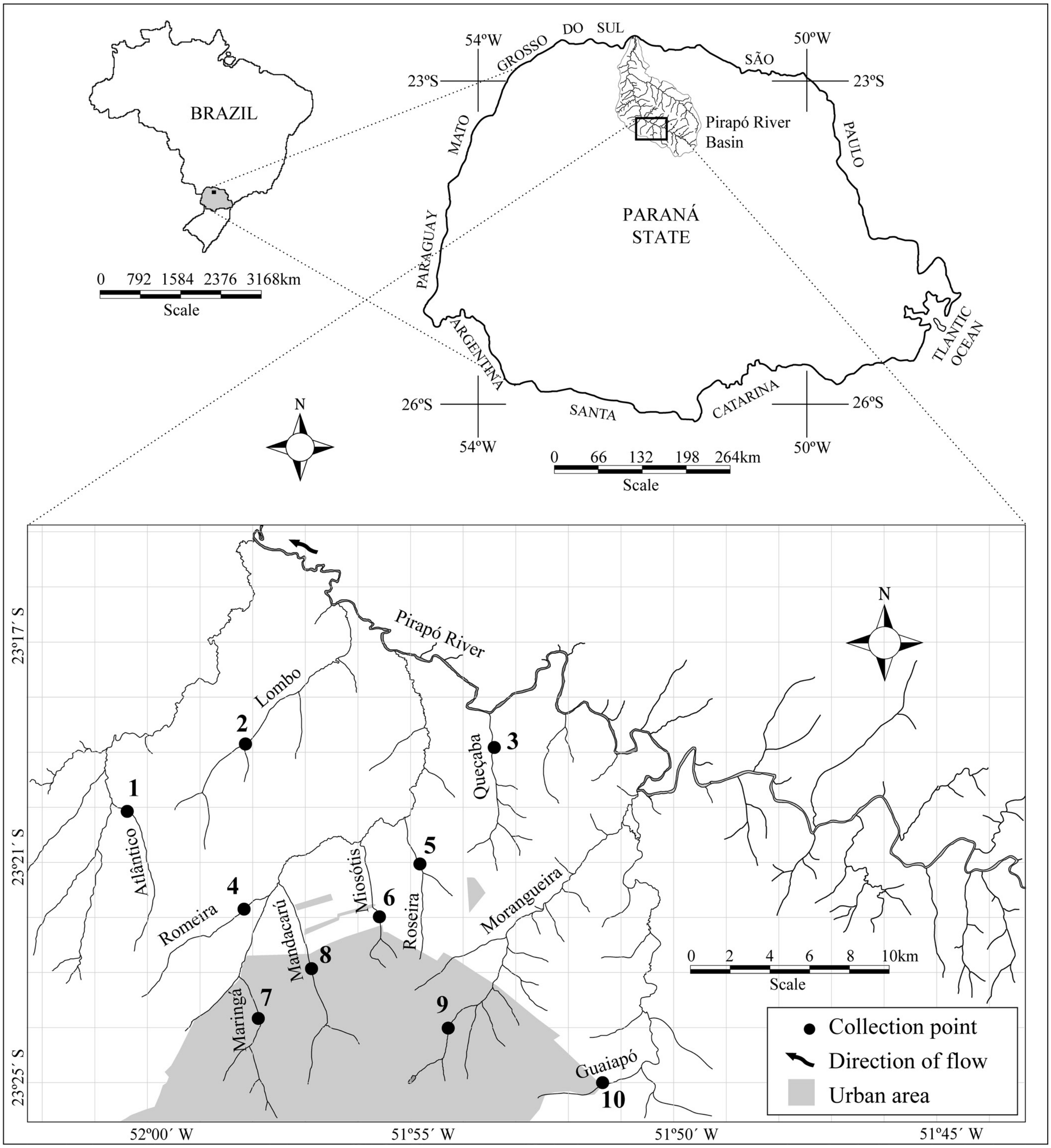

Figure 1. Location of collection points in rural (1-5) and urban (6-10) streams in the Pirapó River Basin, Maringá, Brazil.

(Maack 2002). The annual rainfall levels exceed 1,000 mm, while the average annual temperatures vary between 16 and 20° C, with January being the hottest and most humid month and July the coldest and driest (Passos 2007).

2. *Data sampling*

Data sampling was carried out in April and May 2017, in three mesohabitats (riffles, runs, and pools) of ten streams, five inserted in the rural environment, and five in the urban one (Figure 1), totaling 30 collection points. Before the collection day, we visited several stretches along the streams and selected the one that had the three mesohabitats next to each other, to facilitate data collection. Thus, mesohabitats were visually selected in sequence or very close to each other, according to the characterization presented by Rincón (1999): riffles had fast and turbulent waters, with a substrate composed of large, worn, and round rocks; runs had relatively fast-running waters but were deeper than riffles, with less turbulent waters; pools were deep areas where the current was slow, which allowed for fine sediment in the substrate. The longitudinal extension of each mesohabitat was standardized in ten meters in length, where the following environmental variables were measured: depth (cm) and width (m) of the channel, proportion of flooded vegetation (%), canopy cover by riparian vegetation (%) and substrate type (clay, sand, rock, or civil construction waste; %), current velocity (m/s; with a JDC electronic flowmeter, model Flowatch FL-K2), pH (DIGIMED, model DM-22), dissolved oxygen (mg/L; DIGIMED, model DM-4P) and electrical conductivity (µS/cm; DIGIMED, model DM-32).

The width of the channel was measured upstream, downstream and in the center of each mesohabitat, while the other variables were taken at nine points, also comprising the left and right margins, and an intermediate point. The quantification of the area of flooded vegetation, canopy cover, and type of substrate was done with a 0.25 m^2 wooden square, subdivided into 25 smaller squares of 0,01 m^2, with their values being estimated from the sum of the filled subdivisions. After quantifying the variables, their averages were calculated to characterize the mesohabitats according to their environmental conditions.

The fish collection was done using electrofishing (portable generator of alternating current, 2,500W, 400V, 2A), through three consecutive passes of the puçás in each mesohabitat. As mesohabitats were selected in sequence or very close to each other, before any procedure, they were blocked by multifilament nets with 2 mm between opposite nodes. The captured specimens were anesthetized with benzocaine and sacrificed. After death, they were fixed in a 4% formaldehyde solution and, after taking their morphological measures, transferred to 70° GL alcohol. The collected fish were identified according to Ota et al. (2018), and the exemplary testimonies were deposited in the Ichthyological Collection of the Nupélia/UEM (lots: NUP 20040 to NUP 20128). The collects were made under the license of the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBIO) nº. 25560-1.

3. *Ecomorphological data*

Linear morphometric measurements and areas related to the fish's trunk, fins, head, eyes, and mouth were taken from ten individuals, when possible, of each species using a digital caliper (0.01 mm approximation). The eyes were photographed and the fins were drawn on sheets of sulfite paper, after which their areas were calculated in the program ImageJ (Rasband 2012), through digitized drawings and photographs. Only adult individuals were used since ontogenetic growth can promote changes in morphology (Russo et al. 2007), feeding habits (Novakowski et al. 2004), and habitat use (Gratwicke et al. 2006). The following morphological traits were measured: standard length, maximum body height, body midline height, maximum body width, caudal peduncle length, caudal peduncle height, caudal peduncle width, head length, head height, head width, eye height, mouth height, mouth width, caudal fin height, anal fin length, pectoral fin length, pelvic fin length, eye area, dorsal fin area, anal fin area, caudal fin area, pectoral fin area, and pelvic fin area.

Species with only one individual collected in a given mesohabitat were disregarded from the ecomorphological analysis for that mesohabitat, but considered for the others where they presented more than one individual. This procedure was taken to minimize the influence of species in which few individuals only transit between mesohabitats, but do not have morphological adaptations for that mesohabitat. In this way, even though mesohabitats are blocked with waiting nets, there is the possibility of capturing individuals who passed through before the blockade. Therefore, the following species were disregarded, from a given mesohabitat, from ecomorphological analysis: riffles in a rural environment – *Psalidodon* aff. *fasciatus*, *Astyanax lacustris*, *Imparfinis borodini*, *Poecilia reticulata*, *Rineloricaria* aff. *latirostris*; runs in a rural environment – *Geophagus brasiliensis*, *Hisonotus francirochai*, *Hypostomus* cf. *nigromaculatus*, *Rineloricaria* aff. *latirostris*; runs in an urban environment – *Piabina argentea*; pools in a rural environment – *Bryconamericus stramineus*, *Characidium* aff. *zebra*, *Hoplias* aff. *malabaricus*, *Hypostomus hermanni*, *Oligosarcus paranensis*, *Pimelodella avanhandavae*; pools in an urban environment – *Piabina argentea*. *Gymnotus inaequilabiatus* was also excluded from ecomorphological analysis, due to the absence of even fins which made it impossible to compare them with others concerning their measurements.

From the mean of linear morphometric measurements and area for each species, ecomorphological indices were calculated (Table 1). This procedure allows the evaluation of information restricted to differences between forms and promotes independence of the analysis regarding the size of the specimens. Although body size is recognized as an important factor in ecological relationships between fish (Layman et al. 2005), significant differences in body dimensions can lead to a trend in data variation related exclusively to the size of the specimens. Thus, the use of indices reduces the chances of the analyzes being dominated by a single variable (Winemiller 1991). Some authors made use of indices in their studies, assuming that, by expressing the shape of the morphological structures, the indices may reveal their ecological roles (Winemiller 1991, Willis et al. 2005, Casatti & Castro 2006, Montaña & Winemiller 2010, Montaña et al. 2014, Oliveira et al. 2010, Pagotto et al. 2011). In this study, 21 ecomorphological indices were used to represent the occupation of the trophic and spatial niche by species (Table 1).

4. *Data Analysis*

To characterize mesohabitats according to their environmental conditions, all variables were transformed to zero mean and unit variance and then summarized by Principal Component Analysis (PCA). The broken-stick model was used as a criterion for assessing the significance of the axes. The Analysis of Variance (two-way ANOVA) was applied to evaluate whether there was a separation of the points according to the factors land-use types (rural and urban) and mesohabitats (rifles, runs, and pools) in the first two axes of the PCA.

We applied a mantel correlogram to analyze whether the fish assemblage composition is associated with the spatial distance between the collection points. The first matrix was generated through the Jaccard distance calculated on the presence/absence of the species. The second matrix was obtained from the calculation of the distance, in kilometers, between the collection points in the QGIS program (QGIS Development Team 2018), using the stream network of the Pirapó River basin, downloaded from the website of the Instituto Água e terra do Paraná (IAT 2021), and the geographical coordinates of the collection points.

A second PCA was performed on the correlation matrix of ecomorphological indices, to characterize the tendency for interspecific variation in the multivariate ecomorphological space between fish assemblages. As in the first PCA, the broken-stick model was used, in which the axes with eigenvalues greater than those generated by the

Table 1. Linear morphometric variables and areas used in the calculation of ecomorphological indices and their respective ecological meanings. The following morphological characters were used: Standard Length (SL), Maximum Body Height (MBH), Midline Height (MH), Maximum Body Width (MBW), Caudal Peduncle Length (CPL), Caudal Peduncle Height (CPH), Caudal Peduncle Width (CPW), Head Length (HL), Head Height (HH), Head Width (HW), Eye Height (EH), Mouth Height (MoH), Mouth Width (MoW), Caudal Fin Height (CFH), Anal Fin Length (AFL), Pectoral Fin Length (PcFL), Pelvic Fin Length (PvFL), Eye Area (EA), Caudal Fin Area (CFA), Anal Fin Area (AFA), Pectoral Fin Area (PcFA), Pelvic Fin area (PvFA), Dorsal Fin area (DFA).

Indices	Formula	Meaning
1. Compression index	MBH/MBW	High values indicate fish with a laterally compressed body, which is expected for species that occupy habitats with low current velocity (Gatz Jr. 1979, Watson & Balon 1984).
2. Depression index	MH/MBH	Low values indicate fish with a dorsoventrally depressed body, which is expected for species that explore habitats with high current velocity, as this body shape helps the fish to stay in the water column without having to swim (Watson & Balon 1984).
3. Relative length of caudal peduncle	CPL/SL	Fish with a long caudal peduncle are good swimmers. However, fish adapted to high current velocity, but not necessarily nektonic species, such as the Siluriformes, also have long caudal peduncles (Watson & Balon 1984).
4. Relative height of caudal peduncle	CPH/MBH	Low values indicate high maneuverability (Winemiller 1991, Willis et al. 2005).
5. Relative width of caudal peduncle	CPH/MBW	High values indicate continuous swimmers (Winemiller 1991, Willis et al. 2005).
6. Relative length of head	HL/SL	High values of these indices are found in fish that feed on larger prey, therefore, higher rates are expected for piscivorous species (Watson & Balon 1984, Winemiller 1991, Pouilly et al. 2003, Willis et al. 2005).
7. Relative height of head	HH/MBH	
8. Relative width of head	HW/MBW	
9. Relative height of mouth	MoH/MBH	The relative height of the mouth allows inferring about the relative size of the prey (Gatz Jr. 1979).
10. Relative widht of mouth	MoW/MBW	Index related to the size of the mouth, suggesting relatively large prey for indexes with high values (Gatz Jr. 1979, Winemiller 1991).
11. Vertical eye position	EH/HH	This index is associated with the species' foraging position in the water column. High values indicate benthic fish (eyes located dorsally), while low values indicate nektonic fish (side eyes) (Gatz Jr. 1979).
12. Relative area of eye	$EA/(SL)^2$	This index is related to food detection and provides information on the visual acuity of the species (Pouilly et al. 2003). It can indicate the position of the species in the water column, as species that inhabit deeper areas have smaller eyes (Gatz Jr. 1979, Piet, 1998, Wikramanayake, 1990).
13. Relative area of dorsal fin	$DFA/(SL)^2$	Larger relative areas have greater yaw stabilization capacity (Breda 2005).
14. Relative area of caudal fin	$CFA/(SL)^2$	Large areas are important for acceleration (Oliveira et al. 2010).
15. Aspect ratio of caudal fin	$(CFH)^2/CFA$	Fish with a high aspect ratio of caudal fins are more active and continuous swimmers, in which there is a tendency for a forked caudal fin and reduced area (Keast & Webb 1966, Gatz Jr. 1979)
16. Relative area of anal fin	$AFA/(SA)^2$	Larger relative areas imply greater maneuverability and movement stabilization (Breda 2005).
17. Aspect ratio of anal fin	$(AFL)^2/AFA$	Larger aspect ratios imply a greater ability to perform faster progressive and retrograde movements (Breda 2005).
18. Relative area of pectoral fin	$PcFA/(SL)^2$	Relatively larger areas of the pectoral fin are found in slow-swimming species, which use it for maneuverability (some characids) and may also be high among fish that inhabit high-current regions such as the Siluriformes. Smaller areas are found in pelagic fish (Watson & Balon 1984).
19. Aspect ratio of pectoral fin	$(PcFL)^2/PcFA$	A high ratio indicates long, narrow pectoral fin, which is expected in fish that swim continuously and reach high speed, and consequently prefer pelagic regions (Oliveira et al. 2010).
20. Relative area of pelvic fin	$PvFA/(SL)^2$	Relatively larger areas of the pelvic fin are found in benthic fish and smaller areas in pelagic fish (Breda 2005).
21. Aspect ratio of pelvic fin	$(PvFL)^2/PvFA$	The highest values are found in pelagic fish and are related to the ability to balance. The lower values are associated with fish that prefer rocky habitats to support the body to the substrate (Gatz Jr. 1979).

model were used in ecomorphological analysis. From the PCA, the Euclidean Distance was calculated between the scores of each pair of species, on the axes that presented eigenvalues greater than the broken-stick model, according to the following mathematical expression:

$$D_{jk} = \left[\sum_{i=1}^{n}\left(X_{ij} - X_{ik}\right)^2\right]^2$$

where D_{jk} represents the Euclidean Distance between species *j* and *k*, *n* corresponds to the number of axes used to calculate the distance, and X_{ij} and X_{ik} are the values of the scores of both species on the *i* axes of the PCA (Gotelli & Ellison 2004).

Based on the Euclidean Distance calculation between the pairs of species, it was determined, for each mesohabitat, the mean Nearest-Neighbor Distance (NND), the Standard Deviation of Nearest-Neighbor Distance (SDNND) and the mean Distance to the assemblage Centroid (DC) (Winemiller 1991). The nearest neighbor of a species is the one with whom it has the lowest Euclidean Distance, and the average distance between all the closest neighbors represents the degree of packaging of the species in the ecomorphological space occupied by the assemblage. Thus, the lowest values for NND indicate assemblages with greater packaging in the ecomorphological space, so, species tending to be more similar in terms of body shape. The SDNND is a form of measurement used to represent the evenness of the species packaging in the ecomorphological space. Consequently, the lowest values are related to assemblages in which the distances between the nearest-neighbors are more uniform. The DC represents the volume of the ecomorphological space. To obtain this distance, first, the centroid of the ecomorphological space of the assemblage is determined by calculating the average of the species scores. Then, the mean of the Euclidean distances between the species to the centroid is measured. Thus, higher values indicate the occupation of larger spaces, which may be related to the greater diversity of body shapes and ecological niches explored by the assemblage. The null hypothesis that the values of ecomorphological distances are not significantly different between rural and urban mesohabitats was tested using the two-sample Welch T-test.

Because each stream is considered three times in the ANOVAs (three mesohabitats), stream identity was used as a blocking factor (additive factor) in these analyses, to control its effect on model variance, thus ensuring dependence on mesohabitats. The assumptions of normality and homogeneity of variance were evaluated and met for all ANOVAs by the Shapiro-Wilk and Levene's tests, respectively. All analysis were performed in the R program (R Core Team 2019), using the vegan package (Oksanen et al. 2019).

Results

1. *Environmental condition*

The mean values and standard deviations of the environmental variables used in this study are described in Table S1. The first two axes of the PCA explained 47.05% of the total variation of the environmental data and obtained eigenvalues greater than those generated by the broken-stick criterion. The first axis explained 27.52% and was mainly related to sand (correlation: -0.77), depth (-0.65), rock (0.61), canopy cover by riparian vegetation (0.65), and dissolved oxygen (0.73). On the other hand, the second axis represented 19.54% of the variation and was mainly related to clay (-0.71), width (0.61), and electrical conductivity (0.73). These variables were responsible for separating the collection points mainly by the land-use type, with the most of urban points positioned in the negative portion of the first axis and the positive portion of the second, while most rural points were on the positive side of the first axis and the negative side of the second (Figure 2).

According to ANOVA, carried out on the scores of the first axis of the PCA, there was a significant separation of points for the factors of land-use type (F = 65.79, P <0.01) and mesohabitat (F = 22.27, P <0.01). For the second axis, there was a significant difference for all factors, as well as for the interaction between them (land use type*mesohabitat: F = 5.92, P = 0.01), indicating that the difference between the land-use type depended on the mesohabitat. Tukey's post hoc test showed that, for the first axis, there was a separation between all mesohabitats (Run-Riffle: P = 0.01, Pool-Riffle: P >0.01, Pool-Run: P = 0.01). For the second axis, the Tukey test showed significant separation between the riffles and the pools of rural streams (rural pools – rural riffles: P >0.01), but not among the mesohabitats of urban streams.

2. *Fish assemblage*

A total of 2,195 individuals were sampled belonging to 26 species, 10 families, and six orders (Table 2). Siluriformes was the most representative order in terms of richness with 14 species (53.8%), followed by Characiformes with 9 species (34.6%). Perciformes, Cyprinodontiformes, and Gymnotiformes presented only one individual each, representing 11.5% of the total richness together. Rural streams showed greater species richness than urban streams, with 26 and 9 species, respectively (Table 2). The mantel correlogram revealed that the correlation coefficient values are not associated with the distance classes (Figure S1), indicating that the composition of the fish assemblage is not related to the watercourse distance between the collection points.

3. *Ecomorphological structure*

The first two axes of the PCA, performed on the correlation matrix of ecomorphological indices, explained 66.74% of the total variation of the data and were the only ones who obtained eigenvalues greater than those generated by the broken-stick criterion (Table 3), being then used to characterize ecomorphological diversification among the species studied (Figures 3 and 4). Axis 1 (46.05%) ordered the species, mainly by body shape and relative mouth opening height (Figure 3). Thus, species positioned at the negative portion of the axis showed laterally compressed bodies and relatively smaller mouths. On the other hand, those with scores on the positive portion have dorsoventrally depressed bodies and relatively bigger mouths. Axis 2 (20.69%) showed ecomorphological segregation related mainly to the relative width of the mouth, head length, and areas of the dorsal, caudal, pectoral, and pelvic fins (Figure 3). Therefore, species with scores positioned in the negative portion of the gradient tended to have relatively wider mouths, while the relative length of the head and the relative fins area increased towards the positive portion of the axis.

The gradient formed by the two axes of the PCA showed the morphological diversity of the fish species, which presented different trends of occupation in the mesohabitats (Figure 4). In the rural riffles,

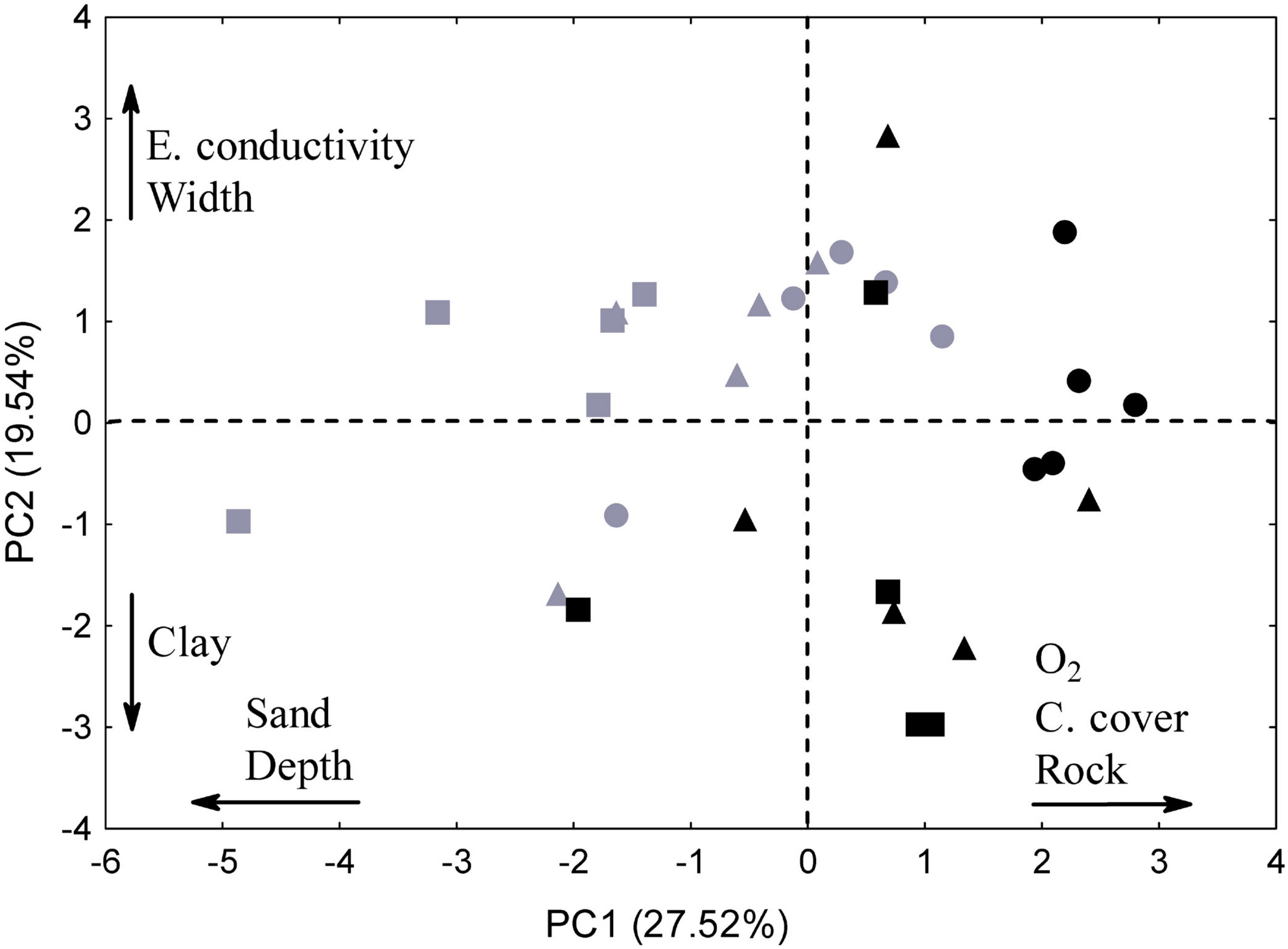

Figure 2. Principal Component Analysis (PCA) based on the environmental variables (C. cover = canopy cover by riparian vegetation and **E. conductivity** = electrical conductivity) collected in the mesohabitats (riffles = circles, runs = triangles and pools = squares) of five rural streams (black symbols) and five urban streams (gray symbols) of the Pirapó river basin.

there was a tendency of species that were positioned in the positive portion of the first axes and the negative portion of the second axes (Figure 4a); In the rural pools, the tendency was of species that were positioned in the negative portion of the first axes and the positive portion of the second axes (Figure 4c); in rural runs, the trend was less evident, but it was similar to the riffles (Figure 4b). On the other hand, practically the same species occupied the three urban mesohabitats (Figure 4d-f). These different trends influenced ecomorphological distances, increasing the morphological similarity in rural mesohabitats compared to urban ones (Table 4). According to ANOVAs, performed on ecomorphological distances, only the Nearest-Neighbor Distance (NND) showed a significant difference, with significance in the interaction between the factors (land-use type*mesohabitat: F = 4.29, P = 0.03). Tukey's post hoc test showed that the significant difference occurred between rural and urban streams, for runs and pools (Table 4).

Discussion

The results show that the land-use type affects the environmental variables and the fish assemblage in the mesohabitats of streams, with the urban environment presenting less preserved environmental conditions and a decrease in species richness. Regarding ecomorphological distances, mesohabitats from urban streams showed assemblages with less morphological similarity between species (i.e. higher values for NND) without significant changes in the volume of ecomorphological space (DC) and in the evenness of the species packaging in the ecomorphological space (SDNND).

In streams, the hydrological and geomorphological differences among mesohabitats influence the distribution of fish species in the channel (Rezende et al. 2009, Alexandre et al. 2010, Wolff & Hahn 2017, Huang et al. 2019). This distribution is associated with the morphology of the species, mainly with the body shape (Gaston et al. 2012). Here, this trend has been corroborated for the mesohabitats of rural streams. In riffles, most species have a dorsoventrally depressed body and well-developed caudal peduncle (e.g., *Imparfinis mirini*, *Phenacorhamdia tenebrosa*, *Hypostomus ancistroides,* and *Hypostomus strigaticeps*); in pools, most species presented a laterally compressed body (e.g., *Astyanax lacustris, Astyanax fasciatus*, *Astyanax paranae* and *Corydoras aenus*); in runs, despite a high relative abundance of *I. mirini*, *A. fasciatus*, *A. lacustris* and *C. aenus*, there was a greater

Table 2. Taxonomic classification, species code, and abundance of the fish species captured in mesohabitats of rural and urban streams from the Pirapó River basin, Paraná State, Brazil.

Taxonomic classification	Code	Rural			Urban		
		Riffle	Run	Pool	Riffle	Run	Pool
OSTEICHTHYES							
CHARACIFORMES							
Characidae							
Astyanax lacustris (Lütken, 1875)	Alac	1	14	19			
Oligosarcus paranensis Menezes & Géry, 1983				1			
Piabarchus stramineus (Eigenmann, 1908)	Pstr	6		1			
Piabina argentea Reinhardt, 1867	Parg	11	3	8	11	1	1
Psalidodon bockmanni (Vari & Castro, 2007)	Pboc			7			
Psalidodon aff. fasciatus (Cuvier, 1819)	Pfas	1	17	14		4	2
Psalidodon aff. paranae (Eigenmann, 1914)	Ppar		6	14			
Erythrinidae							
Hoplias aff. malabaricus (Bloch, 1794)				1			
Crenuchidae							
Characidium aff. zebra Eigenmann, 1909	Czeb	9	4	1			
SILURIFORMES							
Callichthyidae							
Corydoras aeneus (Gill, 1858)	Caen	2	11	12			
Loricariidae							
Hisonotus francirochai (Ihering, 1928)			1				
Hypostomus ancistroides (Ihering, 1911)	Hanc	21	2	1	38	12	4
Hypostomus hermanni (Ihering, 1905)	Hher	10	2	1			
Hypostomus cf. nigromaculatus (Schubart, 1964)	Hnig		3	2	83	22	35
Hypostomus cf. strigaticeps (Regan, 1908)	Hstr	14	4		2	2	
Rineloricaria latirostris (Boulenger, 1900)		1	1				
Heptapteridae							
*Cetopsorhamdia ihering*i Schubart & Gomes, 1959	Cihe	14	4		25	2	
Imparfinis borodini Mees & Cala, 1989		1					
Imparfinis mirini Haseman, 1911	Imir	55	30	6		2	
Pimelodella avanhandavae Eigenmann, 1917				1			
Pimelodella gracilis (Valenciennes, 1835)				2			
Phenacorhamdia tenebrosa (Schubart, 1964)	Pten	24	3				
*Rhamdia quelen (*Quoy & Gaimard, 1824)	Rque	9	7	5	25	21	16
CICHLIFORMES							
Cichliformes							
Geophagus iporangensis Haseman, 1911	Gipo		1	10			
CYPRINODONTIFORMES							
Poeciliidae							
Poecilia reticulata Peters, 1859	Pret	1		2	338	755	369
GYMNOTIFORMES							
Gymnotidae							
Gymnotus inaequilabiatus (Valenciennes, 1839)	Gina	3					

richness of species with dorsoventrally depressed bodies (Table 1). This difference in the body shape of most species between riffles, runs, and pools resulted in lower NND values compared to urban ones, i.e. greater morphological similarity in the assemblage of each mesohabitat.

The high current velocity presented in riffles and runs favors species with a dorsoventrally depressed body (Oliveira et al. 2010, Gaston et al. 2012, Bower & Piller 2015, Bower & Winemiller 2019) because this body shape decreases the high energy cost associated with maintaining the position in the water column in fast waters, due to the hydraulic drag exercised over a large body surface area (Webb 1984, 1988). Also, the well-developed caudal peduncle and larger areas of the pectoral fins allow the body to stabilize on the rocky substrate, as well as movement over short distances

Table 3. Eigenvectors, eigenvalues of the axes, eigenvalue predicted by the broken-stick model, and the percentage of explanation of the first two axes of the PCA based on the 21 ecomorphological indices. The main variables responsible for explaining the species ordering pattern are highlighted.

Ecomorphological indices	**PC1**	**PC2**
Compression index	**-0.31**	0.05
Depression index	0.14	0.03
Relative length of caudal peduncle	0.26	0.07
Relative height of caudal peduncle	**0.28**	-0.11
Relative width of caudal peduncle	-0.20	-0.12
Relative length of head	0.03	**0.42**
Relative height of head	0.26	0.18
Relative width of head	0.22	-0.08
Relative height of mouth	**0.30**	-0.03
Relative width of mouth	0.10	**-0.29**
Vertical eye position	0.27	-0.13
Relative area of eye	**-0.27**	0.11
Relative area of dorsal fin	0.12	**0.40**
Relative area of caudal fin	0.02	0.31
Relative area of anal fin	-0.24	0.07
Relative area of pectoral fin	0.15	0.37
Relative area of pelvic fin	0.24	0.27
Aspect ratio of caudal fin	-0.23	-0.05
Aspect ratio of anal fin	-0.23	0.06
Aspect ratio of pectoral fin	-0.21	0.29
Aspect ratio of pelvic fin	-0.12	0.26
Eigenvalue	9,67	4,34
Predicted eigenvalue: broken strick	3,92	2,81
Variance explained (%)	0,46	0,21

in environments with high current velocity (Oliveira et al. 2010). In contrast, laterally compressed bodies are associated with species that inhabit deeper environments and with lower current velocity (Oliveira et al. 2010, Gaston et al. 2012, Bower & Winemiller 2019), because this body shape provides greater maneuverability for species (Werner 1977, Gerstner 1999), allowing efficient exploration of more structured lentic environments. The absence of a significant difference in the NND between rural and urban riffles may indicate that this mesohabitat presents greater environmental pressures on the fish assemblage than the others, selecting the morphologically similar species regardless of land-use types. According to Bower & Winemiller (2019), the high velocity of the water in the riffles function as universal environmental filters for fish species, producing similar assemblage trait in this mesohabitat.

Contrary to the rural environment, and according to what we expected, mesohabitats in urban streams showed a significant decrease in the morphological similarity of the fish assemblage. In our view, this result was due to two factors. First, there was a loss of morphologically similar species in urban mesohabitats, in such a way that only the most distinct species remained. The environmental changes found in urban streams, such as the decrease in canopy cover by riparian vegetation and dissolved oxygen, and the increase in electrical conductivity and bed silting, are characteristic of urban streams worldwide and have been associated with the loss of endemic species and dominance by exotic ones (Walters et al. 2003). Our results show a significant decrease in endemic species and the dominance of *P. reticulata* in all mesohabitats, which is a species that was introduced in many neotropical streams and became dominant in degraded environments (Araujo et al. 2003, Vieira & Shibatta 2007, Cunico et al. 2012). According to Inward et al. (2011), assemblages exposed to environmental conditions intensely altered by anthropogenic activities tend to have species progressively removed from the ecomorphological space, until only those more distinct from each other remain. This decrease in functional redundancy is one of the main consequences of the simplification of ecosystems by human activities, leading to significant losses in the resilience of assemblages in the face of new disturbances because when only the most distinctly functional species remain, the disappearance of any one of them leads to definitive loss of a function exercised by the assemblage (Laliberté et al. 2010, Bruno et al. 2016).

Second, the species that resisted environmental changes and remained in urban streams showed no difference in composition among mesohabitats. Thus, few species dominated the three urban mesohabitats, being they *Poecilia reticulata, Hypostomus nigromaculatus*, *H. ancistroides* and *Rhandia quelen* (Table 2). The homogenization of species among urban mesohabitats resulted in a significant decrease in morphological similarity (i.e., increase in NND) and similar values of the volume of ecomorphological space compared to rural mesohabitats.

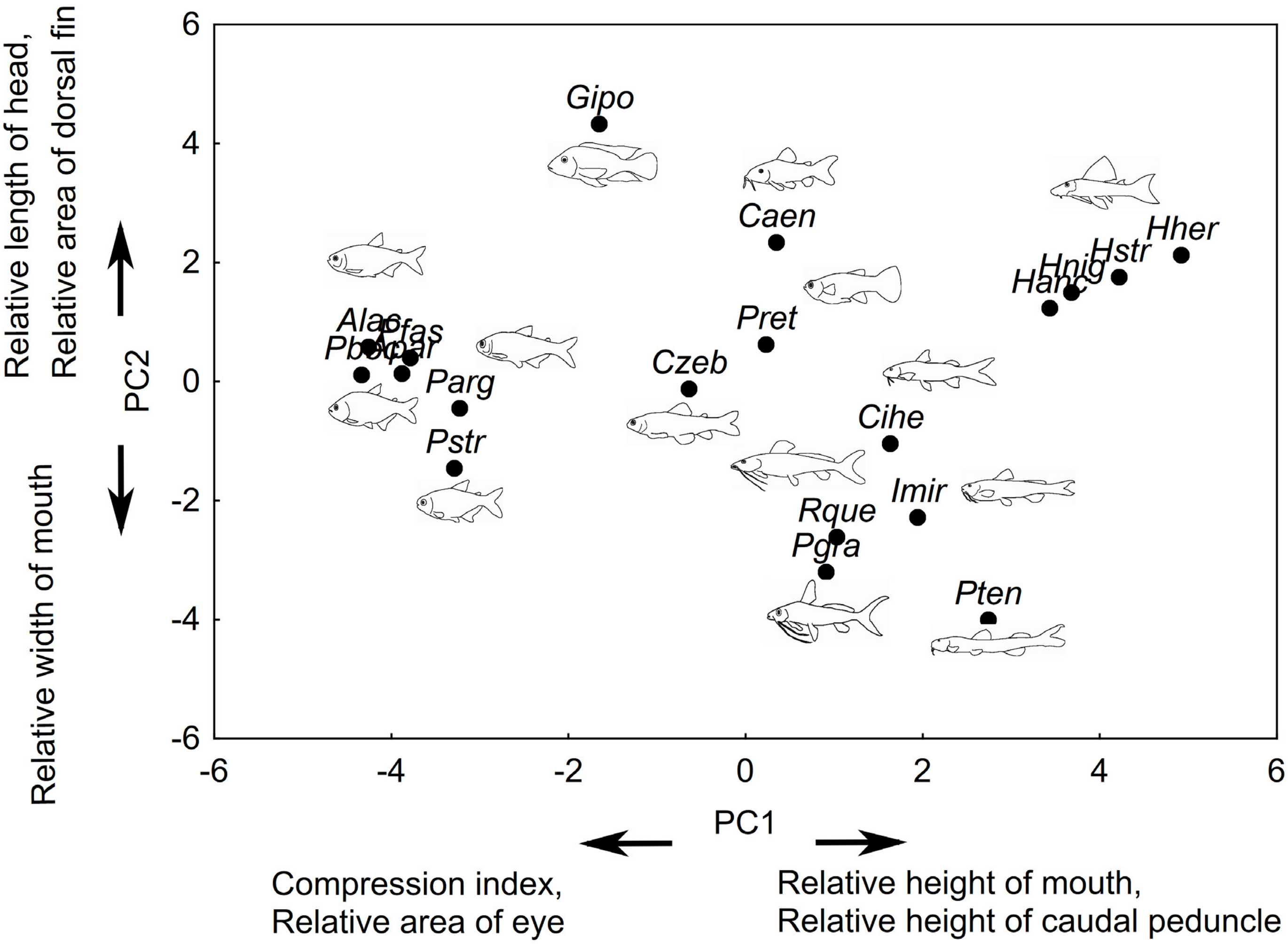

Figure 3. Principal Component Analysis (PCA) based on 21 ecomorphological indices calculated for 19 species. The main variables responsible for explaining the ordering pattern are highlighted in each axis. The species codes are described in Table 2. One species of each genus was designed to improve the visualization of the species' body shape in the ecomorphological space.

This low species turnover among mesohabitats was shown by Teresa & Casatti (2012) in deforested streams and, as in this study, was the cause of the increase in the functional diversity of the fish assemblage. Here, the homogenization of species may have been caused by changes in environmental variables in urban streams. Although urban mesohabitats present hydrological and geomorphological differences as in rural areas, there was a large proportion of sand in the substrate. As mentioned earlier, the sand can bury the rocky substrate, homogenizing the stream (Walters et al., 2003). However, the silting of the channel was not of great importance in the restructuring of the fish assemblage, since all urban streams presented homogeneous assemblages among the mesohabitats, not just those silted up. The cause of species homogenization among mesohabitats was the presence of civil construction waste (such as bricks and tiles), as we observed, during the collections, these artificial substrates served as hiding places for species of the genus *Hypostomus* (*H. ancistroides* and *H. nigromaculatus*) in the pools.

In summary, we can conclude that the urban environment leads to the loss of morphologically similar fish species in the mesohabitats, with only a few functionally distinct species remaining. Although no function played by the fish assemblage has disappeared in urban mesohabitats, the loss of morphological similarity may have future consequences for these streams. As mentioned earlier, this response of species to environmental changes has led to the loss of the assemblage's resilience in the face of future disturbances. Therefore, management projects must be carried out in such ecosystems with the aim of recovering lost species, and, thus, restore the resilience of the fish assemblage.

Supplementary Material

The following online material is available for this article:

Figure S1 - Mantel correlation with the fish assemblage composition and hydrological distance matrices between the collection points. Six distance classes were selected, which presented p values >0.05, indicating that the fish assemblage composition is not spatially structured.

Table S1 - Mean values and standard deviations of the environmental variables measured in the mesohabitats (Me: Ri, riffles; Ru, runs; Po, pools) of streams (Que, Queçaba; Rom, Romeira; Atl, Atlântico; Ros, Roseira; Lom, Lombo; Man, Mandacaru; Mio, Miosótis; Gua, Guaiapó; Mar, Maringá; Mor, Morangueira) in the Pirapó River hydrographic basin. Abbreviations of environmental variables: O2, Dissolved oxygen;

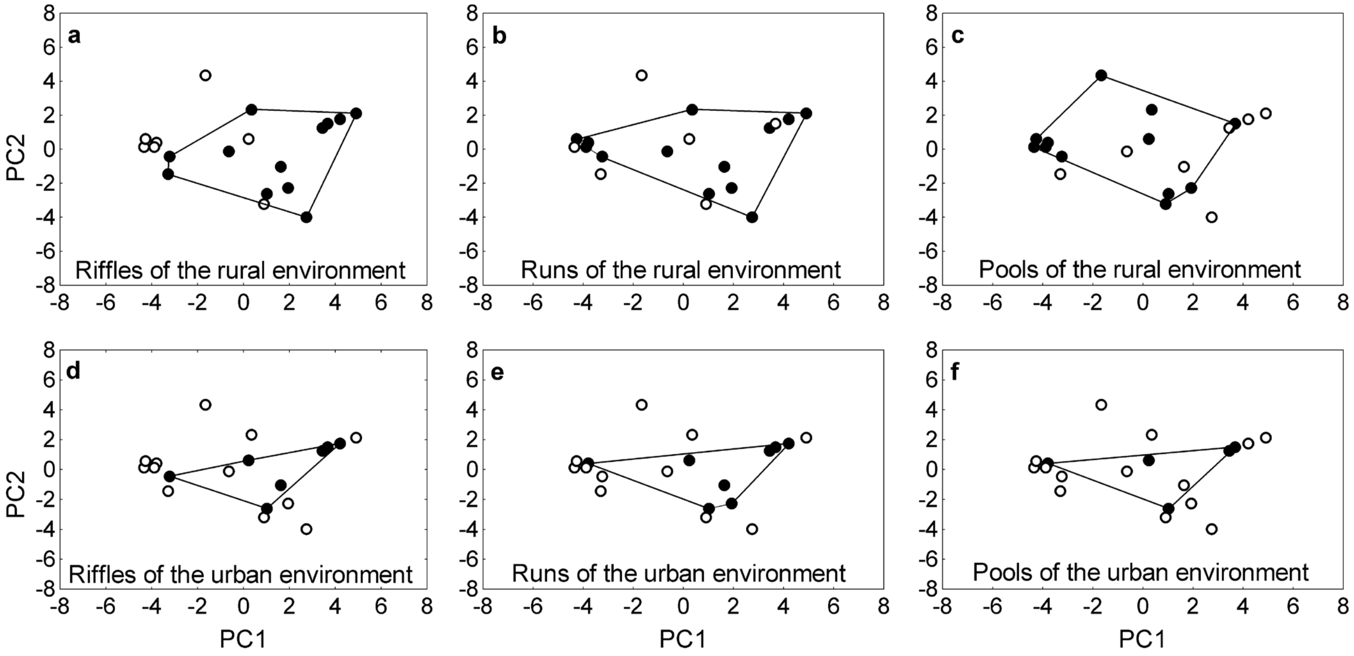

Figure 4. Plots of the first two axes of the Principal Component Analysis based on the 21 ecomorphological indices, showing the species occupation in the ecomorphological space of the mesohabitats of rural (a-c) and urban (d-f) environments. The species collected in each mesohabitat are highlighted (filled symbols) and delimited.

Table 4. Ecomorphological distance values (**NND** = Nearest-Neighbor Distance, **SDNND** = Standard Deviation of the Nearest-Neighbor Distance and **DC** = Distance to the assemblage Centroid) and Welch's T-test (T and P) for each mesohabitat (**Ri** = riffles, **Ru** = runs, and **Po** = pools) of urban and rural streams. For some mesohabitats (X) it was not possible to calculate ecomorphological distances, due to the species richness being less than three.

Streams		**NND**			**SDNND**			**DC**	
Rural	**Ri**	**Ru**	**Po**	**Ri**	**Ru**	**Po**	**Ri**	**Ru**	**Po**
Queçaba	1.57	2.90	1.17	0.80	0.38	1.04	2.88	2.60	2.99
Romeira	1.60	1.35	1.25	0.82	1.40	1.61	1.69	3.43	3.20
Atlântico	0.87	1.93	1.55	0.37	1.51	1.31	3.39	2.10	3.08
Roseira	1.92	1.25	1.19	1.64	1.68	1.77	1.88	1.44	1.61
Lombo	1.27	1.56	X	0.39	1.04	X	2.23	2.99	X
Mean	**1.44**	**1.80**	**1.29**	**0.80**	**1.20**	**1.43**	**2.41**	**2.51**	**2.72**
Urban									
Mandacaru	3.41	3.41	3.56	0.13	0.13	0.33	2.26	2.26	2.79
Miosótis	2.20	2.11	3.41	0.74	1.29	0.13	1.87	2.44	2.26
Guaiapó	2.29	3.56	X	0.92	0.40	X	2.12	2.49	X
Maringá	1.25	1.99	1.82	0.84	1.72	1.69	1.98	2.86	2.17
Morangueira	1.58	3.28	3.28	1.57	0.04	0.04	2.11	2.13	2.13
Mean	**2.15**	**2.87**	**3.02**	**0.84**	**0.72**	**0.55**	**2.07**	**2.44**	**2.34**
P	*0.23*	*0.03*	*>0.01*	-	-	-	-	-	-

Cond, Electric conductivity; Wid, width; Dep, depth; Vel, current velocity; Can, canopy cover by riparian vegetation; Floo, flooded vegetation; San, sand; Civ, civil construction waste; Cla, clay; Roc, rock.

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Author Contributions

Leonardo Antunes Pessoa: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Matheus Tenório Baumgartner: Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intelectual content.

Marcelo Percilio Santana Junior: Contribution to data analysis and interpretation; Contribution to manuscript preparation.

João Paulo Alves Pagotto: Substantial contribution in the concept and design of the study; Contribution to critical revision, adding intelectual content.

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Erivelto Goulart: Substantial contribution in the concept and design of the study; 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.

Ethics

The collects were made under the license of the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBIO) nº. 25560-1.

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Thematic Review

Searching for synthetic mechanisms on how biological traits mediate species responses to climate change

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Abstract: Climate change will likely be the most significant challenge faced by species in this century, and species' ability to cope with climate change depends on their life history and ecological and evolutionary traits. Understanding how these traits mediate species' responses is beneficial for identifying more vulnerable species or prone to extinction risk. Here, we carried out a literature review describing how four traits commonly used in vulnerability assessments (i.e. clutch size, diet breadth, dispersal ability, and climatic tolerance) may determine species vulnerability. We also portray the possible mechanisms that explain how these traits govern species responses to climate change. The literature suggests different mechanisms operating for the evaluated traits. The mechanism of response to climate change differs between species inhabiting tropical and temperate regions: while species from the temperate areas may respond positively to temperature rise, tropical species may be severely affected. Since ectotherms depend on environment temperature, they are more sensitive and present different response mechanisms from endotherms.
Keywords: *Global warming; extinction risk; phenology; physiology; species traits.*

Em busca de mecanismos sintéticos sobre como os atributos biológicos mediam as respostas das espécies às mudanças climáticas

Resumo: A mudança climática provavelmente será o maior desafio enfrentado pelas espécies neste século e a capacidade das espécies em lidar com a mudança climática depende de seus próprios atributos de história de vida, ecológicos e evolutivos. Entender como esses atributos mediam as respostas das espécies é extremamente útil para identificar espécies que são mais vulneráveis ou sujeitas ao risco de extinção. Aqui, realizamos uma revisão da literatura com foco na descrição de como quatro atributos comumente usados em avaliações de vulnerabilidade (tamanho da ninhada, amplitude da dieta, capacidade de dispersão e tolerância climática) podem realmente determinar a vulnerabilidade das espécies. Também retratamos os possíveis mecanismos que explicam como esses atributos governam as respostas das espécies à mudança climática. A literatura sugere diferentes mecanismos operando para os atributos avaliados. O mecanismo de resposta à mudança climática difere entre as espécies que habitam as regiões tropicais e temperadas: enquanto as espécies das regiões temperadas podem responder positivamente ao aumento da temperatura, as espécies tropicais podem ser severamente afetadas. Como os ectotérmicos dependem da temperatura ambiente, eles são mais sensíveis e apresentam mecanismos de resposta diferentes dos endotérmicos.
Palavras-chave: *Aquecimento global; risco de extinção; fenologia; fisiologia; atributos das espécies.*

Introduction

Climate change will likely be the most significant challenge faced by species this century. The observed effects include changes in distribution areas, phenology, morphology, demography, and abundance (Parmesan and Yohe 2003; Parmesan 2006; Lane et al. 2012). Species ability to respond to climate change depends on their life-history traits (Végvári et al. 2010; Angert et al. 2011; Pacifici et al. 2017), which can help predict species that will be more vulnerable and direct conservation efforts (Foden et al. 2013).

In this sense, the use of trait-based Climate Change Vulnerability Assessments (CCVAs) has become popular in studies that assess climate change impact on species vulnerability (Foden et al. 2018). In the context of CCVAs, the term “trait” refers to a wide range of species characteristics (such as diet breadth and climatic tolerance) instead of referring to specific features of an individual (*sensu* Violle et al. 2007). Trait-based CCVAs combine scores based on exposure to climate change (extrinsic factors) with biological characteristics of species (intrinsic factors), which define their sensitivity and adaptive capacity to obtain a general measure of vulnerability (Pacifici et al. 2015).

Vulnerability is assessed based on these three components: exposure, sensitivity, and adaptive capacity, so that species with high exposure, high sensitivity, and low adaptive capacity will be the most vulnerable to climate change (Dawson et al. 2011; Foden et al. 2013). Exposure is determined by the rate and magnitude of climate change within the species’ distribution area. Sensitivity is characterised by the ability to tolerate climate change and is generally associated with physiological tolerance and habitat specialisation. Adaptive capacity refers to the ability of a given species to deal with climate change, whether adapting to new local conditions or dispersing to more suitable areas (Dawson et al. 2011).

Despite the importance of biological traits in determining species vulnerability, there is no agreement on which traits should be used in assessments. Their selection depends on data availability and the opinion of experts (Foden et al. 2013, 2018). Biological traits may help identify species with higher extinction risk (Mckinney 1997; Purvis and Hector 2000). However, species responses depend on the type of threat they are exposed to (González-Suarez et al. 2013). Species that present larger body size is more threatened by hunting, while smaller and ecologically specialised species are more threatened by habitat loss and fragmentation (Owens and Bennett 2000; González-Suarez et al. 2013).

Under the threat of climate change, biological traits might play a fundamental role in species responses, influencing their vulnerability (Jiguet et al. 2007; Angert et al. 2011; Estrada et al. 2015). Clutch size is strongly influenced by climatic variables (Jetz et al. 2008), and species may present rapid physiological adjustments of this trait in response to climatic changes (Baker 1995; Coe and Rotenberry 2003). Species that reproduce frequently or prematurely, with high fecundity, should have greater opportunities to colonise new environments (Angert et al. 2011). Species with generalist diets can change their feeding habits to other resources when climate affects the availability of preferred items (Rubolini et al. 2003; Bojarska and Selva 2012) and, consequently, they might have a higher ability to change their distributions to follow suitable climatic conditions (Angert et al. 2011). Dispersal ability is a crucial trait that allows species to change their distribution areas to follow a suitable climate. Species with higher dispersal ability might respond more quickly to climate change, facing lower extinction risk (Pöyry et al. 2009; Corlett and Westcott 2013). Species that can physiologically tolerate higher climatic variation and live in environments where temperatures are far from their upper thermal limit will be more likely to persist under climate change (Deutsch et al. 2008; Huey et al. 2012). There is a growing interest in using biological traits to assess species vulnerability in response to climate change (Gardali et al. 2012; Foden et al. 2013; Garcia et al. 2014; Böhm et al. 2016; Reside et al. 2016; Borges et al. 2019). However, potentially important traits from some taxa are still frequently unavailable, which leads to the use of morphological proxies, measurements from congeneric species or the knowledge of experts (Foden et al. 2013, 2018).

Identifying the most informative traits and responding to climate change is a priority if we want to assess the vulnerability of different species groups. However, a study showed that less than half of the studies that evaluated the relationship between traits and changes in species distributions have specified hypothesis for the ecological processes involved in the relationship (Estrada et al. 2016). To advise appropriate conservation measures, it is essential to explain the reasons for choosing traits and the specific mechanisms underlying climate change impacts on species of interest (Foden et al. 2018).

We did a literature review to understand how four traits (clutch size, diet breadth, dispersal ability and climatic tolerance) might determine species vulnerability. We also aimed to describe the possible mechanisms that explain how traits influence species responses to climatic changes. Specifically, our goals were: 1) to verify whether it is possible to use the four chosen traits to understand the mechanisms underlying the impacts caused by climate change based on the ecology literature produced so far, and 2) to present and explain the main mechanisms found. Including details regarding these mechanisms will help substantiate trait choice and broaden the discussion about future conservation strategies of assessed species.

Material and Methods

We searched the literature for studies that evaluated variation in the four traits mentioned earlier in response to recent climate change regarding organisms from any taxa within any level (population, community, and ecosystem). We chose these four traits because they are commonly used in CCVAs (Gardali et al. 2012; Reside et al. 2016; Borges et al. 2019) and are more widely available in the literature. As the study’s objective was to present a broad discussion for each trait, more traits would excessively increase the number of pages in the study. The search was carried out in July 2019 in the Thomson Reuters ISI Web of Science online database. It included articles published between 1945 and 2019, using the following search terms: (“trait” OR “clutch size” OR “diet” OR “dispersion” OR “climatic tolerance” OR “thermic tolerance” OR “heat tolerance”) AND (“climate change” OR “global warming” OR “temperature increase”).

We excluded studies that: (1) belonged to Web of Science categories not related to ecology (*e.g.* agronomy, veterinary medicine, tropical medicine), (2) did not relate (directly or indirectly) possible trait changes to climate change, and (3) did not present any explanation (through empirical data) to the mechanisms involved in the observed responses (*e.g.* changes in distribution areas, phenology and abundance). Studies cited by the articles obtained in our search were also included in our synthetic review if they fulfilled the requirements. The search generated a total of 1164 articles. After the exclusions following the criteria mentioned above, 197 articles were evaluated.

Results and Discussion

1. Clutch size

Clutch size is one of the best-studied life-history traits in birds, and its variation throughout the latitude gradient is well known, with larger clutch size in higher latitudes (Lack 1947; Skutch 1949; Ashmole 1963; Ricklefs 1980; Evans et al. 2005; Jetz et al. 2008). As expected, studies that assess clutch size are focused on birds and have been carried out mainly in the temperate region (Table 1). Birds that inhabit temperate and tropical areas adopt different life-history strategies to respond to climate change through other mechanisms (Table 1).

Clutch size is related to species fecundity; thus, it indicates the population ability to recruit. Species with smaller clutch size present low reproductive potential and consequently a slower response to risk factors, which would make them more vulnerable to decline and extinction (Smith and Quin 1996; Pimm 1991; Hero et al. 2005). On the other hand, species with larger clutch size may present a higher ability to respond to climate change, for they present shorter life cycles (Mckinney 1997). Larger clutch size is related to the probability of occupying broader geographic areas, higher dispersal ability and higher ability to colonise changing habitats and explore new opportunities (Duncan et al. 2001; Hero et al. 2005).

Some studies have found a significant relationship between clutch size and environmental variables. In temperate regions (with severe winter), studies with birds have shown that temperature increases have led to larger clutch sizes (Jarvinen 1996; Przybylo et al. 2000; Møller 2002; Husek and Adamík 2008; Table 1). The mechanism involved in this physiological adjustment seems to be related to resource availability. In these regions, the cold climate imposes food shortage (Jarvinen 1986, 1996), and higher temperatures lead to higher food availability, allowing species to have a higher number of broods. Annual variation in temperature, which reflects the seasonality of resources, was the most crucial variable to explain clutch size in a global assessment (Jetz et al. 2008). For example, the clutch size of owls in Finland is strongly determined by the abundance of their prey (voles): warmer years, with thinner snow cover, favour a higher abundance of voles, allowing larger clutch size (Lehikoinen et al. 2011). Such a positive relationship between food availability and mean clutch size in birds is well-known (Lack 1947; Price 1985; Gibbs and Grant 1987). Correlation between clutch size and climatic variables was also confirmed for other groups such as lizards (Smith et al. 1995; Abell 1999) and butterflies (Karlsson and Wiklund 2005; Saastamoinen 2007). In this sense, for species that live in temperate regions, where the cold is a limiting factor for population regulation, climate change may positively impact environmental conditions, increase resource availability, and allow larger clutch size.

In the tropical region, resource seasonality is less intense, and the reproductive season is longer, which allow species to attempt reproduction more frequently per season (Martin, 1996). A higher number of attempts to reproduce may lead to smaller clutch size, as the parents need to save energy to invest in the next clutch (Slagsvold 1984; Farnsworth and Simons 2001). This seems to be a good strategy in the tropics since nest predation is higher than in the temperate region, which would allow the spread of predation risk in numerous reproduction attempts (Cody 1966; Kulesza 1990; Martin 1995; Griebeler et al. 2010; Table1). If clutch size depends on nest predation rate, as proposed by Skutch (1949), if larger broods attract more predators, natural selection will favour smaller clutch sizes in the tropics (Martin et al. 2000). Considering that, a possible consequence of climate change to species that inhabit the tropics is that temperature increase and rainfall decrease might shorten the reproductive season, leading to a reduction in the number of reproduction attempts, which could force species to compensate by increasing clutch size (Lovette and Fitzpatrick 2016).

Table 1. Possible mechanisms that explain how clutch size may influence species responses to climate change and their respective studies.

Pattern	Mechanism	Reference	Taxon	Location
In temperate and boreal regions, temperature increase may favour larger clutches	In cold regions, temperature increase leads to abundance of feeding resources	Jarvinen, 1996	Bird	Finland
		Przybylo et al., 2000	Bird	Sweden
		Moller, 2002	Bird	Denmark
		Husek and Adamik, 2008	Bird	Czech Republic
In the tropics, temperature increase and rainfall decrease may shorten reproductive season, decreasing the number of reproduction attempts and consequently reproductive success	In the tropics, reproductive season is longer and species may have more clutches with fewer eggs to spread predation risk, which is high.	Skutch, 1949	Bird	Central America
		Cody, 1966	Bird	Global
		Slagsvold, 1984	Bird	Norway
		Kulesza, 1990	Bird	Americas
		Martin, 1995	Bird	North America
		Martin, 2000	Bird	America
		Farnsworth and Simons, 2001	Bird	Theoretical model
		Griebeler et al., 2010	Bird	Theoretical model
Aridity may lead to reduction of clutch size	Lack of water may jeopardise egg production	Grant et al., 2000	Bird	Galápagos islands
		Coe and Rotenberry, 2003	Bird	Mojave desert
In the tropics, temperature increase may reduce viability of the first eggs	Temperatures higher than 24-26ºC induce embryonic development before incubation	Deeming and Ferguson, 1992	Bird and reptile	Theoretical model
		Stoleson, 1999	Bird	Venezuela
		Stoleson and Beissinger, 1999	Bird	Venezuela

That would represent a risk for species since the tropics nest predation rate is relatively high, reaching 80-90% (revised by Stutchbury and Morton 2001).

In regions where climate change will cause temperature increase and significant rainfall decrease, making the areas arider, species tend to reduce the clutch size (Grant et al. 2000; Coe and Rotenberry 2003; Table 1). A study in the California desert has shown that, in territories that received water supplementation (treatment), a desert sparrow had a significantly larger clutch size than in non-supplemented territories (control) (Coe and Rotenberry 2003). This result shows that environment variables have an indirect effect (regulating food availability) and act directly on physiology, so that supplemented females can allocate more water to egg production. During the reproductive period, females need a significantly higher amount of water to produce eggs since they contain a high percentage of water (Bartholomew and Cade 1963; Reynolds and Waldron 1999).

Another hypothesis used to explain smaller clutch size in the tropical region than the temperate region is the egg-viability hypothesis (Stoleson and Beissinger 1999; Table 1). According to this hypothesis, in the tropics, where the temperature is higher, extended exposure of the eggs to temperatures higher than 24-26ºC (physiological zero) may trigger embryonic development even when the eggs are not incubated. Such premature development of the embryos below optimum incubation temperature (36-38ºC) results in abnormal growth of some tissues and consequent embryo death (Deeming and Ferguson 1992; Stoleson 1999). Therefore, birds that live in the tropics may lay smaller clutches to start active incubation earlier to keep the viability of the first eggs instead of waiting until many eggs are laid (Stoleson and Beissinger 1999). Based on this hypothesis, in a scenario of temperature increase, it is expected that species initiate incubation earlier and earlier to avoid loss of the first eggs, which can lead to smaller clutch size, since premature incubation or contact with the eggs may interrupt follicular growth and egg-laying (Haywood 1993).

Available evidence shows that species can adjust to climate change through phenotypic plasticity instead of altering their genetic constitution through microevolutionary adaptation (Gienapp et al. 2008). There seems to be low, or no additive genetic variation to clutch size and most intrapopulation variation is due to transitory environmental effects (Gibbs 1988). Species may present fast physiologic responses adjusting the clutch size to environmental changes (Gibbs 1988; Baker 1995; Coe and Rotenberry 2003). For example, the mean clutch size for sparrows in New York was 4.7 eggs, while in Costa Rica, it was two eggs (reviews in Baker 1995). When sparrows captured in Costa Rica were raised in aviaries in New York, their clutch size was 3.50 (+ 0.46) eggs in the first year and 4.62 (+ 0.55) in the second year. Sparrows from New York raised in nearby aviaries under the same feeding conditions, and same pressures had a mean clutch size of 4.89 (+ 0.48) eggs (Baker 1995). This example shows that species do not need several generations to adjust their clutch size to climatic conditions. Therefore, negative impacts on species that will be forced to reduce their clutch size, such as low population recruitment, could occur at a somewhat accelerated pace, thus increasing their vulnerability.

2. *Diet breadth*

In general, studies that assess climatic effects on diet are not focused on a specific taxon, but there is a prevalence of studies with vertebrates living in the temperate region (Table 2). Diet is an important trait that summarises distinct morphological, physiological and behavioural characteristics of a given organism, determining how it interacts with the biotic and abiotic environments (Donnell et al. 2012; Abrahamczyk and Kessler 2014). It is expected that species with specialised diets present narrow niches, low local abundance and restricted geographic distribution (Mckinney 1997). On the other hand, generalist species have flexible behaviour and can change their feeding habits to adapt to changes in resource availability (O'Donoghue et al. 1998). Therefore, the diet breadth of a given species may influence its extinction risk

Table 2. Possible mechanisms that explain how diet may influence species responses to climate change and their respective studies.

Pattern	Mechanism	Reference	Taxon	Location
Climate change may alter resource availability to species in the environment.	Generalists may increase the diversity of ingested items to include new options when their preferred resources are scarce	Folks et al. 2014	Mammal	Texas, USA
		Gray et a. 2016	Mammal	Australia
		Robinson et al. 2018	Mammal	California, USA
		Rubolini et al. 2003	Bird	Northern Italy
		Bojarska and Selva 2012	Mammal	Holarctic
	There might be population decline when preferred food items are scarce	Pearce-Higgins et al. 2010	Bird	United Kingdom
		Fancourt et al. 2018	Mammal	Tasmania
		Víkingsson et al. 2014	Aquatic mammal	Iceland coast
Climate change may force species to alter their phenology and distribution	Species with more flexible diets can change their phenology more easily to follow modifications induced by the climate.	Altermatt 2010	Lepidoptera	Central Europe
	Generalist species can easily change their distribution areas following climate change	Braschler and Hill 2007	Lepidoptera	Great Britain
		Angert et al. 2011	Bird	North America
Alter omnivore diets	In higher temperatures, animals increase herbivory to maximise energy intake	Floeter et al. 2005	Sea fish	Atlantic ocean
		Boersma et al. 2016	Copepoda	North Sea
		Carreira et al. 2016	Tadpole	Iberian Peninsula
		Espinoza et al. 2004	Reptile	South America
		Clarke and O'Connor 2014	Bird and mammal	Global

(Boyles and Storm 2007). Species with a more specialised diet are associated with higher probabilities of negative response to climate change (Pacifici et al. 2017). We will discuss three main mechanisms species may respond to climate change through their diets (Table 2).

Climate change may affect the availability of feeding resources. In regions where these resources will decrease, species with specialised diets will become more sensitive, presenting a higher extinction risk than generalist species (Chessman 2013). Species with broader diet breadth can avoid hunger by changing their diet to the available food item during adverse climatic conditions (Brändle et al. 2002). Such plasticity in the diet is a mechanism that has allowed species to deal with climate-related fluctuations in availability and abundance of resources (Furness 1996; Ancona et al. 2012). Generalist species can increase diet diversity in response to unfavourable changes in the weather when their preferred resources are scarce. They are led to supplement their diets with available resources at the moment (Folks et al. 2014; Gray et al. 2016; Table 2). For example, temperature increase in North Pacific waters alters the availability of sea lion preys, making them change their diet, increasing the diversity of consumed preys (Robinson et al. 2018). In Northern Italy, owls have become more generalist under adverse climatic conditions: increased rainfall and decreased temperature increased the breadth of owls' diets. (Rubolini et al. 2003). Alternatively, species with specialised diets may not respond to resource fluctuation and therefore experience higher extinction risk. For mountain birds, temperature increase can result in population decrease caused by the abundance of preys, insects from the Tipulidae family adapted to cold weather (Pearce-Higgins 2010). Temperature and rainfall increase during winter caused a significant decrease in the Eastern quoll population due to a reduction in the abundance of moth larvae (Fancourt et al. 2018).

Diet type may influence species ability to change their phenologic events (Altermatt 2010) and their distribution area (Angert et al. 2011) to follow climate change. Species that are not able to change their distribution areas fast enough to follow their adequate climatic conditions are at higher risk of extinction (Devictor et al. 2008), as well as those species that cannot change phenology to match species that they depend on for survival (Visser and Both 2005). Generally, diet generalists are expected to be more likely to find adequate resources in new areas. They should, therefore, present a greater ability to change their distributions than specialists, which could be more limited by the phenology of species they depend on (Angert et al. 2011; Buckley and Kingsolver 2012). Broader diets can facilitate the expansion of distribution areas driven by climate (Braschler and Hill 2007) and the establishment and persistence of species in new environments (Estrada et al. 2016). However, a specialist may have a greater probability of following spatial changes if its host species or prey also changes (Betzholtz et al. 2013; Auer and King 2014). Generally, diet specialists could be more affected by climate change since they present narrower distribution, are less likely to leave their habitats (Caldas 2014) and alter their phenologic events (Altermatt 2010) to track adequate climatic conditions.

The temperature increase may cause omnivore species to change their diet, becoming more herbivores and fewer carnivores (Table 2). For ectotherms, low body temperature makes herbivory energetically unfavourable, as it constrains the rate at which energy can be extracted from the diet (Floeter et al. 2005; Boersma et al. 2016). For marine herbivorous fishes, herbivory is only possible above a threshold of 15°C (Floeter et al. 2005). There seems to be a consensus that due to better digestion of vegetal material at high temperatures, ectotherms might maximise energy intake and maintain high metabolic rates in higher temperatures by increasing herbivory (Carreira et al. 2016). This idea is supported by studies that have found that herbivory increases in response to higher temperatures in several groups, such as Copepoda (Boersma et al. 2016), fish (Floeter et al. 2005), tadpoles (Carreira et al. 2016) and reptiles (Espinoza et al. 2004). Even amongst endotherms, herbivores maintain higher body temperature than carnivores (Clarke and O'Connor 2014). Although omnivores can regulate their diet to deal with temperature increase caused by climate change, changing to a more herbivore diet and its adaptive value is variable among species (Carreira et al. 2016). Besides, an increase in herbivory in response to global warming can alter food chains, species interactions, and ecosystems' functioning.

3. *Dispersal ability*

Birds and lepidopterans are the best-represented taxa in studies regarding climatic effects on dispersal ability, and no studies were carried out in the tropical region (Table 3). Understanding species ability to respond to climate change is a fundamental point to identify species that experience higher risk (Møller et al. 2008; Hurlbert and Liang 2012). Species that cannot change their annual cycles and their distributions to follow their suitable climatic conditions will be prone to higher extinction risk (Møller et al. 2008; Corlett and Westcott 2013). In this sense, dispersal ability is a crucial attribute for species. It is expected that those with higher dispersal ability respond more quickly to climate change, presenting lower extinction risk (Pöyry et al. 2009; Angert et al. 2011).

Climate change can affect the dispersal processes of organisms both directly and indirectly (Travis et al. 2013; Table 3). Indirect mechanisms (*e.g.* altering resource availability and climatic suitability of the habitat) may lead species to change their distribution areas. Their annual cycles will be discussed in the following paragraphs (Table 3). On the other hand, climate change may directly interfere with behaviour, affecting the organisms' decisions to stimulate or inhibit dispersal (Table 3). Higher temperatures increase the dispersal of moths (Battisti et al. 2006), butterflies (Cormont et al. 2011) and birds (Møller et al. 2006) and decrease dispersal of lizards (Massot et al. 2008). Flooding increases the dispersal of an aquatic bird in Canada (Roche et al. 2012), and the reduction of snow cover decreases the dispersal of wolverines in the USA (Schwartz et al. 2009). These examples indicate that climatic variables may increase or reduce dispersal depending on the system and the species (Travis et al. 2013). Moreover, species response may depend on weather and landscape configuration (Delattre et al. 2013). In more fragmented landscapes, dispersal distance is longer at lower temperatures, while in continuous landscapes, dispersal distance is longer at higher temperatures.

Recent climate change is quickly altering the location of areas with a suitable climate for certain species (Loarie et al. 2009). To survive, species must move fast enough to follow such changes (Chen et al. 2011; Lenoir and Svenning 2015). Therefore, as expected for the future, climate change might be a significant threat to species persistence since rates of distribution changes should be much higher than those observed in the past (Williams and Blois 2018). Some studies show that many organisms will not be able to disperse fast enough to follow their climatic

Table 3. Effects and possible mechanisms that explain how dispersal influences species responses to climate change and their respective studies.

Effect	Pattern	Mechanism	Reference	Taxon	Location
Direct	Affecting decision to disperse	Increasing/ stimuating dispersion	Battisti et al. 2006	Moth	Europe
			Cormont et al. 2011	Butterfly	Netherlands
			Roche et al. 2012	Bird	Canada
			Møller et al. 2006	Bird	Denmark
			Pärn et al. 2012	Bird	Norway
			Delattre et al. 2013	Butterfly	France
		Decreasing/ inhibiting dispersion	Schwartz et al. 2009	Mammal	USA
			Massot et al. 2008	Lizzard	France
			Bullock et al. 2012	Plant	Great Britain
Indirect	Changing the distribution area	Higher dispersal ability, higher probability of tracking suitable environmental conditions	Pöyry et al. 2009	Butterfly	Finland
			Angert et al. 2011	Plant	Switzerland
			Hill et al. 2002	Butterfly	Great Britain
			Warren et al. 2001	Butterfly	Great Britain
			Krause et al. 2015	Plant	USA
			Methorst et al. 2017	Bird	Palearctic
			Williams and Blois 2018	Mammal	North America
	Changing phenological responses	Short-distance migrants respond more quickly to climate change than long-distance migrants.	Butler 2003	Bird	North America
			Swanson and Palmer 2009	Bird	USA
			Tryjanowski et al. 2002	Bird	Poland
			Tøttrup et al. 2010	Bird	Europe
			Hurlbert and Liang 2012	Bird	North America
			Rubolini et al. 2010	Bird	Germany
			Végvári et al. 2010	Bird	Europe
			Rubolini et al. 2007	Bird	Europe
			Thorup et al. 2007	Bird	Europe

niches, even highly mobile species (Pearson 2006; Devictor et al. 2008, 2012; Schloss et al. 2012). Species with low dispersal ability might lose significant parts of their distribution areas in the future (Krause et al. 2015), hence facing higher extinction risk (Pearson 2006; Corlett and Westcott 2013). Therefore, dispersal ability is a good predictor of species vulnerability to climate change. Both empirical observations (Warren et al. 2001; Hill et al. 2002; Pöyry et al. 2009; Angert et al. 2011) and model projections (Krause et al. 2015; Methorst et al. 2017; Williams and Blois 2018) evidence that higher dispersal ability indicates higher ability to change distribution to follow climate displacement (Table 3).

Recent global warming has already caused significant changes in many species' life cycles (Walther et al. 2002; Parmesan and Yohe 2003). Generally, plants and animals have advanced their phenologies in response to temperature increase (Parmesan and Yohe 2003; Parmesan 2006). However, consumers and predators at higher trophic levels in the food chain might not respond in the same proportion, leading to a mismatch between reproductive period and resource availability (Visser et al. 1998, 2004; Visser and Both 2005). Species that cannot advance their arrival to reproduction sites to match the peak of food abundance may suffer population declines and, consequently, be more prone to extinction (Both et al. 2006; Møller et al. 2008).

Migratory birds should advance the beginning of the migration to follow the phenology of plants and invertebrates in their reproduction areas (Sparks et al. 2005). Indeed, as a response to temperature increase in the last years, migratory birds have arrived earlier in their reproduction sites (Butler 2003; Hurlbert and Liang 2012). However, literature shows that long-distance migrants cannot respond to climatic change as quickly as short-distance migrants do and arrive later (Table 3). This happens because long-distance migrants experience slower temperature increase in wintering areas than their reproduction areas, while short-distance migrants are exposed to warm weather throughout the year (Lehikoinen et al. 2004). Therefore, short-distance migrants have more and better cues to match their phenology with resource phenology (Jones and Cresswell 2010). Thus, long-distance migratory behaviour can represent an essential constraint to responses to climate change, contributing to the decline of some species (Berthold et al. 1998; Møller et al. 2008; Jones and Cresswell 2010; Rubolini et al. 2010).

4. Climatic tolerance

Studies assessing species climatic tolerance are focused on ectotherms, and most of them were carried out on a global scale (Table 4). Tolerance to climatic conditions is one of the most critical factors determining how species are distributed around the globe (Thomas 2010). A variation in climatic tolerance among species is an important characteristic to determine their responses to climate change, as it can alter distribution and survival (Deutsch et al. 2008; Huey et al. 2012; Caldwell et al. 2015; Rugiu et al. 2018). Species with higher thermic tolerance occupy broader geographic areas (Bozinovic et al.

2011) and will deal better with global warming (Calosi et al. 2008; Buckley et al. 2012; Huey et al. 2012). In general, the thermic tolerance of an organism is proportional to the magnitude of temperature variation experienced in its habitat, steeply increasing with latitude (Deutsch et al. 2008). Thus, species from the tropics, which inhabit environments with lower temperature variation throughout the year, have narrower thermic tolerance than species from temperate regions (Deutsch et al. 2008; Huey et al. 2009, 2012; Duarte et al. 2012; Khaliq et al. 2014; Table 4). Deutsch et al. (2008) have reported that heat tolerance in tropical insects is, on average, only one-fifth of the tolerance of insect species from temperate regions. Besides that, tropical species already live in warmer environments, close to their critical temperature, compared to species from the temperate areas, which live in colder environments, far from their critical temperature (Sunday et al. 2012; Araújo et al. 2013; Khaliq et al. 2014). Therefore, even slight temperature increases might be a threat to tropical species.

Heat tolerance is more conserved amongst lineages than cold tolerance, implying that many species might have lost their evolutionary potential to respond to global warming (Addo-Bediako et al. 2000; Huey et al. 2009; Araújo et al. 2013). When organisms are exposed to temperatures close to their upper thermal limit, biological activity suffers from several limitations and might compromise survival (Somero 2011). Furthermore, it is unlikely that species can persist under conditions that surpass their physiological tolerance limits (Calosi et al. 2010). Thus, climatic conditions expected in the future might negatively affect population abundance and potentially compromise their persistence (Rugiu et al. 2018). However, while tropical species might be severely affected, species from temperate regions might benefit from temperature increase, responding with higher population growth rates and aptitude (Deutsch et al. 2008; Caldwell et al. 2015; Carrascal et al. 2016; Table 4).

Such pattern of greater physiological vulnerability to climatic changes in tropical species, when compared to species from temperate areas, has been shown to ectotherms, especially reptiles (Deutsch et al. 2008; Tewksbury et al. 2008; Huey et al. 2009, 2010; Diamond et al. 2012; Duarte et al. 2012; Sunday et al. 2012; Hoffmann et al. 2013; Caldwell et al. 2015). For endotherms, on the other hand, the relationship between higher thermic tolerance in species that experience higher climatic variability was observed in birds but not in mammals (Khaliq et al. 2014). Even though most ectotherms, particularly those from the temperate region, might tolerate projected temperature increases across significant ranges of their distributions, potential vulnerability to projected temperatures increases from polar regions to tropical areas (Khaliq et al. 2014). Unlike the observed pattern for ectotherms (Addo-Bediako et al. 2000; Deutsch et al. 2008), endotherms present low phylogenetic conservatism regarding climatic tolerance to respond to temperature increase through physiological adaptation (Khaliq et al. 2015). In temperate regions, endotherms distribution is limited by extremes of low temperature via physiological cold tolerance of species (Khaliq et al. 2017). Global warming scenarios might benefit species living in those regions, increasing their abundance (Carrascal et al. 2016). In the tropics, endotherms (especially mammals) seem limited by other factors, such as biotic interactions, rather than climatic conditions (Khaliq et al. 2017).

Overall, species that present the lowest climatic tolerances will be more affected by climate change. Species from the tropical region and mainly ectotherms will be more vulnerable to projected temperature increases in the future (Table 4). Endotherms can keep high and constant body temperature, which is generally independent of ambient climatic conditions (MacNab 2012). On the other hand, ectotherms might be more vulnerable as their physiology, locomotion, growth and

Table 4. Possible mechanisms that explain how climatic tolerance may influence species responses to climate change and their respective studies.

Pattern	Mechanisms	Reference	Taxon	Location
Species from tropical regions are more vulnerable to climatic change than species from temperate regions	Species from tropical regions have narrower thermic tolerance and live in environments where the temperature is close to their upper thermal limit	Deutsch et al. 2008	Ectotherms	Global
		Tewksbury et al. 2008	Lizard	Global
		Huey et al. 2009	Lizard	Neotropics
		Sunday et al. 2012	Ectotherms	Global
		Huey et al. 2012	Ectotherms and endotherms	Global
		Diamond et al. 2012	Ant	Global
		Hoffmann et al. 2013	Ectotherms	Global
		Khaliq et al. 2014	Bird and mammal	Global
		Caldwell et al. 2015	Lizard	Tasmania
Species from temperate regions are less vulnerable and may benefit from climate change	Species present broader thermic tolerance and live in environments where the temperature is far from their upper limits	Deutsch et al. 2008	Ectotherms	Global
		Sunday et al. 2012	Ectotherms	Global
		Huey et al. 2012	Ectotherms and endotherms	Global
		Khaliq et al. 2014	Bird and mammal	Global
		Caldwell et al. 2015	Lizard	Tasmania
		Carrascal et al. 2016	Bird	Spain
Ectotherms are more vulnerable to climate change than endotherms	Ectotherms present higher niche conservatism and lower capacity to adjust their physiology	Addo-Bediako et al. 2000	Insect	Global
		Deutsch et al. 2008	Ectotherms	Global
		Sinervo et al. 2010	Lizard	Mexico
		Khaliq et al. 2015	Bird and mammal	Global
		Khaliq et al. 2017	Bird and mammal	Global

reproduction are strongly influenced by ambient temperature (Deutsch et al. 2008). Moreover, warmer temperatures may force ectotherms to spend more time in shelters to avoid lethally high temperatures, restricting the time available for other vital activities such as foraging, territory defence and mating (Sinervo et al. 2010). Due to their low ability to respond to climate change, several ectotherm populations were locally extinct in recent decades, and temperature increase might lead to the extinction of almost 40% of lizard populations and 20% of lizard species globally 2080 (Sinervo et al. 2010).

Conclusions

Overall, the literature review performed regarding the four chosen traits enabled us to present and discuss mechanisms that might explain species responses to climate change. As shown here, response to climate change is highly variable among species and regions. Some species may exhibit a critical response to a specific climate variable. In contrast, others may have a minimal response, and some might even present a contradictory response from what is expected, depending on the region they inhabit. Explaining such variation has become a significant challenge to conservationists in this century. Such explanation would allow the identification of species at higher extinction risk, the definition of the best conservation strategies, and the resources' strategic direction. It was also possible to verify bias concerning region and taxa in the evaluated studies. The tropical region, which holds more sensitive species, was weakly represented, while most studies have focused on the temperate region. For some traits, studies concentrate on a specific group and neglect others; for example, most studies assessing climatic tolerance have concentrated on reptiles.

Species exposed to a higher magnitude of climate warming should present more pronounced biological responses (Chen et al. 2011). However, intrinsic differences between species' life-history traits, physiology and other ecological characteristics are fundamental to determine their vulnerability (Williams et al. 2008; Foden et al. 2013). Assessments of climate change vulnerability that consider both exposure and traits that define sensitivity and adaptive ability could be helpful tools (Foden et al. 2013; Böhm et al. 2016). However, trait choice should be based on empirical evidence that shows the relevance of such traits in determining the vulnerability of assessed species.

This review shows that the four evaluated traits are significant predictors of species responses to climate change, and we present the main mechanisms involved in each response. Therefore, clutch size, diet breadth, dispersal ability and climatic tolerance are essential traits for vulnerability assessments. Even though some evidence might lead us to conclude that species with smaller clutch size, with specialised diets, low dispersal ability and lower climatic tolerance would experience higher risk due to climate change, the set of studies evaluated here indicates that the risk depends on the region and the species group considered. While species from the temperate region could benefit from temperature increase with greater resource availability, increasing clutch size and expanding the distribution area through dispersal, species from the tropics could be severely affected. They have lower climatic tolerance and already live close to their limits of heat tolerance. Vulnerability is higher for ectotherms because, unlike endotherms, they cannot control body temperature and their biological activities depend on the climatic conditions of the environment. Ectotherms from the tropical region will not escape from temperature increase through dispersal (Buckley et al. 2013).

The lack of response in a trait may interfere with the response of another feature. In the temperate region, temperature increase causes advanced flowering in plants and an abundance of insects. Thus, birds that spend the winter in other areas should advance their arrival so that the reproductive period matches food availability. Species that cannot advance their arrival might face food scarcity during reproduction, leading to smaller clutch size. In the tropics, species present lower thermic tolerance, affecting their dispersal ability to follow suitable climatic conditions if they have to cross warmer areas.

As we understand the mechanisms involved in the response of other traits, we will enhance our ability to predict climate change impacts, enabling conservation practices that are more adequate to protect species. The increase of this type of studies could facilitate understanding which characteristics are more informative to each species group within each region. Besides that, understanding the mechanisms through which traits influence species responses to climatic changes may help justify the traits included in vulnerability assessments, improving their results and making them more useful. For that, CCVAs need to be more integrated with the ecology literature to assess how species traits respond to changes in the climate.

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Author Contributions

Fábio Júlio Alves Borges: Originally formulated the idea, performed the literature search, data analysis and wrote the first version of the manuscript.

Rafael Loyola: Commented and revised the manuscript, substantially improving the final version.

Conflict of Interest

The authors declare that they have no conflict of interest.

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Inventory

Diversity of insect galls from Mato Grosso State, Brazil: North Pantanal

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Abstract: The Pantanal Biome occupies 20% of the Brazilian territory extending its distribution over two Brazilian States, Mato Grosso and Mato Grosso do Sul. This Biome is one of Brazil's poorly known regions concerning insect gall and their interactions with host plants. In this study, we characterized for the first time the gall morphology, identified host plants and the gall makers from an area of Brazilian wetlands from Mato Grosso State, known as Pantanal Matogrossense. We sampled Pantanal Biome areas in Poconé municipality, along the Transpantaneira Road, Mato Grosso State, Brazil, in two expeditions, July 2012 and January 2013, with a total effort of 2 hours. We characterized 91 morphotypes of insect galls in 54 host plant species; 28 gall makers in 24 host plant species; the richest host plant families are Fabaceae, Myrtaceae, and Sapindaceae. Psidium guineense Sw. is the super host species. This area in Pantanal Matogrossense is the second in the richness of gall morphotypes (N=91) and average morphotypes/plant species (1.7), comparing phytophysiognomies. Additionally, 15 plant species are new record as host in galler-host plant interaction in the world. This number represents 30% of the total of host plant species sampled in Poconé. This inventory is new knowledge to the Pantanal Matogrossense and representing a unique testimony of insect-plant interactions consumed by the unprecedented fire that occurred in Pantanal Biome in the dry season of 2020.

Keywords: *Biodiversity; Brazilian wetlands; conservation; gall makers; Neotropical region; insect-plant-interaction.*

Diversidade de galhas de insetos do Estado do Mato Grosso, Brasil: Pantanal Norte

Resumo: O Bioma Pantanal ocupa 20% do território brasileiro estendendo sua distribuição sobre dois Estados brasileiros, Mato Grosso e Mato Grosso do Sul. Esta é uma das regiões menos estudadas do Brasil com relação aos insetos e suas interações. Neste estudo, caracterizamos pela primeira vez a morfologia de galhas, identificamos plantas hospedeiras e galhadores em áreas do Pantanal Norte, conhecido como Pantanal Matogrossense. As amostragens foram feitas em áreas do Bioma Pantanal, no município de Poconé, ao longo da Estrada Transpantaneira, Mato Grosso, Brasil em duas expedições, julho de 2012 e janeiro de 2013. Caracterizamos 91 morfotipos de galhas entomógenas em 54 espécies de plantas hospedeiras; identificamos 28 galhadores em 24 espécies de plantas hospedeiras; as famílias de plantas hospedeiras mais ricas em galhas são Fabaceae, Myrtaceae e Sapindaceae. Psidium guineense Sw. é a espécie superhospedeira. Esta área no Pantanal Matogrossense é a segunda tanto em riqueza de morfotipos de galhas (N=91) quanto na média de morfotipos por espécie de planta hospedeira (1,7), em fitofisionomias comparáveis. Além disso, 15 espécies de plantas são novos registros como hospedeiras para galhas de insetos no mundo. Esse número representa 30% do total de plantas amostradas em Poconé. Todos os dados deste inventário são conhecimentos novos para o Pantanal Mato-grossense e para o estado do Mato Grosso, representando um testemunho único das interações inseto-planta que foram consumidas pelo fogo sem precedentes ocorrido no Bioma Pantanal em sua estação seca de 2020.

Palavras-chave: *Biodiversidade; conservação; galhadores; interação inseto-planta; Pantanal Matogrossense; região Neotropical.*

Introduction

The Pantanal biome occupies 20% of the Brazilian territory (Junk et al. 2013), extending its distribution over two Brazilian States, Mato Grosso and Mato Grosso do Sul. The Brazilian wetlands, called Pantanal popularly, are considered a hyper-seasonal savannah under contrasting stresses due to alternation between periods of drought and prolonged flooding (Eiten 1982, Marengo et al. 2021). Pantanal harbors deciduous or semi-deciduous forests shedding leaves during the dry season, deciduous forest and Cerrado vegetation in inselbergs and evergreen floodplain forests in the lower areas along rivers and channels (Nunes da Cunha et al. 2007). Its vegetation is highly influenced by Chaco Biome (Pott et al. 2011). It is considered a hotspot of biodiversity, with more than 2,000 species of vascular plants (Pott et al. 2011) and more than 2,000 species of animals, except terrestrial invertebrates (Junk et al. 2006), with the seasonal flood-pulsing harboring habitat specialization (*e.g.*, morphological, anatomical and physiological adaptations) (Junk et al. 2013).

The interaction between plants and insects is still unexplored in North Pantanal, South-western of the State of Mato Grosso, in the Midwest region of Brazil. About 15% of the insect galls inventories made in Brazil were carried out in the Midwest region (Araújo et al. 2019). Despite that, only two have been carried out in the Pantanal biome (Julião et al. 2002, Urso-Guimarães et al. 2017). Both in the State of Mato Grosso do Sul, which is strongly influenced by the Cerrado biome. Julião et al. (2002) and Urso-Guimarães et al. (2017) found 182 morphotypes of galls in 104 host plants, of which only nine plant species and three morphotypes were common. The richest plant family in Abobral was Bignoniaceae, and the super host species was Hippocratea volubilis L. (Julião et al. 2002). In Corumbá/Porto Murtinho, Fabaceae was the richest plant family and Serjania sp. the super host species (Urso-Guimarães et al. 2017).

In this study, we present the first survey of gall-inducing insects for the North Pantanal, including the characterization of gall morphology and the identification of host plants. Our study represents the first step to understanding the richness of the history of host plants' interaction and gall-inducing insects in this biodiverse and unique biome.

In the last three months of 2020, the region of Pantanal Sul Matogrossense and Matogrossense (including Poconé) was devastated by an unprecedented fire. These months correspond to the Pantanal winter, in which the waters of the Paraguay River Basin should overflow the river channels and flood the plains around them. In this period, leaves fall, fruits, and branches accumulated in the litter, generating a formidable amount of food, all consumed by the primary consumers that occupy the food chain base and sustain the unique Pantanal biodiversity. But, in the winter of 2020, the flooding did not occur. All available dry matter functioned as fuel and burned large extensions of the Pantanal, destroying much this biome's rich fauna and flora due to deforestation, cleaning, and reforming pastures using improper management practice without control techniques endanger the conservation (Marengo et al. 2021). In this terrible scenario, our inventory represents a unique testimony of insect-plant interactions consumed by the fire.

Material and Methods

1. *Study site*

We conducted this study in two areas: Pousada Rio Clarinho and Transpantaneira Road Km 40, in Poconé Municipality (16°36'03.5" S, 56°43'46.1" W), State of Mato Grosso, Brazil (Fig. 1). This region is localized in the North Pantanal, also called Pantanal Matogrossense (Fig. 1). Its vegetation is considered a Pantanal mosaic because it is influenced by distinct biomes, with the Amazonia to the North, the Cerrado to the East, the Meridional Forests to the South, and the Chaco to the West (Pott et al. 2011). The Cerrado vegetation occupies 36% of the study area region, corresponding to 10% in the sub-region of Poconé (South-western of the State of Mato Grosso) (Silva et al. 2000). The region's climate is the Tropical Climate of Savannah (Aw), with two well-defined seasons (hot and rainy in summer and dry and cold in winter). The seasonal flooding process is divided into four phases: flooding, flood, reflux, and dry (Costa et al. 2010).

2. *Sampling*

We performed two expeditions in a North Pantanal area in Poconé, State of Mato Grosso, Brazil, one in July 2012 and the other in January 2013. We selected two points to the collection, a floodable gallery forest along the Clarinho river (16° 36' 15.6" S/ 56° 43' 18.8" W), and a dry forest (Chaco edge) near the Transpantaneira Road (16° 35' 14.7" S/ 56° 44' 04.5" W), 3 kilometers apart from each other. We sampled along the trails' edges, with a 30-minute effort was made at each sampling point on each expedition, totaling 2 hours of effort following Price et al. (1998). We measured each route's length to quantify the sampled area (Urso-Guimarães et al. 2017), covering 52 meters in floodable gallery forest trail and 129 meters in the dry forest trail. All gall sighted was collected, without limitation of habitus, stem diameter, or plant height. The collection method, labeling, processing samples, identification of plants, and insects followed Urso-Guimarães et al. (2017) and Araújo et al. (2021). The voucher specimens were deposited in the Universidade Federal de São Carlos: plants in the Herbarium SORO, and the insect material in the Laboratório de Sistemática de Diptera.

Results

We found 91 morphotypes of insect galls in 54 host plant species from 39 genera and 19 families (Table 1 and Figs. 2–5). On average, 1.7 gall morphotypes per plant species (for comparisons with other inventories in Pantanal areas, see Table 2). Four host plants are identified only at the family level, 16 at the genus level, and five are completely unidentified. We collected 83 gall morphotypes in the gallery forest and eight in the dry forest. The richest families in morphotypes are Fabaceae (N=19, 20.9%), Myrtaceae (N=14, 15.4%), and Sapindaceae (N=11, 12%). The richest plant genera in gall morphotypes were *Bauhinia* (N=11, 12%), *Serjania* (N=8, 8.8%), *Psidium* (N=7, 7.7%), and *Combretum* (N=5, 5.5%). The plant species considered super host were *Psidium guineense* Sw. (N=7, 7.7%), *Combretum laxum* Jacq., and the Unidentified sp. 3 (N=5, 5.5% each).

The galls were induced mostly in leaves (N=67, 74%) and stem (N=19, 24%); the globoid (N=32, 35%) and lenticular (N=31, 34%) gall shapes are predominant. The colors green and brown were found in equal proportion (N=43; 47% each) and the glabrous galls are dominant (N=70; 77%).

In this inventory, fifteen plant species are new records as a host plant for insect galls in the world: *Amaioua intermedia* Mart. ex Schult. & Schult.f., *Annona cornifolia* A.St.-Hil., *Bauhinia mollis* (Bong.) D.Dietr., *B. pentandra* (Bong.) D.Dietr., *B. platypetala* Burch. ex Benth., *Byrsonima cydoniifolia* A.Juss., *Coccoloba cujabensis* Wedd,

Table 1. Characterization of insect galls recorded in North Pantanal in Poconé, Mato Grosso State, Brazil organized by host plant. Figures refer to the picture of the gall morphotype. All galls are uni-chambered. New records of plants species as host of galls in the world are marked with asterisk.

Host plat family	Host plant species	Host plant organ	Gall shape	Gall color	Trichome	Collection site	Figures
Anacardiaceae	*Astronium graveolens* Jacq.	Leaf, stem	Cylindrical	Green/brown	Yes	Gallery forest	2A
Annonaceae	*Annona cornifolia* A.St.-Hil.*	Leaf	Cylindrical	Green	No	Gallery forest	2B
Bignoniaceae	*Dolichandra quadrivalvis* (Jacq.) L.G.Lohmann*	Stem	Globoid	Green/brown	No	Dry forest	2C
Bignoniaceae	*Dolichandra quadrivalvis* *	Stem	Fusiform	Green/brown	No	Dry forest	2C
Bignoniaceae	Bignoniaceae sp.1	Stem	Globoid	Green	No	Gallery forest	2D
Bignoniaceae	Bignoniaceae sp.1	Stem	Fusiform	Green	No	Gallery forest	2D
Bignoniaceae	Bignoniaceae sp.2	Stem	Globoid	Brown	No	Gallery forest	2E
Bignoniaceae	Bignoniaceae sp.2	Tendril	Fusiform	Brown	No	Gallery forest	2E
Chrysobalanaceae	*Couepia* sp.	Leaf	Lenticular	Green/brown	No	Gallery forest	2F, 2G
Chrysobalanaceae	*Leptobalanus gardneri* (Hook.f.) Sothers & Prance *	Leaf	Lenticular	Brown	No	Gallery forest	2H
Chrysobalanaceae	*Leptobalanus humilis* (Cham. & Schltdl.) Sothers & Prance	Leaf	Lenticular	Brown	No	Gallery forest	2I
Chrysobalanaceae	*Licania* sp.	Leaf	Lenticular	Brown	No	Gallery forest	2J
Combretaceae	*Combretum laxum* Jacq.	Leaf	Cylindrical	Green	Yes	Gallery forest	2K
Combretaceae	*Combretum laxum*	Leaf	Globoid	Brown	Yes	Gallery forest	2L
Combretaceae	*Combretum laxum*	Leaf	Lenticular	Green	Yes	Gallery forest	2M
Combretaceae	*Combretum laxum*	Leaf	Conical	Green	Yes	Gallery forest	2M, 2N
Combretaceae	*Combretum laxum*	Leaf	Globoid	Green/brown	No	Gallery forest	2O, 2P
Combretaceae	*Terminalia argentea* Mart. & Zucc.	Leaf	Lenticular	Brown	Yes	Dry forest	2Q
Dilleniaceae	*Davilla elliptica* A.St.-Hil.	Leaf	Lenticular	Brown	No	Gallery forest	2R
Euphorbiaceae	*Maprounea guianensis* Aubl.	Leaf	Lenticular	Light yellow	No	Gallery forest	2S
Fabaceae	*Andira vermifuga* (Mart.) Benth.*	Leaf	Lenticular	Brown	No	Dry forest	2T
Fabaceae	*Bauhinia* cf. *pulchella* Benth.	Stem	Globoid	Brown	No	Gallery forest	2U, 2V
Fabaceae	*Bauhinia* cf. *pulchella*	Leaf	Globoid	Brown	No	Gallery forest	2X
Fabaceae	*Bauhinia* cf. *pulchella*	Stem	Globoid	Brown	No	Gallery forest	2Z
Fabaceae	*Bauhinia* cf. *pulchella*	Stem	Fusiform	Brown	No	Gallery forest	2Z
Fabaceae	*Bauhinia mollis* (Bong.) D. Dietr.*	Leaf	Globoid	Brown	Yes	Dry forest	3A
Fabaceae	*Bauhinia mollis* *	Leaf	Lenticular	Brown	No	Gallery forest	3B
Fabaceae	*Bauhinia pentandra* (Bong.) D. Dietr.*	Leaf	Globoid	Brown	Yes	Gallery forest	3C
Fabaceae	*Bauhinia pentandra**	Stem	Fusiform	Brown	No	Gallery forest	3D
Fabaceae	*Bauhinia pentandra**	Stem	Globoid	Brown	No	Gallery forest	3D
Fabaceae	*Bauhinia pentandra**	Stem	Globoid	Brown	No	Gallery forest	3E
Fabaceae	*Bauhinia platypetala* Burch. ex Benth. *	Leaf	Globoid	Brown	Yes	Gallery forest	3F, 3G
Fabaceae	Fabaceae sp.	Leaf	Globoid	Brown	No	Gallery forest	3H, 3I
Fabaceae	Fabaceae sp.	Leaf	Lenticular	Brown	No	Gallery forest	3H, 3I
Fabaceae	Fabaceae sp.	Leaf	Lenticular	Brown	No	Gallery forest	3J
Fabaceae	*Galactia glaucescens* Kunth*	Leaf	Globoid	Brown	No	Gallery forest	3K
Fabaceae	*Galactia glaucescens* *	Stem	Globoid	Brown	No	Dry forest	3L
Fabaceae	*Hymenaea courbaril* L.	Leaf	Lenticular	Brown	No	Gallery forest	3M, 3N
Fabaceae	*Senegalia* sp.	Leaf	Amorphous	Green	No	Gallery forest	3O
Lamiaceae	*Aegiphila* sp. 1	Leaf	Amorphous	Green	No	Gallery forest	3P
Lamiaceae	*Aegiphila* sp. 2	Leaf bud	Globoid	Brown	No	Gallery forest	3Q
Malpighiaceae	*Byrsonima crassifolia* (L.) Kunth	Leaf	Conical	Green/red	No	Gallery forest	3R, 3S
Malpighiaceae	*Byrsonima crassifolia* (L.)	Leaf	Conical	Light yellow	Yes	Gallery forest	3T, 3U

continue...

....continuation

Malpighiaceae	*Byrsonima cydoniifolia* A.Juss.*	Leaf	Conical	Green	No	Gallery forest	3V, 3X
Moraceae	*Ficus* sp.	Leaf	Lenticular	Purple	No	Gallery forest	3Z
Myrtaceae	*Campomanesia* sp.	Leaf	Globoid	Green	No	Gallery forest	4A
Myrtaceae	*Campomanesia* sp.	Leaf, stem	Globoid	Green	No	Gallery forest	4B
Myrtaceae	*Eugenia* cf. *florida* DC.	Leaf	Globoid	Green/red	No	Gallery forest	4C
Myrtaceae	*Eugenia* cf. *florida*	Leaf	Lenticular	Green	Yes	Gallery forest	4D
Myrtaceae	*Eugenia* sp.	Leaf	Lenticular	Black	No	Gallery forest	4E
Myrtaceae	*Myrcia neolucida* A.R.Lourenço & E.Lucas*	Leaf	Lenticular	Black	No	Gallery forest	4F
Myrtaceae	*Psidium guineense* Sw.	Leaf	Lenticular	Brown	No	Gallery forest	4G
Myrtaceae	*Psidium guineense*	Leaf	Globoid	Green	Yes	Gallery forest	4H
Myrtaceae	*Psidium guineense*	Stem	Fusiform	Brown	No	Gallery forest	4I
Myrtaceae	*Psidium guineense*	Leaf	Globoid	Green	No	Gallery forest	4J
Myrtaceae	*Psidium guineense*	Stem	Globoid	Brown	No	Gallery forest	4K
Myrtaceae	*Psidium guineense*	Leaf	Lenticular	Brown	No	Gallery forest	4L
Myrtaceae	*Psidium guineense*	Stem	Fusiform	Brown	No	Gallery forest	4L
Myrtaceae	Myrtaceae sp.	Stem	Globoid	Brown	No	Gallery forest	4M
Polygonaceae	*Coccoloba cujabensis* Wedd.*	Leaf	Lenticular	Green	Yes	Gallery forest	4N
Polygonaceae	*Coccoloba cujabensis**	Leaf	Lenticular	Brown	No	Gallery forest	4R
Polygonaceae	*Coccoloba cujabensis**	Stem	Globoid	Brown	No	Gallery forest	4S
Polygonaceae	*Polygonum acuminatum* Kunth*	Leaf	Lenticular	Green/grey	No	Gallery forest	4P
Polygonaceae	*Symmeria paniculata* Benth.*	Leaf	Lenticular	Brown	No	Gallery forest	4N–O
Polygonaceae	*Triplaris gardneriana* Wedd.*	Leaf	Globoid	Green	No	Gallery forest	4Q
Rubiaceae	*Amaioua intermedia* Mart. ex Schult. & Schult.f.*	Leaf, stem	Cylindrical	Green/brown	Yes	Gallery forest	4T
Rubiaceae	*Psychotria* sp.	Leaf bud	Fusiform	Brown	No	Gallery forest	4U
Salicaceae	*Casearia* sp.	Leaf	Globoid	Green	Yes	Gallery forest	4V
Sapindaceae	*Magonia pubescens* A. St.-Hil.	Leaf vein	Globoid	Green	No	Dry forest	4X
Sapindaceae	*Matayba* sp.	Leaf	Globoid	Brown	Yes	Dry forest	4Z
Sapindaceae	*Paullinia* sp.	Leaf	Lenticular	Green	No	Gallery forest	5A
Sapindaceae	*Serjania caracasana* (Jacq.) Willd.*	Leaf	Lenticular	Brown	No	Gallery forest	5B
Sapindaceae	*Serjania caracasana**	Leaf	Lenticular	Green	Yes	Gallery forest	5C
Sapindaceae	*Serjania caracasana**	Leaf	Cylindrical	Light green	Yes	Gallery forest	5D
Sapindaceae	*Serjania erecta* Radlk.	Leaf	Lenticular (Wrinkle)	Green	No	Gallery forest	5E
Sapindaceae	*Serjania erecta*	Leaf	Conical	Green	Yes	Gallery forest	5F
Sapindaceae	*Serjania erecta*	Stem	Globoid	Brown	No	Gallery forest	5G
Sapindaceae	*Serjania erecta*	Leaf	Conical	Green/pink	Yes	Dry forest	5H
Sapindaceae	*Serjania* sp.	Leaf	Lenticular	Brown	No	Gallery forest	5I
Smilacaceae	*Smilax* sp.	Leaf	Amorphous	Green	No	Gallery forest	5J, 5K
Solanaceae	*Cestrum* sp.	Leaf	Conical	Green	Yes	Gallery forest	5L
Symplocaceae	*Symplocos* sp.	Stem	Conical	Green	No	Gallery forest	5M
Unidentified	Unidentified sp. 1	Leaf	Rosette	Brown	No	Gallery forest	5N
Unidentified	Unidentified sp. 2	Leaf	Lenticular	Brown	No	Gallery forest	5O
Unidentified	Unidentified sp. 3	Leaf	Lenticular	Green	No	Gallery forest	5P
Unidentified	Unidentified sp. 3	Leaf	Globoid	Green	No	Gallery forest	5P
Unidentified	Unidentified sp. 3	Leaf	Pineapple	Green	No	Gallery forest	5Q
Unidentified	Unidentified sp. 3	Leaf	Cylindrical	Green/brown	No	Gallery forest	5R
Unidentified	Unidentified sp. 3	Leaf	Globoid	Green	No	Gallery forest	5R
Unidentified	Unidentified sp. 4	Stem, tendril	Fusiform	Green	No	Gallery forest	5S
Unidentified	Unidentified sp. 5	Leaf	Lenticular	Green	No	Gallery forest	5T

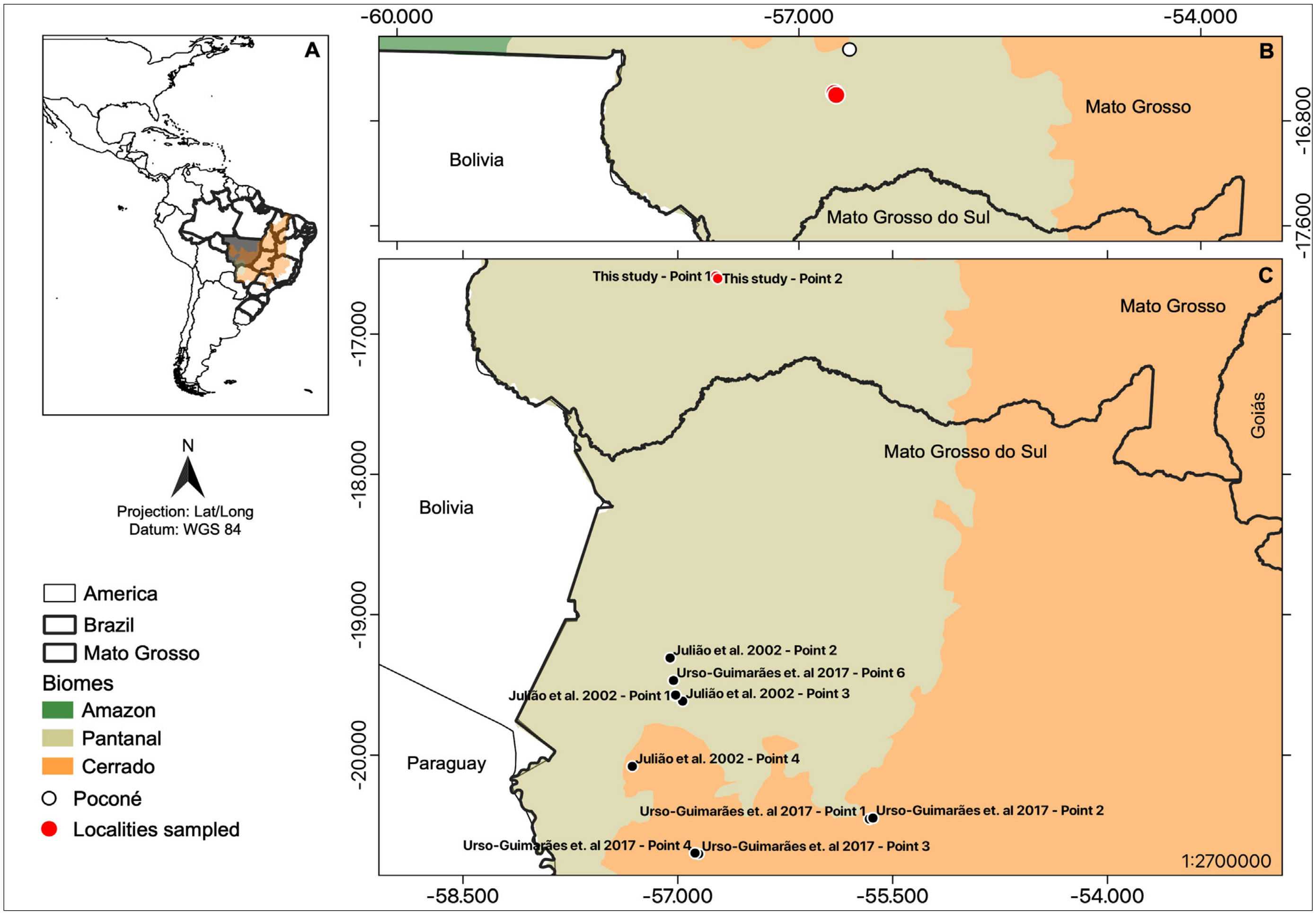

Figure 1. A. Map of South America indicating the Mato Grosso State and Cerrado and Pantanal Biomes extension in Brazil. B. Map of the of Cerrado and Pantanal areas with the sampling localities of North Pantanal in Poconé. C. Map of the sampling localities of Urso-Guimarães et al. (2017) (Point 1- Universidade Estadual do Mato Grosso do Sul (UEMS), Aquidauana; Point 2 – Distrito de Camisão, Aquidauana; Point 3 – Sede da Fazenda Califórnia, Bodoquena; Point 4 – Base de Estudos do Pantanal, Corumbá; Point 5- Fazenda São Bento, Corumbá; Point 6 – Trilha Fazenda Retiro Conceição, Porto Murtinho; Point 7 – Trilha da Fazenda Campo Florido, Porto Murtinho) and of Julião et al. (2002) (Point 1 – Rio Vermelho; Point 2 – Base de Estudos do Pantanal; Point 3 – MS-184 Highway; Point 4 – Fazenda São Bento) in Mato Grosso do Sul, Brazil.

Dolichandra quadrivalvis (Jacq.) L.G.Lohmann, *Galactia glaucescens* Kunth, *Leptobalanus gardneri* (Hook.f.) Sothers & Prance, *Myrcia neolucida* A.R.Lourenço & E.Lucas, *Polygonum acuminatum* Kunth, *Serjania caracasana* (Jacq.) Willd., *Symmeria paniculata* Benth., and *Triplaris gardneriana* Wedd (Flora do Brasil 2020).

From the insect galls, 28 (30.8%) of the gall inducers were obtained and identified in 24 host plant species. Among the insect inducers, 60.7% belong to Diptera (N=17) and 21.4% to Hymenoptera (N=7), 7.1% to Hemiptera, and Thysanoptera (N=2 each), and 3.6% to Coleoptera (N=1). Associated fauna and other details are in Table 3. The gall inducers of 63 morphotypes are undetermined because the galls were collected empty, the specimens obtained were damaged or the morphological information in the instars obtained was insufficient to the identification. As in all surveys, the species of Cecidomyiidae were the predominant gall inducer species (Table 3).

Discussion

The morphotype richness found in the gallery forests was significantly higher (N=83) when compared with the dry forest (N=8). The leaves are the organ most attacked by the gall makers in all environments (Araújo et al. 2019), except for few studies with stems as the most affected organ always associated with dry environments (Veldtman & McGeoch 2003, Fernandes et al. 2002, Carneiro et al. 2009, Coelho et al. 2013, Toma & Mendonça 2013, Kuzmanich et al. 2018). Thus, the host plant species' leaves loss during the dry season must have influenced the low number of galls found in the dry forest.

Fabaceae and Myrtaceae are two of the richest plant families in Pantanal (Pott et al. 2011). Pattern recovered in our study corroborating the hypothesis that families with the highest number of plant species also have the highest number of gall-forming species associated with them in all Brazilian biomes (Araújo et al. 2019, Santos-Silva & Araújo 2020). Sapindaceae appears as the third richest family, because of *Serjania* Mill. It is a super host genus, with eight gall morphotypes in only three species, the same situation found by Urso-Guimarães et al. (2017) in Corumbá. These results show the super host species' contribution to increasing the local richness of the insect-plant interactions, independently of plant species richness (Veldtman & McGeoch 2003).

Comparing with other studies in South Pantanal, our average (1.7) is similar to the other areas, Abobral region (1.7, Julião et al. 2002), and Corumbá/Porto Murtinho areas (1.4, Urso-Guimarães et al. 2017) (Fig.

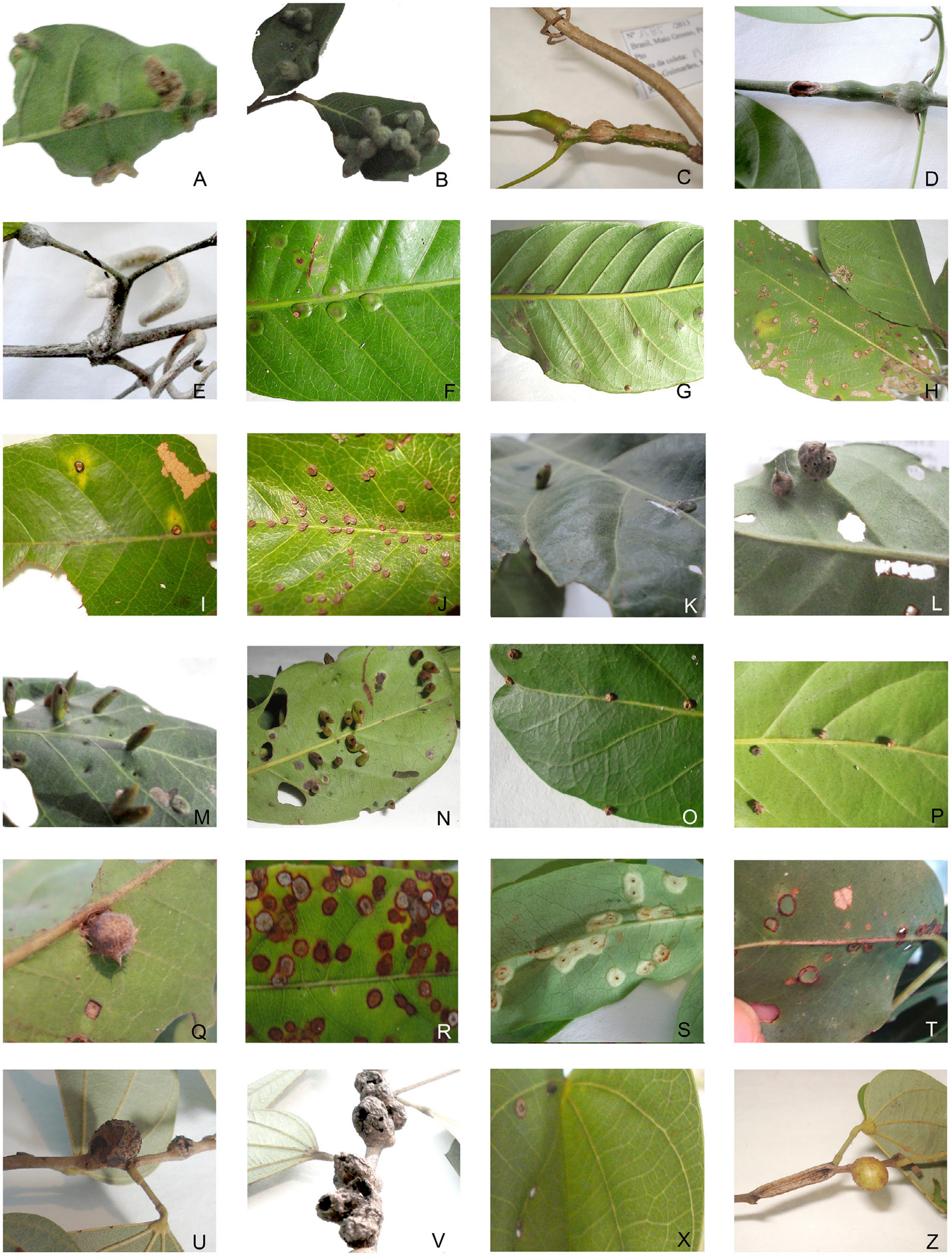

Figure 2. Insect galls of North Pantanal in Poconé, Mato Grosso State, Brazil in host plants indicated. Anacardiaceae. A. *Astronium graveolens*, Annonaceae. B. *Annona cornifolia*, Bignoniaceae. C. *Dolichandra quadrivalvis*, D. Bignoniaceae sp.1, E. Bignoniaceae sp.3, Chrysobalanaceae. F–G. *Couepia* sp., H. *Leptobalanus gardneri*, I. *Leptobalanus humilis*, J. *Licania* sp., Combretaceae. K–P. *Combretum laxum*, Q. *Terminalia argentea*, Dilleniaceae. R. *Davilla elliptica*, Euphorbiaceae. S. *Maprounea guianensis*, Fabaceae. T. *Andira vermifuga*, U–Z. *Bauhinia* cf. *pulchella*.

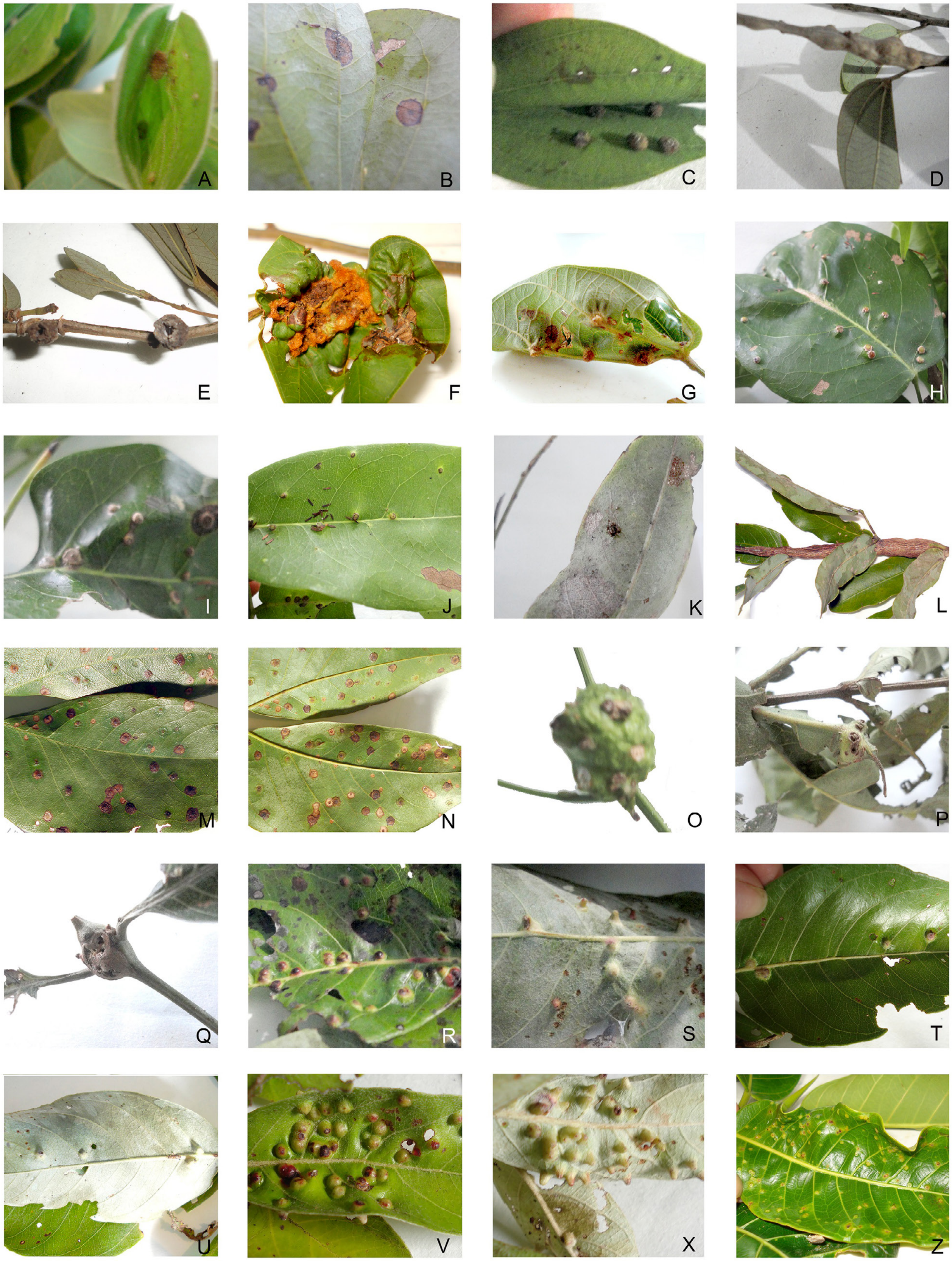

Figure 3. Insect galls of North Pantanal in Poconé, Mato Grosso State, Brazil in host plants indicated. Fabaceae. A–B. *Bauhinia mollis*, C–E. B. *pentandra*, F–G. *B. platypetala*, H–J. Fabaceae sp., K–L. *Galactia glaucescens*, M–N. *Hymenaea courbaril*, O. *Senegalia* sp., Lamiaceae. P. *Aegiphila* sp. 1, *Q. Aegiphila* sp., 2. Malpighiaceae. R–U. Byrsonima crassifolia, V–X. B. *cydoniifolia*, Moraceae. Z. *Ficus* sp.

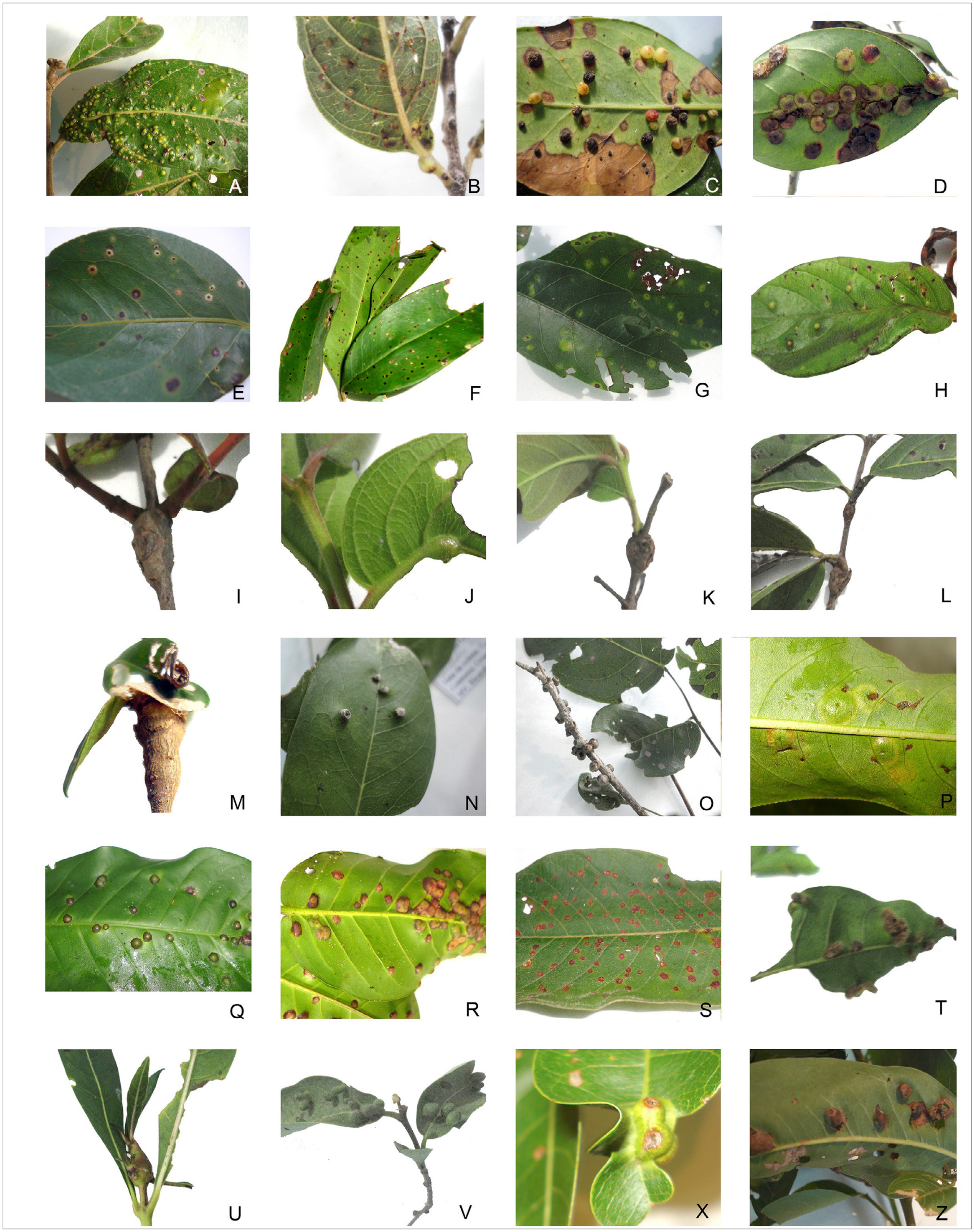

Figure 4. Insect galls of North Pantanal in Poconé, Mato Grosso State, Brazil in host plants indicated. Myrtaceae. A–B. *Campomanesia* sp. C–D. *Eugenia* cf. *florida*, E. *Eugenia* sp., F. *Myrcia neolucida*, G–L. *Psidium guineense*, M. Myrtaceae sp., Polygonaceae. N–O. *Symmeria paniculata*, P. *Polygonum acuminatum*, Q. *Triplaris gardneriana*, R–S. *Coccoloba cujabensis*, Rubiaceae. T. *Amaioua intermedia*, U. *Psychotria* sp., Salicaceae. V. *Casearia* sp., Sapindaceae. X. *Magonia pubescens*, Z. *Matayba* sp. 3.

Figure 5. Insect galls of North Pantanal in Poconé, Mato Grosso State, Brazil in host plants indicated. Sapindaceae. A. *Paullinia* sp., B–D. *Serjania caracasana*, E–H. *Serjania erecta*, I. *Serjania sp.*, Smilacaceae. J–K. *Smilax sp.*, Solanaceae. L. *Cestrum* sp., Symplocaceae. M. *Symplocos* sp., Unidentified. N. Unidentified sp. 1, O. Unidentified sp. 2, P–R. Unidentified sp. 3, S. Unidentified sp. 4, T. Unidentified sp. 5.

Table 2. Richness of gall morphotypes and plant super-hosts families and species from localities in Brazilian Pantanal areas.

Inventories	Locality/ Brazilian States	Biome	Richness				Super-host	
			Gall morphotypes	Plant species	Plant family	Average morphotype/ plant species	Families	Species
Urso-Guimarães, Koch & Castelo (this study)	Poconé/MT	Pantanal (Gallery Forest, Chaco)	91	54	19	1.7	Fabaceae (19), Myrtaceae (14), Sapindaceae (11)	*Psidium guineense* (N=7), *Combretum laxum* (N=5), Unidentified sp. 3 (N=5)
Julião et al. (2002)	Abobral region/MS	Pantanal	133	75	37	1.8	Bignoniaceae (18), Fabaceae (13), Sapindaceae (11), Hippocrateaceae (7)	*Hippocratea volubilis* (6), *Inga vera* (5)
Urso-Guimarães et al. (2017)	Corumbá, Porto Murtinho/ MS	Pantanal (Gallery Forest, Chaco)	52	38	16	1.4	Fabaceae (12), Sapindaceae (11), Apocynaceae (5)	*Serjania* sp. 2 (4)

Table 3. Gall makers and associated fauna in galls of North Pantanal in Poconé, Mato Grosso State, Brazil.

Host plat family	Host plant species	Gall inducer	Associated fauna
Anacardiaceae	*Astronium graveolens*	Diptera, Cecidomyiidae	not observed
Chrysobalanaceae	*Couepia* sp.	Hymenoptera	not observed
Chrysobalanaceae	*Licania* sp.	Hemiptera, Cicadidae	not observed
Combretaceae	*Combretum laxum*	Diptera, Cecidomyiidae	not observed
Combretaceae	*Combretum laxum*	Hymenoptera, Perilampidae	not observed
Combretaceae	*Combretum laxum*	Diptera, Cecidomyiidae	not observed
Combretaceae	*Terminalia argentea*	Hymenoptera	not observed
Fabaceae	*Bauhinia pentandra*	Hymenoptera, Chalcidoidea	not observed
Fabaceae	*Bauhinia pentandra*	Hymenoptera, Chalcidoidea	not observed
Fabaceae	*Bauhinia platypetala*	Diptera, Cecidomyiidae, *Schizomyia* sp.	not observed
Fabaceae	*Senegalia* sp.	Coleoptera, Curculionidae, Scolytinae	not observed
Lamiaceae	*Aegiphila* sp. 1	Diptera, Cecidomyiidae	Hymenoptera, Chalcidoidea; Hemiptera
Lamiaceae	*Aegiphila* sp. 2	Diptera, Cecidomyiidae	not observed
Malpighiaceae	*Byrsonima crassifolia*	Thysanoptera, Phlaeothripidae	not observed
Malpighiaceae	*Byrsonima cydoniifolia*	Diptera, Cecidomyiidae	not observed
Moraceae	*Ficus* sp.	Diptera, Cecidomyiidae	not observed
Myrtaceae	*Eugenia* cf. *florida*	Diptera, Cecidomyiidae, *Bruggmanniella* sp.	Coleoptera, Curculionidae; Hymenoptera, Ichneumonidae; Hemiptera, Cicadellidae
Myrtaceae	*Eugenia* cf. *florida*	Diptera, Cecidomyiidae, Oligotrophini	Psocoptera
Polygonaceae	*Symmeria paniculata*	Diptera, Cecidomyiidae	Hemiptera, Cicadelidae
Rubiaceae	*Amaioua intermedia*	Diptera, Cecidomyiidae	not observed
Rubiaceae	*Psychotria* sp.	Diptera, Cecidomyiidae	not observed
Salicaceae	Casearia sp.	Hemiptera	not observed
Sapindaceae	*Serjania caracasana*	Thysanoptera, Phlaeothripidae	not observed
Sapindaceae	*Serjania caracasana*	Diptera, Cecidomyiidae, *Youngomyia* sp.	Psocoptera
Solanaceae	*Cestrum* sp.	Diptera, Cecidomyiidae	not observed
Unidentified	Unidentified sp. 1	not observed	Psocoptera
Unidentified	Unidentified sp. 3	Hymenoptera, Torymidae	not observed
Unidentified	Unidentified sp. 4	Diptera, Cecidomyiidae	Hymenoptera
Unidentified	Unidentified sp. 5	Diptera	empty gall

1, Table 3). From the richest plant genera in gall morphotypes, *Bauhinia* L. (Fabaceae) and *Serjania* (Sapindaceae) are species-rich genera. The plant species considered super host were *Psidium guineense* (N=7, 7.7%), *Combretum laxum*, and the Unidentified sp. 3 (N=5, 5.5% each) (Table 2). For the first time, *P. guineense* and *C. laxum* are reported as super hosts of gall morphotypes in the world.

The predominance of galls in leaves and stems with the globoid and lenticular shapes, the green and brown colors and glabrous is a pattern also found in Pantanal Sul-matogrossense (Julião et al. 2002, Urso-Guimarães et al. 2017) and in other biomes (Araújo et al. 2019).

We found 91 morphotypes of galls in 54 host plants, of which 87 are new registers. Only four morphotypes are common to the studies of Julião et al. (2002) and Urso-Guimarães et al. (2017): the lenticular, brown, and glabrous on leaves of *Bauhinia mollis*, the fusiform in stems of *Psidium guineense*, the globoid, green, and glabrous on leaves of *Magonia pubescens* A.St.-Hil., and the globoid, green, and glabrous on leaves of *Serjania caracasana*. Thus, Brazilian Pantanal has 269 morphotypes of galls in 157 plant species, of which only two species are common of the three studies, *Eugenia florida* DC. and *S. caracasana*.The fifteen new records of host plants found in this inventory represent 30% of the total host plant species sampled in the Poconé survey (Table 2).

We also found that only three plant species, *Coccoloba cujabensis*, *Symmeria paniculata*, and *Triplaris gardneriana*, occur in Pantanal and Cerrado areas. These species occur exclusively in Mato Grosso and Mato Grosso do Sul States, which means the insect's interactions and these species are endemic. The low endemicity was expected because the plant species distributed in North Pantanal undergoes other biomes' influence in its composition (Pott et al. 2011).

The interactions among plants and associated entomofauna are still unknown and threatened with extinction due to deforestation. Mato Grosso State is currently one of the agricultural frontiers in Brazil. The maintenance and encouragement of taxonomic studies, such as the SISBIOTA – Diptera Brazil Program (2010-2015), are necessary to understand gall inducers' richness. Before studies funded by the SISBIOTA, only of gall inducers (*Termitomastus leptoproctus* Silvestri, 1901 and *Schizomyia tuiuiu* Urso-Guimarães & Amorim, 2002 – Diptera, Cecidomyiidae) were registered in Mato Grosso State. Three new species of cecidomyiids found in this survey are under the process of description, one species of each of the genera *Bruggmanniella* Tavares, *Schizomyia Kieffer*, and *Youngomyia* Felt.

This inventory became a unique testimony of insect-plant interactions in Pantanal Biome in Brazil that may have been completely devastated by fire in the dry season of 2020. We hope that with its enormous resilience, the Pantanal biome will recover the unique biodiversity lost by fire. We also expected that international organizations help Brazilian institutions to pressure the Federal Government to adopt measures for the conservation of Pantanal, a biome from South America, but is essential for humanity.

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Author Contributions

Maria Virginia Urso-Guimarães: Substantial contribution in the concept and design of the study, data collection, data analysis and interpretation, manuscript preparation, critical revision, adding intellectual content.

Ingrid Koch: Substantial contribution in the data analysis and interpretation, manuscript preparation, critical revision, adding intellectual content.

Ana Carolina Devides Castello: Substantial contribution in the data analysis and interpretation, manuscript preparation, 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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Short Communication

Phoretic association between *Hisonotus chromodontus* (Loricariidae: Hypoptopomatinae) and *Ichthyocladius* sp. (Diptera: Chironomidae) larvae in Amazonian streams

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Abstract: Larvae of non-biting midges in the family Chironomidae can be found in association with several species of fish in the family Loricariidae. In this study, we describe the first record of phoretic interaction between larvae of *Ichthyocladius* sp. and the fish *Hisonotus chromodontus* in streams in the Amazon basin. Between July 2010 and March 2019, fish were collected from three streams of the Teles Pires River basin in the state of Mato Grosso, Brazil. We investigated the attachment site of chironomid larvae on the body of fish and the frequency of attachment. A total of 1.241 specimens of *H. chromodontus* were collected, among which nine hosts were found carrying in the ventral region a single *Ichthyocladius* sp. specimen. All *Ichthyocladius* sp. were attached to a spicule of fish between the pectoral and pelvic fins, in which they were observed at the fourth developmental stage at the beginning of the cocoon construction (1.50 mm). In addition, a pre-pupa larva (2.60 mm) and an empty cocoon (2.50 mm) were reported. The Loanda stream had the highest occurrence of this type of association (of 12 fish examined, three had larvae). The other two streams reported a lower occurrence: the Baixada Morena stream had three fish associated with larvae amongst 1105 fish examined, whereas the Selma stream had three out of 124 fish infested by larvae. The occurrence of only one larva per host can be related to the small body area of the host fish (average standard length = 26.60 mm and average weight = 0.31 g). We observed that the larvae prefer fixation sites in the vicinity of the pectoral and pelvic fin of the fish, which is presumably associated with the fact that chironomids feed on algae and debris suspended by the movement of loricariids. These streams differ with respect to the presence of riparian forests, which may affect resource availability and thereby influence ecological interactions between the species.

Keywords: *Interspecific Interaction; Invertebrate–fish Interaction; Phoresy; Tapajos River basin; Non-biting midges; Siluriformes.*

Associação forética entre *Hisonotus chromodontus* (Loricariidae: Hypoptopomatinae) e larvas de *Ichthyocladius* sp. (Diptera: Chironomidae) em riachos amazônicos

Resumo: Larvas de mosquitos da família Chironomidae podem ser encontradas em associação com várias espécies de peixes da família Loricariidae. Neste estudo, descrevemos o primeiro registro de interação forética entre larvas de *Ichthyocladius* sp. e o *Hisonotus chromodontus* em riachos da bacia amazônica. Entre julho de 2010 e março de 2019, foram coletados peixes em três riachos da bacia do rio Teles Pires, no estado de Mato Grosso, Brasil. Nós investigamos o local de fixação das larvas de quironomídeos no corpo dos peixes e a frequência da fixação. Um total de 1.241 espécimes de *H. chromodontus* foram coletados, entre os quais nove hospedeiros foram encontrados carregando, na região ventral, um único espécime de *Ichthyocladius* sp. Todos os *Ichthyocladius* estavam aderidos a uma espícula do peixe entre as nadadeiras peitoral e pélvica, onde foram observados no quarto estágio de desenvolvimento, no início da construção do casulo (1,50 mm), além de uma pré-pupa (2,60 mm) e um casulo vazio (2,50 mm). O riacho Loanda apresentou a maior ocorrência de hospedeiros na associação (de 12 peixes examinados, três estavam com larvas) e o menor registro foi para o riacho Selma (dos 1105 peixes examinados, três estavam infestados). A ocorrência de apenas uma larva por hospedeiro pode estar relacionada à pequena área corporal do peixe hospedeiro (comprimento padrão médio = 26,60 mm e peso médio = 0,31 g). Observamos que as larvas preferem locais de fixação nas proximidades da nadadeira peitoral e pélvica dos peixes, o que está presumivelmente associado ao fato dos quironomídeos se alimentarem de algas e detritos suspensos pelo movimento dos loricarídeos. Os riachos diferem com relação à presença de matas ciliares, que podem afetar a disponibilidade de recursos e, assim, influenciar as interações ecológicas entre as espécies.

Palavras-chave: *Interação Interespecífica; Interação Invertebrado-peixe; Forésia; Bacia do rio Tapajós; Mosquitos; Siluriformes.*

Introduction

Ecological interactions can be considered harmonious, such as commensalism and mutualism, or discordant, such as parasitism and predation (Ricklefs & Relyea 2016). Phoresy is a form of temporary interspecific commensalism, in which a phoretic organism enters an association with another organism for purpose of dispersal, with no harm being caused to its host or disruption of trophic processes (Hunter & Rosario 1988, Houck & O'Connor 1991, Bartlow & Agosta, 2021**).** Phoretic interactions have been documented mostly in terrestrial taxa (Badets & Du Preez 2014, White et al. 2017, Bartlow & Agosta, 2021). In freshwater environments, porpoises carrying candirus fish (Araújo-Wang et al. 2019), several species of fish carrying candirus fish (Zuanon & Sazima 2005, Adriaens et al. 2010), and mussel larvae as phoretic organisms on fish (Modesto et al. 2018) have been recorded. Furthermore, interactions between non-biting midges larvae and freshwater fish provide examples of phoretic associations between fish and insects (Fittkau 1974, Pinder 1986, Mendes et al. 2004, Trivinho-Strixino 2014).

Non-biting midges in the family Chironomidae (Diptera) can typically be found in sediments and on aquatic vegetation but can also enter phoretic associations with other aquatic organisms (Trivinho-Strixino 2014). For example, the larvae of *Ichthyocladius* Fittkau 1974 (Chironomidae: Orthocladiinae) and others larvae midges belonging to this group have been observed in association with the siluriformes fish of families Astroblepidae, Loricariidae, and Trichomycteridae (Fittkau 1974, Pinder 1986, Mendes et al. 2004, Trivinho-Strixino 2014). Loricariidae fish (armored catfish) have been described as hosts of *Ichthyocladius* larvae, including *Ancistrus*, *Chaetostoma*, *Corumbataia*, *Harttia*, *Hemipsilichthys*, *Hisonotus*, *Hypostomus*, *Kronichthys*, *Neoplecostomus*, *Otothyropsis*, *Pareiorhaphis*, and *Pareiorhina* (Vilella 2002, Mendes 2004, Roque et al. 2004, Sydow et al. 2008, Henriques-Oliveira & Nessimian 2009, Dala-Corte & Melo 2018, Mattos et al. 2018). The first observations of phoretic interactions between loricariids and *Ichthyocladius* larvae were recorded in rivers of the Amazon basin (Freihofer & Neil 1967), whereas in Brazil, other occurrences have recorded in the south (Vilella 2002, Sydow et al. 2008, Dala-Corte & Melo 2018) and southeast Atlantic watersheds (Mendes 2004, Roque et al. 2004, Henriques-Oliveira & Nessimian 2009, Mattos et al. 2018).

During previous ecological studies on streams in the Teles Pires River sub-basin, we collected specimens of the loricariid fish *Hisonotus chromodontus* Britski & Garavello 2007 (Loricariidae: Hypoptopomatinae), a species restricted to the Tapajos basin, Amazonia (Dagosta & de Pinna 2019), some of which were unexpectedly found to be transporting *Ichthyocladius* sp. larvae. In the present study, we provide the first record of the phoretic association between *H. chromodontus* and *Ichthyocladius* sp. in streams of the South Amazon.

Material and Methods

1. *Study area*

Between July 2010 and March 2019, we collected fish from three first- to third-order streams, the Loanda (11°25′33.1″S and 55°16′39.3″W), Baixada Morena (11°29′43.9″S and 55°21′44.0″W) and Selma (11°36′03.2″S and 55°25′41.5″W), which are tributaries of the right bank of the Teles Pires River and differ among them in relation to preservation. The Loanda stream is characterized by an intact riparian forest, sandy substrate, and an absence of macrophytes (Cabeceira 2014), whereas the Selma stream lacks riparian forest and has areas of rapids, sand, and pebble substrate, and supports the growth of macrophytes. The Baixada Morena stream is also devoid of riparian forest in the area sampled and is considered to have undergone considerable environmental damage.

2. *Fish collection and recording of fish–insect interactions*

Fish were collected by two or three individuals using 0.5-mm-mesh nets. The collected specimens were euthanized with Eugenol anesthetic, fixed in formalin solution (10%), and subsequently transferred to 70% ethanol (modified from Mendonça et al. 2005). Voucher specimens were deposited in the fish collection of the Tropical Ichthyology Laboratory (LIT) of the Federal University of Mato Grosso, Sinop University Campus (voucher specimens with fixed larvae: LIT 3143, LIT 3144 and LIT 3145), and at the Ichthyological Collection of the Center of Research in Limnology, Ichthyology and Aquaculture (NUPELIA) of the State University of Maringá (voucher specimens: NUP 22680). The fish were weighed (g), measured (mm), examined for the presence of chironomid larvae, and photographed with the aid of Leica S9 stereomicroscope (×50 magnification) to record development (larval and pupal phases) (Trivinho-Strixino 2014) and the sites of attachment of phoretic organisms on fish.

The larvae were identified to the genus level by using morphological character-based identification keys presented by Trivinho-Strixino

(2014). According to Trivinho-Strixino (2014) and Luiz Carlos de Pinho (personal communication) the identification of immature chironomid species (larvae and pupae), is only possible through the observation of the male genitalia adult.

Results

A total of 1.241 specimens of *H. chromodontus*, with mean standard lengths and weights ranging from 27 to 38 mm and 0.19 to 0.38 g, were collected. Among these, nine fish were found to be carrying a single *Ichthyocladius* sp. larva. The Loanda and Selma streams had the highest (of 12 fish examined, three had larvae) and the smallest (of the 1105 fish examined three fish were infested) occurrence of the interaction, respectively (see Table 1). All chironomids were observed in the ventral region between the pectoral and pelvic fins to the host (Figure 1 a), attached by fixing the distal part of the abdomen (prolegs) to the fish spicule, leaving the larval head free (Figure 1b). Attached *Ichthyocladius* sp. were observed at the fourth developmental stage at the beginning of the cocoon construction (Figure 2 a and b). In addition, we found a pre-pupa larva (Figure 2 c) and an empty cocoon (Figure 2 d).

Discussion

We report here the first record of phoresy between insect-fish for the South of the Brazilian Amazon, involving a loricariid host with restricted distribution in the Tapajós River basin. Free-living larvae of chironomidae (Figure S1) has limited dispersal capacity and the interactions with a fish can benefit it with no detrimental effects on their fish hosts. The phoresy recorded in this study represents a commensal interaction that benefits chironomid larvae (White et al. 2017, Silknetter et al. 2020). The findings of the present study, in which we detected only a single larva attached to each host, contrast with those of other studies that have reported means of 12.21 (Sydow et al. 2008) and 13.2 (Mattos et al. 2018) *Ichthyocladius* larvae associated with loricariid fish species. These studies have described loricariid hosts with relatively large body lengths of 104 mm (Sydow et al. 2008), 93 mm (Dala-Corte & Melo 2018), and 63 mm (Mattos et al. 2018), compared with the maximum length of 43 mm SL for the *Hisonotus chromodontus* specimens collected in the three streams we investigated.

Sydow et al. (2008) examined the relationship between the total length of three species of loricariid (*Ancistrus* cf. *multispina* (104.2 mm), *Pareiorhaphis hypselurus* (62.5 mm), and *Pareiorhaphis nodulus* (37.6 mm)) and the quantity of associated chironomids. The larval density is higher in larger fish; for example, *P. nudulus* (a host with two larvae) had a mean length three times shorter than that of the other two species, as *Pareiorhaphis hypselurus* and *Ancistrus* cf. *multispina*, which had the density of larvae of 2.57 and 12.21, respectively. Similarly, Dala-Corte & Melo (2018) examined the distribution of *Ichthyocladius* larvae on the loricariid *Pareiorhaphis hypselurus* and found that smaller (36 mm) and larger (93 mm) fish had correspondingly small and large chironomid infestations, respectively. Large-sized hosts can carry a larger number of chironomid larvae on their body because they have a greater surface area, as well as a greater swimming range, thereby providing phoretic organisms with access to the larger amounts of suspended food particles (Sydow et al. 2008, Dala-Corte & Melo 2018).

The *Ichthyocladius* larvae associated with fish gain advantages with respect to diet (continuous access to debris and algae available on the host body), mobility (avoiding unfavorable habitat sites), protection against predators (larvae are camouflaged by the host) and environmental disturbance (commensal species vulnerable to environmental disturbance exploit hosts to evade areas exposed to such disturbance) (Tokeshi 1993). As observed herein, larvae prefer attachment sites in the vicinity of pectoral and pelvic fin of fish, which is presumably associated with the fact that chironomids feed on algae and debris suspended by the movement of loricariids (Henriques-Oliveira et al. 2003, da Silva et al. 2008, Sydow et al. 2008, Mattos et al. 2018). *Ichthyocladius* larvae have thick posterior pseudopods bearing strong claws that facilitate attachment to the host, and construct cocoons shaped like fish scales attached to the spines of host fish fins (Trivinho-Strixino 2014). In this regard, it can be speculated that the symbionts have preferred sites for attachment on the surface of the host body and that there is competition for these sites. Alternatively, larvae may not show any site-specific preference and colonize all sites equally but remain attached to those sites that offer better resources or protection against predators *(*Dala-Corte & Melo 2018). The dispersal of an organism by phoretic interaction involves locating, fixing and detaching from the host (Bartlow & Agosta 2021). The success of this interaction is clear from our findings, as we found both larvae in the initial fixation phase and an empty cocoon trapped in the host.

Hisonotus species feed on periphyton, with a diet composed of diatoms, Chlorophyceae, and organic matter (Casatti 2002, Teresa & Casatti 2012), and numerous studies have shown that the availability of periphyton in streams is dependent on riparian coverage and may influence the growth of loricariid fish species with this type of diet (Bojsen & Barriga 2002, Teresa & Casatti 2012, Fernandes et al. 2013, Gomes et al. 2020). Therefore, it is possible that the degradation of the vegetation cover has a negative influence on the ecological interactions of the streams studied here.

Supplementary Material

The following online material is available for this article:

Table 1. Occurrence of *Ichthyocladius* sp. larvae on the loricariid *Hisonotus chromodontus* in three streams in the Teles Pires River basin. SL = standard length (mm); min = minimum; max = maximum.

Stream	Number of *H. chromodontus* collected	SL (mm) Average (min–max)	Weight (g) Average (min–max)	Hosts	Larvae
Selma	1105	21.95 (17.83–26.40)	0.19 (0.07–0.32)	3	3
Baixada Morena	124	27.90 (26.73–29.31)	0.38 (0.35–0.42)	3	3
Loanda	12	29.90 (26.60–35.10)	0.36 (0.32–0.40)	3	3
Total	1241	26.6	0.311	9	9

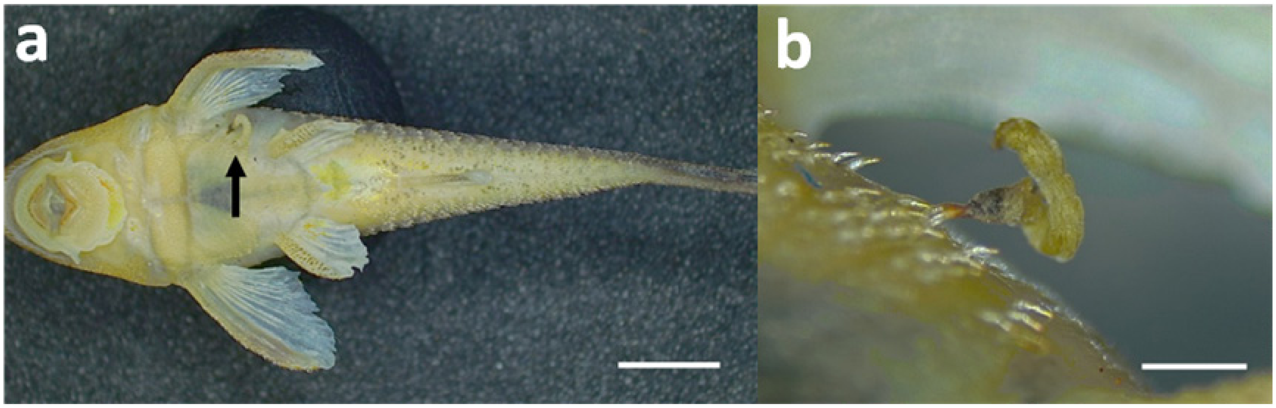

Figure 1. Ventral view of *Hisonotus chromodontus* (26 mm SL and 0.18 g weight) with an arrow indicating the position of a larvae of *Ichthyocladius* sp. between pectoral and pelvic fins, (a) *Ichthyocladius* sp. larva (2.10 mm) attached to a distal part of the abdomen (proleg) to a spicule (b). Scale bar: 1 mm.

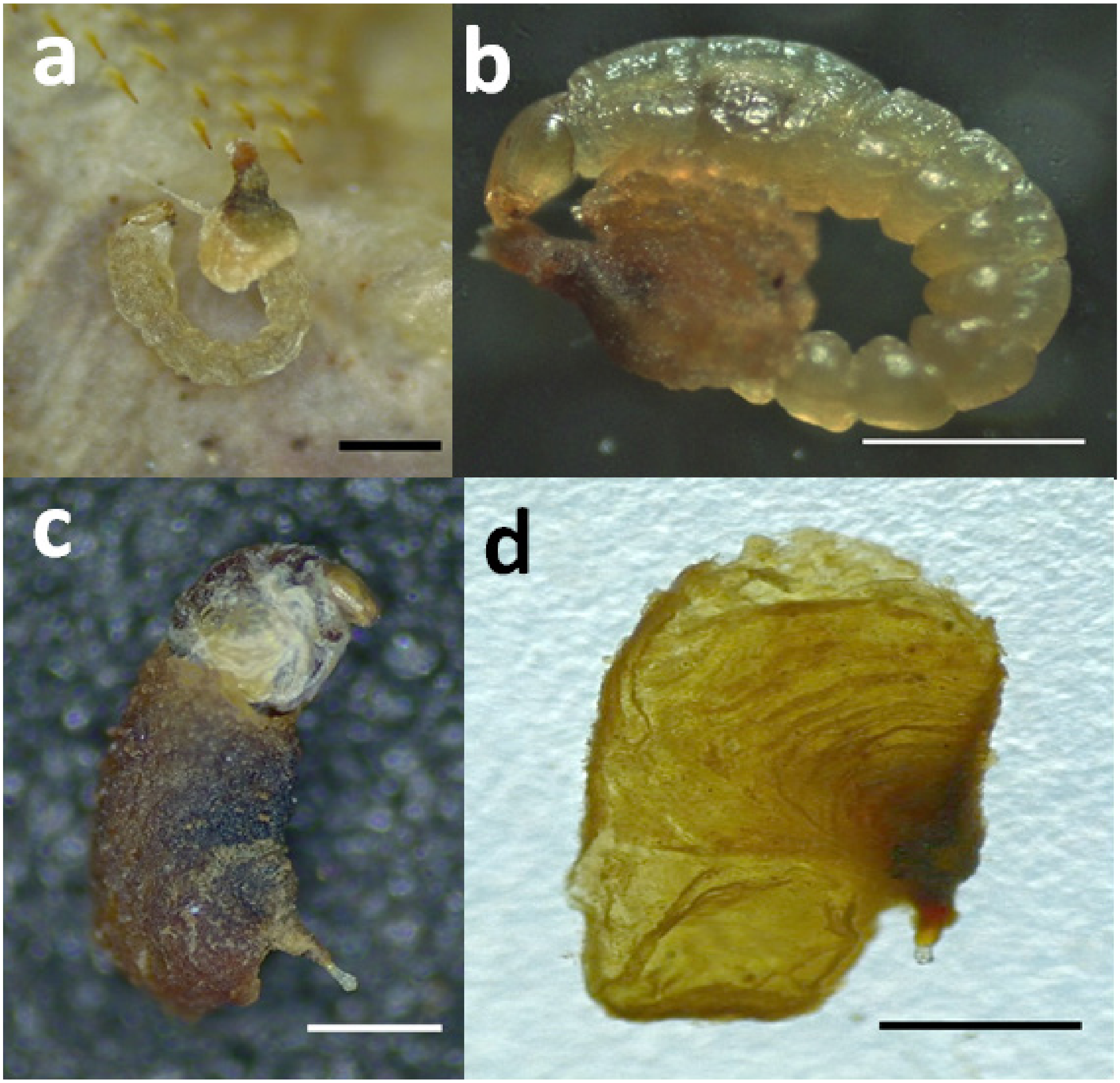

Figure 2. *Ichthyocladius* sp. development phases: (a) larva (1.10 mm) attached on the distal part of the abdomen, (b) initial pupal phase (1.50 mm), (c) prepupal (2.60 mm), (d) empty cocoon (2.50 mm). Scale bar: 1 mm.

Figure S1 - Free-living larvae of *Ichthyocladius* sp. (indicated by arrow) fixed in a submerged log near two specimens of *Hisonotus chromodontus* in an Amazonian stream.

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Author Contributions

Andressa Cristina Costa: Substantial contribution in the concept, design of the study, data collection, data analysis, interpretation and manuscript preparation.

Fábio Martins de Almeida: Substantial contribution in the concept, design of the study, data collection, data analysis and interpretation.

João Otávio Santos Silva: Contribution to data collection, critical revision and adding intellectual content.

Talles Romeu Colaço-Fernandes: Contribution to data collection, critical revision and adding intellectual content.

Lucélia Nobre Carvalho: Substantial contribution in the data analysis, interpretation, manuscript preparation, critical revision, funding acquisition and academic supervision.

Conflicts of Interest

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

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Inventory

Checklist of mammals from Goiás, central Brazil

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Abstract: The state of Goiás, in central Brazil, is covered mainly by the Cerrado domain, with the Alto Paraná Atlantic Forest occupying its central-southern portion. Goiás is one of the 20 Brazilian federative units without a mammal checklist. In this study, we provide the first checklist of mammals from Goiás state. We recorded mammal species based primarily on the analysis of specimens housed in scientific collections as well as on literature with associated voucher material. We listed 191 mammalian species belonging to 125 genera, 31 families and 10 orders, which represents 25.2% of the mammal species occurring in Brazil. The most speciose orders were Chiroptera (90 spp.), followed by Rodentia (43 spp.), Carnivora (19 spp.) and Didelphimorphia (17 spp.). The following orders accounted for a smaller portion of the state diversity: Cetartiodactyla (7 spp.), Cingulata (7 spp.), Primates (4 spp.), Pilosa (2 spp.), Lagomorpha (1 sp.), and Perissodactyla (1 sp.). A total of 28 species (14.7%), mainly represented by medium and large-sized mammals, are nationally threatened while 12 (6.3%) are globally threatened. Our results indicate great portions of the state lacking a proper survey of mammals, especially the northwestern portion. We discuss species richness, distribution and conservation status of the mammals of Goiás state in national and regional scenarios. We highlight the need for mammal inventories based on complementary survey techniques with the collection of vouchers in order to provide karyologic, molecular, morphologic, parasitologic, and ecological data. These informations are the basis for integrative studies that lead to the understanding of current mammalian richness and diversity. Indeed, knowledge on species richness distribution in the state will guide conservation strategies, especially in areas undergoing habitat loss and fragmentation, such as the central-southern portion of Goiás.

Keywords: *Atlantic Forest; Bats; Cerrado; Inventory; Large mammals; Small non-volant mammals.*

Lista de Mamíferos de Goiás, Brasil central

Resumo: O estado de Goiás, no Brasil central, é coberto principalmente pelo domínio do Cerrado, com a Mata Atlântica do Alto Paraná ocupando sua porção centro-sul. Goiás é uma das 20 unidades federativas brasileiras que ainda não possui uma lista de espécies de mamíferos. Neste estudo, apresentamos a primeira lista de mamíferos para o estado. Registramos as espécies de mamíferos com base principalmente na análise de espécimes depositados em coleções científicas, bem como na literatura apresentando material testemunho associado. Listamos 191 espécies pertencentes a 125 gêneros, 31 famílias e 10 ordens, as quais representam 25,2% das espécies de mamíferos que ocorrem no Brasil. As ordens mais especiosas foram Chiroptera (90 spp.), seguida pelas ordens Rodentia (43 spp.), Carnivora (19 spp.) e Didelphimorphia (17 spp.), com as demais ordens respondendo por uma porção menor da diversidade: Cetartiodactyla (7 spp.), Cingulata (7 spp.), Primates (4 spp.), Pilosa (2 spp.), Lagomorpha (1 sp.) e Perissodactyla (1 sp.). Um total de 28 espécies (14,7%), principalmente representadas por mamíferos de médio e grande porte, estão ameaçadas nacionalmente e 12 (6,3%) encontram-se globalmente ameaçadas. Nossos resultados indicaram grandes porções do estado ainda não devidamente pesquisadas em relação aos seus mamíferos, com informações escassas e fragmentadas, principalmente no que diz respeito à sua porção noroeste. Discutimos a riqueza de espécies, a distribuição e o estado de conservação dos mamíferos do estado de Goiás nos cenários nacional e regional. Ressaltamos a importância da realização de inventários que utilizem técnicas complementares de amostragem, incluindo a coleta de material testemunho, proporcionando a obtenção de dados cariotípicos, moleculares, morfológicos, parasitológicos e ecológicos. Estas informações são a base de estudos integrativos, os quais aumentam nossa compreensão a respeito da riqueza e diversidade atual dos mamíferos. O conhecimento a respeito da distribuição da riqueza de espécies em Goiás é essencial para embasar estratégias de conservação, tão necessárias em áreas que vem sofrendo com a perda e fragmentação de seus hábitats naturais, como a porção centro-sul do estado.

Palavras-chave: *Cerrado; Inventário; Mamíferos de médio e grande porte; Mata Atlântica; Morcegos; Pequenos mamíferos não voadores.*

Introduction

The number of mammalian species has increased through time; currently, more than 6,400 species are recognized worldwide, with the Neotropics considered as the third most species-dense biogeographic region (Burgin et al. 2018; 2019). Within this region, Brazil is the richest country, which might be related to its large area and environmental heterogeneity (Quintela et al. 2020). This diverse country holds 759 native species, distributed in 249 genera, 51 families and 11 orders (Abreu et al. 2020; Quintela et al. 2020).

Although there is an enormous potential to describe new species [*e.g.*, many have been recently surveyed, while many groups need taxonomic reviews (Gonçalves & Oliveira 2014; Nascimento & Feijó 2017; Bezerra et al. 2020)] and a great field for research on their ecology, biogeography, and population genetics, among others, we are facing an unfavorable scenario for conservation biology in the country (Quintela et al. 2020). The Cerrado and Atlantic Forest domains harbor a high mammalian diversity and endemism (Paglia et al. 2012; Gutiérrez & Marinho-Filho 2017; Quintela et al. 2020), and have been severely threatened by anthropogenic impacts, moreover were listed, among only 34 other regions, as biodiversity hotspots for the world conservation (Myers et al. 2000; Mittermeier et al. 2004). More than 80% of the remnants of the Brazilian Atlantic Forest are smaller than 50 ha (Ribeiro et al. 2009), and for the Cerrado, more than 50% of its original area (approximately 2 million km^2) have been converted into pasture and agricultural areas (Klink & Machado 2005; Strassburg et al. 2017).

Considering the large Brazilian territory, its environmental heterogeneity and conservation status, currently only seven federative units have checklists of mammals available: Amapá (Silva et al. 2013), Espírito Santo (Moreira et al. 2008), Mato Grosso (Brandão et al. 2019), Mato Grosso do Sul (Cáceres et al. 2008; Tomas et al. 2017), Santa Catarina (Cherem et al. 2004), São Paulo (Vivo 1998; Vivo et al. 2011), and Rio de Janeiro (Rocha et al. 2004). A checklist is the first step in order to plan inventories, conduct biogeographic and systematic studies, and develop conservation actions; thus, a review of the mammal records for each Brazilian state is warranted (Brandão et al. 2019). In this study, we provide the first checklist of mammals from Goiás state, with comments on their distribution and conservation.

Material and Methods

1. *Study site*

The state of Goiás is located in central Brazil (12° to 19° S, 46° to 53° W) and is represented by two ecoregions: Cerrado and Alto Paraná Atlantic Forest (Dinerstein et al. 2017) (Figure 1). Goiás has the seventh largest territorial extension among the 27 federative units in the country, with approximately 340,106 km^2 (IMB 2020), representing 4% of the national territory. It is almost entirely characterized by the Cerrado domain, with its remnants being severely fragmented mainly by cattle ranching and agriculture activities (Prado et al. 2012), as well as other threats such as hydroelectric dams and mining (Melo & Soares 2005).

The Brazilian savanna is composed of a continuous mosaic represented by different phytophysiognomies ranging from grasslands to closed canopy forests (Eiten 1972). However, the distribution of these phytophysiognomies throughout the domain is not equitable (*e.g.*, while gallery forests represent only 5% of the total area of the Cerrado, the *stricto sensu* cerrados cover about 70% of the landscape) (Ribeiro et al. 1998; Oliveira et al. 2017). The Cerrado in Goiás also ranges through a great elevational gradient, from valleys and depressions

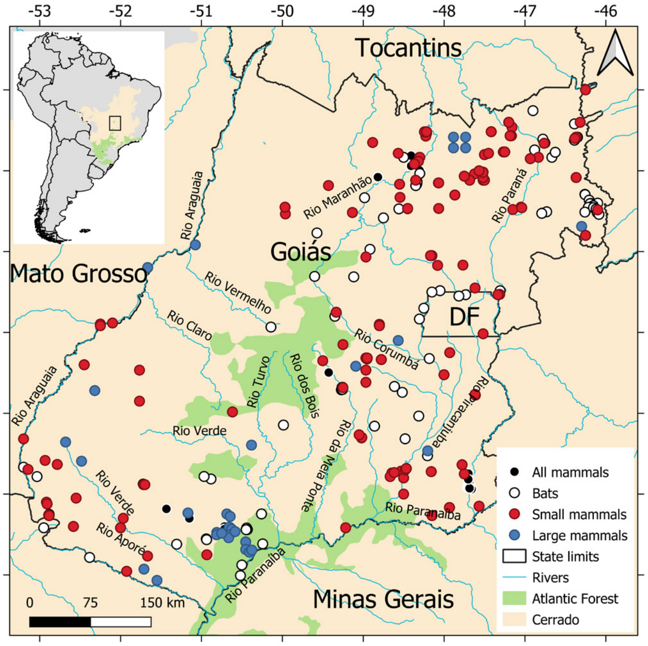

Figure 1. Map of Goiás state in central Brazil. Sampling points for mammalian species according to records listed in Table 1 (see Supplementary Material S1 for access to the references and coordinates). Ecoregions and rivers (adapted from Dinerstein et al. 2017). Black lines indicate the political geographic boundaries.

mainly located at its western portion at the Araguaia river margins, to highlands located at the Brazilian Central Plateau in its central and eastern portions (Cardoso & Marcuzzo 2014). The Chapada dos Veadeiros and Serra Geral do Paranã, at its northeastern border, are the most elevated regions, ranging from 800 to 1,700 meters high (NASA 2002). Three main hydrographic basins delimit and cross the Cerrado in Goiás: the Araguaia at west, Tocantins at central, and São Francisco at its eastern border. The other ecoregion, the Alto Paraná Atlantic Forest, is represented by forest patches in its central-southern portion (Figure 1), mainly located at river margins and valleys of the Paraná hydrographic basin, also at the Brazilian Central Plateau slopes (RADAMBRASIL 1982). Goiás climate is classified as Köppen's Aw – tropical with dry winters (Setzer 1966). The mean annual temperature is around 23ºC, and the mean annual pluviosity around 1,500 mm. However, the temperature and rainfall regime define two distinct seasons: the hot and wet season during the months of October to April, with temperatures around 26-27ºC, concentrating 85% of the rainfall; and the cold and dry season, ranging from May to September, with a total pluviosity around 200 mm, and mean temperatures around 21ºC (Cardoso & Marcuzzo 2014).

These environmental features, together with the climatic fluctuations during the Tertiary and Quaternary periods, have shaped the biogeography and evolutionary history of the Cerrado, leading to the great biodiversity and endemism currently found, with the neighboring forested domains playing a major role (Da Silva & Bates 2002; Werneck 2011).

2. *Data collection*

We recorded mammal species based primarily on the analysis of specimens housed in mammalian scientific collections: American Museum of Natural History, New York, USA (AMNH); Laboratório de Biodiversidade Animal, Universidade Federal de Jataí, Goiás, Brazil (CJ); Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, Instituto Oswaldo Cruz, Fiocruz, Rio de Janeiro, Brazil (LBCE); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MN); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Universidade de Brasília, Brasília, Brazil (UnB, CMVUNB [Coleção de Mamíferos Voadores da Universidade de Brasília]); Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (UFMG); Universidade Federal da Paraíba, João Pessoa, Brazil (UFPB). We tried to include at least one voucher per species to attest the presence of each taxon in the state (see Table 1).

We also searched for articles about mammals from Goiás in the following databases: Scientific Eletronic Library Online (Scielo, www.scielo.org), Web of Science (WoS, http://portal.isiknowledge.com), Scopus® (www.scopus.com) and Periódicos CAPES (http://www.periodicos.capes.gov.br/). The combination of the keywords "Goiás AND mammals", "Cerrado AND mammals", "savanna AND mammals" were used. We also used the database of the Brazilian Digital Library of Theses and Dissertations of the Brazilian Institute of Sciences and Technology (BDTD 2020). The bibliography with voucher material (records based on photographic evidences – of camera trap, tracks or direct observations - were also considered as vouchers in the case of medium and large-sized mammals) were cited in Table 1 and included as Supplementary Material (S1). The recorded localities were classified by mammal group (bats, small non-flying mammals and medium and large mammals) and plotted in a map (Figure 1) in order to give a general picture of the surveyed areas in Goiás state.

We followed the updated and annotated checklists of mammals from Brazil (Abreu et al. 2020; Quintela et al. 2020) for taxonomic hierarchical categories and nomenclature of the mammal taxa. Since these checklists differ in the treatment of some taxa, we cited our decisions bellow. We used the name Cetartiodactyla Montgelard, Catzeflis & Douzery, 1997 for the order including members of Artiodactyla Owen, 1848 and Cetacea Brisson, 1762; we used the name *Dicotyles* Cuvier, 1816 for the genus of the collared peccary according to Acosta et al. (2020); both decisions followed Abreu et al. (2020). For the taxonomic nomenclature of Chiroptera we followed Garbino et al. (2020). We considered *Conepatus amazonicus* Hershkovitz, 1994 as a valid taxon; we also treated *Cabassous squamicaudis* (Lund, 1845) as a valid species; both decisions followed Quintela et al. (2020). Here we used the concept of *Marmosa demerarae* (Thomas, 1905) of Silva et al. (2019a) following Quintela et al. (2020). We treated *Calomys mattevii* Gurgel-Filho, Feijó & Langguth 2015 as a junior synonym of *C. expulsus* (Lund, 1840), according to Gutiérrez & Marinho-Filho (2017); *Sylvilagus minensis* as a valid species based on Ruedas et al. (2017) and Silva et al. (2019b); and we did not treat *Galea flavidens* as valid, according to Bezerra (2008), differing from the previous checklists. The concept of *Holochilus sciureus* follows the recent study of Prado et al. (2021). Conservation statuses are based on the Brazilian (ICMBio/MMA 2018) and international (IUCN 2020) red lists of threatened species.

Results and Discussion

A total of 191 mammalian species, distributed in 125 genera, 31 families and 10 orders were recorded for Goiás state. The richest order is Chiroptera, with 90 species, followed by Rodentia (43 spp.), Carnivora (19 spp.), and Didelphimorphia (17 spp.). The other orders comprise less diverse groups: Cetartiodactyla (7 spp.), Cingulata (7 spp.), Primates (4 spp.), Pilosa (2 spp.), Lagomorpha (1 sp.), and Perissodactyla (1 sp.) (Table 1). These results corroborate the richness pattern found in Brazil and in the world, where the most diverse mammals are bats and rodents (Burgin et al. 2018; Abreu et al., 2020; Quintela et al. 2020), as well as the pattern found in the Cerrado domain, where Chiroptera represents the richest order followed by the Rodentia, Didelphimorphia and Carnivora (Carmignotto et al. 2012). However, bats presented a much higher proportion in the state (47%) compared to the Cerrado (35%), while the opposite trend was found for rodents (22% in Goiás and 34% for the Cerrado), evidencing the lack of studies on this latter group in the state.

A total of 28 species (14.7%) are included in some national threat category (four as endangered – one armadillo, one bat, two rodents - and 24 as vulnerable – one marsupial, one armadillo, one anteater, five bats, one primate, two rodents, nine carnivores, a tapir, two deers, one peccary), while 12 species (6.3%) are globally threatened (three as endangered and nine as vulnerable), 10 (5.2%) are considered as Near Threatened (NT), and 12 (6.3%) as Data Deficient (DD), with this later category mostly represented by rodents and bats (Table 1). The high percentage of threatened and DD species highlight the need to increase our efforts regarding further studies and conservation of target mammalian species and/or poorly surveyed regions in the state.

1. *Didelphimorphia*

We recorded 10 genera and 17 species from the family Didelphidae for Goiás state. These taxa include members from two subfamilies: Caluromyinae (2 spp.) and Didelphinae (15 spp.), as well as from three Didelphinae tribes: Marmosini (6 spp.), Didelphini (5 spp.) and Thylamyini (4 spp.). These numbers represent 26% of the 65 Brazilian didelphids (Abreu et al. 2020) and equates richness with other Brazilian states, such as Mato Grosso do Sul (17 spp.– Tomas et al. 2017) and Rio de Janeiro (14 spp. – Rocha et al. 2004).

In relation to general distribution patterns, 53% of these taxa (9 spp.) are widely distributed, and shared between the Cerrado and forested domains, such as the Amazonian and Atlantic Forests. This is the case of *Caluromys lanatus*, *C. philander*, *Chironectes minimus*, *Marmosa murina*, *M. demerarae*, *M. paraguayana*, *Monodelphis americana*, *Philander canus* and *P. quica*. The other half (47% - 8 spp.) is represented by Cerrado endemics (*Thylamys velutinus*) and by taxa shared with other open formations, such as the Caatinga, Pantanal and Chaco, which include *Cryptonanus chacoensis*, *Gracilinanus agilis*, *Didelphis albiventris*, *Lutreolina crassicaudata*, *Monodelphis domestica*, *M. kunsi* and *Thylamys karimii*. These data reveal the composite nature of the didelphid fauna of the state, characterized by inhabitants of forested and open formations, due to the presence of a vegetation mosaic, typical of the Cerrado domain (Carmignotto et al. 2012), and the semideciduous seasonal forest fragments, which still persist in the state (Ribeiro & Walter 2008; IBGE 2011).

Considering the local distribution patterns, we can cite six didelphids that are rare in Goiás, with few records restricted to different portions of the state: *Marmosa paraguayana* and *Philander quica*, both widely distributed in the Atlantic Forest of southeastern Brazil, are restricted to the southeast of Goiás (Carmignotto 2005; Silva et al. 2019a), suggesting a closer relationship between this region and the Atlantic Forest; *Caluromys philander* and *Monodelphis americana*, which occur on both forested domains (Amazon and Atlantic Forest), present few and scaterred records in southwestern (only *Caluromys*), central and northern portions of the state (Carmignotto 2005; Cáceres et al. 2008; Pavan et al. 2014); *Lutreolina crassicaudata*, a marsupial with a disjunct distribution in South America, is restricted to its southern portion (Cáceres et al. 2008; Carmignotto et al. 2014); and *Thylamys velutinus*, a Cerrado endemic species, is restricted to southwestern and northeastern portion of the state, in two protected areas (Parque Nacional das Emas and Parque Nacional da Chapada dos Veadeiros) (Bonvicino et al. 2002, 2005; Carmignotto & Monfort 2006; Carmignotto et al. 2014). Besides the restricted distribution in the state, this latter species is also threatened in Brazil, classified as vulnerable (Rossi et al. 2018). *Thylamys karimii*, although presenting a wider distribution, is also treated as vulnerable at the IUCN Red List (Carmignotto et al. 2016). In the case of *L. crassicaudata*, it is also important to note that the records from Goiás delimit the northeastern range of the southern portion of its distribution in South America (Martínez-Lanfranco et al. 2014).

The richest didelphid communities were found within conservation units, such as the Parque Nacional das Emas (10 spp.– Carmignotto et al. 2014), Parque Nacional da Chapada dos Veadeiros (8 spp.– Bonvicino et al. 2002; 2005), Parque Estadual da Serra de Caldas Novas (6 spp.– Carvalho et al. 2002; Costa et al. 2003; Carmignotto 2005), and areas very well sampled, such as the region of the Hydroelectric dam of Serra da Mesa (11 spp.– Carvalho et al. 2002; Costa et al. 2003; Carmignotto 2019) and the region of Anápolis (7 spp. – Carmignotto 2005). So, the majority of the records were based on few and well sampled localities, ranging from six to 11 didelphids, while the other regions of the state are still poorly sampled (most of them with records of only one species) (Carmignotto 2005).

Indeed, there are some didelphid taxa that need additional taxonomic comments: *Cryptonanus chacoensis* has proven to be a species complex, composed of very similar taxa in morphology, but distinct at molecular levels, with at least three putative species for the state (Carmignotto et al. 2014; Fegies et al. in press). The cited records for the state are all part of *C. chacoensis* complex (see de la Sancha and D'Elía 2014), including those cited as *G. emiliae* by Carvalho et al. (2002) and as *C. agricolai* (Gardner 2008; Gomes et al. 2015). Recent revisionary studies on the genus *Marmosa* subgenus *Micoureus* have also shown genetically and geographically structured populations within *M. demerarae* (Silva et al. 2019a), with populations from central Brazil treated as distinct taxa, such as *M. limae* Thomas, 1920 by Voss et al. (2020) and Abreu et al. (2020), or *M. domina* Thomas, 1920 by Bonvicino *et al.* (2021). For *Philander*, molecular and morphological studies have also shown that populations from central Brazil can be treated as a distinct taxon: *P. canus*, but the limits of the geographic distribution between this species and *P. quica*, the species from southeastern Brazil, are not delimited yet. Both species are recorded in Goiás, but several records in the state need to be reexamined based on molecular and morphological grounds (Costa 2003; Voss et al. 2018).

2. *Cingulata*

We recorded seven species of Cingulata for Goiás state, wich represents 58.3% of the species listed for Brazil (Quintela et al. 2020). According to other Brazilian states' checklists, armadillos range from five species in São Paulo (Vivo et al. 2011) and Amapá (Silva et al. 2013), to nine species in Mato Grosso (Brandão et al. 2019). The occurrence of the southern three-banded armadillo *Tolypeutes matacus* was mentioned in an interview for the region of the Parque Nacional das Emas, but only in the past (Rodrigues et al. 2002). Considering that there is no reliable record or voucher material for the species in Goiás, *T. matacus* was not included in the list.

The largest populations of Brazilian three-banded armadillo *Tolypeutes tricinctus* occurs in areas of Bahia on the border with Goiás

Table 1. Checklist of mammals from Goiás state, Brazil. Records are based primarily on the analysis of specimens housed in scientific collections (numbers between brackets) and on literature with associated voucher material (numbered citations). Conservation statuses are based on the Brazilian and international red lists of threatened species (ICMBio/MMA 2018 and IUCN 2020, respectively). Acronyms for conservation status categories: DD = data deficient, EN = endangered, NT = near threatened, P/R = pending (re)evaluation, VU = vulnerable. For scientific collections acronyms, please see Material and Methods.

Taxon	Common Name	Record	ICMBio	IUCN
DIDELPHIMORPHIA Gill, 1872				
DIDELPHIDAE Gray, 1821 (17 species)				
Caluromys lanatus (Olfers, 1818)	Brown-eared Woolly Opossum	18, 82, 103 [MN 20963, UnB 2564]		
Caluromys philander (Linnaeus, 1758)	Bare-tailed Woolly Opossum	82, 83 [MZUSP 1160]		
Chironectes minimus (Zimmermann, 1780)	Water Opossum	13, 19, 80, 82, 84 [MN 37815]		
Cryptonanus chacoensis (Tate, 1931)	Chacoan Gracile Opossum	13, 101 [CRB 3067]		
Didelphis albiventris Lund, 1840	White-eared Opossum	3, 13, 18, 19, 79, 80, 82, 98 [MN 43054, MN 46514, UnB 1119]		
Gracilinanus agilis (Burmeister, 1854)	Agile Gracile Opossum	3, 13, 18, 19, 79, 81, 82, 83, 88, 101 [MN 46574, MN 67080, UnB 1198]		
Lutreolina crassicaudata (Desmarest, 1804)	Little Water Opossum	13, 19, 82, 83 [MN 71673, UnB 1927]		
Marmosa demerarae (Thomas, 1905)	Woolly Mouse Opossum	3, 79, 80, 82, 87 [MN 46883, MN 67082]		
Marmosa murina (Linnaeus, 1758)	Linnaeus's Mouse Opossum	13, 19, 82, 83, 102 [UnB 2551]		
Marmosa paraguayana (Tate, 1931)	Tate's Woolly Mouse Opossum	87 [UnB 2987]		
Monodelphis americana (Müller, 1776)	Faint-striped Opossum	3, 82, 85 [MN 46570]		
Monodelphis domestica (Wagner, 1842)	Gray Short-tailed Opossum	3, 13, 18, 79, 80, 82, 85, 90, 100 [MN 67084, MN 46574, MN 46583]		
Monodelphis kunsi Pine, 1975	Pygmy Short-tailed Opossum	13, 18, 80, 82, 85, 90 [MZUSP SAMA 53]		
Philander canus (Osgood, 1913)	Gray Four-eyed Opossum	13, 80, 82, 86, 89 [UnB 1577]	P/R	P/R
Philander quica (Temminck, 1824)	Gray Four-eyed Opossum	82 [UFMG 769]		
Thylamys karimii (Petter, 1968)	Karimi's Fat-tailed Mouse Opossum	4, 80 [MN 36285, MZUSP 32242, UnB 1158]		VU A2c+3c
Thylamys velutinus (Wagner, 1842)	Dwarf Fat-tailed Mouse Opossum	3, 4 [MZUSP 32098, MN 66461]	VU A2c	NT
CINGULATA Illiger, 1811				
CHLAMYPHORIDAE Bonaparte, 1850(5 species)				
Cabassous squamicaudis (Lund, 1845)	Southern Naked-tailed Armadillo	16, 19, 21-23, 25 and 77	P/R	P/R
Cabassous tatouay (Desmarest, 1804)	Greater Naked-Tailed Armadillo	2		DD
Euphractus sexcinctus (Linnaeus, 1758)	Yellow Armadillo	1, 2, 12, 16, 19, 21, 23, 25 and 77 [UnB 1628, UnB 2221, UnB 2235]		
Priodontes maximus (Kerr, 1792)	Giant Armadillo	1, 16, 20, 22, 23 and 25	VU A2cd	VU A2cd
Tolypeutes tricinctus (Linnaeus, 1758) *	Brazilian Three-banded Armadillo	78, [Photo (Supplementary Material S2)]	EN A2cd	VU A2cd
DASYPODIDAE Gray, 1821 (2 species)				

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Dasypus novemcinctus Linnaeus, 1758	Nine-banded Armadillo	1, 2, 11, 12, 19, 21, 22, 23, 25, 77, 115 [UnB 1118, UnB 1602, MZUSP 4130, MN 24460]		
Dasypus septemcinctus Linnaeus, 1758	Brazilian Lesser Long-nosed Armadillo	1, 18, 115 [MN 59336]		
PILOSA Flower, 1883				
MYRMECOPHAGIDAE Gray, 1825 (2 species)				
Myrmecophaga tridactyla Linnaeus, 1758	Giant Anteater	1, 2, 11, 12, 16, 17, 19-25 and 77 [MN 55699, UnB 1603-UnB1607]	VU A2c	VU A2c
Tamandua tetradactyla (Linnaeus, 1758)	Southern Tamandua	1, 2, 11, 12, 16, 17, 19, 21, 22, 23, 25, and 77 [UnB 1238, UnB 2063]		
CHIROPTERA Blumech, 1779				
EMBALLONURIDAE Gervais, 1855 (8 species)				
Centronycteris maximiliani (Fischer, 1829)	Maximilian's Shaggy Bat	42		
Diclidurus ingens Hernández-Camacho, 1955	Greater Ghost Bat	65		
Peropteryx kappleri Peters, 1867	Greater Dog-like Bat	42 and 65		
Peropteryx macrotis (Wagner, 1843)	Lesser Dog-like Bat	34, 41, 42, 51 and 52 [CJ 41, CJ 491, 492]		
Peropteryx trinitatis Miller, 1899	Trinidadian Dog-like Bat	65		
Rhynchonycteris naso (Wied-Neuwied, 1820)	Proboscis Bat	7, 34 and 42 [UnB 431]		
Saccopteryx bilineata (Temminck, 1838)	Greater White-lined Bat	34 and 42		
Saccopteryx leptura (Schreber, 1774)	Brown White-lined Bat	31 and 65 [CJ 53]		
FURIPTERIDAE Gray, 1866 (1 species)				
Furipterus horrens (F. Cuvier, 1828)	Smoky Bat	32, 34, 35, 41 and 42 [CJ 508]	VU A3	
MOLOSSIDAE Gervais, 1856 (14 species)				
Cynomops planirostris (Peters, 1865)	Southern Dog-faced Bat	1, 40, 41 and 57 [CJ 302, CJ 303]		
Eumops glaucinus (Wagner, 1843) *	Wagner's Bonneted Bat	[CJ 01, CJ 43, CJ 67]		
Eumops maurus (Thomas, 1901)	Guianan Bonneted Bat	49		DD
Eumops perotis (Schinz, 1821) *	Greater Bonneted Bat	[UnB 1024]		
Molossops temminckii (Burmeister, 1854)	Dwarf Dog-faced Bat	1, 7, 27, 28, 32, 34, 40, 42, 46, 50, 51, 53, 55-58 and 65 [CMVUNB 1190, 1191, 1193]		
Molossus currentium Thomas, 1901	Corrientes Mastiff Bat	65		
Molossus molossus (Pallas, 1766)	Palla's Mastiff Bat	1, 40, 62, 65 and 67 [CJ 05, CJ 21, CJ 22]		
Molossus rufus É. Geoffroy, 1805	Black Mastiff Bat	65 [CJ 557]		
Neoplatymops mattogrossensis (Vieira, 1842)	Mato Grosso Dog-faced Bat	34, 37 and 42		
Nyctinomops laticaudatus (É. Geoffroy, 1805)*	Geoffroy's Free-tailed Bat	[UnB 791]		
Nyctinomops macrotis (Gray, 1840)	Big Free-tailed Bat	34 and 42		
Promops centralis Thomas, 1915	Crested Mastiff Bat	65		
Promops nasutus (Spix, 1823)	Brown Mastiff Bat	65		
Tadarida brasiliensis (I. Geoffroy, 1824)	Brazilian Free-tailed Bat	51 and 65		
MORMOOPIDAE Saussure, 1860 (3 species)				
Pteronotus gymnonotus (Wagner, 1843)	Big Naked-backed Bat	1, 40, 41, 59 and 65 [CJ 14]		
Pteronotus personatus (Wagner, 1843)	Wagner's Mustached Bat	7 [CJ 630]		

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Pteronotus rubiginosus (Wagner, 1843)	Ferruginous Mustached Bat	1, 7, 33-35, 40-42, 46, 50, 51, 56 and 65		
NATALIDAE Gray, 1866 (1 species)				
Natalus macrourus (Gervais, 1856)	Brazilian Funnel-eared Bat	34, 38, 41, 42 and 52	VU A3c	NT
NOCTILIONIDAE Gray, 1821 (2 species)				
Noctilio albiventris Desmarest, 1818	Lesser Bulldog Bat	7		
Noctilio leporinus (Linnaeus, 1758)	Greater Bulldog Bat	27, 28, 31 and 55 [CMVUNB 1198-CMVUNB 1203]		
PHYLLOSTOMIDAE Gray, 1825 (49 species)				
Carollia brevicauda (Schinz, 1821)	Silky Short-tailed Bat	43 [UnB 1557]		
Carollia perspicillata (Linnaeus, 1758)	Seba's Short-tailed Bat	1, 7, 18, 27, 31, 32, 34, 35, 40-42, 46, 47, 50-53, 55-59, 60, 62 and 66 [CMVUNB 1153-CMVUNB 1157]		
Desmodus rotundus (É. Geoffroy, 1810)	Common Vampire Bat	1, 7, 18, 32, 33-35, 41, 42, 46, 50-53, 55-59, 60, 62 and 66 [CMVUNB 1262-1264]		
Diaemus youngi (Jentink, 1893)	White-winged Vampire Bat	69		
Diphylla ecaudata Spix, 1823	Hairy-legged Vampire Bat	32, 35, 41, 46, 50, 55 and 59 [CJ 503, CMVUNB 1277]		
Anoura caudifer (É. Geoffroy, 1818)	Lesser Tailless Bat	7, 18, 32, 35, 39-41, 51, 55, 57, 58, 62 and 66 [CMVUNB 1145, CMVUNB 1159]		
Anoura geoffroyi Gray, 1838	Geoffroy's Tailless Bat	1, 7, 34, 39, 40-42, 46, 50, 51, 53, 56-58 [CJ 50, CJ 204, CJ 210]		
Choeroniscus minor (Peters, 1868)	Lesser Long-tailed Bat	41		
Glossophaga soricina (Pallas, 1766)	Pallas's Long-tongued Bat	1, 7, 18, 28, 31, 32, 34, 35, 39-42, 46, 50-53, 55-58, 61, 62, 66 and 67 [CMVUNB 1249, CMVUNB 1252]		
Glyphonycteris behnii (Peters, 1865)	Behn's Big-eared Bat	51	VU A4c	DD
Hsunycteris thomasi (J. A. Allen, 1904) *	Thomas´s nectar bat	[UnB 1567]		
Lionycteris spurrelli Thomas, 1913	Chestnut Long-tongued Bat	7, 32, 34, 42 and 66 [CJ 556]		
Lonchophylla bokermanni Sazima, Vizotto & Taddei, 1978	Bokermann's Nectar Bat	42		EN B1ab (iii)
Lonchophylla dekeyseri Taddei, Vizotto & Sazima, 1983	Dekeyser's Nectar Bat	1, 7, 35, 40, 41, 56, 50, 52, 53, 55, 63 and 66 [CMVUNB 1290, CMVUNB 1291]	EN C2a (iiLon)	EN C2a (i)
Lonchophylla mordax Thomas, 1903	Goldman's Nectar Bat	42		NT
Xeronycteris vieirai Gregorin & Ditchfield, 2005	Vieira's Long-tongued Bat	68	VU A4c	DD
Lonchorhina aurita Tomes, 1863	Tome's Sword-nosed Bat	7, 32, 34, 35, 41, 42, 52, 56, 59 and 66 [CJ 502]	VU A3c	
Micronycteris megalotis (Gray, 1842)	Little Big-eared Bat	32, 34, 35, 41, 42, 52, 57 and 59 [CJ 49, CJ 55, CJ 232]		

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Micronycteris minuta (Gervais, 1856)	White-bellied Big-eared Bat	1, 40, 41, 46, 50, 51, 53 and 55 [CJ 48, CMVUNB 1251, CMVUNB 1261]
Chrotopterus auritus (Peters, 1856)	Woolly False Vampire Bat	1, 32, 40, 41, 51, 52, 55, 56, 58 and 60 [CJ 27, CMVUNB 1266]
Gardnerycteris crenulatum (É. Geoffroy, 1810)	Striped Hairy-nosed Bat	7, 34, 42, 51, 57 and 58 [CJ 215, CJ 261]
Lophostoma brasiliense Peters, 1866	Pygmy Round-eared Bat	7, 42, 46, 50, 51, 58 and 60 [CJ 208]
Lophostoma carrikeri (J. A. Allen, 1910)	Carriker's Round-eared Bat	54
Lophostoma silvicola d'Orbigny, 1836	White-throated Round-eared Bat	7, 34, 42 and 51 [CJ 900, UnB 647]
Macrophyllum macrophyllum (Schinz, 1821)	Long-legged Bat	32, 34 and 42 [CJ 547]
Mimon bennettii (Gray, 1838)	Southern Golden Bat	18, 34, 35, 41, 42, 46, 48, 50-53, 55, 57 and 58 [CMVUNB 1161, UnB 1420]
Phylloderma stenops (Peters, 1865)	Pale-faced Bat	41
Phyllostomus discolor (Wagner, 1843)	Pale Spear-nosed Bat	1, 7, 34, 40, 42, 46, 50, 51, 57, 58, 62 and 62 [CJ 301, 304, 305]
Phyllostomus elongatus (É. Geoffroy, 1810)	Lesser Spear-nosed Bat	7 [CJ 549]
Phyllostomus hastatus (Pallas, 1767)	Greater Spear-nosed Bat	7, 18, 27, 28, 31, 34, 35, 41, 42, 46, 50, 51, 53, 56, 57, 59, 60 and 62 [CJ 231, 335, 336]
Tonatia bidens (Spix, 1823)	Greater Round-eared Bat	34, 42 and 55 [CMVUNB 1265, CMVUNB 1283]
Tonatia maresi Williams, Willig & Reid, 1995	Maresi Round-eared Bat	7
Trachops cirrhosus (Spix, 1823)	Fringe-lipped Bat	34, 41, 42, 53 and 66 [CJ 19, CJ 493]
Artibeus cinereus (P. Gervais, 1856)	Gervais´s fruit-eating Bat	7, 18, 40, 46, 50, 51, 53, 56-58, 60 and 62 [CJ 200, CJ 256]
Artibeus concolor Peters, 1865	Brown Fruit-eating Bat	44, 46 and 50
Artibeus lituratus (Olfers, 1818)	Great Fruit-eating Bat	1, 7, 18, 34, 40-42, 46, 50, 51, 56-58, 60, 62, 64 and 67 [CJ 68, CJ 286, CJ 287]
Artibeus obscurus (Schinz, 1821)	Dark Fruit-eating Bat	34, 42 and 55 [CMVUNB 1178-CMVUNB 1181]
Artibeus planirostris (Spix, 1823)	Flat-faced Fruit-eating Bat	1, 7, 32, 34, 40-42, 46, 50, 51, 56-60, 62, 64 and 67 [CJ 29, CJ 69, CJ 101]
Chiroderma doriae Thomas, 1891	Brazilian Big-eyed Bat	32 and 42
Chiroderma villosum Peters, 1860	Hairy Big-eyed Bat	7, 34 and 42 [UnB 39]
Mesophylla macconnelli Thomas, 1901	Macconnell's Bat	34, 42, 44, 51 and 58 [CJ 12]
Platyrrhinus brachycephalus (Rouk & Carter, 1972)	Short-headed Broad-nosed Bat	32

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Platyrrhinus incarum (Thomas, 1912)	Incan Broad-nosed Bat	7, 34, 42, 46, 50, 51, 53, 56-58 and 60 [CJ 220, CJ 288, CJ 423]		
Platyrrhinus lineatus (É. Geoffroy, 1810)	White-lined Broad-nosed Bat	1, 7, 18, 26, 28, 31, 32, 34, 35, 40-43, 46, 50, 51, 53, 55-58, 62, 63 and 66 [CMVUNB 1168, CMVUNB 1260]		
Sturnira lilium (É. Geoffroy, 1810)	Little Yellow-shouldered Bat	1, 7, 18, 32, 34, 40-42, 51, 55-58, 60 and 62 [CMVUNB 1250]		
Sturnira tildae de la Torre, 1959	Tilda´s Yellow-shouldered Bat	42 and 60 [UnB 1554]		
Uroderma bilobatum Peters, 1866	Tent-making Bat	7, 34 and 42 [UnB 888]		
Uroderma magnirostrum Davis, 1968	Brown Tent-making Bat	7, 34, 42 and 55 [CMVUNB 1278]		
Vampyressa pusilla (Wagner, 1843)	Southern Little Yellow-eared Bat	32, 34, 41, 42 and 45 [CJ 10]		DD
VESPERTILIONIDAE Gray, 1821 (12 species)				
Eptesicus andinus J. A. Allen, 1914	Andean Brown Bat	29 and 30		
Eptesicus brasiliensis (Desmarest, 1819)	Brazilian Brown Bat	1, 27, 28, 34, 35, 40, 42 and 65		
Eptesicus chiriquinus Thomas, 1920	Chiriqui Brown Bat	65		
Eptesicus diminutus (Osgood, 1915)	Little Serotine	7, 51 and 58 [CJ 398, UnB 769]		
Eptesicus furinalis (d' Orbigny & Gervais, 1847)	Argentine Brown Bat	7, 55, 62 and 65 [CMVUNB 1246, CMVUNB 1258]		
Histiotus velatus (I. Geoffroy, 1824)	Tropical Leaf-eared Bat	65 [UnB 1038]		
Lasiurus blossevilli (Lesson, 1826)	Southern Red Bat	1, 40 and 51 [CJ 40, CJ 46, CJ 56]		
Lasiurus villosissimus (Palisot de Beauvois, 1796) *	Hoary Bat	[CJ 399]		
Lasiurus ega (Gervais, 1856)	Southern Yellow Bat	28, 51 and 58 [CJ 229]		
Myotis albescens (É. Geoffroy, 1806)	Silver-tipped Myotis	42, 56 and 65 [CJ 631]		
Myotis nigricans (Schinz, 1821)	Black Myotis	34, 41, 42, 51, 56, 57, 60 and 65 [CJ 326, CJ 381, CJ 382]		
Myotis riparius Handley, 1960	Riparian Myotis	65		
PRIMATES Linnaeus, 1758				
ATELIDAE Gray, 1825 (1 species)				
Alouatta caraya (Humboldt, 1812)	Black-and-gold Howler Monkey	1, 12, 16, 18, 21-23 and 77 [UnB 2061, UnB 2175]		
CALLITHRICHIDAE Gray, 1821 (1 species)				
Callithrix penicillata (É. Geoffroy, 1812)	Black-pencilled Marmoset	19, 21, 22 and 54 [UnB 1116]		
CEBIDAE Gray, 1831 (2 species)				
Sapajus cay (Illiger, 1815)	Pantanal Capuchin	23	VU A2cd	
Sapajus libidinosus (Spix, 1823)	Bearded Capuchin	12, 17-19, 22, 26 and 77		
LAGOMORPHA Brandt, 1855				
LEPORIDAE Fischer, 1817 (1 species)				
Sylvilagus minensis Thomas, 1901	Brazilian Cottontail Rabbit	12, 17, 19, 22, 23, 79 and 99 [MN 43003, UnB 2636]	P/R	P/R

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RODENTIA Bowdich, 1821				
CAVIIDAE Fischer, 1817 (4 species)				
Cavia aperea Erxleben, 1777	Brazilian Guinea Pig	1 and 94 [UnB 1625]		
Galea spixii (Wagler, 1831)	Spix's Yellow-toothed Cavy	6 [MN 2615, MN 22583, MZUSP 25304]		
Kerodon acrobata Moojen, Locks & Langguth, 1997	Acrobata Rock Cavy	8 [MN 22728-MN 22730, UnB 2525, UnB 2523)	VU B1ab(iii, v)	DD
Hydrochoerus hydrochaeris (Linnaeus, 1766)	Capybara	1, 12, 16, 17, 19, 21, 22, 25 and 77 [UnB 2247]		
CRICETIDAE Fischer, 1817 (29 species)				
Akodon gr. *cursor* *	Montane Akodont	82 [AMNH 134567, MN 5176, MZUSP MRT 7903]		
Calomys expulsus (Lund, 1840)	Rejected Vesper Mouse	3, 79, 93 and 110 [MN 61583, MN 61588, MN 71958, UnB 1178]		
Calomys tener (Winge, 1887)	Delicate Vesper Mouse	93 and 110 [MN 61575, MN 67075]		
Cerradomys maracajuensis (Langguth & Bonvicino, 2002)	Maracaju Rice Rat	97 [LBCE 7475]		
Cerradomys marinhus (Bonvicino, 2003)	Marinho's Rice Rat	13, 97, 105 [UnB 1901]		
Cerradomys scotti (Langguth & Bonvicino, 2002)	Lindbergh's Rice Rat	3, 13, 97, 105, 106 and 112 [MN 61674, MN 61684, MN 67089]		
Cerradomys subflavus (Wagner, 1842)	Flavescent Cerradomys	105, 106 and 112 [MN 437, AMNH 134562]		
Euryoryzomys lamia (Thomas, 1901)	Monster Rice Rat	3, 104, 106 and 112 [MN 67090]	EN B1ab(iii)	VU B2ab(i, iii)
Holochilus sciureus Wagner, 1842	Amazonian Marsh Rat	107 [MN 34181]	P/R	P/R
Hylaeamys megacephalus (G. Fischer, 1814)	Large-headed Rice Rat	3, 13, 79, 98 and 106 [MN 46867, MN 46866, MN 67092, UnB 1167]		
Kunsia tomentosus (Lichtenstein, 1830)	Woolly Giant Rat	13 [MN 62579, UnB 1706]		
Neacomys amoenus Thomas, 1903	Common Spiny Mouse	98 [UFPB CRB 70]	P/R	P/R
Necromys lasiurus (Lund, 1841)	Hairy-tailed Bolo Mouse	3, 13, 79 and 82 [MN 46828, MN 67073]		
Nectomys rattus (Pelzeln, 1883)	Common Water Rat	3, 13, 79 and 106 [MN 67075, UnB 383]		
Oecomys catherinae Thomas, 1909	Atlantic Forest Rat	91 and 113 [MN 62174]		
Oecomys cleberi Locks, 1981	Cleber Arboreal Rat	113 [UnB 1716]		DD
Oecomys roberti (Thoms, 1904) *	Robert's Oecomys	82 [MZUSP MRT 7965]		
Oligoryzomys mattogrossae (J. A. Allen, 1916)	Mato Grosso Colilargo	3, 13, 79, 92, 104 and 108 [MN 67089]	P/R	P/R
Oligoryzomys moojeni Weksler & Bonvicinno, 2005	Moojen's Colilargo	3 and 104 [MN 50307, MN 67087]		DD
Oligoryzomys nigripes (Olfers, 1818)	Black-footed Colilargo	104 [MN 5210]		
Oligoryzomys rupestris Weksler & Bonvicino, 2005	Highlands Colilargo	3 [MN 50286]	EN B2ac(iii, iv)	DD
Oligoryzomys stramineus Bonvicino & Weksler, 1998	Straw-colored Colilargo	79 [MN 46406, MN 46410]		
Oxymycterus dasytrichus (Schinz, 1821)	Atlantic Forest Hocicudo	70 [MN 32890]		
Oxymycterus delator Thomas, 1903	Spy Hocicudo	3, 13, 70 and 111 [UnB 2084, MN 46619, MN 71657]		

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Pseudoryzomys simplex (Winge, 1887)	False Oryzomys	1, 3 and 106 [UnB 2084, MN 46619, MN 71657]		
Rhipidomys macrurus (Gervais, 1855)	Cerrado Rhipidomys	71 and 72 [UnB 1581]		
Rhipidomys cf. *mastacalis*	Tree Rat	71 and 72 [MN 37350]		
Thalpomys cerradensis Hershkovitz, 1990	Cerrado Mouse	98 [UnB 1157]	VU A2c+3c	
Wiedomys cerradensis Gonçalves, Almeida & Bonvicino, 2005	Cerrado Wiedomys	73 [UnB 2593]		
CUNICULIDAE G. S. Miller & Gidley, 1918 (1 species)				
Cuniculus paca (Linnaeus, 1766)	Lowland Paca	1, 11, 16, 17, 18, 20, 23, 25 and 77 [UnB 2232]		
DASYPROCTIDAE Bonaparte, 1838 (2 species)				
Dasyprocta azarae Lichtenstein, 1823	Azara's Agouti	1, 11, 17-20, 22, 23 and 74 [MN 71690]		DD
Dasyprocta leporina (Linnaeus, 1758)	Red-rumped Agouti	74 [MZUSP 3944]		
ECHIMYIDAE Gray, 1825 (6 species)				
Carterodon sulcidens (Lund, 1838)	Owl's Spiny Rat	10 [MN 54368, UnB 2716]		DD
Clyomys laticeps (Thomas, 1909)	Broad-headed Spiny Rat	13, 96 [UnB 2155, UnB 2717]		
Dactylomys dactylinus (Desmarest, 1817)	Amazon Bamboo Rat	5 [UnB 2067-UnB 2071]		
Proechimys longicaudatus (Rengger, 1830)	Long-tailed Spiny Rat	13 and 98 [MN 71668]		
Proechimys roberti Thomas, 1901	Robert's Spiny Rat	3 [MN 50219, MN 67093]		
Thrichomys pachyurus (Wagner, 1845)	Paraguayan Punaré	3, 79, 95 and 109 [MN 66132]	P/R	P/R
ERETHIZONTIDAE Bonaparte, 1845 (1 species)				
Coendou prehensilis (Linnaeus, 1758)	Brazilian Porcupine	1, 11, 16-19, 21, 23, 75 and 77 [AMNH 134062]		
CARNIVORA Bowdich, 1821				
CANIDAE Fischer, 1817 (4 species)				
Cerdocyon thous (Linnaeus, 1766)	Crab-eating Fox	1, 9, 12, 17-23, 25 and 77 [MN 68181]		
Chrysocyon brachyurus (Illiger, 1815)	Maned Wolf	1, 12, 16-21, 23, 25 and 77 [MN 68175]	VU A3c; E	NT
Lycalopex vetulus (Lund, 1842)	Hoary Fox	1, 16-21, 23, 25 and 77 [MN 68180]	VU A2cd+3cd	
Speothos venaticus (Lund, 1842)	Bush Dog	1, 21 [MN 68179, UnB 3275]	VU C1	NT
FELIDAE Fischer, 1817 (7 species)				
Leopardus braccatus (Cope, 1889)	Pampas Cat	1, 23, 76 and 77 [UnB 2237]	VU C1	NT
Leopardus pardalis (Linnaeus, 1758)	Ocelot	9, 12, 16-20, 22-24, 25 and 77 [UnB 2021]		
Leopardus emiliae (Thomas, 1914)	Emilia Oncilla Cat	114 [MZUSP 19900]		P/R
Leopardus wiedii (Schinz, 1821)	Margay	9, 18, 21 and 23	VU C1	NT
Panthera onca (Linnaeus, 1758)	Jaguar	1, 9, 20 and 77	VU A2bcd+3cd; C1	NT
Puma concolor (Linnaeus, 1771)	Puma	1, 9, 12, 16-20, 22, 23, 25 and 77 [UnB 2026]	VU C1	
Herpailurus yagouaroundi (É. Geoffroy, 1803)	Jaguarundi	1, 18, 21-23, 25 and 77 [UnB 1889]	VU C1	

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MEPHITIDAE Bonaparte, 1845 (1 species)				
Conepatus amazonicus (Lichtestein, 1838)	Striped Hog-nosed Skunk	17-19, 21 and 77 [MN 59335]	P/R	P/R
MUSTELIDAE Fischer, 1817 (4 species)				
Eira barbara (Linnaeus, 1758)	Tayra	1, 9, 11, 17-23, 25 and 77		
Galictis cuja (Molina, 1782)	Lesser Grison	18 and 19 [MN 68975]		
Lontra longicaudis (Olfers, 1818)	Neotropical Otter	1, 16-19, 21, 23 and 25		NT
Pteronura brasiliensis (Gmelin, 1788)	Giant Otter	[MZUSP 3161, MZUSP 3162]	VU	EN
PROCYONIDAE Gray, 1825 (3 species)				
Nasua nasua (Linnaeus, 1766)	South American Coati	1, 11, 9, 16-22 and 77 [MN 55094]		
Potos flavus (Schreber, 1774)	Kinkajou	24		
Procyon cancrivorus (Cuvier, 1798)	Crab-eating Raccoon	1, 9, 11, 12, 16-19, 21-23, 25 and 77		
PERISSODACTYLA Owen, 1848				
TAPIRIDAE Gray, 1821 (1 species)				
Tapirus terrestris (Linnaeus, 1758)	Lowland Tapir	1, 18- 23, 25 and 77 [MN 53701]	VU A2bcd+3bcd	VU A2cde+3cde
CETARTIODACTYLA Montgelard, Catzeflis & Douzery, 1997				
CERVIDAE Goldfuss, 1820 (4 species)				
Blastocerus dichotomus (Illiger, 1815)	Marsh Deer	1 and 77	VU A4ade	VU A4cde
Mazama americana (Erxleben, 1777)	Red Brocket	1, 12, 18, 19, 23 and 77		DD
Mazama gouazoubira (Fischer, 1814)	Gray Brocket	1, 17, 18, 23, 25 and 77		
Ozotoceros bezoarticus (Linnaeus, 1758)	Pampas Deer	1 and 77 [MN 55093]	VU A4cde; C1	NT
TAYASSUIDAE Palmer, 1897 (2 species)				
Dicotyles tajacu (Linnaeus, 1758)	Collared Peccary	1, 12, 16-19, 21-23, 25 and 77		
Tayassu pecari (Link, 1795)	White-lipped Peccary	1, 23 and 78 [MN 68178, MN 68182]	VU A2bcde+3bcde	VU A2bcde+3bcde
INIIDAE Gray, 1846 (1 species)				
Inia araguaiaensis Hrbek, Farias, Dutra & da Silva, 2014	Araguaian river Dolphin	15	P/R	P/R

***New record for the state of Goiás.** Sources: 1- Rodrigues et al. (2002); 2- Sanderson & Silveira (2003); 3- Bonvicino et al. (2005); 4- Carmignotto & Monfort (2006); 5- Bezerra et al. (2007); 6- Bezerra (2008); 7- Zortéa & Darc (2019); 8- Bezerra et al. (2010); 9- Calaça et al. (2010); 10- Bezerra et al. (2011); 11- Bernardo & Melo (2013); 12- Ribeiro & Melo (2013); 13- Carmignotto et al. (2014); 14- Colodetti (2014); 15- Hrberk et al. (2014); 16- Araújo et al. (2015); 17- Estrela et al. (2015); 18- Gomes et al. (2015); 19- Hannibal et al. (2015); 20- Cabral et al. (2017); 21- Miranda et al. (2017); 22- Oliveira & Hannibal (2017); 23- Calaça et al. (2018); 24- Miranda et al. (2018); 25- Oliveira et al. (2019); 26- Pelzeln (1883); 27- Vieira (1942); 28- Vieira (1955); 29- Davis (1965); 30- Davis (1966); 31- Piccinini (1974); 32- Coimbra et al. (1982); 33- Trajano & Gnaspini-Netto (1991); 34- Trierveiler 1998; 35- Bredt et al. (1999); 36- Salles et al (1999); 37- Avilla et al. (2001); 38- Taddei & Uieda (2001); 39- Zortéa (2003); 40- Coelho (2005); 41- Esbérard et al. (2005); 42- Fracasso & Sales (2005); 43- Nunes (2005); 44- Zortéa & Tomaz (2006); 45- Longo et al. (2007); 46- Tomaz (2007); 47- Tomaz et al. (2007); 48- Gregorin et al. (2008); 49- Sodré et al. (2008); 50- Tomaz & Zortéa (2008); 51- Zortéa & Alho (2008); 52- Silva et al. (2009); 53- Tomaz (2009); 54- Zortéa et al. (2009); 55- Bezerra & Marinho-Filho (2010); 56- Gomes (2010); 57- Zortéa et al. (2010); 58- Graciolli et al. (2010); 59- Chaves et al. (2012); 60- Pina et al. (2013); 61- Oprea (2013); 62- Teixeira et al. (2015); 63- Moratelli & Dias (2015); 64- Assunção (2016); 65- Arias-Aguilar et al. (2018); 66- Bichuette et al. (2018); 67- Benvindo-Souza et al. (2019); 68-Dias & Oliveira (2020); 69- Hope et al. (2019); 70- Oliveira & Gonlçalves (2015), 71- Andrades-Miranda et al. (2002); 72- Tribe (2015), 73- Bezerra et al. (2013), 74- Patton & Emmons (2015), 75-Voss (2015), 76- Bagno et al. (2004); 77- Giozza et al. (2017); 78- This study; 79- Bonvicino et al. (2002); 80- Carvalho et al. (2002); 81- Costa et al. (2003); 82- Carmignotto (2005); 83- Cáceres et al. (2008); 84- Brandão et al. (2014); 85- Pavan et al. (2014); 86- Voss et al. (2018); 87- Silva et al. (2019); 88- Creighton & Gardner (2008); 89- Patton & Silva (2008); 90- Pine & Handley (2008); 91- Carleton & Musser (2015); 92- Weksler et al. (2017); 93- Salazar-Bravo (2015); 94- Dunnum (2015); 95- Pessôa et al. (2015); 96- Bezerra & Oliveira (2010); 97- Bonvicino et al. (2014); 98- Bonvicino et al. (1996); 99- Bonvicino et al. (2015); 100- Caramaschi et al. (2011); 101- Faria et al. (2013a); 102- Faria et al. (2013b); 103- Fonseca & Astúa (2015); 104- Moreira et al. (2020); 105- Percequillo et al. (2008); 106- Prado & Percequillo (2013); 107- Prado et al. (2021); 108- Weksler et al. (2017); 109- Basile (2003); 110- Bonvicino & Almeida (2000); 111- Oliveira (1998); 112- Percequillo (1998); 113- Suérez-Villota et al. (2018); 114- Nascimento & Feijó (2017); 115- Feijó et al. (2018).[see Supplementary Material S1 for cited references].

(Marinho-Filho et al. 1997; Bocchiglieri et al. 2010; Marinho-Filho & Guimarães 2010; Feijó et al. 2015) and had been mentioned in other studies as of potential occurrence for the state (Anacleto et al. 2006; Gutiérrez & Marinho-Filho 2017). A visual observation (photo in Supplementary Material S2) of an adult specimen was done in the Mambaí region by a researcher (D. Sampaio) in 2013, corroborating the presence of *T. tricinctus*, and representing a new record for Goiás (Table 1). This species has been classified as endangered in the Brazilian red list (Reis et al. 2018) and vulnerable in the IUCN red list (IUCN 2020).

In general, species of Cingulata listed for the state are common and widely distributed, being found in different types of environments and domains. The nine-banded armadillo (*Dasypus novemcinctus*) and the yellow armadillo (*Euphractus sexcinctus*) are the most frequent species (Rodrigues et al. 2002; Bernardo & Melo 2013; Calaça et al. 2018; Feijó et al. 2018), being tolerant to disturbed environments, although they are rare in places where they suffer intense hunting pressure (Cabral et al. 2017). We consider *Cabassous squamicaudis* as a full species as treated by Feijó & Langguth (2013). This species co-occurs with *Cabassous tatouay* in Goiás (Rodrigues et al. 2002; Sanderson & Silveira, 2003; Rocha et al. 2019) and, as well as for other species of armadillos, the number of records varied between studies, depending on the type of habitat, and the degree of conservation of surveyed areas. *Tolypeutes tricinctus* and *C. tatouay* were the rarest species throughout its range in Cerrado, including Goiás (Anacleto et al. 2006; Ubaid et al. 2010).

Studies on armadillos remain incipient in Goiás, but the studies evaluating the ecology of the giant armadillo *Priodontes maximus* are worth mentioning, developed in the Parque Nacional das Emas (Silveira et al. 2009; Vynne et al. 2009). Considered as the largest and most conspicuous armadillo species, *P. maximus* generally is more sensitive, being recorded in more preserved environments of the Cerrado (Anacleto & Marinho-Filho 2001; Silveira et al. 2009; Carter et al. 2016; Lemos et al. 2020). According to Anacleto & Marinho-Filho (2001), high densities of the species can be observed in Goiás, but their populations have been drastically reduced, being listed as vulnerable (VU) (ICMBio/MMA 2018; IUCN 2020). Habitat loss, fragmentation, fires and roadkill are the main threats for the species (Silveira et al. 1999; Hannibal et al. 2018; Lemos et al. 2020).

We reinforce the north and northeastern areas of the state as regions of knowledge gaps for Cingulata, mainly the Paranã Valley, as well as the southwestern of Goiás, including the region of Serranópolis and Serra do Caiapó. This latter region was informally mentioned as area of occurrence of *T. matacus*, but requires further studies to confirm the presence of this species.

3. *Pilosa*

Only two species of the order Pilosa occur in Goiás state, the giant anteater (*Myrmecophaga tridactyla*) and the southern tamandua (*Tamandua tetradactyla*), both representing the family Myrmecophagidae. These species comprised 16.6% of Pilosa members found in Brazil (Quintela et al. 2020). In other Brazilian states, Pilosa richness varied from one (in Santa Catarina – Cherem et al. 2004) to five species (in Amapá – Silva et al. 2013, and Mato Grosso – Brandão et al. 2019).

Giant anteaters are considered common in Goiás state, being a frequently registered species in mammalian studies conducted in the region (Rodrigues et al. 2002; Gomes et al. 2015; Cabral et al. 2017; Oliveira et al. 2019). Concerning locomotor habits, *M. tridactyla* is terrestrial and *T. tetradactyla* is scansorial (Paglia et al. 2012), but both occur in open (open grasslands and scrubland) and forested areas (woodland savanna, semideciduous and riparian forests). However, *M. tridactyla* prefers open formations, while *T. tetradactyla* selects forested areas (Desbiez & Medri 2010).

The giant anteater is categorized as a vulnerable species (ICMBio/MMA 2018; IUCN 2020). Human activities such as agriculture, deforestation, hunting, roadkill, and fire are the main threats for population establishment (Miranda et al. 2014a). On the other hand, *T. tetradactyla* is classified as Least Concern, even though the knowledge on its population density is scant. This species suffers the same threats as those cited for *M. tridactyla* (Miranda et al. 2014b).

4. *Chiroptera*

We recorded 90 species of bats including five new records for the Goiás state. Only Thyropteridae, one of the nine families occurring in Brazil, has not yet been registered in the state. Phyllostomidae is the most speciose family (49 spp.), followed by Molossidae (14 spp.), Vespertilionidae (12 spp.), Emballonuridae (8 spp.), Mormoopidae (3 spp.), Noctilionidae (2 spp.), Furipteridae (1 sp.), and Natalidae (1 sp.).

The first bat collected in the region currently corresponding to Goiás state dates back to 1819, by Auguste de St-Hilaire (I. Geoffroy St.-Hilaire 1824). In his study, Isidore St-Hilaire describes the species *Vespertilio hilarii*, later synonymized as *Eptesicus brasiliensis* (Carter & Dolan 1978; Gardner 2008). Gervais (1855) cited the occurrence of six species for Goiás based on F. Castelnau's expedition to the "Province of Goiás". One of the species, *Vespertilio chiloensis* (= *Myotis chiloensis*), was not considered here because it must be an incorrect identification, since the species has a distribution restricted to Chile and southwestern Argentina (Gardner 2008). The third record was made in 1823 by Dr. Johann Emanuel Pohl, on an expedition to Goiás (Pelzeln 1883). The only city in Goiás mentioned by Pelzeln is the old state capital, Goiás city. However, the exact locality of the record is imprecise, since the expedition entered the state along the border with Minas Gerais state, along the Rio das Velhas, and proceeded in the direction to the river that, according to this author, is probably the Araguaia River (Pelzeln 1883).

The panorama of the number of bat species registered for Goiás over the years shows four peaks, with the highest increase in 1982, 1998, 2005, and 2017-2020 (Figure 2). The first increment concerns to the study of Coimbra et al. (1982), with the contribution to the zoogeography and ecology of bats in Cerrado regions of central Brazil. In 1998, a single study added 21 new species. It refers to Fernanda Trierveiler's unpublished master dissertation in the Serra da Mesa hydroelectric reservoir region, in northern Goiás (Trierveiler 1998). Moreover, five articles published in 2005 resulted in the third peak of species addition with 11 new records, 64% of those by Fracasso & Salles (2005). This paper stands out for being the only one based on fossil material and including recent (non-fossil) material deposited in a scientific collection (the Museu Nacional, Universidade Federal do Rio de Janeiro, MN). Bezerra & Marinho-Filho (2010) added five new records (*Diphylla ecaudata*, *Tonatia bidens*, *Artibeus obscurus*, *Uroderma magnirostrum* and *Eptesicus furinalis*), based on voucher specimens collected mainly at limestone outcrops of northeastern Goiás. More recently, 18 additional species have been reported (Arias-Aguilar et al. 2018; Hope et al. 2019; Zortéa & Darc 2019; Dias & Oliveira 2020; Hintze et al. 2020; present study).

Arias-Aguilar et al. (2018) added eight species, and the new species recorded can be attributed to the sampling methodology used by the

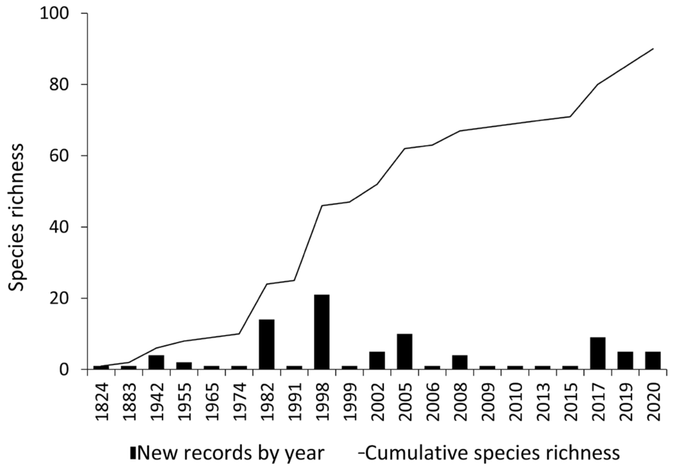

Figure 2. Temporal trend in cumulative species richness for Chiroptera in Goiás state. The 2020 year refers to the present study.

authors, which was the acoustic recording. This is the first bioacoustic study applied to survey bats in the state of Goiás. The most recent study published with Chiroptera in Goiás was that of Zortéa & Darc (2019), which surveyed the central-northern portion of the state (Ceres, Rialma, and Pilar de Goiás localities), adding four new records to the state. Dias & Oliveira (2020) provided the first record of *Xeronycteris vieirai* for the state, and the present study added five new occurrences with data obtained from the collection of the Universidade de Brasília, UnB (*Eumops perotis*, *Nyctinomops laticaudatus*, and *Hsunycteris thomasi*) and the Universidade Federal de Jataí, CJ (*Eumops glaucinus* and *Lasiurus villosissimus*).

In general, the new records added here are expected, since these species occur within neighboring states (Bianconi & Pedro 2017; Sartore et al. 2017; Zortéa et al. 2017). It is important to mention that the previous record of *E. perotis* for Goiás, provided by Sartore et al. (2017) and based on the study of Eger (1977), is erroneous. Eger (1977) refers to the material deposited at the Institut Royal des Sciences Naturelles de Belgique (IRSNB) that was attributed to a location in Goiás state named "Parano do Manhana" (sic). In a careful investigation, Suckow et al. (2010) rectified this information indicating that the correct location is "Paranã do Manhana", a locality in the upper Amazonas River. Bichuette et al. (2018) registered 66 species in a recent review of bats from Goiás and the Federal District. Two species considered by these authors were not considered in our study: *Cynomops abrasus* and *Histiotus laephotis*. Although these species are likely to occur in Goiás, especially *C. abrasus*, we have not found supporting material to attest their occurrence in the state.

The order Chiroptera is one of the most representative of mammals globally, a pattern reflected in Brazil, and also in this study. According to Aguiar et al. (2016), at least 118 species occur in the Cerrado, of which 76% occur in Goiás, as found in the present study. Concerning Brazil, Goiás comprises about 50% of the 181 recognized species (see Garbino et al. 2020). These figures show that Goiás state presents a high bat species diversity, playing a significant role for the conservation of this group in Brazil.

Comparatively to other Brazilian states, bat species richness found in Goiás is only surpassed by the observed in the states of Pará (120 spp.), Amazonas (110 spp.) (Bernard et al. 2011), and Mato Grosso (99 spp.- Brandão et al. 2019), which owns more than 8% of its territory within the Amazon domain. Mato Grosso do Sul holds 73 species (Tomas et al. 2017), while São Paulo presents 79 species (Vivo et al. 2011).

The family Phyllostomidae is the most diverse in Brazil (93 spp.- Garbino et al. 2020), a pattern reflected in our study. Phyllostomidae bats are most commonly captured in the understory with mist nets, the country's most-used capturing method (Delgado-Jaramillo et al. 2020). Families such as Molossidae and Vespertilionidae are also diverse, but they demand complementary methods to be registered (*e.g.*, bioacoustics inventory), which is still rarely used in Brazil. Other species not registered in Goiás are likely to occur due to close records in the state's frontiers, as the record of *Pygoderma bilabiatum* in the IBGE's Reserve in the city of Brasília, Federal District (Schneider et al. 2011).

Regarding endemism, three species considered endemic to the dry diagonal of Brazil [*Lonchophylla bokermanni, Lonchophylla dekeyseri* (Cerrado), and *Xeronycteris vieirai* (Cerrado and Caatinga)] are found in Goiás (Aguiar et al. 2010; Zortéa et al. 2017; Dias & Oliveira 2020).

We found registers of seven threatened bat species in Goiás, six of which are included in the Brazilian red list (ICMBio/MMA 2018): *Furipterus horrens* (Vulnerable), *Natalus macrourus* (Vulnerable), *Glyphonycteris behnii* (Vulnerable), *Lonchophylla dekeyseri* (Endangered), *Lonchorhina aurita* (Vulnerable), and *Xeronycteris vieirai* (Vulnerable). IUCN lists *Lonchophylla dekeyseri* and *L. bokermanni* as Endangered (Aguiar 2016; Aguiar & Bernard 2016), but the Brazilian red list does not include *L. bokermanni* in any threat category. *Glyphonycteris behnii*, *X. vieirai*, *Eumops maurus* and *Vampyressa pusilla* are classified as data deficient according to IUCN red list (IUCN 2020).

Despite the remarkable diversity of bats reported here, Goiás still stands out as one of the Brazilian states with the lowest bat sampling locations (Bernard et al. 2011), thus it is indicated by Aguiar et al. (2020) as a priority area for bat inventories. Bat records are concentrated mainly in the southern and eastern portions of the state (Mambaí region) (Figure 1). The number of species can be higher, if we consider the lack of bioacoustic studies. For example, in addition to the 20 species recorded by Arias-Aguilar et al. (2018), several sonotypes were not identified by them, including complexes from several families.

Many of the Cerrado areas were converted into agriculture, especially soy monoculture, which reduced this domain to just 20% of the original area (Strassburg et al. 2017). Goiás is home to a large portion of the Cerrado domain. Currently, the economy model based on agriculture affects bat assemblages changing habitat structure and leading to reduced shelter and food availability, which can potentially cause local and even permanent extinctions according to a climate modeling study (Aguiar et al. 2016). In addition, the reduction of habitat availability imposed by the expansion of agriculture contributes to the loss of environmental quality. This scenario favors the susceptibility of contact with pollutants in water resources, in the air, and in ingested food (Bayat et al. 2014; Souza et al. 2020), which can jeopardize animal immune responses and increase the chances of contracting diseases, leading to the decline of bat populations (Naidoo et al. 2016; Miguel et al. 2019).

There are indications that the southern and southeastern parts of the Cerrado (including areas in Goiás) are potential regions of high habitat suitability for many bat species in a dispersion scenario motivated by climate change (Aguiar et al. 2016). This adds value to the region for long-term conservation of chiropterans and further emphasizes the need for inventory efforts and updating species richness and distribution in the state. These data are essential for elaborating effective landscape management strategies to guarantee the persistence of suitable habitats for bat species and their ecosystem services, such as pollination, agricultural pest predation, and seed dispersion.

5. *Primates*

We recorded four primate species in Goiás state, belonging to three genera and three families, which represents only 2.7% of this group diversity in the country (Jerusalinsky & Melo 2018). In the Brazilian states, richness of primates varied from three (in Santa Cataria – Cherem et al. 2004) to 25 species (Mato Grosso – Brandão et al. 2019). Primate richness in the Cerrado is considered lower (5 spp.) compared to Amazon and Atlantic Forest (Paglia et al. 2012).

The four primate species recorded here are common in its geographical range. *Alouatta caraya*, *Sapajus libidinosus* and *Callithrix penicillata* are abundant in Goiás, and display great environmental plasticity, occuring even in urban fragments (Grande et al. 2020). Black-pencilled marmosets can reach high densities and be more common in degraded areas (Grande et al. 2020), and were not registered in protected areas such as Parque Nacional das Emas (Rodrigues et al. 2002), and Chapada dos Veadeiros (Ferreguetti et al. 2019). The geographical distribution of *Sapajus cay* reaches Goiás state (IUCN 2020), where it was recorded in Atlantic Forest enclaves in the municipalities of Aporé and Itajá, southwestern of the state (Calaça et al. 2018; Gusmão et al. 2018). Habitat loss has been the main threat for capuchin monkeys. In the last 48 years, the populations of *S. cay* declined about 30%, which led the species to be currently categorized as Vulnerable in the Brazilian red list (Rímoli et al. 2018).

6. *Carnivora*

In Goiás state, richness of Carnivora order was extremely representative, with five families, 15 genera and 19 species. In comparative terms with Brazilian Carnivora richness, these data represent 53% of total species (36 spp., Quintela et al. 2020). When compared to other state lists, Goiás ranges around 90-95% of Carnivora species found in Mato Grosso (21 spp., Brandão et al. 2019) and Mato Grosso do Sul states (20 spp., Tomas et al. 2017). In contrast, Goiás holds two more Carnivora species than São Paulo (17 spp., Vivo et al. 2011), and six more than Amapá state (13 spp., Silva et al. 2013). The species found here correspond to 90% of carnivora mammals recorded for the Cerrado (21 spp., Paglia et al. 2012).

Most carnivores species listed for Goiás present a large geographic distribution in Neotropical region (IUCN 2020). In the Cerrado domain, *Cerdocyon thous*, *Chrysocyon brachyurus*, *Speothos venaticus*, *Leopardus pardalis*, *L. emiliae*, *L. wiedii*, *Herpailurus yagouaroundi*, *Puma concolor*, *Panthera onca*, *Nasua nasua*, *Procyon cancrivorus*, *Galictis cuja* and *Eira barbara* occur in open and forested environments, covering several physiognomies (Juarez & Marinho-Filho 2002; Marinho-Filho et al. 2002; Leuchtenberger et al. 2013; Lima et al. 2014). On the other hand, species such as *Lontra longicaudis* and *Pteronura brasiliensis* inhabit mainly forests (Leuchtenberger et al. 2013), while *Lycalopex vetulus*, *Leopardus braccatus* and *Conepatus amazonicus* occur almost exclusively in open areas (Juarez & Marinho-Filho 2002; Marinho-Filho et al. 2002; Feijó & Langguth 2013; Nascimento et al. 2021). Recently, Miranda et al. (2018) recorded an individual of *Potos flavus* roadkilled over a highway in southwest Goiás, adding a recent record for the state, and corroborating its presence for the Cerrado. The kinkajou occurs exclusively in forested habitats (Marinho-Filho et al. 2002), and this individual was close to a forest, which reinforces the importance of conservation of these physiognomies in the Brazilian savanna (Miranda et al. 2018).

We recorded 47.4% 9 spp.) of carnivora categorized as vulnerable (*C. brachyurus*, *L. vetulus*, *S. venaticus*, *L. braccatus*, *L. wiedii*, *P. onca*, *H. yagouaroundi*, *P. concolor* and *P. brasiliensis*) according to the Brazilian Red List (ICMBio/MMA 2018). Carnivora is the most threatened Brazilian mammal group, being habitat destruction the biggest challenge for the conservation of these animals. In the Atlantic Forest, Carnivora species richness is affected by the amount of native vegetation cover (Regolin et al. 2017). In the Cerrado, there is higher occupancy of *C. brachyurus* and *P. concolor* in strictly protected areas (Ferreira et al. 2020). Further, the conflict with humans (i.e., retaliation), roadkills, urbanization, fires and diseases are other concerns about Carnivora conservation (Beisiegel 2017).

7. *Perissodactyla*

The lowland tapir (*Tapirus terrestris*) represents the unique species of Perissodactyla confirmed for Goiás. The species is widely distributed in Brazil and common in several regions of the state, recorded in open and forested environments, as well as in crop lands (Rodrigues et al. 2002; Cabral et al. 2017; Oliveira et al. 2019). However, in southeastern Goiás, the presence of lowland tapir is rare, occurring only in landscapes with higher native habitat amount (Rocha et al. 2018). Lowland tapir is nationally and globally threatened, categorized as vulnerable (ICMBio/MMA 2018; IUCN 2020). According to the Brazilian red list (ICMBio/MMA 2018), *T. terrestris* reaches different threatened categories across the Brazilian domains (*e.g.*, regionally extinct - Caatinga, endangered - Cerrado and Atlantic Forest, near threatened - Pantanal, and least concern - Amazon) (Medici et al. 2018). In the Brazilian Cerrado, agricultural expansion and consequent low percentage of native remnants are the highest threats to lowland tapir populations (Medici et al. 2012).

8. *Cetartiodactyla*

We recorded seven species of Cetartiodactyla for Goiás state, representing only 12% of the group species richness cited for Brazil (Quintela et al. 2020). This richness is similar to those registered in other states of the country, with six species in Mato Grosso do Sul (Tomas et al. 2017) and nine species in Mato Grosso (Brandão et al. 2019), but lower than richness found in other states that harbor aquatic mammal species (*e.g.*, São Paulo, with 33 species – Vivo et al. 2011). Collared peccary and White-lipped peccary, species of Tayassuidae, present a wide geographical range in the Brazilian territory (Desbiez et al. 2012; Keuroghlian et al. 2012). *Dicotyles tajacu* is more resistant to environmental degradation, managing to survive even in devastated areas (Sowls 1997; Desbiez et al. 2012), while *Tayassu pecari* in Brazil is classified as vulnerable (Keuroghlian et al. 2018). This species is in peril in regions most impacted by human action such as southeastern Goiás, where the most recent records date from approximately ten years ago (Keuroghlian et al. 2012).

Mazama americana and *M. gouazoubira* are considered common, occurring in all domains of Brazil, with the red brocket evaluated as data deficient, and the gray deer as least concern in the IUCN Red List (Duarte et al. 2012a; b; Duarte & Vogliotti 2016). *Ozotoceros bezoarticus* is classified as vulnerable in Brazil, due to population decline and geographical isolation

(Gonzalez et al. 2010; Duarte et al. 2012c; Duarte et al. 2018) and as near threatened in the IUCN Red List (González et al. 2016). Despite being very common in some areas in the southwestern region of Goiás (Rodrigues et al. 2002), the subspecies *Ozotoceros bezoarticus bezoarticus* is considered vulnerable due to a 98% decrease in its distribution area, which depends on preserved open vegetation formations in the Cerrado (Weber & Gonzalez 2003; Duarte & Gonzalez 2010; Duarte et al. 2012c). *Blastocerus dichotomus* is the largest species of deer in Brazil, being classified as vulnerable in nacional and international red lists (Duarte et al. 2012d, 2016, 2018). It inhabits floodplains of the great rivers and their affluents. The highest concentrations of marsh deer can be observed in the Pantanal and in the region of Ilha do Bananal in the Araguaia River (Tiepolo & Tomas 2009; Duarte et al. 2012d).

Inia araguaiaensis was recently described as a distinct species of *Inia*, being restricted to the Araguaia-Tocantins basin (Hrbek et al. 2014; Siciliano et al. 2016). Although its status is not yet recognized by the IUCN and Ministério do Meio Ambiente (MMA), Hrbek et al. (2014) suggest the classification to be considered as vulnerable due to the great threats in its occurence area, such as agricultural and industrial development, and hydroelectric dams, that contributes to the fragmentation of populations.

9. Lagomorpha

The Lagomorpha order is represented by a single genus in Brazil, *Sylvilagus*, which was treated as monotypic, represented by *S. brasiliensis* with several subspecies until recently. Currently, this complex taxonomic history began to be elucidated based on phylogenetic relationships among South American populations. Ruedas et al. (2017) recognized at least three distinct species for the country: *S. brasiliensis*, *S. minensis* and *S. tapetillus*, with other taxonomic issues yet to be clarified (Silva et al. 2019b). In Goiás state, only *S. minensis* is expected to occur (Bonvicino et al. 2015; Ruedas et al. 2017). In general, Brazilian cottontail rabbits are considered common, with a wide distribution and preference for edges of forest habitats, although they are also recorded in open environments, bamboo forests and disturbed areas (Emmons & Feer 1997; Silva Júnior et al. 2005; Borges et al. 2014; Dias et al. 2019). *Sylvilagus minensis* was one of the most common medium-large mammal species recorded in fragmented areas of the southwestern region of the state (Gomes et al. 2015; Rocha et al. 2018), being associated with forest environments (Gomes et al. 2015). However, the species was not recorded in some conservation units, such as the Parque Nacional das Emas (Rodrigues et al. 2002) and the Parque Nacional Chapada dos Veadeiros (Ferreguetti et al. 2019), which present a predominance of shrublands. Due to recent taxonomic rearrangements, *S. minensis* has not yet been evaluated by the IUCN and MMA.

10. Rodentia

A total of 29 genera and 43 species, belonging to six rodent families, occur in Goiás state. These species and families are divided in two infraorders (*sensu* D'Elía et al. 2019), as follows: infraorder Hystricognathi, including the families Caviidae (4 spp.), Cuniculidae 1 sp.), Dasyproctidae (2 spp.), Echimyidae (6 spp.), and Erethizontidae (1 sp.); and infraorder Myomorphi, represented only by the family Cricetidae (29 spp.). The total number of species represents *ca.* 16% of the 258 rodent species of Brazil (Quintela et al. 2020). This richness is comparable to that found in other Brazilian states (*e.g.*, Rio de Janeiro state - 49 spp.; Rocha et al. 2004), which ranges from 33 species in Mato Grosso do Sul (Tomas et al. 2017) to 67 species in Mato Grosso state (Brandão et al. 2019). Below we describe the rodent richness in both infraorders.

10. 1. Hystricognathi

Seven rodent families represent the infraorder Hystricognathi in Brazil, being five of them found in Goiás state. Among these families, we account a total richness of 12 genera and 14 species, distributed as described above. Comparing to other states of central-western Brazil, this richness fits in a range of nine genera and 10 species in Mato Grosso do Sul (Tomas et al. 2017) to 15 genera and 20 species in Mato Grosso state (Brandão et al. 2019).

Concerning the general distribution patterns in Goiás state, 64% (9 spp.) of the Hystricognathi species are forest vegetation inhabitants, with six species widely distributed (i.e., *Cavia aperea*, *Coendou prehensilis*, *Cuniculus paca*, *Dasyprocta azarae*, *Dasyprocta leporina*, and *Hydrochoerus hydrochaeris*), occurring on the forested environments of the Cerrado, as well as in other domains of Brazil, especially in the Atlantic Forest (Patton et al. 2015). Two exceptions regarding widely distributional ranges are *Cavia aperea*, which has no records in Amazon (Dunnum 2015), and *Dasyprocta leporina*, with no records in Pantanal and Caatinga (Patton & Emmons 2015). Three species with restricted range distribution in the state also inhabit forested formations, being two species only shared between Cerrado and Amazon (i.e., *Dactylomys dactylinus* – Bezerra et al. 2007, and *Proechimys roberti* – Patton & Leite 2015), and one species shared among Cerrado, Pantanal, and Amazon (i.e., *Proechimys longicaudatus* – Patton & Leite 2015).

Species occurring in open vegetation domains account for 36% of the total (5 spp., i.e., *Galea spixii*, *Carterodon sulcidens*, *Clyomys laticeps*, *Kerodon acrobata*, and *Thrichomys pachyurus*). In this group, we have the only Hystricognathi species found in Goiás state that are Cerrado endemics (3 spp.): *Carterodon sulcidens*, distributed in eastern Goiás (Bezerra et al. 2011); *Kerodon acrobata*, restricted to north and northeastern Goiás (Moojen et al. 1997; Bezerra et al. 2010; Zappes et al. 2014); and *Thrichomys pachyurus*, ranging throughout Goiás, except the southern end of the state (Nascimento et al. 2013; Bonvicino et al. 2020 – specimens with 2n =30, FNa= 56). In regards to the remaining two species, one is shared between Cerrado and Caatinga (*Galea spixii* – Bezerra 2008), and the other between Cerrado and Pantanal (*Clyomys laticeps* – Bezerra & Oliveira 2010).

Regarding the conservation status, two species are considered under some threaten level. The narrowly distributed species *Kerodon acrobata*, figures as vulnerable at Brazilian red list, and as data deficient in the IUCN, due mainly to habitat loss and illegal hunt, since it is a game species (Bezerra et al. 2010, Roach 2016). The second species, *Dasyprocta azarae*, is classified as data deficient in the IUCN Red List, but faces population decline tendency due to decreasing number of mature individuals, habitat loss and ilegal hunt (Catzeflis et al. 2016).

There are some taxa needing taxonomic review. *Galea spixii* have proven to be a species complex, composed of distinct morphological groups, and needs to be studied based on molecular data, including the description and redescription of some taxa (Bezerra 2008; Dunnum 2015); *G. flavidens* (Brandt, 1835) listed for Goiás by Bonvicino et al. (2005), is not considered here since it has no designated holotype, and "Brasil" as type locality (Brandt 1835), and can be considered a synonym of the fossil species *Cavia bilobidens* (Winge, 1888), which is considered related to *G. spixii* (Paula Couto 1950, Bezerra 2008); *Proechimys* is the most speciose genus of the family Echimyidae and needs revision in both molecular and morphological grounds, including here the represented species groups *P. longicaudatus* and *P. guyannensis*, which includes *P. longicaudatus* and *P. roberti*, respectively (Patton & Leite 2015).

10.2. Myomorphi

The highly diverse infraorder Myomorphi is represented in Brazil by the family Cricetidae, subfamily Sigmodontinae (Patton et al. 2015). We recorded 17 genera and 29 species for Goiás state, belonging to five tribes (*sensu* Salazar-Bravo et al. 2016): Akodontini (6 spp.), Oryzomyini (18 spp.), Phyllotini (2 spp.), Thomasomyini (2 spp.), and Wiedomyini 1 sp.). This number of sigmodontine species is similar to the ones found in other Brazilian states, such as Rio de Janeiro, with 32 species (Rocha et al. 2004), and Mato Grosso do Sul, with 22 species (Tomas et al. 2017), but is lower than that found in Mato Grosso state, with 42 species (Brandão et al. 2019).

In relation to general distribution patterns, 10% (3 spp.) of Cricetidae species are widely distributed and are shared between the Cerrado and forested domains such as the Amazon and Atlantic Forests. This is the case of *Necromys lasiurus*, *Nectomys rattus,* and *Pseudoryzomys simplex*. Species occurring in Cerrado and Atlantic Forest domains represent 38% (11 spp., *Akodon* gr. *cursor*, *Calomys tener*, *Cerradomys subflavus*, *Oecomys catherinae*, *Oligoryzomys mattogrossae*, *Oligoryzomys rupestris*, *Oligoryzomys stramineus*, *Oligoryzomys nigripes*, *Oxymycterus dasytrichus*, *Rhipidomys macrurus* and *Rhipidomys mastacalis*), and in Cerrado and Amazon, 14% (4 spp., *Cerradomys maracajuensis*, *Hylaeamys megacephalus*, *Neacomys amoenus* and *Oecomys roberti*). The remaining species, 24% (7 spp.), are Cerrado endemics (*Cerradomys marinhus*, *Euryoryzomys lamia*, *Holochilus sciureus* [*sensu* Prado et al. 2021], *Oecomys cleberi*, *Oligoryzomys moojeni*, *Thalpomys cerradensis* and *Wiedomys cerradensis*) or are shared between Cerrado and other open formations, such as Chaco, Pampas or Caatinga, representing 14% (4 spp., *Calomys expulsus*, *Cerradomys scotii*, *Kunsia tomentosus* and *Oxymycterus delator*).

Some species are known from only one locality in Goiás, as is the case of: *Cerradomys maracajuensis*, recorded at Serranópolis, southern Goiás; *Kunsia tomentosus*, recorded only at Parque Nacional das Emas, in southwestern Goiás; *Neacomys amoenus*, recorded in Baliza, at western Goiás; *Oligoryzomys rupestris*, a species with a disjunct distributional range, and endemic to highly elevated rupestrian grasslands, recorded in Parque Nacional da Chapada dos Veadeiros at northern Goiás; *Akodon* gr. *cursor*, *Oecomys roberti* and *Oxymycterus dasytrichus*, all recorded only in the region known as 'Mato Grosso de Goiás' at the central portion of Goiás state; and *Wiedomys cerradensis*, recorded in São Domingos, eastern Goiás. Other species, typical of forested formations, also have few records in the state, such as *Euryoryzomys lamia*, restricted to eastern Goiás.

Here we provide the first published records for *Akodon* gr. *cursor* and *Oecomys roberti* based on examined material housed at scientific collections. These records are for Anápolis (*Akodon* gr. *cursor*) and Petrolina de Goiás (*Oecomys roberti*) (see Carmignotto, 2005; Table 1 – present study).

Among the abovementioned species, five are classified under some threaten category, being two of them classified as endangered in the Brazilian red list (*Euryoryzomys lamia* and *Oligoryzomys rupestris*) and one as vulnerable (*Thalpomys cerradensis*). The IUCN red list accounts for four species, being three classified as data deficient (*Oecomys cleberi*, *Oligoryzomys moojeni*, *Oligoryzomys rupestris*) and one as vulnerable (*Euryoryzomys lamia*). Among the cricetid rodents of Goiás state, the later species, *Euryoryzomys lamia* is included in the more severe threaten categories of both Brazilian and IUCN red lists. This species has occupancy area of less than 2,000 km^2 and is known from only four locations, two of them are already completely destroyed due to agriculture (Percequillo & Weksler 2018). All threatened and data deficient species have in common the relatively small distribution, habitat loss due to convertion for agribusiness, and a few or no population study (see ICMBio/MMA 2018, IUCN 2020).

There are some species needing taxonomic review: *Rhipidomys macrurus* and *Rhipidomys mastacalis* have proven to be species complexes, composed of taxa morphologically similar, but distinct at molecular levels (Costa et al. 2011; Lanes 2020), as well as *Oecomys catherinae* (Suárez-Villota et al. 2018). So, specimens from Goiás cited as *Oecomys trinitatis* by Carleton and Musser (2015) and as *Oecomys rex* by Costa (2001), as well as those cited as *Oecomys* sp.1 (2n = 60), *O. trinitatis* (2n = 54) and *Oecomys* gr. *catherinae* (morphological data) by Carmignotto (2005), refer to *O. catherinae* species complex of Suárez-Villota et al. (2018), represented by at least two distinct lineages in the state. A specimen (MN 36150 from 55 km N Niquelândia, GO) cited by Andrades-Miranda et al. (2000) with 2n = 60 and FNa = 64, and treated as *Hylaeamys yunganus* (see also Moreira et al. 2020), was not included in the present checklist, since the voucher material was not examined by us nor other authors working with this genus (Prado & Percequillo 2013; Percequillo 2015), being its taxonomic identity waiting to be confirmed.

The rodent fauna of Goiás state is also a composite, characterized by inhabitants of forested and open formations due to the presence of a vegetation mosaic (grasslands, shrublands, and forests) typical of the Cerrado domain (Carmignotto et al. 2012), and also by the presence of Seasonally Dry Tropical Forest remnants that still persist in the state (Ribeiro & Walter 2008; IBGE 2011). The connection between the Atlantic Forest and Amazon through forest formations of the Cerrado is already described (Costa 2003), as well as the mammal fauna shared between Cerrado and Caatinga (Carmignotto et al. 2012). Richest rodent communities were found in conservation units, such as the Parque Nacional das Emas (13 spp., Carmignotto et al. 2014) and the Parque Nacional da Chapada dos Veadeiros (14 spp., Bonvicino et al. 2002, 2005), as well as in regions under hydroelectric dam projects, such as the Serra do Facão dam reservoir (16 spp., Gomes et al. 2015) and the Serra da Mesa dam reservoir (12 spp., Carmignotto 2019), at southeastern and northeastern of Goiás state, respectively. Furthermore, a significant number of species is also found in areas of extensive cattle ranching intermixed with natural landscapes, such as the Cadoz farm (11 spp., Bonvicino et al. 2011) and Vão dos Bois farm (9 spp., Bonvicino et al. 2002), in northeastern Goiás state. Besides the relevant richness present in conservation units, endemic and rare species were also recorded in regions affected by hydroelectric reservoirs, where it was observed a high diversity loss due to landscape flooding (*e.g.*, Carmignotto 2019), highlighting the real need for strategic efforts to conserve rodent communities of Goiás state.

10.3. Potential rodent species in Goiás state

Among potential species which could occur in the state, we speculate that in the central region of Goiás it is possible to find records of *Akodon lindberghi*, *Gyldenstolpia planaltensis*, *Thalpomys lasiotis* and *Phyllomys centralis*. These species have been recorded in Federal District of Brazil, which is within Goiás state, and neighboring federative unities such as Mato Grosso and Minas Gerais states (Andrade et al. 2004; Ribeiro & Marinho-Filho 2005; Bezerra 2011; Machado et al. 2018).

Conclusions

Goiás state harbors a rich mammalian fauna, especially for bats, rodents, carnivores, and marsupials. Regardless of state geographical size, the number of species listed for Goiás is higher than the listed for other Brazilian states, except for Mato Grosso and São Paulo. The mammalian fauna of Goiás is characterized by inhabitants of open (*e.g.* Cerrado and Caatinga) and forested environments (*e.g.*, Amazon and Atlantic Forest), due to the presence of a vegetation mosaic in the Cerrado domain. Gallery forests and semideciduous forests contribute to mammal richness in central Brazil, and habitat selectivity seems to be more evident for small mammals. Medium and large-sized mammals tend to be more generalists in terms of habitat and are widely distributed across Goiás state.

Another pattern found here is that the studies reporting largest numbers of mammal species for Goiás state were carried out in conservation units, and some species have been found only inside these protected areas. Thus, we highlight the need to increment the number of conservation units in the state, especially regarding the central and southeastern portion of Goiás, which was once represented by a large area part of Alto Paraná Atlantic Forest ecoregion, but now is represented by few, scattered and small remnants, with no conservation units (Giustina et al. 2018). We also conclude that there are still great portions of the state lacking a proper mammal survey. There is scant and fragmented information about mammals based on specimens housed in scientific collections, especially from the northwestern portion of Goiás. Thus, the increase in the number of inventories in the state, including complementary survey techniques (see Srbek-Araujo & Chiarello 2004; Bovendorp et al. 2017; Arias-Aguilar et al. 2018), and the collection of vouchers and tissue samples to provide correct species delimitation and identification, will allow a better understanding on the biodiversity and conservation of mammals in Goiás state.

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Supplementary Material

The following online material is available for this article:

Table S1. Literature data with records of mammal species for Goiás state, central Brazil.

Figure S1. Visual observation of *Tolypeutes tricinctus* in Mambaí, Goiás.

Author Contributions

Wellington Hannibal: Substantial contribution in the concept and design of the study. Contribution to critical revision, adding intellectual content.

Marlon Zortéa: Contribution to data collection and manuscript preparation – Bats; Contribution to critical revision, adding intellectual content.

Analice M. Calaça: Contribution to data collection and manuscript preparation - Medium and large-sized mammals, Contribution to critical revision, adding intellectual content.

Ana Paula Carmignotto: Contribution to data collection and manuscript preparation - Non-volant small mammals, Contribution to critical revision, adding intellectual content.

Alexandra M. R. Bezerra: Contribution to data collection and manuscript preparation - Non-volant small mammals, Contribution to critical revision, adding intellectual content.

Henrique G. Carvalho: Contribution to data collection and manuscript preparation – Bats;

Cibele R. Bonvicino: Contribution to data collection and manuscript preparation - Non-volant small mammals, Contribution to critical revision, adding intellectual content.

Ana C. M. Martins: Contribution to data collection and manuscript preparation – Bats; Contribution to critical revision, adding intellectual content.

Ludmilla M. S. Aguiar: Contribution to data collection and manuscript preparation – Bats:

Marcelino B. de Souza: Contribution to data collection and manuscript preparation – Bats;

Ingrid de Mattos: Contribution to data collection and manuscript preparation – Bats; Contribution to critical revision, adding intellectual content.

Roniel F. Oliveira: Contribution to data collection and manuscript preparation - Medium and large-sized mammals; Contribution to critical revision, adding intellectual content.

Daniel Brito: Contribution to data collection and manuscript preparation – Bats;

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Jânio C. Moreira: Contribution to data collection and manuscript preparation - Medium and large-sized mammals;

All authors reviewed the manuscript 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.

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Erratum

Erratum: Checklist of mammals from Goiás, central Brazil

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Table 1, page 6, column "Record", where it was written:
1, 2, 11, 12, 16, 17, 19-25 and 77 [MN 55699, UnB 1603-UnB1607]
Should read:
1, 2, 11, 12, 16, 17, 19-25 and 77 [MN 53699, UnB 1603-UnB 1607]

Table 1, page 9, column "Record", where it was written:
12, 17, 19, 22, 23, 79, 99 [MN 43003, UnB 2636]
Should read:
12, 17, 19, 22, 23, 79, 99 [MN 43004, UnB 2636]

Table 1, page 10, column "Record", where it was written:
6 [MN 2615, MN 22583, MZUSP 25304]
Should read:
6 [MN 2615, MN 22853, MZUSP 25304]

Table 1, page 10, column "Record", where it was written:
105, 106, 112 [MN 437, AMNH 134562]
Should read:
105, 106, 112 [MN 32445, AMNH 134562]

Table 1, page 10, column "Record", where it was written:
13 [MN 62579, UnB 1706]
Should read:
13 [MN 62570, UnB 1706]

Table 1, page 10, column "Record", where it was written:
91, 113 [MN 62174]
Should read:
91, 113 [MN 62179]

Table 1, page 10, column "Record", where it was written:
3, 13, 79, 92, 104,108 [MN 67089]
Should read:
3, 13, 79, 92, 104,108 [MN 67086]

Table 1, page 11, column "Record", where it was written:
1, 3, 106 [UnB 2084, MN 46619, MN 71657]
Should read:
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Short Communication

Limnoperna fortunei - Updating the geographic distribution in the Brazilian watersheds and mapping the regional occurrence in the Upper Uruguay River basin

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HERMES-SILVA, S., RIBOLLI, J., ÁVILA-SIMAS, S., ZANIBONI-FILHO, E., CARDOSO, G.F.M., NUÑER, A.P.O., ***Limnoperna fortunei*** **- Updating the geographic distribution in the Brazilian watersheds and mapping the regional occurrence in the Upper Uruguay River basin**. Biota Neotropica 21(3): e20201175. https://doi.org/10.1590/1676-0611-BN-2020-1175

Abstract: *Limnoperna fortunei* is an invasive alien species (IAS) that cause serious ecological and economic problems in Brazilian freshwater environments. Due to its high dispersion capacity and the lack of new records in peer-reviewed journals we carried out an extensive survey to update the distribution of *L. fortunei* in the Brazilian hydrographic basins. We also performed a detailed investigation of its distribution in the Upper Uruguay River basin using a molecular method. We presented new records, showing the invasion in new basins and a wide distribution in the basins previously infested. Additionally, we confirmed that the Upper Uruguay River is fully colonized by the golden mussel, being distributed in the lentic, lotic, and transitional lotic/lentic environments presented in this region. This update is an important tool for the implementation of guidelines and the development of safety protocols and sanitary barriers to avoid the dispersion of this IAS to new environments..

Keywords: *Biological invasion; dispersion; freshwater; golden mussel; bivalves.*

Limnoperna fortunei - Atualização da distribuição geográfica nas bacias hidrográficas brasileiras e mapeamento da ocorrência regional na bacia do Alto Rio Uruguai

Resumo: *Limnoperna fortunei* é uma espécie exótica invasora que causa sérios problemas ecológicos e econômicos em ambientes de água doce do Brasil. Devido à sua elevada capacidade de dispersão e à falta de novos registros em publicações científicas, o objetivo deste estudo foi realizar uma extensa pesquisa para entender e alertar sobre o atual cenário de distribuição de *L. fortunei* nas bacias hidrográficas brasileiras. Também realizamos uma investigação mais detalhada sobre a distribuição da espécie na bacia do Alto Rio Uruguai, utilizando um método molecular. Apresentamos novos registros de ocorrência da espécie, mostrando a invasão em novas bacias e uma ampla distribuição nas bacias anteriormente infestadas. Além disso, confirmamos que o Alto Rio Uruguai está totalmente colonizado pelo mexilhão-dourado, estando distribuído pelos ambientes lênticos, lóticos e de transição existentes na região. Esta atualização se mostra como uma importante ferramenta para a implementação de diretrizes e o desenvolvimento de protocolos de segurança e barreiras sanitárias para evitar a dispersão desta espécie invasora em novos ambientes.

Palavras-chave: *Invasões biológicas; dispersão; água doce; mexilhão-dourado; bivalves.*

Introduction

Limnoperna fortunei, known as golden mussel, is a freshwater bivalve considered an invasive alien species (IAS) in South America with great potential for dispersion that causes substantial impacts on community structure and ecosystems function, and also generate substantial economic damages (Darrigran et al. 2020).

IAS are defined as species living outside of their natural geographical range due to human actions that can maintain a self-sustainable population and cause environmental or socio-economic impact (Turbelin et al. 2017). The dispersion of the IAS increased mainly due to rapid technological advances and globalization observed during the last decades (Karatayev et al. 2007, Darrigran et al. 2020). These biological invasions accelerate biodiversity loss, and compromise the supporting, provisioning, regulating, and cultural services (Vilà & Hulme 2017).

Native from China and Southeast Asia, *L. fortunei* is currently dispersed in Hong Kong, Taiwan, Japan, and South America, where it was first registered in 1991 in the Río de La Plata estuary (Pastorino et al. 1993). Since then, it has spread throughout the continent (Argentina, Bolivia, Paraguay, Uruguay, and Brazil) (Fusaro et al. 2020).

The *L. fortunei* dispersion success is mainly related to some biological attributes of the species, such as free-living planktonic larvae, sessile byssate adult (Boltovskoy 2015), and high fecundity (Callil et al. 2012). Besides, the golden mussel can survive in extreme environmental conditions and highly polluted waters (Karatayev et al. 2007), tolerate long exposures to air (Andrade et al. 2020), low calcium concentrations, and wide water temperature variations (Karatayev et al. 2007).

In many Brazilian rivers, heavy traffic of boats, mainly for fishing, occurs with no control measures against golden mussel spread (i.e., not preventing the spread associated with hull fouling, live fishing baits, or even water inside the boat and engine). Also, ships with ballast water navigate in some Brazilian watersheds. Hence, we hypothesize that the spread of the *L. fortunei* is much more extensive than it is known.

The combination of golden mussel high dispersion capacity with the lack of records in peer-reviewed journals showing new occurrences of golden mussels in Brazilian watersheds motivated us to update *L. fortunei* distribution in the Brazilian territory.

Therefore, the objective of the present study was to update the scenario of distribution of *L. fortunei* in Brazilian hydrographic basins through bibliographic survey and by point data. We also intend to present a more comprehensive investigation of the golden mussel distribution in the Upper Uruguay River basin, giving particular attention to tributaries, transitional stretches, bays, and the main body of all five hydroelectric power plants reservoirs located in this area.

Material and Methods

To update the distribution of the golden mussel among the Brazilian river basins, we performed an extensive survey of new publications in Medline, Web of Science, Scopus, ERIC, CSA, Biological Abstracts, Scielo, and Google Scholar databases, searching for scientific papers, books, thesis, and abstracts, published between 2016 and 2020, which have the terms "Limnoperna fortunei AND Brazil" or "Limnoperna fortunei AND Brasil". This search updates the data published by Hydroelectric Invasive Species Bioengineering Center (CBEIH), which presents golden mussel distribution until 2016 (CBEIH 2020). Approximately 250 publications were found in the survey, but only 60 of them addressed *L. fortunei* samplings.

Also, we create a network of professionals associated to the hydroelectric power plants (HPP) located in different Brazilian watersheds, that includes generation and environment staffs, engineers, consultants, and researchers, to report the presence of the golden mussel in each HPP and, when known, the year of the invasion.

The HPP studied were selected by hydrographic basin, excluding those with registered presence of the golden mussel, and selecting those positioned in the upper, middle or lower stretch of the rivers, for which no presence was cited in the literature in the analyzed period.

A total of 66 HPP was selected, distributed in the Southeast Atlantic Basin (*n*=13; Aimorés, Baguari, Candonga, Guilman Amorim, Ilha dos Pombos, Mascarenhas, Nilo Peçanha, Paraibuna, Pereira Passos, Porto Estrela, Sá Carvalho, Salto Grande, Simplício), in the Parana River Basin (*n*=11; Amador Aguiar I and II, Camargos, Funil, Itumbiara, Itutinga, Jaguara, Miranda, Nova Ponte, Piraju, Salto Santiago), in the Amazon Basin (*n*=11; Balbina, Belo Monte, Cachoeira Caldeirão, Colíder, Curuá-Una, Dardanelos, Jirau, Santo Antônio, São Manoel, Sinop, Teles Pires), in the San Francisco River Basin (*n*=10; Itaparica, Moxotó, Paulo Afonso I, II, III and IV, Queimado, Retiro Baixo, Três Marias, Xingó), in the Araguaia-Tocantins River Basin (*n*=7; Cana Brava, Estreito, Lajeado, Peixe Angical, São Salvador, Serra da Mesa, Tucuruí), in the South Atlantic Basin (*n*=6; 14 de Julho, Castro Alves, Itaúba, Jacuí, Monte Claro, Passo Real), in the Paraguay River Basin (*n*=3; Jauru, Manso, Ponte de Pedra), in the East Atlantic Basin (*n*=3; Irapé, Itapebi, Santa Clara), in the Parnaiba River Basin (*n*=1; Boa Esperança), and in the Uruguay River Basin (*n*=1; Passo Fundo).

In September 2018, we also performed a field survey in Campos Novos, Barra Grande, Machadinho, Itá, and Foz do Chapecó reservoirs, all located in the Upper Uruguay River basin, to evaluate the presence of the golden mussel through a molecular method.

In each reservoir, we investigated ten sites distributed in the main reservoir body and in the surrounding areas, which include tributaries, transitional stretches, and bays, totalizing 50 sampling sites. We filtered water from these sites in a plankton net (53µm), collected just below the surface with a motor pump (Tschá et al. 2012). Two replicates, separated by a distance of approximately 30 m, were performed at each site, and the 200 l filtered in each replicate were mixed in one bottle (400 l of filtered water). Samples were fixed with 95% ethanol (1:4 water:ethanol proportion) and kept on ice until arriving at the laboratory, in which the storage was made at -20°C until processing.

Plankton samples were filtered again in a 100-micron nylon mesh to remove large particles that could impair DNA extraction and subsequently filtered in smooth membranes (0.22 µm) using a vacuum pump. Total DNA was extracted with the PureLink™ Microbiome DNA Purification Kit (Invitrogen™). The DNA was quantified in NanoDrop Lite (Thermo Scientific) and standardized at a concentration of 10 ng/µl using ultra-pure water.

Polymerase Chain Reactions (PCR) were adapted from Pie et al. (2006) and Boeger et al. (2007), using universal 18S-1100R
(5'-GATCGTCTTCGAACCTCTG-3') and 18S-7F
(5'-GATCGTCTTCGAACCTCTG-3'), and specific primers Limno-COIR1
(5'-TCCAACCAGTCCCTACTCCACCCTCTA-3') and Limno-COIF1
(5'-TTTAGAGTTAGCACGTCCTGGTAGGTT-3').
We carried out the PCR in 25 µL mixes containing 1.5 mM of $MgCl2$, 0.5 mM of dNTPs, 1X reaction buffer, 1U of Taq platinum (Invitrogen), 2.0 mM of each specific primers (Limno-COIR1 and

Limno-COIF1), 0.2 mM of each universal primers (18S), 0.5 ng/µL of BSA and 0.8 ng/µL of DNA. Standard cycling parameters were adapted from Pie et al. (2006), with initial denaturation at 94 °C for 4 min, followed by 35 cycles of 94 °C for 30 s, annealing temperature of 59 °C for 30 s, extension at 72 °C for 60 s, followed by a final elongation step at 70 °C for 3 min. We visualized the PCR products on 1.5% agarose. All negative PCR amplifications were tested twice to confirm the absence of amplification.

Results

We identified three new records of *L. fortunei* in the 60 publications available between 2016 and 2020, one of them in a new invaded basin (Online Resource 1). This record was published in 2019 and referred to 10 specimens of *L. fortunei* collected in October 2010 in the bay-estuary complex of Santos, São Vicente, and Bertioga Channel, in the Southeast Atlantic Basin (Senske et al. 2019). The other records refer to basins were *L. fortunei* was already present, such as the San Francisco River Basin, were *L. fortunei* was collected in the lower stretch of the river (Melo 2018), and the Paraná River Basin, in the Salto Santiago HPP (Borges et al. 2017).

From our network, we had feedback from 44 collaborators, 15 of them notifying new records of *L. fortunei* and 29 indicating the absence of the invasive species (Online Resource 2). Additionally, three new records from not selected plants were also notified, expanding the network to 69 HPP and 18 new records.

Two other new records were registered in a river stretch with no HPP, both in the north and east channels of the water transposition system of the San Francisco River, which enabled the invasion of *L. fortunei* in the Eastern Northeast Atlantic Basin.

These 23 new records (3 from publications and 20 from collaborators) were plotted in Figure 1, complementing the information related to golden mussel distribution in Brazilian watersheds previously available (CBEIH 2020).

The PCR analysis showed bands in 42 of the 50 collected samples, which confirmed the presence of *L. fortunei* in the plankton and revealed that it is widely distributed in the five reservoirs of the Upper Uruguay River (Figure 2).

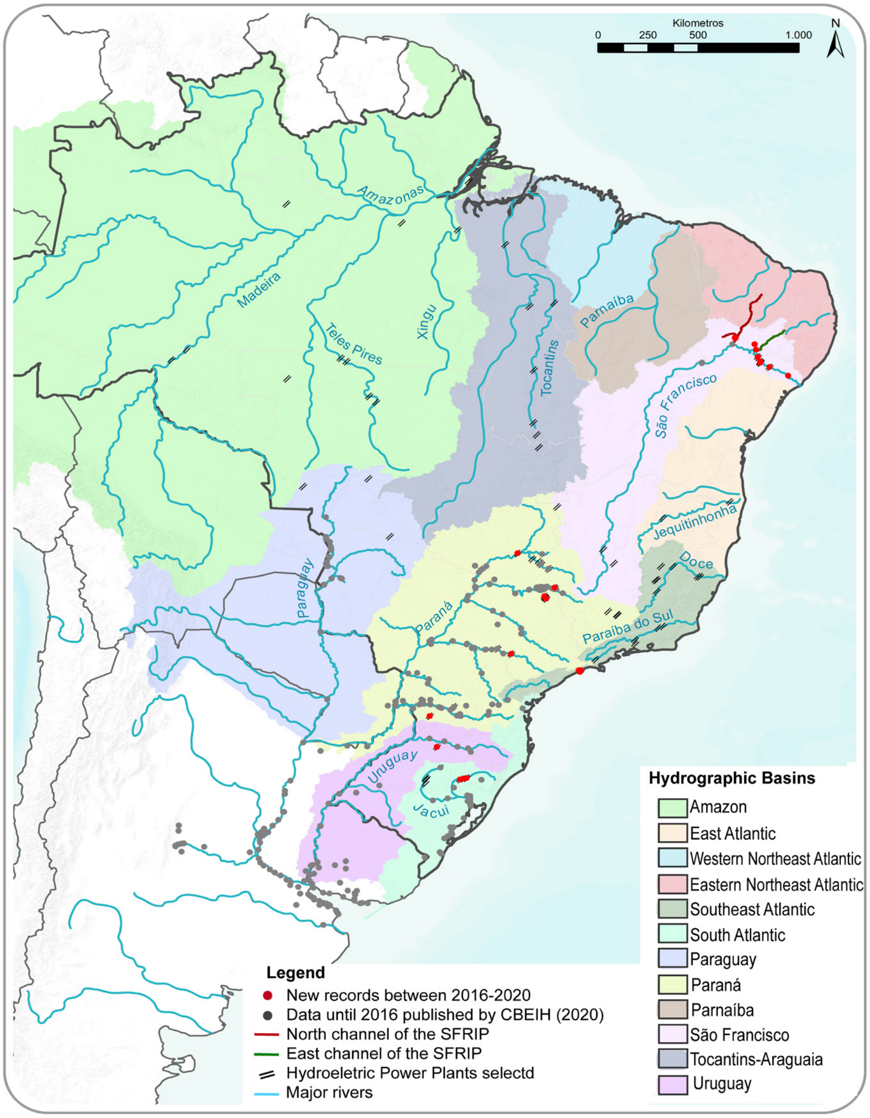

Figure 1. Distribution of the golden mussel *Limnoperna fortunei* in South America, updating the distribution in the Brazilian watershed. Dots represent the presence of *L.fortunei.* Data until 2016 are from CBEIH (2020). Double strokes represent the Hydroelectric Power Plants selected. SFRIP means São Francisco River Integration Project

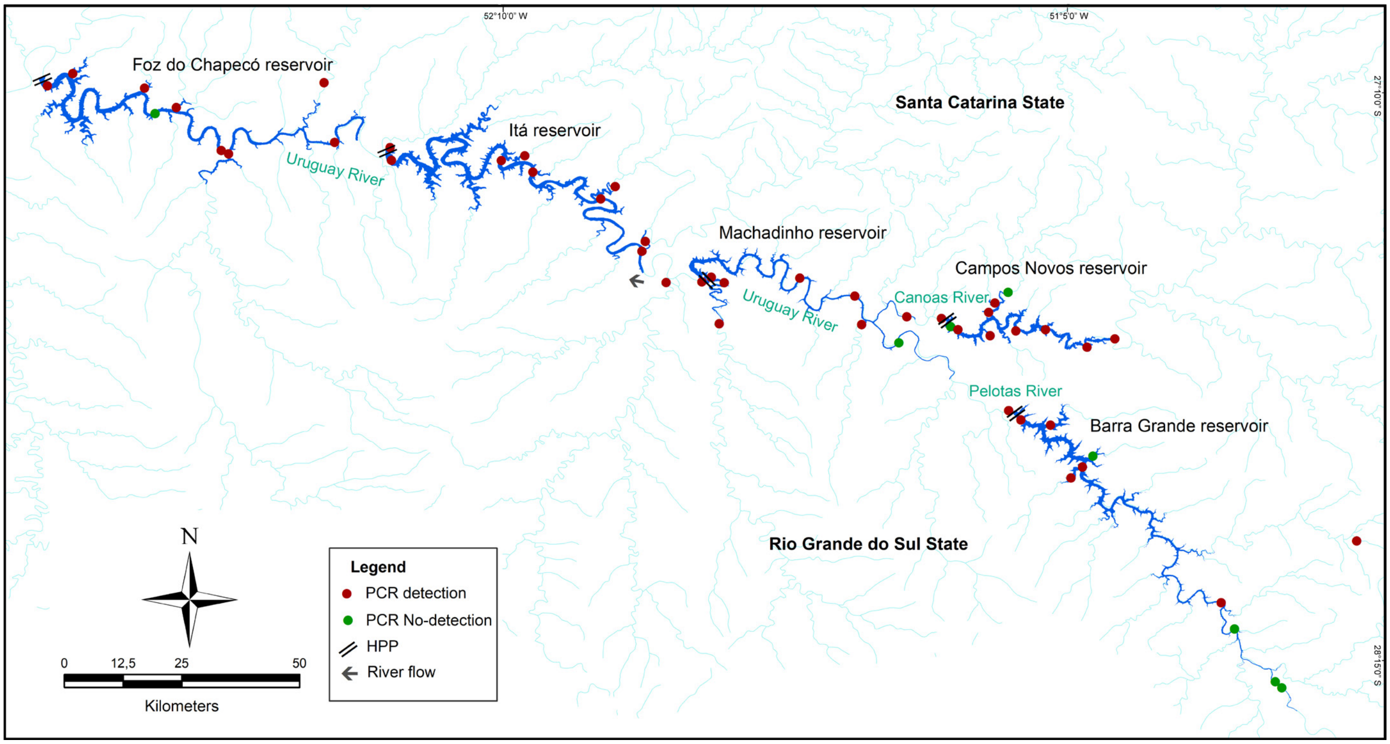

Figure 2. Distribution of the golden mussel *Limnoperna fortunei* in the Upper Uruguay River Basin. Red dots: presence of *L. fortunei*. Green dots: absence of *L. fortunei*

Discussion

Brazil has twelve hydrographic basins, and in five of which (Uruguay, South Atlantic, Paraná, Paraguay, and San Francisco) the invasion by *L. fortunei* had already been reported in the CBEIH mapping 2016 (CBEIH 2020).

The present survey identified two new watersheds invaded by the species: the Southeast Atlantic Basin and the Eastern Northeast Atlantic Basin. Thus, only five Brazilian hydrographic basins (Eastern Atlantic Basin, Araguaia-Tocantins, Parnaiba, Amazon, and Western North Atlantic) are still free of this invasive species.

The new records here identified showed that in the last four years (2016-2020), *L. fortunei* was more widely distributed in basins previously infested, in some cases reaching their upper stretches and in others dispersing downstream with the current.

The biological traits of the golden mussel allow a wide dispersion in the environment invaded by the species (Boltovskoy 2015, Giglio et al. 2016), and are remarkably efficient in downstream colonization. The presence of a planktonic larval phase in the life cycle of the species, which can last from 10 to 20 days depending on the water temperature (Cataldo et al. 2005), permits the dispersion over long stretches in rivers with currents.

However, as highlighted by Boltovskoy (2015), the natural geographic barriers end up being insurmountable for the natural dispersion of the golden mussel. Therefore, human activity acts as the primary vector of the species dispersion between basins (Boltovskoy 2015), either through the transit of boats (commercial or recreational), aquaculture (Oliveira et al. 2015) or even through the construction of water transposition systems between basins. In this way, human action ends up being responsible for taking the species to new watersheds and enabling the invasion of the species upstream in the watersheds it is already present (known as the dispersion jumps) (Oliveira et al. 2015).

The invasion of *L. fortunei* in the São Francisco River basin was recorded in 2015 by Barbosa et al. (2016) in the middle stretch of the basin in Sobradinho HPP, and also in the inlet of the north axis of the irrigation channels (near the municipality of Cabrobó, PE) of the São Francisco River Integration Project (SFRIP). In the next year (2016) the species dispersed to other reservoirs located in this region (Itaparica, Moxotó, Paulo Afonso I, II, III, IV, and Xingó), and around 2018 through the two channels of the transposition system (north and east), reaching a new hydrographic basin, the Eastern Northeast Atlantic Basin. As a result, golden mussel dispersion throughout the northeastern region of the country seems to be a matter of time, considering that the SFRIP irrigation channels reach four states in this region (Pernambuco, Paraíba, Rio Grande do Norte, and Ceará).

Despite this, the upper stretch of the São Francisco basin remains free from *L. fortunei* invasion, as confirmed by the absence of golden mussel records above the Três Marias dam, even with its proximity to environments with a high abundance of golden mussel for several years, such as the Grande and Paranaíba rivers (Parana River Basin). In these rivers, an intense sport and commercial fishing activity and possible transit of boats between basins are registered (Oliveira et al. 2015).

The sampling carried out in the Upper Uruguay River region in 2018 confirmed the prognosis presented by Oliveira et al. (2015), who suggested, from some records and personal observations, that the golden mussel would fully colonize the Uruguay River in a few years. The species is now present in more than 80% of the sampled environments in the Uruguay River, spread in lentic, lotic, transitional lotic/lentic environments and in tributaries of that river. This is possibly the dispersion condition of golden mussels in places where the species is already registered.

In general, we can say that the lack of connectivity between the basins and the low navigability in many river stretches has helped in decelerating the dispersion of *L. fortunei* within the Brazilian territory. In rivers that are barely navigable or do not have commercial navigation, the golden mussel ends up not dispersing as intensely. Pessotto & Nogueira (2018) did not find larvae of this species in the upper stretches of the Grande and Paranaíba rivers in samples carried out in 2010, although low larval densities were already recorded in the lower stretches of these rivers in 2006 (Campos et al. 2012).

Based on the updated map of areas invaded by *L. fortunei*, managers can concentrate efforts to implement safety protocols or sanitary barriers to avoid the dispersion of the golden mussel to new areas. Aside from the need to monitor the dispersion of the golden mussel, through the standardization of a monitoring protocol, it is essential to implement sanitary controls and authorities inspections between basins, because only them can prevent the last five Brazilian basins from being colonized by this invasive alien species.

Supplementary Material

The following online material is available for this article:

Online Resource 1 - List of the 60 publications found between 2016 and 2020 addressing *L. fortunei* samplings(new records are in bold).

Online Resource 2 - Summary of the information obtained from the network of collaborators, indicating the presence or absence of the golden mussel and year of the observation. (NI means 'Not Informed'; NA means that the contact was 'Not Answered').

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Grasiela Fagundes Minatto Cardoso: project administration and manuscript revision.

Alex Pires de Oliveira Nuñer: funding acquisition, project administration, and manuscript 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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Short Communication

Blooming meal: flower eating by the Blue-crowned Trogon *Trogon curucui*

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Abstract: Flowers provide birds with a range of dietary resources, although few data are available on flower eating for birds that have mixed diets. We report here a new food type for the Blue-crowned Trogon (*Trogon curucui*), describing two flower eating events. The individuals fed on the yellow trumpet tree flowers (*Handroanthus* spp.) at the peak of the dry season in the Cerrado and Pantanal biomes. The birds picked up the flowers by sally-glean flying and a brief hovering, and then perched on a nearby branch to swallow the flower whole. Florivory appears to be seasonal and, while a minor component of this species' diet, flowers may be an important alternative resource during periods when fruits are scarce.
Keywords: *feeding behavior, flowers as food, Trogonidae, Cerrado, Pantanal.*

Refeição florida: consumo de flores pelo surucuá-de-barriga-vermelha *Trogon curucui*

Resumo: As flores fornecem às aves uma variedade de recursos alimentares, embora poucos dados estejam disponíveis sobre o consumo de flores por aves de dieta mista. Relatamos aqui um novo item alimentar para o surucuá-de-barriga-vermelha (*Trogon curucui*), descrevendo dois eventos de ingestão de flores. Os surucuás se alimentaram das flores de ipê-amarelo (*Handroanthus* spp.) no ápice da estação seca nos biomas Cerrado e Pantanal. As aves apanharam as flores em voo "sally-glean" e em seguida pousaram em um ramo próximo para engoli-las por inteiro. A florivoria parece ser sazonal e embora seja um componente secundário da dieta desta espécie, as flores podem ser um recurso alternativo importante durante os períodos em que os frutos são escassos.
Palavras-chave: *comportamento alimentar, flores como alimento, Trogonidae, Cerrado, Pantanal.*

Introduction

Trogonidae (Aves, Trogoniformes) are forest dwellers that include eight genera and 43 species with a Pantropical distribution, except in Australasia (Collar 2020). African species are exclusively insectivores, whereas the Asian and Neotropical species have mixed diets of arthropods and fruits, with occasional small vertebrate preys, although the exact composition of the diet varies considerably among the different taxa (Remsen et al. 1993, Sick 1997, Collar 2000, Pizo 2007, Winkler et al. 2020). For species of the genus *Trogon*, analyses of the stomach contents of 17 species revealed a mixed diet of arthropods and fruits (Schubart et al. 1965, Remsen et al. 1993).

Florivory (or floral herbivory) is defined as the consumption of all or part of the structure of a flower, which may damage the floral bud or mature flower prior to the development of the seed capsule (Burgess 1991). Floral components are an important feeding resource for many Brazilian birds (Silva and Rubio 2007, Parrini & Raposo 2008, 2010, Parrini 2015). Nevertheless, the consumption of flowers by omnivorous birds and the importance of floral resources in their diets are still poorly understood. Most studies focus on the consumption of nectar for acquisition of nutrients, energy, and water (Silva 2019), typically without causing damage to the flowers (Parrini 2015). However, some studies describe feeding on petals and other floral components by several bird species (Sazima & Sazima 2007, Silva & Rubio 2007, Parrini & Pacheco 2013, Parrini 2015, Silva 2019).

We describe herein two events of flower eating by the Blue-crowned Trogon, *Trogon curucui*, during the dry season in the Brazilian Cerrado savanna and Pantanal wetland biomes. This species is reported as having a typical *Trogon* diet of invertebrates and fruit (Remsen et al. 1993).

Material and Methods

The records from the Cerrado were obtained in the village of Brejo do Peixe (5º24’56” S, 43º31’34” W), in the municipality of Parnarama, eastern Maranhão (Figure1). The observations were conducted in September, at the peak of the dry season, which coincides with the blooming of the yellow trumpet tree (*Handroanthus* sp.). The vegetation of the studied area is composed of extensive areas of Cerrado *sensu lato*, interspersed with tracts of *Mauritia flexuosa* palm swamps (veredas), small villages, and subsistence farmland. The local climate is highly seasonal, with a dry season from June to November and a rainy season from December to May. Another observation was obtained on the Transpantaneira highway (16º20’21” S, 56º38’40” W), in the municipality of Poconé, southern Mato Grosso. The vegetation of this studied area is composed of extensive swampland typical of the Pantanal, interspersed with tracts of gallery forests, and large cattle-raising farms. The climate is highly seasonal, with a dry season from May to September and a rainy season from October to April (Tarifa 1986). The observations at both areas were conducted using Nikon 10x42 or Pentax 10x50 binoculars, and the photographs were taken with a Canon 7D camera.

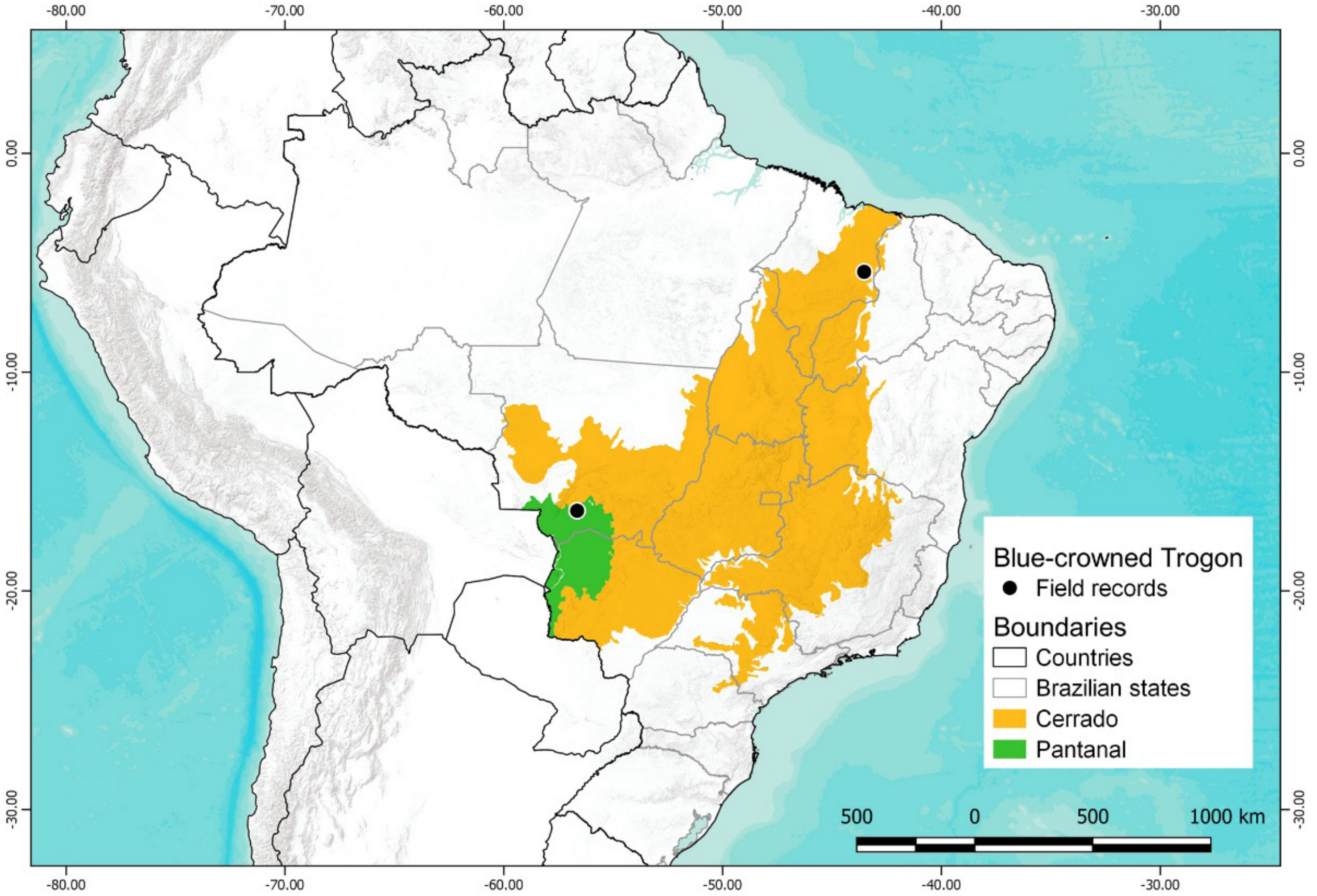

Figure 1. Map with the biomes Cerrado and Pantanal in Brazil, and the two field records of Blue-crowned Trogon (*Trogon curucui*) consuming trumpet tree (*Handroanthus* spp.) flowers.

https://doi.org/10.1590/1676-0611-BN-2020-1154.

Results

On the Transpantaneira highway, on September 1982, at approximately 13:00 h, a pair of *T. curucui* was observed on a full blooming yellow trumpet tree (*Handroanthus* cf. *ochraceus*). The two birds were perched near one another and flew towards a flowering branch three or four times, using a sally-glean flight and picked a flower while hovering briefly. The birds then returned to their perch to swallow the flower whole. The female was observed picking and swallowing two flowers, while the male did this once before the pair left the perch and disappeared from view.

At the village of Brejo do Peixe, at 10:40 h on 9 September 2019, a flock of six Blue-crowned Trogon individuals was observed moving in the crown of a yellow trumpet tree (*Handroanthus* sp.) in full bloom. During the intense movements of the individuals among the crowns of the trees adjacent to the trumpet tree, a female Blue-crowned Trogon was observed carrying a yellow flower in its bill. Afterwards the flower was swallowed whole. Subsequently, a male was observed perching alongside a number of flowers and then descended in a short, rapid flight to collect a flower after a sally-glean maneuver, which consisted of swooping down onto a food item and capturing it in a brief hovering. The bird then perched in an adjacent tree and swallowed the flower whole (Figure 2).

Discussion

Our observations validate and document flower eating for the Blue-crowned Trogon, *Trogon curucui*, an apparently uncommon feeding behavior among Trogonidae. In an observational dietary study of three *Trogon* species in the Atlantic Forest, a single unidentified flower was eaten by a Green-backed Trogon *T. viridis* individual during the dry season (Pizo 2007). On the other hand, the Cuban Trogon *Priotelus temnurus* seems to feed mostly on flowers, besides fruits and insects (Collar 2020).

Many *Trogon* species, including *T. curucui*, have a mixed diet composed mainly of fruits and arthropods. Schubart et al. (1965) analyzed 10 individuals of *T. curucui* (including *T. variegatus*), and found that 60% of the stomach contents were composed exclusively by arthropods while 40% had a mix of arthropods, fruits, seeds, and plant tissue. Remsen et al. (1993) analyzed 36 individuals and found that 52.8% of the stomach contents was composed by arthropods only, while 44.4% contained a combination of fruits and arthropods (2.8% contained unidentified material).

While feeding on flowers, trogons and other birds may obtain a considerable combination of nutrients and sugars, such as glucose, fructose, and saccharose, particularly when fleshy fruits are scarce (Baker & Baker 1983, Terborgh 1986, Galetto & Bernardello 2003). Indeed, the flowers of trumpet trees (*Handroanthus* and *Tabebuia*) produce nectar with a high (23–30%) concentration of sugars (Barros 2001; Souza et al. 2004). *Handroanthus ochraceus* blooms profusely for about one month during the dry season, and the time of the trogon feeding event recorded at Parnarama coincided with the 11:00 h peak of nectar concentration recorded for *H. ochraceus* and *Tabebuia aurea* (Barros 2001). In addition to making available an important alternative source of nutrients and energy, flowers may meet the birds' requirements for water, a scarce resource in the dry season (Mlcek & Rop 2011, Silva et al. 2015, Silva 2019). The fleshy petals of *Acca sellowiana* may be an important nutritional resource for nestlings of the Sayaca Tanager *Thraupis sayaca*, the Chestnut-backed Tanager *Stilpnia preciosa*, and other passerines as well, when fruits are scarce (Sazima & Sazima 2007).

The consumption of flowers is considered an opportunistic behavior in many birds and recorded mostly during the dry season when the availability of fruit and water is reduced (Parrini 2015, Silva 2019). Floral resources can be exploited in a number of ways, both destructive and non-destructive. Hummingbirds (Trochilidae) and a number of passeriforms feed on nectar and act as pollinators without changing the flower structure (Parrini & Raposo 2010), whereas some species of Cracidae, Psittacidae, Ramphastidae, Thraupidae, and Icteridae are known to be flower predators (Ragusa-Netto 2005, Parrini & Pacheco 2013, Parrini 2015, Mendes et al. 2017, Valtuille et al. 2017).

Primarily frugivorous birds may also occasionally include flowers in their diets, independently of the scarcity of fruit, as is the example of the Saffron Toucanet *Pteroglossus bailloni* in the Brazilian Atlantic Forest, and the Emerald Toucanet *Aulacorhynchus prasinus* in Costa Rica (Riley & Smith 1986, Galetti et al 2000). It thus seems that at least some toucans may feed regularly on non-fruit foods, even if in small amounts, in particular during the breeding season (Riley & Smith 1986). However, the Toco Toucan *Ramphastos toco* appears to eat flowers opportunistically in the Pantanal biome (Ragusa-Netto 2006).

In the Pantanal, Blue-throated Piping-Guan *Pipile cumanensis* regularly eats the flowers of the pink trumpet tree (*Handroanthus impetiginosus*) during the dry season, when it may congregate in blooming trees together with Chaco Chachalaca *Ortalis canicollis*, Bare-faced Curassow *Crax fasciolata*, and Chestnut-bellied Guan *Penelope ochrogaster* (Del Hoyo et al. 2020). In the Pantanal, which has an intense dry season, the Yellow-chevroned Parakeet *Brotogeris chiriri*, Peach-fronted Parakeet *Eupsittula aurea*, and Turquoise-fronted Parrot *Amazona aestiva*, exploited *Erythrina fusca* ripping the flowers off the

Figure 2. A Blue-crowned Trogon (*Trogon curucui*) male swallows a whole trumpet tree flower (*Handroanthus* sp.) in the Cerrado savanna at Brejo do Peixe,

branch to feed on nectar, while the Chestnut-eared Aracari *Pteroglossus castanotis* and *R. toco* swallowed the flowers whole (Parrini & Raposo 2010). On the other hand, the Sayaca Tanager, the Palm Tanager *Thraupis palmarum*, and the Grayish Saltator *Saltator coerulescens* were observed tearing off and eat the petals (Parrini & Raposo 2010). As would be expected, wide-gaped birds swallow the flowers whole, whereas narrow-gaped ones feed on flower pieces.

Despite the apparent rarity and seasonality, feeding on flowers by the Blue-crowned Trogon indicates that this bird searches actively for alternative sources of nutrients to meet water and nutrients requirements during periods of fruit scarcity. However, studies on the relationship between birds and blooming trumpet trees (*Handroanthus* and *Tabebuia*) in the Cerrado and Pantanal are still scarce. Both these biomes have an intense dry season when they are vulnerable to extensive wildfires, which may have a significant impact on the abundance of feeding resources for birds during this part of the year. Thus, availability of alternative food, such as flowers, may be fundamental to their survival.

The Blue-crowned Trogon and Green-backed Trogon are phylogenetically close (Espinosa de los Monteros 1998, Moyle 2005), and both species occasionally feed on flowers (Pizo 2007; present paper). The Cuban Trogon *Priotelus temnurus* is placed among the first branching lineages in the phylogeny of the Neotropical trogons (Espinosa de los Monteros 1998, Moyle 2005), and feed mostly on flowers (Collar 2020). Given the absence of flower-eating in most *Trogon* species, we submit that this feeding behavior could have been lost throughout the evolution of the variable feeding habits of most Neotropical trogons (Collar 2020, Winkler et al. 2020). Alternatively, florivory is actually a rare behavior and has been mostly unnoticed. We predict that a few additional flower eating *Trogon* species will be reported with further observational, natural history-oriented studies, especially in biomes with marked seasonal differences.

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Author Contributions

Gustavo Gonsioroski: Contribution to data collection; manuscript preparation; contribution to critical revision, adding intellectual content.

Ivan Sazima: Contribution to data collection; manuscript preparation; contribution to critical revision, adding intellectual content.

Marcos Augusto Rodrigues Silva: Contribution to data collection; manuscript preparation.

Flávio Kulaif Ubaid: 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

Besides the map, photographs and descriptions included here, other data was compiled from published literature, and appropriated cited along the manuscript.

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Thematic Review

Insect galls of the Brazilian Cerrado: associated fauna

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Abstract: Insect galls host a rich and diverse fauna of secondary dwellers, which compose the associated fauna. In Brazil, many inventories of insect galls in Cerrado areas have recorded secondary dwellers. These records were scattered in several papers. This study gathered literature data to provide an overview of the arthropod fauna associated with insect galls in the Brazilian Cerrado. We searched for scientific publications in online academic databases and retrieved 16 papers with data on the secondary dwellers. We limited our search to the period from 1988 to 2020. We updated the name of plant species and verified endemism and geographic distribution in Flora do Brasil 2020. We provided plant species uses based on the Tropical Useful Plants 2014. We found 163 gall morphotypes with secondary dwellers (16.8% of the total of gall morphotypes of the Brazilian Cerrado) on 94 plant species in 37 families. Asteraceae, Fabaceae, Myrtaceae, and Malpighiaceae exhibited the greatest number of records. These are the richest families in insect galls in the Brazilian Cerrado. Most arthropod fauna were recorded in galls of Cecidomyiidae (Diptera). Most records were in leaf galls, the predominant galled organ. Parasitoids were more frequent than successors, inquilines, and predators. Eulophidae and Eurytomidae were the most frequent parasitoid families. Inquilines were represented by Coleoptera, Diplopoda, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Psocoptera, and Thysanoptera; successors by Acari, Araneae, Cecidomyiidae (Diptera), Coleoptera, Collembola, and Formicidae (Hymenoptera), whereas predators by Pseudoscorpiones and Diptera. Most records were presented in suprageneric categories, showing that the taxonomic knowledge is very deficient. 29 plant species are endemic to Brazil and totaled 45 gall morphotypes with secondary dwellers; 46 plant species are useful and host secondary dwellers in 62 gall morphotypes. These data add ecological and economic importance to these arthropods..

Keywords: *Parasitoids; inquilines; predators; successors; galling-insects.*

Galhas de insetos do Cerrado Brasileiro: fauna associada

Resumo: As galhas de insetos abrigam uma fauna rica e diversificada de habitantes secundários que compõem a fauna associada. No Brasil, muitos inventários de galhas de insetos em áreas de Cerrado registram habitantes secundários. Estes registros, dispersos em vários artigos, foram reunidos para fornecer uma visão ampla da fauna de artrópodes associados às galhas de insetos no Cerrado brasileiro. Buscamos publicações científicas nas bases de dados acadêmicas virtuais e encontramos 16 artigos com informações de habitantes secundários. Limitamos nossa busca ao período de 1988 a 2020. Atualizamos o nome das espécies botânicas e verificamos sua distribuição geográfica e endemismos no site Flora do Brasil 2020. Fornecemos os usos das espécies vegetais com base no site Tropical Useful Plants 2014. Encontramos 163 morfotipos de galhas com habitantes secundários (16,8% do total de morfotipos de galhas do Cerrado brasileiro) em 94 espécies de plantas de 37 famílias. Asteraceae, Fabaceae, Myrtaceae e Malpighiaceae exibiram o maior número de registros. Estas são as famílias mais ricas em galhas de insetos no Cerrado brasileiro. A maioria da fauna de artrópodes foi assinalada em galhas de Cecidomyiidae (Diptera). A maioria dos registros foi em galhas foliares, órgão vegetal com maior riqueza de galhas. Os parasitoides foram mais frequentes que os sucessores, inquilinos e predadores. Eulophidae e Eurytomidae foram as famílias de parasitoides mais frequentes. Os inquilinos foram representados por Coleoptera, Diplopoda, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Psocoptera, e Thysanoptera; os sucessores por Acari, Araneae, Cecidomyiidae (Diptera), Coleoptera, Collembola e Formicidae (Hymenoptera); enquanto os predadores por Pseudoscorpiones e Diptera. A maioria dos registros foi apresentada em categorias supragenéricas, mostrando que o conhecimento taxonômico é muito deficiente. Vinte e nove plantas são endêmicas do Brasil e totalizam 45 morfotipos de galhas com habitantes secundários; 46 espécies vegetais são úteis e hospedam habitantes secundários em 62 morfotipos de galhas. Estas informações acrescentam importância ecológica e econômica a estes artrópodes.

Palavras-chave: *Parasitoides; inquilinos; predadores; sucessores; insetos galhadores.*

Introduction

Galls are a classic example of niche construction (Gilbert 2009). They represent discrete microhabitats that support relatively closed communities of specialist inhabitants (Shorthouse & Rohfritsch 1992, Williams 1994, Crespi et al. 1997). Galls are abnormal plant growths induced by various parasitic organisms, mainly insects. Insect galls provide the inducers with food and shelter at the expense of the host plant (Tooker et al. 2008). Galls serve as ''incubators'' for the developing insects in which they gain nutrition and protection from both abiotic factors (e.g., sun irradiation, wind, rain and snow) and natural enemies such as pathogens, predators and parasitoids (Price et al. 1987, Stone & Schonrogge 2003). Galls act as a ''nutrient sink'' into which the plant translocates concentrated soluble nutrients for the growth of those cells. These nutrients, which are especially rich in amino acids, are then used by the gall-inducer for its own growth (White 2010).

Gall tissues are attractive for non-galling herbivores as food sources (Sugiura & Yamazaki 2009, Yamazaki & Sugiura 2016). There is a rich and diverse fauna of secondary dwellers of galls. They compose the associated fauna and include parasitoids, predators, cecidophages, successors, inquilines, kleptoparasites and symbionts (Luz & Mendonça-Júnior 2019).

In Brazil, there are several inventories of insect galls in Cerrado areas, mainly in the states of Minas Gerais and Goiás (Araújo et al. 2014). The Cerrado is the second largest phytogeographical domain of Brazil, occupying an area of ca. 2 million km^2 (23% of the national territory) (Oliveira & Ratter 2002) and one of the phytogeographical domains with the highest plant diversity in the world, containing over 12,000 species (Klink & Machado 2005, Mendonça et al. 2008). Furthermore, the Cerrado is considered one of the world`s biodiversity hotspots and a priority conservation area (Myers et al. 2000). Cintra et al. (2020) published a dataset of host plants and their gall-inducing insects for the Brazilian Cerrado, which represented a major effort to compile species lists of host plant communities for galling insects of the Neotropical region. However, Cintra et al. (2020) did not address the associated fauna.

Gall-inducers can influence the distribution and abundance of organisms in diverse communities by providing a physical structure that can be later used as shelter from the physical environment, protection from natural enemies as well as food resources. Therefore, they alter the local environment through habitat modification or amelioration of abiotic stress, with direct and indirect effects on other components of communities and ecosystem properties (Cuddington et al. 2007). This valuable role of gall-inducers as ecosystem engineers (Cornelissen et al. 2016) reinforces the importance of studying the associated fauna and knowing its composition, richness and ecological interactions.

The present study aims to compile data on arthropods associated with insect galls in the Brazilian Cerrado and answer the following questions: i) which guilds are represented? ii) which is the most frequent? iii) which is the most diverse? iv) what is the composition of each one? v) which plants host these guilds? vi) how many gall morphotypes host them? vii) do these guilds occur in endemic or useful hosts? vii) which galling insects stand out for sheltering the secondary fauna more often?

Material and Methods

We searched for papers in online academic databases: ISI Web of Knowledge, Google Scholar, Scielo, Scopus and JStor, using the terms "insect gall"/"galhas de insetos", "inventories"/"inventários, and "Brazilian Savanah"/"Cerrado. We found 32 papers, 16 of them with data on the associated fauna. We used the Flora do Brasil 2020 website to verify botanical names and plant endemisms. We also looked for data on plant uses in the site Useful Tropical Plants 2014.

We organized tables, according to the level of plant identification: species – Table 1, genus – Table 2, and family – Table 3. These tables include the following data: host plant, galled organ, gall-inducer, associated fauna, food habit, locality and reference. Whenever the name of host plant species was updated, we presented the original name in brackets after the reference.

We counted the number of gall morphotypes only for host plant species. We compared morphotypes in the same plant species when recorded by different authors to avoid repeated counting. We adopted this procedure only when gall illustrations were available.

Concerning the guilds of the associated fauna, we kept the term "inquiline" as used in the original publications, although we recognize problems in its use, since it includes cecidophages, kleptoparasites, and inquilines. However, original data are insufficient to allow re-categorization.

Results

We found records of the associated fauna in 163 gall morphotypes, 94 plant species and 37 plant families. Fabaceae (N=52) (31.9%), Asteraceae (N=15) (9.2%), Myrtaceae, and Malpighiaceae (N=10 each) (6.1%) had the greatest number of gall morphotypes with records of the associated fauna (Table 4).

Most records (N=105) (64.4%) were in galls of Diptera, mainly Cecidomyiidae (N=102) (62.6%), but galls of Hemiptera, Lepidoptera, Hymenoptera, Coleoptera, and Thysanoptera also hosted secondary dwellers (Table 5), Hemiptera were the second most common gall-inducers, but with very low percentage (4.3% only). Leaf galls had the most records (N=117) (71.8%), followed by stem galls (N=43) (26.4%). Galls on buds, spines and reproductive structures also hosted secondary dwellers. Some galls were induced in two plant organs or more (Table 6).

Parasitoids were the most frequent guild, being reported in 147 gall morphotypes (90.2%). They were followed by successors, inquilines, and predators, reported in 13 (8.0%), 12 (7.4%) and three (1.8%) gall morphotypes, respectively, showing that these guilds were infrequent (Table 7).

Parasitoids were represented by 12 Hymenopteran families. Among them, Eulophidae, Eurytomidae, Torymidae, and Encyrtidae were the most frequent, with records in 41gall morphotypes (29.7% of the parasitized morphotypes), 20 (13.6%), 14 (9.5%) and 12 (8.2%), respectively.

Sucessors included insects of three orders (Coleoptera, Diptera and Hymenoptera), as well as other arthropods (Acari, Araneae, and Collembola); inquilines included insects of seven orders (Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Psocoptera, and Thysanoptera), and Diplopoda, whereas predators were the least diverse, being represented by Pseudoscorpiones and Diptera; all of these taxa were recorded in few gall morphotypes (from 5 to 1) (Table 8).

Concerning the taxonomic knowledge, only four species, *Anthonomus vis* Clark, 1992 (Coleoptera), *Meunieriella spinosa* Urso-Guimarães, 2019 (Diptera), *Salina celebensis* (Schäffer, 1898), and

Table 1. Data on arthropods associated with insect galls in the Brazilian Cerrado: host plant species, gall-inducer, host organ, secondary dweller, ecological guild, locality, and reference. Plant origin: (1) native to Brazil, (2) endemic to Brazil, (3) naturalized. Ecological guild: (Inq) inquiline, (Par) parasitoid, (Pre) predator, (Suc) successor, (Und) undetermined.

Host plant	Gall-inducer	Host organ	Secondary dweller	Locality	Reference
ANNONACEAE					
Annona coriacea Mart. (1)	Cecidomyiidae (Diptera)	Leaf	Eulophidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
Annona crassiflora Mart. (1)	Sternorrhyncha (Hemiptera)	Leaf	Braconidae (Par) Eurytomidae (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Duguetia furfuracea (A. St-Hil.) Saff. (1)	Undetermined	Leaf	Hymenoptera (Par)	Caetité (BA)	Nogueira et al. 2016
APOCYNACEAE					
Aspidosperma australe Müll-Arg. (1)	Cecidomyiidae	Flower bud	Eurytomidae (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
	Hemiptera	Leaf	Hymenoptera (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
ARALIACEAE					
Didymopanax morototoni (Aubl.) Decne. & Planch. (1)	Undetermined	Leaf	Eulophidae (Par)	Goiânia (GO)	Santos et al. 2010 (as *Schefflera morototoni* Aubl)
ASTERACEAE					
Baccharis microcephala (Less.) DC (1)	Cecidomyiidae	Leaf	Eulophidae 1 (Par) Eulophidae 2 (Par)	Tiradentes (MG)	Maia & Fernandes 2004
	Cecidomyiidae	Bud	Eulophidae (Par) *Galeopsomyia* sp. (Eulophidae) (Par) *Eurytoma* sp. (Eurytomidae) (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Baccharis reticularia DC. (2)	Cecidomyiidae	Leaf	Platygastridae (Par)	Tiradentes (MG)	Maia & Fernandes 2004
	Lasiopteridi (Cecidomyidae)	Leaf	Heteroptera (Hemiptera) (Und)	Tiradentes (MG)	Maia & Fernandes 2004
Baccharis serrulata (Lam.) (2)	Cecidomyiidae	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Eremanthus capitatus (Spreng.) MacLeish (2)	Coleoptera	Stem	Formicidae (Suc)	Caetité (BA)	Nogueira et al. 2016
Eremanthus erythropappus (DC.) MacLeish (2)	*Asphondylia serrata* Maia, 2004 (Cecidomyiidae)	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia 2004, Maia & Fernandes 2004 (as *Vannilosmopsis erythropapa* Schult)
Moquiniastrum barrosoae (Cabrera) G. Sancho (1)	Undetermined	Stem	Sciaridae (Diptera) (Inq)	Silvânia (GO)	Bergamini et al. 2017 (as *Gochnatia barrosii* Cabrera)
Mikania lindbergii Baker (2)	*Neolasioptera* sp. (Cecidomyiidae)	Stem	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Moquiniastrum paniculatum (Less.) G. Sancho (2)	Cecidomyiidae	Leaf	Eulophidae (Par) Eurytomidae (Par)	Belo Horizonte (MG)	Fernandes et al. 1988 (as *Moquinía panículata* (Less) D.C.)
Moquiniastrum pulchrum (Cabrera) G. Sancho (1)	Cecidomyiidae	bud	Eulophidae (Par) Pteromalidae (Par) Torymidae (Par)	Altinópolis (SP)	Ribeiro et al. 2019
Porophyllum ruderale (Jacq.) Cass. (1)	Cecidomyiidae	Stem	Hymenoptera (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
Verbesina macrophylla (Cass.) S.F.Blake (1)	Cecidomyiidae	Bud	Araneae (Suc) Lepidoptera (Inq)	Caetité (BA)	Silva et al. 2018a

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Vernonanthura polyanthes (Spreng.) Vega & Dematteis (1)	*Tomoplagia rudolphi* (Lutz & Lima, 1918) (Diptera, Tephritidae)	Stem/Bud	Braconidae (Par) Eulophidae (Par) Hymenoptera (Par) Hymenoptera (Inq)	Belo Horizonte Tiradentes Delfinópolis	Fernandes et al. 1988 Maia & Fernandes Urso-Guimaraes et al. 2003 (as *Vernonía polyanthes* Less.)
	Asphondylia sp. (Cecidomyiidae)	Leaf/ Stem	Chalcididae (Par) Torymidae (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
BIGNONIACEAE					
Handroanthus ochraceus (Cham.) Mattos (1)	Lopesiini (Cecidomyiidae)	Leaf	Helconinae (Braconidae) (Par) Hemiptera (Inq)	Delfinópolis (MG)	Urso-Guimarães et al. 2003 (as *Tabebuia ochracea* (Cham.) Standl.)
BORAGINACEAE					
Cordia sellowiana Cham. (2)	Cecidomyiidae	Leaf	Braconidae (Par) Eulophidae (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
	Cecidomyiidae	Leaf	Hymenoptera (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
	Cecidomyiidae	Stem	Hymenoptera (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
BURSERACEAE					
Protium heptaphyllum (Aubl.) March. (1)	Cecidomyiidae	Leaf/ Stem	Torymidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Cecidomyiidae	Leaf	Eulophidae (Par)	Goiânia (GO)	Santos et al. 2010
CALOPHYLLACEAE					
Calophyllum brasiliense (1)	*Lopesia elliptica* Maia, 2002 (Cecidomyiidae)	Leaf	Eulophidae (Par) Eurytomidae (Par) Pteromalidae (Par)	Tiradentes (MG)	Madeira et al. 2002, Maia & Fernandes 2004 (as *Calophyllum* sp.)
	Thysanoptera	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004 (as *Calophyllum* sp.)
	Contarinia gemmae Maia, 2002 (Cecidomyiidae)	Bud	Hymenoptera (Par)	Tiradentes (MG)	Madeira et al. 2002, Maia & Fernandes 2004 (as *Calophyllum* sp.)
CANNABACEAE					
Celtis iguanaea (Jacq.) Sarg. (1)	Undetermined	Leaf	Encyrtidae (Par)	Goiânia (GO)	Santos et al. 2010
CARYOCACEAE					
Caryocar brasiliense Cambess. (1)	Cecidomyiidae	Leaf	Eulophidae (Par) Eurytomidae (Par) Torymidae (Par)	Hidrolândia (GO)	Silva et al. 2018b
	Diaspididae (Hemiptera)	Leaf	Encyrtidae (Par)	Altinópolis (SP)	Ribeiro et al. 2019
CELASTRACEAE					
Plenckia populnea Reissek (1)	Cecidomyiidae	Stem	Braconidae (Par)	Hidrolândia (GO)	Silva et al. 2018b
COMBRETACEAE					
Combretum leprosum Mart. (1)	Cecidomyiidae	Leaf	Hymenoptera (Par) Hymenoptera (Par) Lepidoptera (Inq)	Caetité (BA)	Nogueira et al. 2016 Silva et al. 2018a Vieira et al. 2018
CONNARACEAE					
Connarus suberosus Planch. (1)	Cecidomyiidae	Leaf	Hymenoptera (Par)	Silvânia (GO)	Bergamini et al. 2017
DILLENIACEAE					

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Davilla brasiliana DC. (1)	Cecidomyiidae	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
	Asphondylia sp. (Cecidomyiidae)	bud	*Clinodiplosis* sp. (Cecidomyiidae) (Inq) Lepidoptera (Inq)	Tiradentes (MG)	Maia & Fernandes 2004
Davilla elliptica A. St-Hil. (1)	Cecidomyiidae	Leaf	Eulophidae (Par)	Serra dos Pireneus (GO)/ Silvânia (GO)	Araújo et al. 2011 Bergamini et al. 2017
EBENACEAE					
Diospyros burchellii DC. (1)	Lepidoptera	Stem	Hymenoptera (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
ERYTHROXYLACEAE					
Erythroxylum frangulifolium A. St-Hil. (2)	Eulophidae (Hymenoptera)	Bud/Stem	Hymenoptera (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
Erythroxylum suberosum A. St-Hil. (1)	Undetermined	Stem	Eurytomidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Myrciariamyia admirabilis Maia, 2007 (Cecidomyiidae)	leaf	Eulophidae (Par) Encyrtidae (Par) Torymidae (Par)	Tiradentes/ Serra do Cipó (MG)/ Hidrolândia (GO)	Maia & Fernandes 2004, 2007 Silva et al. 2018b
EUPHORBIACEAE					
Croton floribundus Spreng. (1)	*Clinodiplosis* sp. (Cecidomyiidae)	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
	Cecidomyiidae	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
	Couridiplosis vena Maia, 2004 (Cecidomyiidae)	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia 2004 Maia & Fernandes 2004
	Undetermined	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Sapium glandulosum (L.) Morong (1)	*Neolithus fasciatus* Scott, 1882 (Triozidae, Hemiptera)	Fruit/ Inflorescence/ Leaf/ Stem	Encyrtidae (Par) Eurytomidae (Par) Pteromalidae (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
FABACEAE					
Anadenanthera peregrina (L.) Spreng. (1)	Undetermined	Leaf	Hymenoptera (Par)	Goiânia (GO)	Santos et al. 2010
Andira cuyabensis Benth. (2)	Undetermined	Leaf	Acari (Suc)	Barreiras (BA)	Lima & Calado 2018
Andira humilis Max ex Benth. (2)	Cecidomyiidae	Leaf	Eulophidae (Par) Eurytomidae (Par)	Barreiras (BA)	Lima & Calado 2018
Andira paniculata Benth. (1)	Cecidomyiidae	Leaf	Encyrtidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
	Cecidomyiidae	Leaf	Encyrtidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
	Cecidomyiidae	Leaf	Encyrtidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
	Cecidomyiidae	Leaf	Hymenoptera (Par)	Caldas Novas (GO)	Santos et al. 2012
Andira fraxinifolia Benth. (2)	Cecidomyiidae	Leaf/ Stem	Hymenoptera (Par)	Belo Horizonte (MG)	Fernandes et al. 1988 (as *Andira parvifolia* Mart. ex Benth.)
Bauhinia brevipes Vogel (1)	Undetermined	Leaf	Acari (Suc)	Barreiras (BA)	Lima & Calado 2018

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	Schizomyia macropillata Maia, 2005 (Cecidomyiidae)	Leaf	Eulophidae (Par) Collembola: *Seira mendoncae* (Suc) *Salina celebensis* (Suc)	Barreiras (BA)	Maia & Fernandes 2005 Lima & Calado 2018
	Cecidomyiidae	Stem	Acari (Suc) Encyrtidae (Par)	Barreiras (BA)	Lima & Calado 2018
	Cecidomyiidae	Stem	Braconidae (Par) Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018b
Bauhinia cupulata Benth. (1)	Cecidomyiidae	Leaf	Salina celebensis	Barreiras (BA)	Lima & Calado 2018
Bauhinia holophylla (Bong.) Steud. (2)	*Schizomyia tuiuiu* Urso-Guimarães & Amorim, 2002 (Cecidomyiidae)	Leaf	Rileynae (Eurytomidae) (Par)	Altinópolis (SP)	Urso-Guimarães & Amorim 2002 Ribeiro et al. 2019
Bauhinia rufa (Bong.) Steud. (1)	Cecidomyiidae	Leaf	Eupelmidae (Par) Torymidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Cecidomyiidae	Leaf	Torymidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Cecidomyiidae	Stem	Eupelmidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Cecidomyiidae	Stem	Eupelmidae (Par) Tetracampidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Cecidomyiidae	Stem	Torymidae (Par)	Silvânia (GO)	Bergamini et al. 2017
Bauhinia ungulata L. (1)	Cecidomyiidae	Leaf	Eulophidae (Par)	Goiânia (GO)	Santos et al. 2010
Calliandra macrocalyx Harms (2)	Undetermined	Bud	Hymenoptera (Par)	Caetité (BA)	Silva et al. 2018a
Copaifera depilis Dwyer (2)	Undetermined	Stem	Hymenoptera (Par)	Barreiras (BA)	Santos et al. 2018
	Undetermined	Leaf	Hymenoptera (Par)	Barreiras (BA)	Santos et al. 2018
Copaifera langsdorffii Desf. (1)	Hymenoptera	Bud/ Leaf/ Stem	Encyrtidae (Par) Eurytomidae (Par) Pteromalidae (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
	Cecidomyiidae	Leaf/ Stem	Hymenoptera (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
	Cecidomyiidae	Leaf	Pteromalidae (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
	Contarinia sp. (Cecidomyiidae)	Leaf	Platygasteridae (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
	Cecidomyiidae	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
	Cecidomyiidae	Stem	Hymenoptera (Par)	Caetité (BA)	Nogueira et al. 2016
	Cecidomyiidae	Stem	Hymenoptera (Par)	Caetité (BA)	Nogueira et al. 2016
	Undetermined	Leaf	Hymenoptera (Par)	Caetité (BA)	Nogueira et al. 2016
	Undetermined	Leaf	Hymenoptera (Par)	Caetité (BA)	Nogueira et al. 2016
Copaifera luetzelburgii Harms (2)	Undetermined	Leaf	Hymenoptera (Par)	Barreiras (BA)	Santos et al. 2018
	Undetermined	Leaf	Hymenoptera (Par)	Barreiras (BA)	Santos et al. 2018
	Undetermined	Leaf	Hymenoptera (Par)	Barreiras (BA)	Santos et al. 2018
	Undetermined	Leaf	Hymenoptera (Par)	Barreiras (BA)	Santos et al. 2018
	Undetermined	Stem	Hymenoptera (Par)	Barreiras (BA)	Santos et al. 2018
Copaifera sabulicola J. Costa & L.P. Queiroz (2)	Undetermined	Stem	Hymenoptera (Par) Acari (Suc)	Barreiras (BA)	Santos et al. 2018
	Undetermined	Stem	Formicidae (Suc)	Barreiras (BA)	Santos et al. 2018
	Undetermined	Leaf	Coleoptera (Suc)	Barreiras (BA)	Santos et al. 2018

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Hymenaea courbaril L. (1)	Cecidomyiidae	Leaf	Eurytomidae (Par)	Barreiras (BA)	Lima & Calado 2018
	Cecidomyiidae	Leaf	Acari (Suc)	Barreiras (BA)	Lima & Calado 2018
Inga bahiensis Benth. (1)	Undetermined	Leaf	Coleoptera (Inq)	Caetité (BA)	Silva et al. 2018a
Inga cylindrica (Vell.) Mart. (1)	Cecidomyiidae	Leaf	Eulophidae (Par)	Goiânia (GO)	Santos et al. 2010
	Cecidomyiidae	Leaf	Eulophidae (Par)	Goiânia (GO)	Santos et al. 2010
Inga ingoides (Rich.) Willd. (1)	Cecidomyiidae	Leaf/ Stem	Braconidae (Par) Eurytomidae (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
	Cecidomyiidae	Leaf	Hymenoptera (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
Inga edulis Mart. (1)	*Neolasioptera* sp. (Cecidomyiidae)	Leaf	Spalangiinae (Pteromalidae) (Par) *Meunieriella spinosa* Urso-Guimarães, 2019 (Cecidomyiidae) (Suc)	Delfinópolis (MG)	Urso-Guimarães et al., 2003 Urso-Guimarães, 2019
Lonchocarpus cultratus (Vell.) A.M.G. Azevedo & H.C. Lima (1)	*Euphaleurus* sp. (Psyllidae, Hemiptera)	Leaf	Hymenoptera (Par)	Belo Horizonte (MG)	Fernandes et al. 1988 (as *Lonchocarpus guilleminianus* (Tui.) Malme)
Machaerium aculeatum Raddi (2)	*Anadiplosis* sp. (Cecidomyiidae)	Leaf	Eulophidae (Par) Eurytomidae (Par) Platygastridae (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
Mimosa gemmulata Barneby (1)	Undetermined	Stem	Hymenoptera (Par)	Caetité (BA)	Nogueira et al. 2016
	Cecidomyiidae	Leaf	Hymenoptera (Par)	Caetité (BA)	Silva et al. 2018a
LAMIACEAE					
Leonotis nepetifolia (3)	*Asphondylia canastrae* Urso-Guimarães & Amorim, 2002 (Cecidomyiidae)	Inflorescence	Toryminae (Torymidae) (Par) Rileynae (Eurytomidae) (Par)	Delfinópolis (MG)	Urso-Guimarães & Amorim 2002 Urso-Guimarães et al. 2003
LAURACEAE					
Nectandra cuspidata Nees (1)	Cecidomyiidae	Leaf	Eulophidae (Par)	Goiânia (GO)	Santos et al. 2010
	Cecidomyiidae	Leaf	Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018b
	Undetermined	Leaf	Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018b
MALPIGHIACEAE					
Byrsonima pachyphylla Griseb. (1)	Cecidomyiidae	Leaf	Hymenoptera (Par)	Caldas Novas (GO)	Santos et al. 2012
Byrsonima starnardii W. R. Anderson (2)	Cecidomyiidae	Leaf	Hymenoptera (Par)	Caetité (BA)	Nogueira et al. 2016
Byrsonima variabilis A. Juss. (2)	Undetermined	Stem	Eulophidae (Par) Eupelmidae (Par) Eurytomidae (Par) Ichneumonidae (Par) Platygastridae (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Byrsonima verbascifolia (L.) DC. (1)	Cecidomyiidae	Leaf	Eulophidae (Par) Eulophidae (Par) Eurytomidae (Par) Torymidae (Par) Signiphoridae (Par)	Silvânia (GO)/ Tiradentes (MG)	Bergamini et al. 2017 Maia & Fernandes 2004
	Lepidoptera	Stem	Eurytomidae (Par)	Silvânia (GO)	Bergamini et al. 2017

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Diplopterys pubipetala (A. Juss.) W.R. Anderson & C. C. Davis (1)	*Clinodiplosis bellum* Urso-Guimarães & Garcia-Neto, 2015 (Cecidomyiidae)	Leaf	Eulophinae (Par) Entedoninae (Par) Torymidae (Par)	Altinópolis (SP)	Urso-Guimarães & Garcia-Neto, 2015 Ribeiro et al. 2019
	Dasineura sp. (Cecidomyiidae)	Leaf	*Lestodiplosis* sp. (Cecidomyiidae) (Pre) Eurytomidae (Par)	Altinópolis (SP) Hidrolândia (GO)	Ribeiro et al. 2019 Silva et al. 2018b
	Phlaeothripidae (Thysanoptera)	Leaf	Eulophidae (Par)	Hidrolândia	Silva et al. 2018b
Peixotoa goiana C. E. Anderson (2)	Undetermined	Leaf	Hymenoptera (Par)	Silvânia (GO)	Bergamini et al. 2017
	Cecidomyiidae	Leaf	Torymidae (Par) Phlaeothripidae (Thysanoptera) (Inq)	Silvânia (GO)	Bergamini et al. 2017
MALVACEAE					
Luehea divaricata Mart. (1)	Coleoptera	Leaf	Hymenoptera (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
Luehea cf. divaricata Mart.	Cecidomyiidae	Leaf/ Stem	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Pseudobombax longiflorum (Mart. & Zucc.) A. Robyns (1)	Lepidoptera	Leaf	Hymenoptera (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
Sida micrantha A.St.-Hil. (1)	Cecidomyiidae	Leaf/ Stem	Hymenoptera (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
MELASTOMATACEAE					
Leandra aurea (Cham.) Cogn. (1)	Lepidoptera	Bud	*Anthonomus vis* Clark, 1992 (Curculionidae) (Inq) *Fiebrigella* sp. (Chloropidae) (Pre) *Lestodiplosis* sp. (Cecidomyiidae) (Pre) Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004 Bená & Vanin 2013
	Lepidoptera	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Macairea radula (Bonpl.) DC. (1)	Gelechiidae (Lepidoptera)	Leaf	Chalcididae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
	Undetermined	Leaf	Microgastrinae (Braconidae) (Par)	Delfinópolis (MG)	Urso-Guimarães et al. 2003
Miconia theaezans (Bonpl.) Cogn. (1)	Cecidomyiidae	Bud	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Pleroma candolleanum (Mart. ex DC.) Triana (2)	Cecidomyiidae	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004 (as *Tibouchina candolleana* (DC.) Cogn.)
MYRTACEAE					
Eugenia punicifolia (Kunth) DC. (2)	Undetermined	Leaf	Hymenoptera (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
	Stephomyia epeugeniae Gagné, 1994 (Cecidomyiidae)	Leaf	Eulophidae (Par)	Belo Horizonte (MG)	Fernandes et al. 1988 (as *Eugenia ovalifolia*)

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	Stephomyia sp. (Cecidomyiidae)	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004 (as *Eugenia* cfr. *ovalifolia*)
	Undetermined	Stem	Hymenoptera (Par)	Caetité (BA)	Vieira et al. 2018a
Myrcia retorta Cambess. (2)	*Dasineura* sp. (Cecidomyiidae)	Leaf	Eulophidae (Par)	Belo Horizonte (MG)	Fernandes et al. 1988 (as *Myrcia itambensis* O. Berg.)
	Triozoida sp. (Psyllidae, Hemiptera)	Leaf	Encyrtidae (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
	Cecidomyiidae	Leaf	Eulophidae (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
Myrciaria tenella (DC.) O. Berg. (1)	*Myrciariamyia fernandesi* Maia, 2004 (Cecidomyiidae)	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Psidium brownianum Mart. ex DC. (2)	Undetermined	Leaf	Pseudoscorpiones (Pre)	Caetité (BA)	Silva et al. 2018a
Psidium salutare var. *pohlianum* (O. Berg.) Laundrum (2)	Psyllidae (Hemiptera)	Leaf	Eulophidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
NYCTAGINACEAE					
Guapira opposita (Vell.) Reitz (1)	Cecidomyiidae	Stem	Hymenoptera (Par)	Caetité (BA)	Vieira et al. 2018
Neea theifera Oerst. (1)	Cecidomyiidae	Leaf	Hymenoptera (Par)	Caldas Novas (GO)	Santos et al. 2012
OCHNACEAE					
Ouratea floribunda (A. St-Hil.) Engl. (2)	Cecidomyiidae	Leaf	Hymenoptera (Par)	Belo Horizonte (MG)	Fernandes et al. 1988
PIPERACEAE					
Piper arboreum Aubl. (1)	Undetermined	Leaf	Eulophidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
	Cecidomyiidae	Leaf	Eulophidae (Par)	Goiânia (GO)	Santos et al. 2010
PROTEACEAE					
Roupala montana Aubl. (1)	Cecidomyiidae	Leaf	Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018b
RUBIACEAE					
Borreria cfr. brachystemonoides Cham. & Schltdl. (1)	Cecidomyiidae	Stem	Encyrtidae (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Chomelia pohliana Müll.Arg (2)	Undetermined	Spine base	Lygaeidae (Hemiptera) (Inq)	Delfinópolis (MG)	Urso-Guimarães et al. 2003
SALICACEAE					
Casearia sylvestris Sw. (1)	Undetermined	Stem	Hymenoptera (Par)	Silvânia (GO)	Bergamini et al. 2017
SAPINDACEAE					
Serjania obtusidentata Radlk. (2)	Cecidomyiidae	Leaf	Eulophidae (Par)	Goiânia (GO)	Santos et al. 2010
SIPARUNACEAE					
Siparuna guianensis Aubl. (1)	Undetermined	Stem	Torymidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Cecidomyiidae	Stem	Eurytomidae (Par)	Hidrolândia (GO) Silvânia (GO)	Silva et al. 2018b Bergamini et al. 2017
	Undetermined	Stem	Torymidae (Par)	Silvânia (GO)	Bergamini et al. 2017
SMILACACEAE					

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CONTINUATION...

Smilax oblongifolia Pohl ex Griseb. (2)	Cecidomyiidae	Leaf	Hymenoptera (Par) *Polyxenus* (Diplopoda) (Inq) Psocoptera (Inq) Eulophidae (Par) *Camptoneuromyia* sp. (Cecidomyiidae) (Inq)	Delfinópolis (MG) Altinópolis (SP)	Urso-Guimarães et al., 2003 (as Smilax coriifolia A. DC.) Ribeiro et al. 2019
STYRACACEAE					
Styrax pohlii A.DC. (1)	Cecidomyiidae	Leaf	Eulophidae (Par)	Goiânia (GO)	Santos et al. 2010
	Diptera	Stem	Hymenoptera (Par)	Goiânia (GO)	Santos et al. 2010
	Cecidomyiidae	Leaf	Hymenoptera (Par)	Goiânia (GO)	Santos et al. 2010
TRIGONIACEAE					
Trigonia nivea Cambess. (1)	Cecidomyiidae	Leaf	Hymenoptera (Par)	Caetité (BA)	Nogueira et al. 2016
VERBENACEAE					
Lantana fucata Lindl. (1)	*Neolasioptera* sp (Cecidomyiidae)	Stem	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004 (as *Lantana lilacina* Desf.)
	Cecidomyiidae	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Lippia alba (Mill.) N. E. Br. ex Britton & P. Wilson (1)	Cecidomyiidae	Leaf	Hymenoptera (Par)	Caetité (BA)	Vieira et al. 2018
VOCHYSIACEAE					
Qualea grandiflora Mart. (1)	Undetermined	Leaf	Eulophidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
	Hymenoptera	Leaf	Collembola (Suc)	Barreiras (BA)	Lima & Calado 2018
	Cecidomyiidae	Stem	Hymenoptera (Par)	Caldas Novas (GO)	Santos et al. 2012
Qualea multiflora Mart. (1)	Cecidomyiidae	Leaf	Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018b
	Cecidomyiidae	Leaf	Braconidae (Par) Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018b
Qualea parviflora Mart. (1)	Undetermined	Leaf	Eulophidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
	Cecidomyiidae	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
			Encyrtidae (Par)	Hidrolândia (GO)	Silva et al. 2018b
	Cecidomyiidae	Leaf	Lepidoptera (Inq)	Caetité (BA)	Silva et al. 2018a

Seira mendoncae Bellini & Zeppelini, 2008 (Collembola); and five genera, *Camptoneuromyia* Felt, 1908, *Clinodiplosis* Kieffer, 1895, *Lestodiplosis* Kieffer, 1894 (Cecidomyiidae), and *Fiebrigella* Duda, 1921 (Chloropidae), and *Polyxenus* Latreille, 1802 were identified. All other records were at suprageneric levels.

We found 36 host plant genera with records of the associated fauna on undetermined species. They included 24 plant families and totaled at most 55 gall morphotypes (Table 2). Among plant families, five were represented only by undetermined species, namely: Chrysobalanaceae, Loranthaceae, Lythraceae, Meliaceae, and Metteniusaceae. Therefore, they were not included in the Table 1. Adding them, the number of host plant families with records of associated fauna rises to 42. Concerning genera data, *Arrabidaea* DC. (Bignoniaceae), *Hirtella* L. (Chrysobalanaceae), *Doliocarpus* Rol. (Dilleniaceae), *Manihot* Mill. and *Sebastiania* Spreng, (Euphorbiaceae), *Emmotum* Dsv. ex Ham. (Metteniusiaceae), *Struthanthus* Mart. (Loranthaceae), *Diplusodon* Pohl. (Lythraceae), *Heteropterys* Kunth. and *Thryallis* L. (Malpighiaceae), *Tibouchina* Aubl. (Melastomataceae), *Guarea* F. Allam ex L. and *Trichilia* P. Browne (Meliaceae), *Camponanesia* Ruiz et Pav. (Myrtaceae), and *Paullinia* L. (Sapindaceae) are added, increasing the number of host genera to 108. The following arthropod taxa were recorded as secondary dwellers: Hymenoptera: Braconidae, Chalcididae, Elasmidae, Encyrtidae, Eulophidae, Eurytomidae, Formicidae, Perilampidae, Pteromalidae, Tanaostigmatidae, Torymidae, and Trichogrammatidae; Diptera: Sciaridae and Brachycera; Thysanoptera; Collembola: *Salina celebensis, Salina* sp. and *Seria mendoncae*; Acari; Araneae; and Pseudoscorpiones. Among them, Elasmidae, Perilampidae, Tanaostigmatidae, Trichogrammatidae, and Brachycera are added, increasing the richness of parasitoid families from 12 to 16, and including Brachycera in the "inquilines" guild. Records at family level (Table 3) added Acanthaceae, Solanaceae, Tiliaceae and Turneraceae, increasing from 42 to 46 the number of host families with associated fauna.

Multiparasitism was recorded in 23 gall morphotypes (15.6% of the total of parasitized gall morphotypes). The number of parasitoid taxa in the same gall morphotype varied from two to five. The highest numbers were recorded in galls on *Byrsonima variabilis* (Malpighiaceae),

Table 2. Data on arthropods associated with insect galls in the Brazilian Cerrado: host plant (identification at genus level), gall-inducer, host organ, secondary dweller, ecological guild, locality, and reference. Ecological guild: (Inq) inquiline, (Par) parasitoid, (Suc) successor.

Host plant	Gall-inducer	Host organ	Secondary dwellers	Locality	Reference
Apocynaceae					
Aspidosperma sp.	Cecidomyiidae	Leaf	Pteromalidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Asteraceae					
Moquiniastrum sp.	Cecidomyiidae	Leaf	Hymenoptera (Par)	Caetité (BA)	Silva et al. 2018
Bignoniaceae					
Arrabidaea sp.	Cecidomyiidae	Leaf	Torymidae (Par)	Goiânia (GO)	Santos et al. 2010
	Cecidomyiidae	Stem	Torymidae (Par)	Goiânia (GO)	Santos et al. 2010
Boraginaceae					
Cordia sp.	Hymenoptera	Leaf	Acari (Suc)	Barreiras (BA)	Lima & Calado 2018
Chrysobalanaceae					
Hirtella sp.	Cecidomyiidae	Leaf	Torymidae (Par)	Silvânia (GO)	Bergamini et al. 2017
Combretaceae					
Combretum sp.	Phlaeothripidae (Thysanoptera)	Leaf	Eurytomidae (Par) *Seria mendoncae* (Collembola) (Suc)	Barreiras (BA)	Lima & Calado 2018
Connaraceae					
Connarus sp.	Undetermined	Stem	Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Dilleniaceae					
Doliocarpus sp.	Cecidomyiidae	Stem	Elasmidae (Par) Eurytomidae (Par) Eulophidae (Par) Torymidae (Par) Sciaridae (Inq)	Silvânia (GO)	Bergamini et al. 2017
Erythroxylaceae					
Erythroxylum sp.	Cecidomyiidae	Leaf	Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018
	Cecidomyiidae	Leaf	Pteromalidae (Par)	Hidrolândia (GO)	Silva et al. 2018
	Cecidomyiidae	Leaf midvein	Pteromalidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Euphorbiaceae					
Croton sp.	Undetermined	Leaf	Hymenoptera (Par)	Caetité (BA)	Vieira et al. 2018
Manihot sp.	Undetermined	Leaf	Eulophidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
	Cecidomyiidae	Leaf	Pteromalidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Sebastiania sp.	Cecidomyiidae	Leaf	Eulophidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
Fabaceae					
Andira sp.	Cecidomyiidae	Stem	Eulophidae (Par)	Tiradentes (MG)	Maia & Fernandes 2004
	Cecidomyiidae	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Bauhinia sp.	Cecidomyiidae	Leaf vein	Eulophidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
	Cecidomyiidae	Leaf	Braconidae (Par) Eulophidae (Par) Torymidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Lepidoptera	Stem	Araneae (Suc)	Caetité (BA)	Silva et al. 2018
	Cecidomyiidae	Leaf	Braconidae (Par) Eulophidae (Par) Pteromalidae (Par)	Hidrolândia (GO)	Silva et al. 2018
	Undetermined	Stem	Braconidae (Par)	Hidrolândia (GO)	Silva et al. 2018
	Lepidoptera	**Stem**	**Torymidae (Par)**	**Hidrolândia (GO)**	**Silva et al. 2018**
Inga sp.	Cecidomyiidae	Leaf midvein	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Loranthaceae					
Struthanthus sp.	Undetermined	Leaf	Hymenoptera (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
Lythraceae					
Diplusodon sp.	Undetermined	Stem	Brachycera (Diptera) (Inq)	Silvânia (GO)	Bergamini et al. 2017
Malpighiaceae					

Byrsonima sp.	Cecidomyiidae	Leaf	Trichogrammatidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
Heteropterys sp.	Undetermined	Leaf	Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Peixotoa sp.	Cecidomyiidae	Leaf	Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Thryallis sp.	Undetermined	Leaf	Hymenoptera (Par)	Caetité (BA)	Nogueira et al. 2016
Malvaceae					
Luehea sp.	Cecidomyiidae	Leaf	*Salina celebensis* (Suc) *Salina* sp. (Suc)	Barreiras (BA)	Lima & Calado 2018
Melastomataceae					
Miconia sp.	Cecidomyiidae	Leaf/Stem	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Miconia sp.	Undetermined	Stem	Hymenoptera (Par)	Goiânia (GO)	Silva et al. 2015
Tibouchina sp.	Cecidomyiidae	Leaf	Perilampidae (Par)	Altinópolis (SP)	Ribeiro et al. 2019
Meliaceae					
Guarea sp.	Cecidomyiidae	Leaf	Thysanoptera (Inq)	Caetité (BA)	Silva et al. 2018
Trichilia sp.	Undetermined	Stem	Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Metteniusaceae					
Emmotum sp.	Undetermined	Stem	Hymenoptera (Par) Formicidae (Suc)	Caetité (BA)	Nogueira et al. 2016
Myrtaceae					
Campomanesia sp.	Undetermined	Leaf	Hymenoptera (Par)	Caetité (BA)	Vieira et al. 2018
Eugenia sp.	Undetermined	Leaf	Hymenoptera (Par)	Caetité (BA)	Vieira et al. 2018
Myrcia sp.	Cecidomyiidae	Leaf	Hymenoptera (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
	Cecidomyiidae	Bud	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
	Cecidomyiidae	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
	Thysanoptera	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
	Undetermined	Stem	Eurytomidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Nyctaginaceae					
Guapira sp.	*Lopesia bilobata* Maia, 2004 Cecidomyiidae	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia 2004 Maia & Fernandes 2004
	Asphondyliini (Cecidomyiidae)	Stem	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
	Cecidomyiidae	Leaf	Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Piperaceae					
Piper sp.	*Parametasphondylia piperis* Maia & Santos, 2007 (Cecidomyiidae)	Leaf/stem	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004 Maia & Santos 2007
	Cecidomyiidae	Leaf midvein	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Sapindaceae					
Paullinia sp.	Cecidomyiidae	Stem	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
	Undetermined	Leaf bud	Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Serjania sp.	Cecidomyiidae	Leaf	Eulophidae (Par) Torymidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Cecidomyiidae	Stem	Eurytomidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Smilaceae					
Smilax sp.	Undetermined	Leaf	Eulophidae (Par) Torymidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Styracaceae					
Styrax sp.	Undetermined	Leaf	Eupelmidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011

five (Eulophidae, Eupelmidae, Eurytomidae, Ichneumonidae, and Platygastridae) in stem galls and four (Eulophidae, Eurytomidae, Torymidae, and Signiphoridae) in leaf galls. Four taxa of parasitoids (Elasmidae, Eurytomidae, Eulophidae, and Torymidae) were also reported in galls on *Doliocarpus* sp. (Dilleniacaeae).

Different inquilines – *Clinodiplosis* sp. (Cecidomyiidae) and Lepidoptera were found in a bud gall on *Davilla brasiliana* DC. (Dilleniaceae), as well as *Polyxenus* sp. (Diplopoda) and Psocoptera in a leaf gall on *Smilax oblongifolia* Pohl ex Griseb (Smilacaceae). Two successors – *Seria mendoncae* and *Salina celebensis* (Collembola)

Table 3. Data on arthropods associated with insect galls in the Brazilian Cerrado: host plant (identification at family level), gall-inducer, host organ, secondary dweller, ecological guild, locality, and reference. Ecological guild: (Inq) inquiline, (Par) parasitoid, (Suc) successor.

Host plant	Gall-inducer	Host organ	Secondary dweller	Locality	Reference
Acanthaceae	Undetermined	Leaf midvein	Chalcididae (Par)	Silvânia (GO)	Bergamini et al. 2017
Anacardiaceae	Undetermined	Leaf	Eurytomidae (Par)	Silvânia (GO)	Bergamini et al. 2017
Asteraceae	Cecidomyiidae	Leaf	Encyrtidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
	Undetermined	Leaf	Eulophidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Undetermined	Stem	Torymidae (Par) Sciaridae (Diptera) (Inq)	Silvânia (GO)	Bergamini et al. 2017
	Undetermined	Stem	Eulophidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Undetermined	Stem	Hymenoptera (Par)	Caetité (BA)	Silva et al. 2018
Celastraceae	Undetermined	Leaf	Eulophidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Undetermined	Stem	Eurytomidae (Par) Torymidae (Par)	Silvânia (GO)	Bergamini et al. 2017
Connaraceae	Cecidomyiidae	Inflorescence	Eurytomidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Erythroxylaceae	Undetermined	Leaf	Araneae (Suc) Hemiptera (Inq)	Caetité (BA)	Silva et al. 2018
Euphorbiaceae	Undetermined	Leaf/ Stem	Eulophidae (Par) Eurytomidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Fabaceae	Cecidomyiidae	Bud	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
	Neolasioptera sp. (Cecidomyiidae)	Stem	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Malpighiaceae	Cecidomyiidae	Leaf	Eulophidae (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
	Undetermined	Stem	Pseudoscorpiones (Pre)	Caetité (BA)	Nogueira et al. 2016
	Undetermined	Leaf midvein	Hymenoptera (Par)	Caetité (BA)	Nogueira et al. 2016
	Phlaeothripidae (Thysanoptera)	Leaf	Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018
	Undetermined	Stem	Hymenoptera (Par)	Caetité (BA)	Vieira et al. 2018
	Cecidomyiidae	Leaf	Hymenoptera (Par)	Caetité (BA)	Vieira et al. 2018
	Undetermined	Leaf	Hymenoptera (Par)	Caetité (BA)	Vieira et al. 2018
Malvaceae	Undetermined	Leaf	Eurytomidae (Par) Torymidae (Par)	Silvânia (GO)	Bergamini et al. 2017
Melastomataceae	Undetermined	Leaf	Hymenoptera (Par)	Serra dos Pireneus (GO)	Araújo et al. 2011
	Undetermined	Stem	Sciaridae (Inq)	Silvânia (GO)	Bergamini et al. 2017
	Undetermined	Stem	Torymidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Meliaceae	Undetermined	Leaf	Eulophidae (Par)	Silvânia (GO)	Bergamini et al. 2017
Moraceae	Undetermined	Stem	Araneae (Suc)	Caetité (BA)	Silva et al. 2018
Myrtaceae	Undetermined	Leaf	Eulophidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Cecidomyiidae	Leaf	Hymenoptera (Par)	Silvânia (GO)	Bergamini et al. 2017
	Undetermined	Leaf	Eurytomidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Cecidomyiidae	Stem	Torymidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Phlaeothripidae) (Thysanoptera)	Leaf	Collembola (Suc)	Barreiras (BA)	Lima & Calado 2018

	Undetermined	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
	Sternorrhyncha (Hemiptera)	Leaf	Hymenoptera (Par)	Tiradentes (MG)	Maia & Fernandes 2004
Rubiaceae	Cecidomyiidae	Stem	Eupelmidae (Par) Tanaostigmatidae (Inq)	Silvânia (GO)	Bergamini et al. 2017
	Undetermined	Stem	Torymidae (Par)	Silvânia (GO)	Bergamini et al. 2017
	Undetermined	Leaf	Araneae (Suc) Hemiptera (Suc)	Caetité (BA)	Silva et al. 2018
Sapindaceae	Undetermined	Stem	Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018
	Cecidomyiidae	Leaf	*Seria mendoncae* (Suc) *Salina celebensis* (Suc) Hymenoptera (Par) Phlaeothripidae (Suc)	Barreiras (BA)	Lima & Calado 2018
	Undetermined	Stem	Eulophidae (Par)	Hidrolândia (GO)	Silva et al. 2018
Solanaceae	Undetermined	Bud	Hymenoptera (Par)	Caetité (BA)	Silva et al. 2018
Tiliaceae	Undetermined	Leaf	Hymenoptera (Par)	Goiânia (GO)	Silva et al. 2015
Turneraceae	Undetermined	Stem	Hymenoptera (Par)	Caetité (BA)	Silva et al. 2018

were recorded in a leaf gall on *Bauhinia brevipes* Vogel (Fabaceae); and two predators in a bud gall on *Leandra aurea* (Cham.) Cogn. (Melastomataceae). Furthermore, 17 gall morphotypes hosted more than one ecological guild: successors + inquilines (N=2), parasitoids + inquilines (N=7), parasitoids + successors (N=5), predators + parasitoids (N=2) and parasitoids + predators + inquilines (N=1).

Almost all recorded plant species are native to Brazil, except *Leonotis nepetifolia* (L.) R.Br which is naturalized. Among the native species, 29 are endemic to Brazil (30.8%) (Table 1). The endemic plants host secondary dwellers in 50 gall morphotypes. Nine hosts are restricted to the Cerrado: *Bauhinia holophylla* (Bong.) Steud., *Copaifera depilis* Dwyer, *C. luetzelburgii* Harms, *C. sabulicola* J. Costa & L.P. Queiroz (Fabaceae), *Byrsonima starnardii* W. R. Anderson, *Peixotoa goiana* C. E. Anderson (Malpighiaceae), *Pleroma candolleanum* (Mart. ex DC.) Triana (Melastomataceae), *Psidium salutare* var. *pohlianum* (O. Berg.) Laundrum (Myrtaceae) and *Ouratea floribunda* (A. St-Hil.) Engl. (Ochnaceae), whereas *Calliandra macrocalyx* Harms (Fabaceae) is restricted to the Caatinga. Nevertheless, this plant species is cited in the present paper, because it was recorded in a transition area between the Cerrado and the Caatinga. The endemic plants host four different ecological guilds: 1) parasitoids of seven Hymenopteran families (Braconidae, Encyrtidae, Eulophidae, Eupelmidae, Eurytomidae, Ichneunomidae, and Platygastridae), 2) successors (Formicidae, Acari, and Coleoptera), 3) predators (Pseudoscorpiones), and 4) inquilines (Lygaeidae: Hemiptera, and *Camptoneuromyia* sp.: Cecidomyiidae).

Forty-six host plant species are useful and host secondary dwellers in 62 gall morphotypes. Several species have multiple uses, but most (33) (71.7%) are used in carpentry and/or cabinet making, 27 (58.7%) are medicinal and 15 (32.6%) are edible (Table 9). The useful plants host parasitoids of eight families (Braconidae, Encyrtidae, Eulophidae, Eurytomidae, Platygastridae, Pteromalidae, Signiphoridae, and Torymidae), inquilinous Lepidoptera, Hemiptera, and *Camptoneuromyia* sp. (Cecidomyiidae); and successors (Acari and Collembola).

Data on the associated fauna are distributed in 12 localities of four Brazilian states: Minas Gerais – Tiradentes (Serra de São José – 21^{0}04'S and 44^{0}08'W) with records in 33 gall morphotypes, Belo Horizonte (Campus Pampulha – 19^{0}48'S and 43^{0}57'W) with 26, Delfinópolis – 20^{0}15'S and 46^{0}45'W with seven, and Serra do Cipó – 19^{0}12-34'S and 43^{0}27-38'W) with one; Goiás – Silvânia (16^{0}38'S and 48^{0}39'W) with 18, Serra dos Pireneus (15^{0}48'S and 48^{0}52'W) with 14, Goiânia (16^{0}36'S and 49^{0}16'W) with 13, Hidrolândia (17^{0}00'S and 49^{0}12'W) with 13, and Caldas Novas (17^{0}42'S and 48^{0}38'W) with 4; Bahia – Barreiras (11^{0}37'S and 44^{0}34'W) with 19 and Caetité (14^{0}05'S and 42^{0}29'W) with 19; and São Paulo (Altinópolis – 21^{0}00'S and 47^{0}23'W) with 16.

Discussion

Cintra et al. (2020) recorded a total 968 gall morphotypes in the Brazilian Cerrado. In the present paper, we reported the associated fauna in 163 gall morphotypes, which corresponds to only 16.8% of the total. This low value appears to suggest that the presence of secondary dwellers are not frequent, but we have to consider that from 32 papers, only 50% addressed the associated fauna. The plant families with the greatest richness of secondary dwellers were the same ones pointed out by Cintra et al. (2020) as those with the highest gall richness.

The associated fauna was reported in all known orders of gall-inducing insects: Diptera Hemiptera, Lepidoptera, Hymenoptera, Coleoptera, and Thysanoptera. The majority was found in galls of Cecidomyiidae, the most frequent inducers in the Brazilian Cerrado. Leaf and stem galls supported most records as they are the most galled plant organs. Some galls hosted more than one ecological guild, which emphasizes the importance of gall-inducers as ecosystem engineers.

Parasitoids were the most frequent secondary dwellers, being represented by 12 Hymenopteran families. Among them, Eulophidae, Eurytomidae, Torymidae, and Encyrtidae predominated. In restinga areas of the Atlantic Forest, Maia & Azevedo (2009) recorded 15 families, almost all represented in the Brazilian Cerrado, except Aphelinidae, Bethylidae, Mymaridae and Scelionidae. On the other hand, Ichneumonidae and Tetracampidae were not recorded by Maia

Table 4. Richness of host plant species and gall morphotypes with records of the associated fauna per plant family in the Brazilian Cerrado. Families with the greatest number of gall morphotypes are highlighted in bold.

Host plant-family	Number of host species	Number of gall morphotypes
Annonaceae	3	3
Apocynaceae	1	2
Araliaceae	1	1
Asteraceae	**12**	**15**
Bignoniaceae	1	1
Boraginaceae	1	3
Burseraceae	1	2
Calophyllaceae	1	3
Cannabaceae	1	1
Caryocaraceae	1	2
Celastraceae	1	1
Combretaceae	1	1
Connaraceae	1	1
Dilleniaceae	2	3
Ebenaceae	1	1
Erythroxylaceae	2	3
Euphorbiaceae	2	5
Fabaceae	**23**	**52**
Lamiaceae	1	1
Lauraceae	1	3
Malpighiaceae	**6**	**10**
Malvaceae	3	4
Melastomataceae	4	6
Myrtaceae	**5**	**10**
Nyctaginaceae	2	2
Ochnaceae	1	1
Piperaceae	1	2
Proteaceae	1	1
Rubiaceae	2	2
Salicaceae	1	1
Sapindaceae	1	1
Siparunaceae	1	3
Smilacaceae	1	1
Styracaceae	1	3
Trigoniaceae	1	1
Verbenaceae	2	3
Vochysiaceae	3	8
Total 35	94	163

Table 5. Richness of gall morphotypes with records of the associated fauna per gall-inducing insect in the Brazilian Cerrado.

Gall-inducing insect	Number of gall morphotypes
Diptera (Cecidomyiidae: 103)	105
Hemiptera	7
Lepidoptera	6
Hymenoptera	3
Coleoptera	2
Thysanoptera	2
Undetermined	38
Total	163

Table 6. Richness of gall morphotypes with records of the associated fauna per host plant organ in the Brazilian Cerrado.

Host plant organ	Number of gall morphotypes
Leaves	109
Stems	32
Bud	8
Flower bud/inflorescence	2
Spine	1
Stem and bud	2
Leaf and stem	7
Bud, leaf and stem	1
Fruit, inflorescence, leaf and stem	1

Table 7. Richness of gall morphotypes with records of the associated fauna per ecological guild in the Brazilian Cerrado.

Guild	Number of gall morphotypes
Parasitoids	147 (90.2%)
successors	13 (8.0%)
Inquilines	12 (7.4%)
Predators	3 (1.8%)
Undetermined	1 (0.6%)

& Azevedo (2009). Parasitoids were also reported in other biomes, as in Pantanal (Urso-Guimarães et at. 2016, Ascendino & Maia 2018), Amazon (Carvalho & Mota 2018), and Caatinga (Costa et al. 2014, Brito et al. 2018), however as a not so diverse guild.

The frequency of successors was similar to that of inquilines, differing from some inventories in Atlantic Forest areas, where inquilines were more frequent than successors (e.g. Maia et al. 2008, Maia & Mascarenhas 2017, Maia & Siqueira 2020). However, other inventories showed similar frequencies between both guilds as in Maia & Carvalho-Fernandes 2016, Flor et al. 2018. The taxa of inquilines~~inquilinous~~ were the same as that reported in the Atlantic Forest (Maia et al. 2008, Maia & Mascarenhas 2017, Maia & Siqueira 2020), except Diplopoda, observed until this moment only in galls from Cerrado areas. Coleoptera, Diptera, and Thysanoptera have been recorded in galls from the Amazon Forest (Maia 2011), whereas *Trotteria* and *Camptoneuromyia* (Cecidomyiidae), Phoridae, Lepidoptera, Coleoptera, Hemiptera, and Hymenoptera in galls from Pantanal (Urso-Guimarães et al. 2016, Ascendino & Maia 2018). Nevertheless, we emphasize that inquilines guild has been

Table 8. Richness of gall morphotypes with records of the associated fauna per ecological guild and arthropod taxon in the Brazilian Cerrado.

Ecological guild	Taxon	Number of gall morphotypes
Inquiline	Sciaridae (Diptera)	1
	Phlaeothripidae (Thysanoptera)	1
	Coleoptera	1
	Lepidoptera	4
	Hemiptera	1
	Lygaeidae (Hemiptera)	1
	Psocoptera	1
	Polyxenus sp. (Diplopoda)	1
	Anthonomus vis (Coleoptera)	1
	Camptoneuromyia sp. (Diptera)	1
	Clinodiplosis sp. (Diptera)	1
	Hymenoptera	1
Parasitoid	Braconidae	9
	Chalcididae	2
	Eulophidae	41
	Encyrtidae	12
	Eupelmidae	4
	Eurytomidae	20
	Hymenoptera	70
	Ichneumonidae	1
	Platygastridae	4
	Pteromalidae	6
	Signiphoridae	1
	Tetracampidae	1
	Torymidae	14
Predator	Lestodiplosis sp. (Cecidomyiidae)	2
	Friebrigella sp. (Chloropidae)	1
	Pseudoscorpionida	1
Successor	Acari	5
	Coleoptera	1
	Formicidae (Hymenoptera)	2
	Collembola	1
	Araneae	1
	Salina celebensis (Collembola)	2
	Seria mendoncae (Collembola)	1
	Meunieriella spinosa (Cecidomyiidae)	1
Undetermined	Heteroptera (Hemiptera)	1

misunderstood as it includes cecidophages, kleptoparasites and true inquilines (Luz & Mendonça-Júnior 2019). Biological data are needed to relocate them in the correct guild. Successors have been reported in galls from other biomes, as Psocoptera in galls from Amazon Forest (Maia 2011) and Caatinga (Brito et al. 2018) and Araneae from the Caatinga (Brito et al. 2018). Predators showed the lowest frequency as in other inventories in Brazil (Maia 2001, Maia et al. 2008, Bregonci et al. 2010, Maia 2013, Maia & Souza 2013, Rodrigues et al. 2014, Maia & Carvalho-Fernandes 2016). Pseudoscorpiones and Diptera (Cecidomyiidae and Chloropidae) were the recorded taxa. In the Atlantic Forest, Pseudoscorpiones and Cecidomyiidae have been reported, as well as Formicidae (Maia 2001, Maia et al. 2008, Bregonci et al. 2010). The record of Chloropidae is known only in the Cerrado until this moment. Cecidomyiidae have been recorded in galls from the Amazon Forest (Maia 2011) and Pantanal (Ascendino & Maia 2018) too, Formicidae and Pseudoscorpiones from Pantanal (Ascendino & Maia 2018).

Taxonomic~~al~~ knowledge of the secondary dwellers is deficient, as only four species have been identified. Besides, there are five records at the genus level, four represented by Diptera: *Camptoneuromyia*, *Clinodiplosis*, *Lestodiplosis* and *Fiebrigella,* and one by Diplopoda. *Camptoneuromyia* comprises only gall inquilines, *Clinodiplosis* includes inquilinous, predaceous as well as gall-inducing species, *Lestodiplosis* is exclusively predator, whereas *Fiebrigella* includes predaceous and parasite species (Gagné & Jaschhof 2017, Smith et al. 2008).

Records of secondary dwellers in insect galls on undetermined plants did not allow us to establish the number of gall morphotypes, since we cannot know whether these morphotypes corresponded to others already recorded in identified species. However, we considered these records as they increased the number of host plant families and genera, as well as the richness of parasitoid and inquilines.

Multiparasitism was observed in 23 gall morphotypes. The fact that two or more parasitoid species attack the same host suggests that they can act together to control the gall-inducer population. Furthermore, multiparasitism can be associated with hyperparasitism, as showed by Maia & Monteiro, 1999. However, hyperparasitism has not yet been recorded in the Cerrado. The presence of two or more guilds in the same gall morphotype exemplifies how the associated fauna can compose complex food webs.

Endemic and useful plants host a diverse fauna of secondary dwellers. Such interactions add ecological importance to these arthropods as they can favor the host plants, acting in the control of the population of the gall-inducers (e.g. parasitoids and predators) or can damage the plants even more in the case of phytophagous dwellers.

Although the Cerrado partially or totally covers 15 states in Brazil (Ribeiro & Walter 2008), records of the associated fauna are restricted to four states: Minas Gerais, Goiás, Bahia, and São Paulo, showing that the current information is punctual and limited to a small fraction of the Cerrado`s territorial extension. The surveyed states correspond to those with research groups in cecidology.

Conclusion

A low percentage of the gall morphotypes from the Brazilian Cerrado hosted secondary dwellers. These galls were found on 94 plant species of 37 families. Other records on undetermined plant species increased the number of plant families to 46. The host families with

Table 9. Uses of host plant species with secondary dwellers in the Brazilian Cerrado.

Host plant	**Uses**					
	Edible	**Medicinal**	**Carpentry and/or cabinet making**	**Fuel and/or charcoal**	**Reforestation**	**Others**
Annona coriacea		x	x			
A.crassiflora	x	x	x			Cork production
Duguetia furfuracea	x	x				
Aspidosperma australe		x			x	
Didymopanax morototoni		x	x		x	Paper industry
Eremanthus erythropappus			x			Living fence
Porophyllum ruderale	x	x				Fungicide
Handroanthus ochraceous			x		x	
Cordia sellowiana			x			
Protium heptaphyllum	x	x	x			Incense Varnishes
Caryocar brasiliense	x	x	x	x		Cosmetic industry
Plenckia populnea			x			
Combretum leprosum		x	x	x	x	
Connarus suberosus		x	x	x		Cork production
Erythroxylum suberosum		x	x			Dye
Croton floribundus		x	x			
Sapium glandulosum				x	x	Latex
Andira cuyabensis		x	x	x		
Andira fraxinifolia		x	x		x	
Bauhinia ungulata		x	x	x	x	
Copaifera langsdorfii	x	x	x	x		Cosmetic industry Varnishes
Hymenaea courbaril	x (tea)	x	x	x		illuminant
Inga cylindrica	x		x	x	x	
Inga ingoides	x		x	x	x	
Lonchocarpus cultratus						
Machaerium aculeatum			x			Soil fertility
Leonotis nepetifolia	x	x				
Nectandra cuspidata			x			
Byrsonima verbascifolia	x	x	x	x		Dye
Luehea divaricata		x	x			Shoe soles
Pseudobombax longiflorum			x		x	Stuffing
Myrciaria tenella	x		x	x		
Psidium salutare var. *pohlianum*	x					
Guapira opposita			x			
Neea theifera	x (tea)	x				Dye
Piper arboreum		x				
Roupala montana			x			
Chomelia pohliana						
Casearia sylvestris		x	x		x	
Siparuna guianensis		x				
Smilax oblongifolia		x				
Styrax pohlii		x	x		x	
Lippia alba	x	x				
Qualea grandiflora			x			
Qualea multiflora			x			
Qualea parviflora			x			Source of tannins

the greatest number of records were the same with the highest richness of insect galls.

Most arthropod fauna were recorded in galls of Cecidomyiidae (Diptera), and on leaves, the predominant galling-insect and the most frequent galled organ. Parasitoids were the most frequent dwellers; among them, Eulophidae and Eurytomidae predominated as in other Brazilian biomes. All arthropod orders reported in the present study were also reported as part of the associated fauna in other Brazilian biomes, except Diplopoda. The taxonomic knowledge of these dwellers is very deficient as in the rest of our country.

Records of secondary dwellers of galls in endemic and useful plants add ecological and economic importance to the associated arthropods as they can favor or damage the host.

Data are restricted to MG, GO, BA and SP, the same states where there are cecidologists. This is the first overview of the fauna associated with insect galls in a Brazilian biome. Studies in other biomes are necessary to consolidate the current knowledge in our country.

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Author Contributions

Valéria Cid Maia: Substantial contribution in the concept and design of the study, contribution to data analysis and interpretation, manuscript preparation and critical revision, and adding intelectual content.

Bruno Gomes Silva: Contribution to data collection and analysis, manuscript preparation and 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

Anurans of a protected area from Mantiqueira Complex, Atlantic Forest of Minas Gerais state, Brazil

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Abstract: The ecological domain of the Atlantic Forest holds a remarkable diversity of anurans with a great degree of endemism, most of which are distributed in high altitude areas, mostly represented by the mountains along the Mantiqueira Complex and Serra do Mar. Despite its biological importance, the region still shows a gap of sampling concerning the amphibians. Thus, we present the first systematic survey of the anuran fauna from Área de Proteção Ambiental Boqueirão da Mira (APABM), in the region of Zona da Mata, Minas Gerais state, Brazil. Two fieldwork expeditions were performed where fifteen sample points were inventoried through active night search and day audiovisual survey in breeding and foraging sites. The anuran fauna of the APABM presented 43 species distributed in 12 families, with the Hylidae family being the richest (17 species). Besides, four species had their distribution increased due to our findings (*Hylodes perere*, *Physalaemus rupestris, Bokermannohyla ibitipoca* and *Ololygon cosenzai*), all of them as endemic to the Mantiqueira Complex. This study revealed that the APABM has a great diversity of anuran species, more representative than adjacent regions such as the Parque Estadual Ibitipoca and close to the richness presented for the Parque Estadual Serra Negra da Mantiqueira. This work demonstrates the great importance of the APABM for conservation, highlighting it as an area of high diversity of the regional anuran species.

Keywords: *Anuran fauna; Inventory; Enviromental Protected Area; Boqueirão da Mira.*

Anuros de uma Unidade de Conservação da Serra da Mantiqueira, Mata Atlântica do estado de Minas Gerais, Brasil

Resumo: O domínio ecológico da Mata Atlântica possui uma notável diversidade de anuros com grande grau de endemismo, a maioria distribuídos em áreas de alta altitude, representadas principalmente pelas montanhas ao longo da Serra da Mantiqueira e Serra do Mar. Apesar de sua importância biológica, a região ainda mostra uma lacuna de amostragem em relação aos anfíbios. Assim, apresentamos o primeiro levantamento sistemático da anurofauna da Área de Proteção Ambiental Boqueirão da Mira (APABM), na região da Zona da Mata, Minas Gerais, Brasil. Foram realizadas duas expedições de campo, onde quinze pontos amostrais foram inventariados por meio de procura ativa noturna e diurna audiovisual em locais de reprodução e forrageio. A anurofauna da APABM apresentou 43 espécies distribuídas em 12 famílias, sendo a família Hylidae a mais rica (17 espécies). Além disso, quatro espécies tiveram sua distribuição ampliada devido aos nossos achados (*Hylodes perere*, *Physalaemus rupestris, Bokermannohyla ibitipoca* e *Ololygon cosenzai*), todas elas sendo endêmicas do Complexo da Mantiqueira. Este estudo revelou que a APABM possui uma grande diversidade de espécies de anuros, mais representativas do que regiões adjacentes como o Parque Estadual do Ibitipoca e próximas à riqueza apresentada pelo Parque Estadual da Serra Negra da Mantiqueira. Este trabalho demonstra a grande importância da APABM para a conservação, destacando-a como uma área de alta diversidade de espécies de anuros regionais.

Palavras-chave: *Anurofauna; Inventário; Área de Proteção Ambiental; Boqueirão da Mira.*

Introduction

The Neotropics contain the greatest diversity of amphibians in the world, distributed throughout important ecoregions such as Amazonia, Atlantic Forest (AF) and Tropical Andes (Frost 2021). The AF comprises about 625 anuran species, of which more than 340 occur as endemic species (Haddad & Prado 2005, Haddad et al. 2013, Rossa-Feres et al. 2017). This significant diversity is due to the region's climate, vegetation structure and topography variation across the land, creating great complexes of mountains (*e.g.,* Serra do Mar and Mantiqueira Complex) (Cruz & Feio 2007, Carnaval & Moritz 2008, Carnaval et al. 2009, Vasconcelos et al. 2014). Nonetheless, the AF has been deeply impacted by urban expansion, mining activities, agriculture and livestock ranching (Morellato & Haddad 2000, Tabarelli et al. 2010), remaining solely around 11.4% -16% of the original extension (SOSMA 2021). Different morphoclimatic conditions and high species diversity, along with the serious degree of threat, aid to classify the AF as a biodiversity hotspot for conservation priorities worldwide (Mittermeier et al. 2004).

Along the AF, the highlands, mostly in the central-southern portion, hold a remarkable diversity of anurans, considered important for maintaining taxonomic diversity and evolutionary history, with a great degree of endemism (Cruz & Feio 2007, Neves et al. 2018, Silva et al. 2018). This is primarily because of heterogeneous habitats and the floristics assemblages, altitudinal gradients and humidity in the region (Cruz & Feio 2007, Vasconcelos et al. 2014). On the other hand, in addition to the human impact already mentioned, the chytridiomycosis has been strengthening the decline of amphibians in the AF (Toledo et al. 2006, Carvalho et al. 2017). This degradation has likely contributed to the decline or extinction of anuran populations in the Mantiqueira Complex (Silva et al. 2018). Lastly, despite the diversity and importance of the highlands, these areas remain poorly know, and inventories of species are still needed in order to better understand the complexity of these environments and fill a gap of sampling.

Another way to mitigate the impact of fragmentation on diversity is restoring lost natural areas by increasing connectivity between protected areas (Cabeza & Moilainen 2001). In the Mantiqueira Complex, the Mantiqueira Ecological Corridor encompasses part of 42 municipalities and embraces significant protected areas like Área de Proteção Ambiental (APA – *Environmental Protected Area*) Fernão Dias, APA Serra da Mantiqueira, Parque Estadual (PE – *State Park*) Serra Negra da Mantiqueira, PE do Ibitipoca, PE da Serra do Papagaio, PE Serra do Brigadeiro, Parque Nacional (PN – *National Park*) do Caparaó and the PN do Itatiaia (Valor Natural 2005). That ecological corridor also holds the APA Boqueirão da Mira (APABM, hereafter) which presents a vegetation mosaic containing a variety of phytophysiognomies (*e.g.,* forest, field, cropland, cloud dwarf forest, cloud forest, anthropic areas) according to Management Plan of the APABM (Lumiar & Xingu Rio 2019). Historically, the region was used in timber extraction, family agriculture and livestock, which explains the occurrence of modified areas (Lumiar & Xingu Rio 2019). Studies related to conservation highlighted the habitat loss and fragmentation, resulted from human exploitation, as the mainly reason for amphibians' population decline (Brooks et al. 2002, Gardner et al. 2007, Verdade et al. 2010). However, the APABM remains poorly sampled for many animal and plant groups, including anurans (Lumiar & Xingu Rio 2019). Faunistic inventories are extremely relevant in order to comprehend biodiversity and, consequently, for conservation action planning (Haddad 1998, Provete 2015). The lack of available data concerning anurans composition along the Mantiqueira Complex, affects negatively the establishment of general biological patterns for tropical species (*e.g.,* reproduction, trophic and thermal relations, population dynamics) (Provete 2015). Thus, we aimed to present herein the anuran species list from APABM located at the southeast portion of Minas Gerais state, with commentaries about those species and filling a gap of sampling for AF, a priority conservation region.

Material and Methods

1. *Study area*

We carried out the present study in the Área de Preservação Ambiental Boqueirão da Mira (APABM) (-22.0527 S, -44.0353 W, WGS84), located in the Zona da Mata region, southeast of Minas Gerais state, in the municipality of Santa Rita de Jacutinga (Figure 1a), Brazil. Placed at the Mantiqueira Ecological Corridor (Costa et al. 1998, Valor Natural 2005), the region belongs to the Mantiqueira Complex, with the altitudinal range varying from 450 to 1746 m above sea level. The APABM has an area of 8.515 ha and is located close to the borderline between Minas Gerais and Rio de Janeiro state (6 km straight line), and to Parque Estadual do Ibitipoca (30 km) and the Parque Estadual Serra Negra da Mantiqueira (6 km) (Figure 1b).

2. *Sampling methods*

We did the survey through 15 sampling points, distributed along different habitats in the APABM (Figure 1a, Table 1): (1) Mata do Espineli, (2) Serra da Água Santa, (3) Estrada Torres Furnas, (4) Brejos da Figueira, (5) Brejos Vila Cruzeiro, (6) Quilombo Hightech, (7) Boqueirão da Mira, (8) Fazenda Santa Clara das Palmeiras, (9) Mata Santa Clara das Palmeiras, (10) Brejos Fazenda Barro Branco, (11) Brejos estrada para Serra da Bandeira, (12) Ribeirão Santa Clara, (13) Lagoa temporária Serra do Chora, (14) Serra da Bandeira and (15) Serrote São Lourenço. More explanation about each area (habitat description, altitude and coordinates) is in the Table 1.

We did the fieldwork in two expeditions with five consecutive days in October and ten consecutive days in November of 2018. We applied the active night search and day audiovisual survey as the method for chasing amphibians, along the breeding and foraging sites (Heyer et al. 1994). The inventory was performed by three researchers, during five hours per day, resulting in a total effort of 75 hours person. Voucher specimens were killed under the process of immersion in water with hydrochloric of benzocaine 250 mg/l, following the recommendations of Portaria CFBio Nº 148/2012. Afterwards, we collected aliquots of liver for future molecular analysis, and those were conditioned in ethanol 100%. We fixed individuals according to the usual techniques described by Gomides et al. (2013) and deposited in the amphibian's collection of Universidade Federal de Juiz de Fora (CAUFJF) (Appendix I) (Colect Permission ICMBio 65519-1). We also gathered data from specimens previously collected within the APABM and deposited in the herpetological collection of Museu de Zoologia João Moojen of the Universidade Federal de Viçosa (MZUFV).

For each recorded species we verified the conservation status according to: List of threatened species for Minas Gerais state (Drummond et al. 2008), Brazilian List of threatened species (ICMBio 2018) and International Union for Conservation of Nature red-list (IUCN 2019).

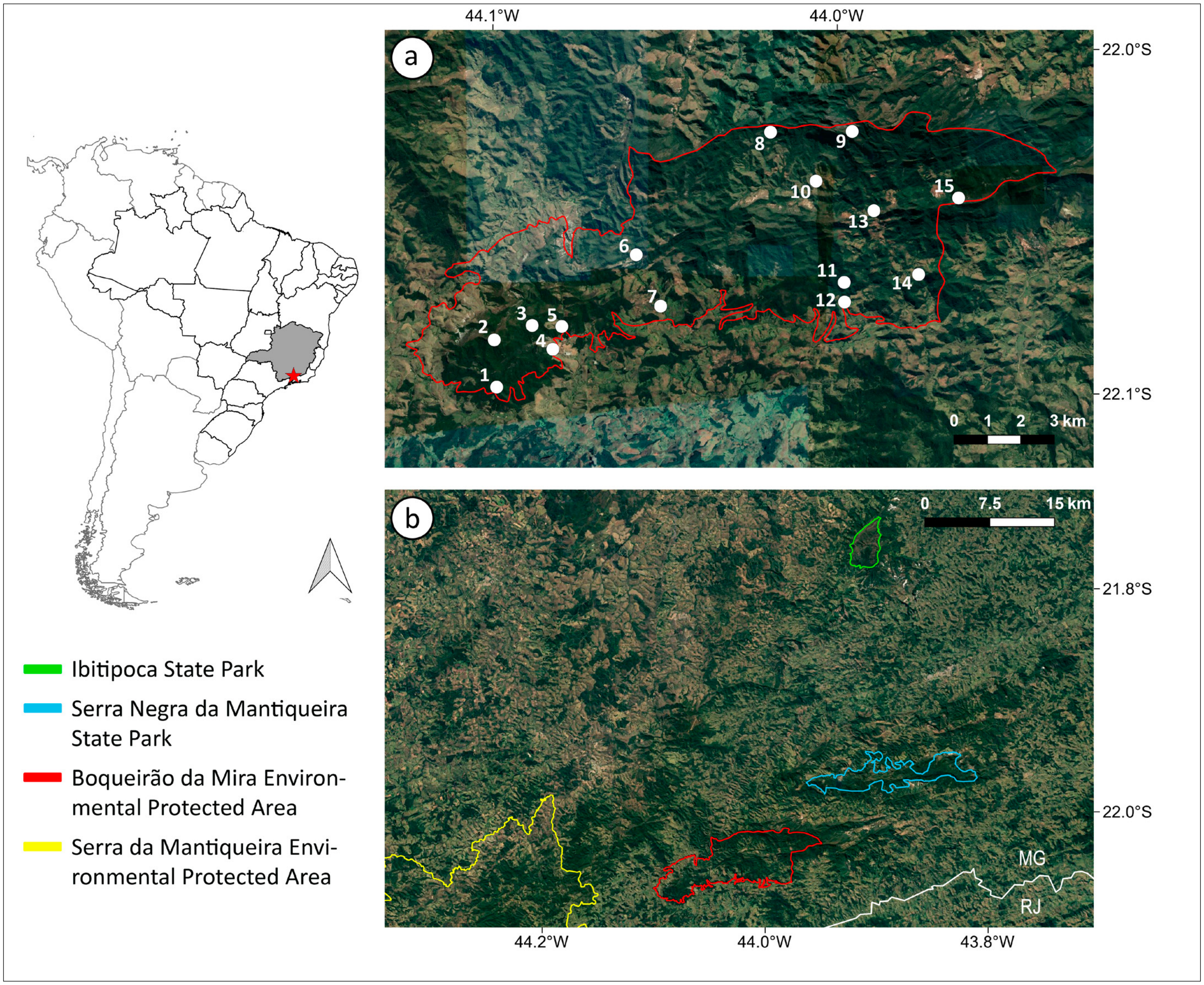

Figure 1. Location of the Área de Proteção Ambiental Boqueirão da Mira (APABM – red star) in the Minas Gerais state (gray background), municipality of Santa Rita de Jacutinga, Southeastern Brazil. (a) Delimitation (red polygon) and sampling areas throughout APABM. The numbers follow Table 1. (b) Proximity between different protected areas in the region connected by the "Serra da Mantiqueira" Ecological Corridor project. White stripe = state border; MG = Minas Gerais state; RJ = Rio de Janeiro state.

Results

We registered a total of 43 anuran species for the Área de Proteção Ambiental Boqueirão da Mira (APABM) (Table 2, Figure 2 - 6), belonging to 12 families: Brachycephalidae (5 species), Bufonidae (2 spp.), Centrolenidae (1 sp.), Craugastoridae (1 sp.), Cycloramphidae (1 sp.), Hemiphractidae (1 sp.), Hylidae (17 spp.), Hylodidae (2 spp.), Leptodactylidae (10 spp.), Microhylidae (1 sp.), Phyllomedusidae (1 sp.) and Odontophrynidae (1 sp.).

We considered Quilombo Hightech as the richest locality among the sampled areas (15 spp.), closely followed by Brejos Figueira (13 spp.) and Serra da Bandeira (12 spp.). *Ischnocnema* gr. *parva*, *Ischnocnema* sp., *Aplastodiscus arildae*, *Ololygon cosenzai*, *Ololygon* sp., *O. flavoguttata*, *Scinax* cf. *perereca*, *Hylodes perere*, *H. lateristrigatus* and *Physalaemus rupestris* were registered only above 1000 m of elevation. On the other hand, other species (*Dendropsophus elegans*, *D. minutus*, *Boana polytaenia*, *Leptodactylus fuscus, L. latrans* and *Rhinella icterica*) were profusely found on several localities.

None of the species we found at APABM were categorized in any threatening level. However, some of them are classified as "Data Deficient" (DD): *Bokermannohyla ibitipoca* and *Physalaemus rupestris* (Drummond et al. 2008); *Hylodes perere* and *Physalaemus rupestris* (ICMBio 2018); and *Ischnocnema izecksohni*, *Bokermannohyla ibitipoca, Physalaemus rupestris* and *Leptodactylus jolyi* (IUCN 2019). Although being out of the IUCN (2019), *Ischnocnema* gr. *parva*, *Vitreorana uranoscopa*, *Bokermannohyla circumdata*, *B. luctuosa* and *Ololygon flavoguttata* are facing population decreasing nowadays (IUCN 2019).

Discussion

In this study, we present the first anuran species list for the Área de Proteção Ambiental Boqueirão da Mira (APABM). Our results (43 species) reveal 6,9% of the known anurans richness for the Atlantic Forest (AF) (625 species; Rossa-Feres et al. 2017) and show a similar

Table 1. Sampling points of Área de Proteção Ambiental Boqueirão da Mira.

Sample point	Locality	Altitude (m)	Latitude	Longitude	Habitat description
1	"Mata do Espineli"	900	-22.0980	-44.0989	Forest at the Serra da Água Santa valley, with open like and forest swamps, creeks and lakes
2	"Serra da Água Santa"	1500	-22.0843	-44.0996	Rocky mountain fields "Campo rupestre"
3	"Estrada Torres Furnas"	1250	-22.0808	-44.0911	Cloud forest; presence of massive antropic activity
4	"Brejos da Figueira"	900	-22.0870	-44.0826	Swamp area, flooded during all months of the year
5	"Brejos Vila Cruzeiro"	600	-22.0745	-44.0513	"Seco" swamp, flooded only in the rainy season
6	"Quilombo Hightech"	1000	-22.0804	-44.0800	Forest with creeks and swamps inside
7	"Boqueirão da Mira"	800	-22.0596	-44.0584	Valley on the Piraputanga river, with forests, and open like swamps
8	"Fazenda Santa Clara das Palmeiras"	680	-22.0733	-43.9979	Valley soaked by the Santa Clara stream, with forest, open like and forest swamps and grassland
9	"Mata Santa Clara das Palmeiras"	900	-22.0676	-43.9980	Huge patch of seasonal forest, with creeks, open like and forest swamps
10	"Brejos Fazenda Barro Branco"	800	-22.0653	-43.9764	Swamp in the edge of a big forest patch
11	"Brejos estrada para Serra da Bandeira"	900	-22.0382	-44.0062	Swamp area in open habitats
12	"Ribeirão Santa Clara"	900	-22.0468	-43.9894	Seasonal forest with the Santa Clara stream
13	"Lagoa temporária Serra do Chora"	1300	-22.0240	-44.0194	Temporary lake surrounded by humid forest
14	"Serra da Bandeira"	1730	-22.0238	-43.9957	Rocky field ("Campo rupestre") with swamps, waterfalls, bromeliads, and cloud forest
15	"Serrote São Lourenço"	1200	-22.0431	-43.9648	Humid forest, waterfalls and forest swamps

diversity amongst other studies in the AF (*e.g.*, Moura et al. 2012, Campos & Lourenço-de-Moraes 2017, Neves et al. 2017a, 2017b, Roberto et al. 2017), with Hylidae presenting the highest richness among the families. This pattern is commonly found in anuran species inventories along the AF, which includes those from the Mantiqueira Complex (Silva et al. 2018). Furthermore, we registered four species that are endemic to the Mantiqueira Complex (*Bokermannohyla ibitipoca*, *Ololygon cosenzai*, *Physalaemus rupestris* and *Hylodes perere*) (Silva & Benmaman 2008, Lacerda et al. 2012, Neves et al. 2017b). In addition, our list shares a great number of species which were also registered by Neves et al. (2017b) to the Serra Negra da Mantiqueira region, which reinforces the importance of connectivity between these highlands. Despite the importance of these areas, both localities might be considered essential for the maintenance of biodiversity in the Brazilian AF altogether (Cruz & Feio 2007, Silva et al. 2018).

Notably, some species we found in our study can be considered as taxonomic uncertainties. *Scinax* cf. *perereca* was recorded in open-like swamps at "Brejos Fazenda Barro Branco" and "Brejos estrada para Serra da Bandeira" (Table 2). We decided to identify as *S.* cf. *perereca* as long as it is a taxonomic complexity, mainly due to morphological similarities among the group (Nunes et al. 2012). The specimens we found here morphologically resemble the true species *S. perereca* Pombal, Haddad & Kasahara, 1995, which is broadly distributed along Southern AF. Likewise, other populations considered as *Scinax* aff. *perereca* have been found in the region (Canelas & Bertoluci 2007, Moura et al. 2012, Pirani et al. 2012, Pimenta et al. 2014, Neves et al. 2017b). Nonetheless, the taxon still remains without a precise identification to the species level. Individuals of *Leptodactylus* cf. *jolyi* of APABM were not identified to the specific level due to the taxonomic complexity presented by this group. The species is morphologically similar to *L. sertanejo* which was described from Uberlândia by Giaretta & Costa (2007) and is considered endemic of Cerrado vegetation. Since *L. sertanejo* was described based on different characteristics of individuals previously recognized as *L. jolyi*, and due to the lack of a clear distribution map for late species, we carefully assume the specimen from APABM as *Leptodactylus* cf. *joyli*. The same name was used by Neves et al. (2017b) after analyzing acoustic parameters between *L. sertanejo, L. jolyi* and *L.* cf. *jolyi* from "Serra Negra da Mantiqueira". All this reveals the need for future revisions regarding the group, with the aid of integrative tools. Moreover, we recorded other four anuran species which we were not able to identify to the species level: *Gastrotheca* sp., *Adenomera* sp., *Ololygon* sp. and *Ischnocnema* sp. Firstly, *Gastrotheca* sp. is an anuran difficulty to find, since it lives and reproduces in the canopy of trees in the AF, becoming difficult to record and rare in scientific collections (Izecksohn & Carvalho-e-Silva 2008). Although we found this species only recording the vocalization high in the trees, which were in accordance with the ones of the genus *Gastrotheca*, it was at the same sort of environment the species usually lives. So, we carefully decided to register this species only at the genus level. Second, both genus *Adenomera* and *Ischnocnema* present a complex taxonomy (Gehara et al. 2013, Cassini et al. 2020), and

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Table 2. Amphibian species recorded at the Área de Preservação Ambiental Boqueirão da Mira. Taxon: (Family/Species); habitat (FA – forest area; OA – open area; OS – open swamp; FS – forest swamp; CF –cloud forest; FC – forest creek; RI – rivers); and sampling point according to the Table 1. * Represents distribution extension records.

Family/Specie	Habitat	Sampling sites
Brachycephalidae		
Ischnocnema izecksohni (Caramaschi & Kisteumacher, 1989)	FA	1, 2, 3, 4, 6, 14, 15
Ischnocnema juipoca (Sazima & Cardoso, 1978)	FA	1, 6, 14
Ischnocnema gr. *parva*	FA	14, 6
Ischnocnema gr. *lactea*	FA	1, 6, 14
Ischnocnema sp.	CF	14
Bufonidae		
Rhinella icterica (Spix, 1824)	FA, OA	1, 2, 3, 4, 5, 6, 9, 14, 15
Rhinella ornata (Spix, 1824)	FA,OA	8, 9, 10
Centrolenidae		
Vitreorana uranoscopa (Müller, 1924)	RI	9
Craugastoridae		
Haddadus binotatus (Spix, 1824)	FA	1, 2, 3, 6, 7, 9, 12, 15
Cycloramphidae		
Thoropa miliaris (Spix, 1824)	OA	14
Hemiphractidae		
Gastrotheca sp.	FA	15
Hylidae		
Aplastodiscus arildae (Cruz & Peixoto, 1987)	FA, CF	6, 14
Bokermannohyla circumdata (Cope, 1871)	FA	13
Bokermannohyla ibitipoca (Caramaschi & Feio, 1990) *	CF	13
Bokermannohyla luctuosa (Pombal & Haddad, 1993)	CF	3
Dendropsophus decipiens (A. Lutz, 1925)	OS	8, 10, 11
Dendropsophus elegans (Wied, 1824)	OS	1, 4, 5, 7, 8, 9, 10, 11
Dendropsophus minutus (Peters, 1872)	OS	1, 4, 5, 7, 8, 9, 10, 11
Boana albopunctata (Spix, 1824)	OS	1, 4, 5, 7, 10, 11
Boana faber (Wied, 1821)	OS	1, 4, 5, 7, 10, 11
Boana pardalis (Spix, 1824)	OS	1, 4, 5, 7, 10, 11
Boana polytaenia (Cope, 1870)	OS	4, 5, 10, 11
Ololygon cosenzai (Lacerda, Peixoto & Feio, 2012) *	CF	3, 14
Ololygon flavoguttata (A. Lutz & B. Lutz, 1939)	CF	3, 6, 14
Ololygon sp.	CF	10, 11
Scinax eurydice (Bokermann, 1968)	OS	5
Scinax fuscovarius (A. Lutz, 1925)	OS	4, 5
Scinax cf. *perereca*	OS	10, 11
Hylodidae		
Hylodes perere Silva & Benmaman, 2008 *	FC	6, 14, 15
Hylodes lateristrigatus (Baumann, 1912)	FC	1
Leptodactylidae		
Adenomera marmorata Steindachner, 1867	OA	
Adenomera sp.	OA	6
Leptodactylus furnarius Sazima & Bokermann, 1978	OS	4
Leptodactylus fuscus (Schneider, 1799)	OS	2, 3, 4, 5, 6, 9
Leptodactylus cf. *jolyi* Sazima & Bokermann, 1978	OS	3
Leptodactylus labyrinticus (Spix, 1824)	OS	2, 3, 4, 6, 9, 13
Leptodactylus latrans (Steffen, 1815)	OS	2, 3, 4, 6, 9, 13
Physalaemus cuvieri Fitzinger, 1826	OS	3, 4, 6, 13
Physalaemus rupestris Caramaschi, Carcerelli & Feio, 1991 *	CF	13, 14
Physalaemus signifer (Girard, 1853)	FS	10
Microhylidae		
Elaschistocleis cesarii (Miranda-Ribeiro, 1920)	OS	5, 6
Phyllomedusidae		
Phyllomedusa burmeisteri Boulenger, 1882	FS	5, 10, 11
Odontophrynidae		
Proceratophrys boiei (Wied, 1824)	FA	1

molecular integrative approaches could elucidate the species complex hypothesis in both groups and arise with new candidate species or an accurate identification. For that reason, we prefer to assign both species only at the genus level. Also, we highlight the need for future investigations regarding this topic using molecular approaches. Finally, regarding the *Ololygon* sp., we recorded this species only in one sampling point ("Serra da Bandeira") at 1.700m above sea level. It corresponds to two individuals that we were not able to reach the proper identification till specific level. We firmly believe that could be an undescribed species, but further specimens sampling and examination should clarify this assumption.

Four species had their distribution increased according to our findings in this study. Firstly, *Bokermannohyla ibitipoca* (Figure 3f) was described to the Parque Estadual (PE) Ibitipoca, in an area of cloud savanna and cloud shrubland with gallery forests along the creek (Caramaschi & Feio 1990, Moreira et al. 2018), and it was recorded in a temporary pond at the APABM. Although the species has already been found in PE Serra Negra da Mantiqueira (Neves et al. 2017b), PE Serra do Brigadeiro (Feio et al. 2003; Moura et al. 2012) and Serra da Boa Vista (Moura et al. 2008), is categorized as Data Deficient (Drummond et al. 2008, IUCN 2019). Now, we increase its distribution, coming out with a new occurrence record. *Hylodes perere* (Figure 5a), a medium-sized torrent frog, registered at three sampling points (*see* Table 2), is also categorized as Data Deficient (ICMBio 2018, IUCN 2019). The species is described to the PE Serra Negra da Mantiqueira and it is known only for the type locality heretofore (Silva & Benmaman 2008). Herein we increase the range distribution of the species to the APABM region and even presenting a short distance, this is the first record for *H. perere* outside Serra Negra da Mantiqueira. Additionally, we increase the number of locality records of *Physalaemus rupestris* (Figure 6b), originally described only to the type locality, in the PE Ibitipoca (Caramaschi et al. 1991). We registered *P. rupestris* in a temporary high elevation pond and in a forest swamp (Table 2). Besides our record, the species has been found at the Serra Negra da Mantiqueira (Oliveira et al. 2009, Neves et al. 2017b). Lastly, *Ololygon cosenzai* (Figure 4c) , described by Lacerda et al. (2012) to the PE Serra do Brigadeiro, was found in high elevations forests at the "Estrada Torres Furnas" and "Serra da Bandeira" (Table 2). Exclusively inhabiting bromeliads and belonging to *O. perpusillus* species group (Peixoto 1987, Brasileiro et al. 2005), *O. cosenzai* has been also found in other places throughout the Mantiqueira Complex (Neves et al. 2016, 2017b). The species conservation status was not evaluated neither by IUCN (2019) nor Brazilian List of threatened species (ICMBio 2018).

Conclusively, despite the fact of most of the species recorded presenting a wide distribution along the AF, several species exhibit a restricted distribution and/or have been included as "Data Deficient" in Lists of Threatened Species (Drummond et al. 2008, ICMBio 2018, IUCN 2019). This reinforces the necessity of standing the APABM as an essential part of the maintenance of Mantiqueira Complex's biodiversity. Finally, our findings contribute to the struggle against the Wallacean shortfall (Lomolino 2004), since we presented new

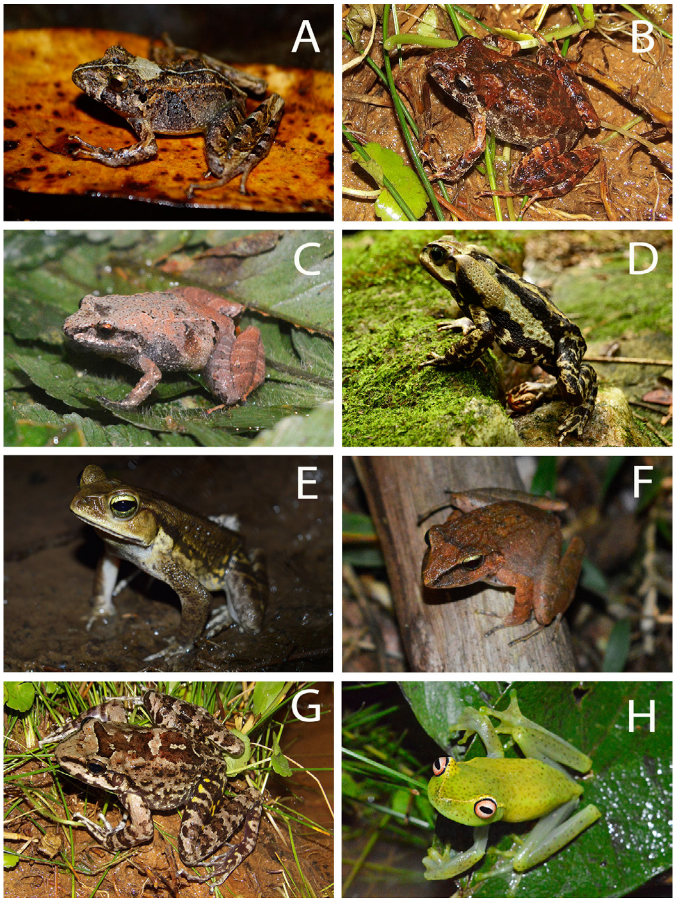

Figure 2. Anuran species from Área de Proteção Ambiental Boqueirão da Mira: (A) *Ischnocnema izecksohni*; (B) *I. juipoca*; (C) *I.* gr. *parva*; (D) *Rhinella icterica*; (E) *R. ornata*; (F) *Haddadus binotatus*; (G) *Thoropa miliaris*; and (H) *Aplastodiscus arildae*.

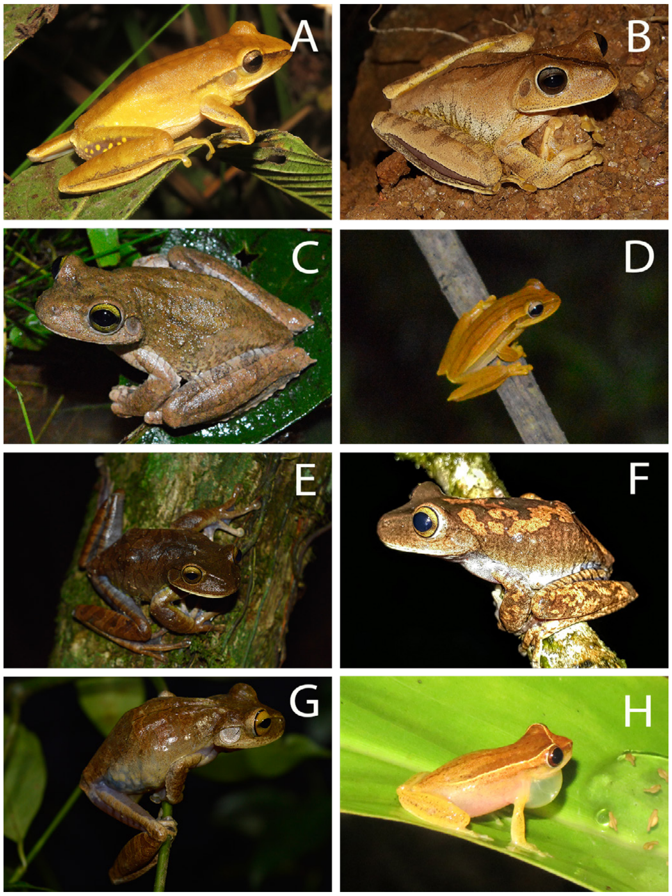

Figure 3. Anuran species from Área de Proteção Ambiental Boqueirão da Mira: (A) *Boana albopunctata*; (B) *B. faber*; (C) *B. pardalis*; (D) *B. polytaenia*; (E) *Bokermannohyla circumdata*; (F) *B. ibitipoca*; (G) *B. luctuosa*; and (H) *Dendropsophus decipiens*.

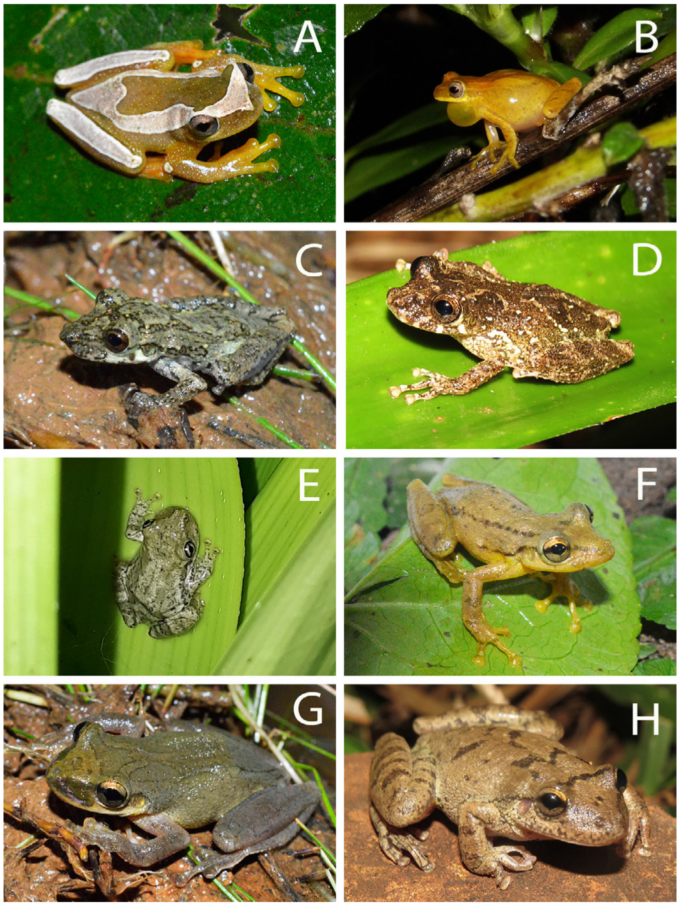

Figure 4. Anuran species from Área de Proteção Ambiental Boqueirão da Mira: (A) *Dendropsophus elegans*; (B) *D. minutus*; (C) *Ololygon cosenzai*; (D) *O. flavoguttata*; (E) *Ololygon* sp.; (F) *Scinax* cf. *perereca*; (G) *S. eurydice*; and (H) *S. fuscovarius*.

records and distribution for some species and filled a gap of anurans composition in the Zona da Mata region, at Minas Gerais state, Brazil, a fragmented AF area.

Supplementary Material

The following online material is available for this article: Appendix I.

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Author Contributions

Lúcio Moreira Campos Lima: Substantial contribution to the conception and design of the work; contribution to data analysis

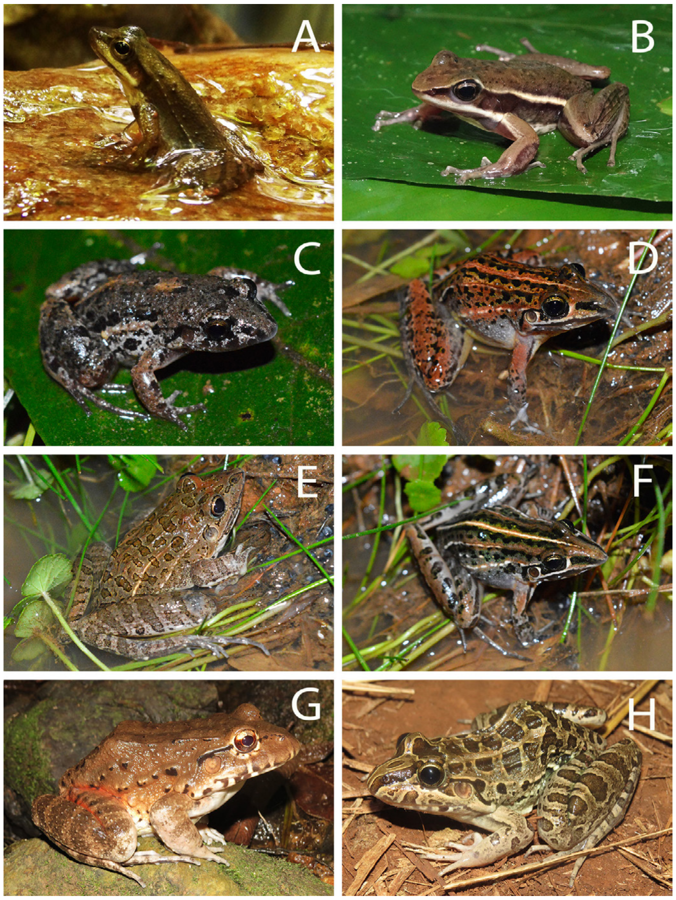

Figure 5. Anuran species from Área de Proteção Ambiental Boqueirão da Mira: (A) *Hylodes perere*; (B) *H. lateristrigatus*; (C) *Adenomera marmorata*; (D) *Leptodactylus furnarius*; (E) *L. fuscus*; (F) *L.* cf. *jolyi*; (G) *L. labyrinthicus*; and (H) *L. latrans*. Photo (B) Clodoaldo Assis.

Figure 6. Anuran species from Área de Proteção Ambiental Boqueirão da Mira: (A) *Physalaemus cuvieri*; (B) *P. rupestris*; (C) *Elachistocleis cesarii*; (D) *Proceratophrys boiei*; and (E) *Phyllomedusa burmeisteri*.

and interpretation; contribution to data acquisition; contribution to manuscript preparation.

André Yves: Substantial contribution to the conception and design of the work; contribution to data analysis and interpretation; contribution to data acquisition; contribution to manuscript preparation.

Victor Gomes de Almeida: Contribution to manuscript preparation; contribution to data acquisition.

Matheus Oliveira Neves: Contribution to data analysis and interpretation; contribution to critical revision, adding intellectual content.

Bernadete Maria de Sousa: Contribution to critical revision, adding intellectual content.

Conflicts of Interest

The author(s) declare(s) that they have no conflict of interest related to the publication of this manuscript.

Ethics

The authors presente the license Colect Permission ICMBio 65519-1 it's material and methods item of the Principal.doc document.

Data Availability

All inventory data is exposed in the principal.doc document.

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Inventory

Checklist and contribution to the knowledge of the odonatofauna of Paraíba state, Brazil

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Abstract: We present the first listing of odonatan species (Insecta: Odonata) that occur in the state of Paraíba, Brazil. There are 49 species and 29 genera registered, making Paraíba the third in number of species among the Brazilian states of northeastern region. The families with the largest number of species were Libellulidae, with 31 species and 15 genera, followed by Coenagrionidae with 11 species and 7 genera. Interior regions of the state are under-sampled, which should still lead to an underestimated number of species. In addition, we present taxonomic notes of two species collected during our expeditions: males of *Progomphus dorsopallidus* Byers, 1934 and females of *Macrothemis griseofrons* Calvert, 1909. Here, we detail important characteristics and present figures to aid their morphological identifications.

Keywords: *Brazilian northeastern; List of species; Anisoptera; Zygoptera; Progomphus dorsopallidus; Macrothemis griseofrons.*

Checklist e contribuição para o conhecimento da odonatofauna do Estado da Paraíba, Brasil

Resumo: Apresentamos a primeira lista de espécies de libélulas (Insecta: Odonata) que ocorrem no estado da Paraíba, Brasil. Há 49 espécies e 29 gêneros registrados, tornando a Paraíba a terceira em número de espécies entre os estados brasileiros da região Nordeste. As famílias com maior número de espécies foram Libellulidae, com 31 espécies e 15 gêneros, seguido por Coenagrionidae com 11 espécies e 7 gêneros. As regiões do interior do estado estão sub amostradas, o que deve levar a um número subestimado de espécies. Além disso, apresentamos notas taxonômicas de duas espécies coletadas durante nossas expedições: machos de *Progomphus dorsopallidus* Byers, 1934 e fêmeas de *Macrothemis griseofrons* Calvert, 1909. Aqui, detalhamos características importantes e apresentamos figuras para auxiliar em suas identificações morfológicas.

Palavras-chave: *Nordeste brasileiro; Lista de espécies; Anisoptera; Zygoptera; Progomphus dorsopallidus; Macrothemis griseofrons.*

Introduction

Odonates (Insecta: Odonata) are an important group of aquatic insects participating in food chains either as an effective predator or as prey for vertebrates (May 2019). They have great appeal to the general public, being considered as “flag species”, and have been used as animal models for behavior investigations and more recently as signals of environmental quality (Amorín et al. 2010, Cordoba-Aguilar 2009). In Brazil, 749 species are registered (Olaya 2019), however, with heterogeneous taxonomic knowledge in the different states.

Available mainly in the central-south region (e.g. Koroiva et al. 2017, Rodrigues et al. 2018, Vilela et al. 2020), lists of odonatan species are still scarce in the northeastern region of Brazil, despite the increase in knowledge of this region in recent years. Considering the nine Brazilian federal states in the Northeastern region, odonatological information is available for six states. The State of Alagoas has about 48 species (see Santos et al. 2020) while Ceará and Piauí have 73 and 26 species, respectively (Takiya et al. 2016). The State of Bahia has 56 species (Firme et al. 2019), however, more than three times this number has already been registered and not yet published (M. Rodrigues com. Pers.). Recently, Santos et al. (2020) released a survey of 34 species for Sergipe, while Bastos et al. (2019) identified 48 species for the State of Maranhão.

Absent from this list is the State of Paraíba. This state is located in the eastern portion of the Northeastern of Brazil, occupies 0.66% of the Brazilian territory and only the 20th position of territorial extension of Brazilian states (Mendes et al. 2012). The mosaic vegetation found in Paraíba ranges from Atlantic Forest biome along the coast to a semiarid region (Caatinga) in the interior. The first biome is considered a hotspot’ region of biodiversity in the world, being the most threatened rainforest in Brazil (Rezende et al. 2018). The other biome (Caatinga), despite being considered intact for a long time, nowadays is known to have a great anthropic effect on its ecosystem mainly caused by cattle industry and bad management of water resources (Silva & Barbosa 2017). Regarding odonates, few studies have been dedicated to increasing knowledge about its fauna in Paraíba and almost all of which are restricted to taxonomic descriptions and specific information about species of large distribution (e.g. Machado 1995, Carvalho & Bravo 2014, Nobre 2016).

Considering this information gap, the main objective of this study was to present the diversity of odonatan species in Paraiba state through the bibliographic record and recent sampling excursions. Additionally, we provide some taxonomic notes on two poorly known species found in the Northeastern region of Brazil: *Progomphus dorsopallidus* Byers, 1934, a species rare in collections that we provide additions to male description and *Macrothemis griseofrons* Calvert, 1909, whose female description was also augmented, both collected during our expeditions.

Material and Methods

1. *Study area*

The state of Paraíba has an area of 56.467 km² (IBGE 2019) and stands out for the predominant presence of the Caatinga Biome. The state is bordered by the states of Pernambuco, Ceará and Rio Grande do Norte (Figure 1). The relief of the state is characterized by plains, plateaus and tabular and flat depressions, with about 90% of the territory located below 600 m in altitude (IDEME 2014). The hydrographic network consists of eleven basins, where the water system is characterized by the predominance of temporary rivers, due to long periods of drought in the interior of the state, and the presence of important perennial rivers, such as Paraíba and Piranhas rivers. In order to mitigate the effects of the dry seasons, many dams were built throughout the state (IDEME 2014). According to the Köppen climate classification, the different regions of the state can be classified as “As”, “Bsh”, “Aw” and “Am” types (Francisco et al. 2015). The average annual precipitation varies between 300 mm in the western and central region of the state to 1900 mm in the coastal sector and the average temperatures are above 24° C (Francisco et al. 2015).

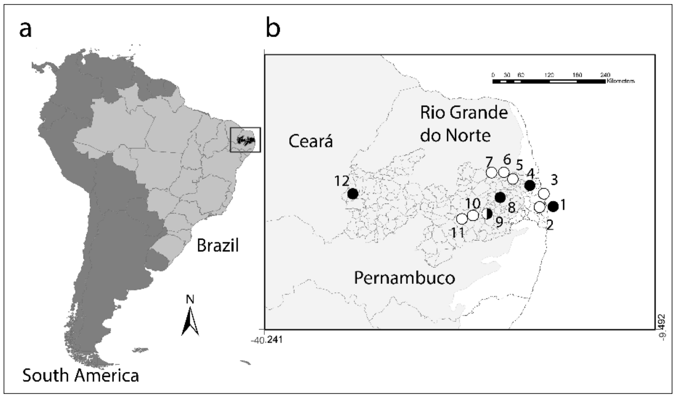

Figure 1. Sampling area. (a) Map of South America (dark grey) highlighting the geopolitical division of Brazil (grey) and Paraíba State (black); (b) Municipalities with Odonata recorded in Paraíba State highlighting Caatinga (soft grey) and Atlantic forest biomes (white). Black circle, municipalities with sampling recorded in the literature; white circle, municipalities with sampling carried out in this study; half black circle, municipality with sampling carried out by both the literature and this study. Municipalities: 1, João Pessoa; 2, Santa Rita; 3, Lucena; 4, Mamanguape; 5, Caiçara; 6, Tacima; 7, Araruna; 8, Areia; 9, Campina Grande; 10, Boa Vista; 11, Cabaçeiras; 12, Cajazeiras.

2. *Taxonomic list elaboration*

To prepare the species list, we carried out samplings and followed the methodology used by Koroiva et al. (2020a). First, we conducted samplings in eight municipalities (23 sampling sites) in Paraíba during 2020 and 2021: Araruna (-6.596052, -35.726025; -6.505297, -35.767449; -6.49901, -35.763893), Boa Vista (-7.369703, -36.308986), Cabaceiras (-7.365301, -36.243216; -7.379293, -36.300225; -7.376817, -36.309105; -7.376034, -36.322289), Caiçara (-6.611859, -35.470029), Campina Grande (-7.277802, -35.970657; -7.277554, -35.971868; -7.274477, -35.964059; -7.269109, -35.974413; -7.275961, -35.966894; -7.275912, -35.965903; -7.277288, -35.972267), Lucena (-6.894775, -34.874688; -6.896821, -34.878103; -6.897269, -34.881032), Santa Rita (-7.151667, -34.961308; -7.000965, -34.98836) and Tacima (-6.590482, -35.46025; -6.48637, -35.643069) (Figure 1). Odonata sampling, euthanasia, and transport was authorized by the Brazilian Biodiversity Information and Authorization System (SISBIO), Chico Mendes Institute for Biodiversity Conservation (ICMBio), Ministry of Environment (MMA) (SISBIO authorization number 74324-2). The field samplings followed the methodology presented in Vilela et al. (2020). We also obtained information from the Entomological Collection of the Department of Systematics and Ecology of the Federal University of Paraíba (DSEC), where all the specimens sampled in this project were also deposited.

Additional data were collected in 12 publications (Bastos et al. 2019, Belle 1983, Costa et al. 2002, 2006, Machado 1995, 2010, Nobre 2016, Pinto & Carvalho 2012, Pinto 2013, Lacerda & Machado 2019, St. Quentin 1973, Takiya et al. 2016), published between 1973 and 2019, and on the website "Catalogo Taxonômico da fauna do Brasil" (http://fauna.jbrj.gov.br; "Taxonomic Catalog of Fauna of Brazil" in English; Pinto 2021). Additionally, we present the municipality where the specimens were sampled in Paraíba state, when the data was available (Figure 1). In cases where there is no previous record of the species from Paraíba state by other document, these must be considered new records. For the systematic classification, we follow Paulson & Schorr (2020) and Lorenzo-Carballa et al. (2021).

3. *Taxonomic notes*

Specimens of *P. dorsopallidus* and *M. griseofrons* were collected during an expedition to the Pai Mateus farm (also known as Tapera farm), Cabaceiras (site 11), Paraíba state, Brazil (Figure 1), between June and July 2020. This farm is located in the permanent preservation area of Cariri - Lajedo do Pai Mateus (Silva et al. 2017) and has a farm hotel and two important natural tourist attractions, "Lajedo do Pai Mateus" and "Lajedo Manoel de Souza".

Specimens were scanned with an Epson V600 Perfection at colored 1200 dpi with 200% magnification. Illustrations were made using trace paper and scanned with Epson V600 Perfection at black and white 1200 dpi with 100% magnification. Morphological terminology for *P. dorsopallidus* follows Belle (1973, 1994), for *M. griseofrons* we follow Garrison et al. (2006), and Costa (1991) except for wing venation. We follow Riek & Kukalová-Peck (1984) for wing venation characters. All measurements are in millimeters (mm). Photos of *Progomphus dorsopallidus* Holotype kindly sent by Dr. Erika Tucker from the Insect Collection Manager from the University of Michigan, MI, USA.

Abbreviations: AL, abdomen length (including cercus); Ax, antenodal crossveins; Ce, cercus; Ep; epiproct; FW, fore wing; HW, hind wing; Pa, paraproct; Pt: costal edge of FW pterostigma; Px, postnodal crossveins; S1–10, abdominal segments; TL, total length (including cercus).

Results

1. *Species list*

The total number of Odonata species registered in Paraíba is 49 (Table 1). We sampled 410 specimens from 36 species and 22 genera. Some species registered in this study are presented in Figures 2 and 3. The total number of genera registered for the state is 29, distributed in six families: Libellulidae is the family with the largest number of records, with 15 genera and 31 species, followed by Coenagrionidae with 7 genera and 11 species, Gomphidae with 4 genera and 4 species. Calopterigydae, Heteragrionidae and Lestidae presented one genus and one species.

2. *Taxonomic notes*

Additions to the original male description of *Progomphus dorsopallidus* Byers, 1934

(Figures 4-7)

Material examined. 1♂, Brazil, Paraíba State, Cabaceiras, Fazenda do Lajedo do Pai Mateus (-7.3760, -36.3222), 437m, 25.vii.2020, R. Koroiva & V.G.N. Gomes-Koroiva leg.

Head. Mouthparts light brown, bearing dark setae; eyes dark brown (blue-grey when alive); antenna dark brown, dorsal portion of scape grey, remainder dark brown; postclypeus, antefrons, postfrons light brown; vertex dark brown; postocellar ridge dark brown, with a deep concavity at its middle; occiput dark green at its middle, black margins with a fringe of pale setae; posterior area of head pale colored laterally, darkening toward the middle.

Thorax. Anterior lobe of prothorax dark brown, with pale spots on each side; medial lobe dark brown; posterior lobe rounded, mostly pale, darkening toward the base. Pterothorax mostly pale green/brown colored with darker marks as follows: mesepisternum pale green with two thin stripes parallel to middorsal carina, slightly surpassing its anterior 1/2, a thick antehumeral stripe covering most of its lower 1/2, connected with a smaller stripe that surpasses the suture to mesepimeron; mesepimeron brown, with a small stripe covering its upper 1/2; metepisternum brown, with a thick stripe covering most of its middle portion; metepimeron brown, with a thin stripe covering its upper 1/2.

Wings. Hyaline, with a light brown tinge, venation brown; pterostigma light brown with dark contours on all four wings, occupying 5.5−6 cells on left wings and 5 cells on right wings. Fore wings (FW) with 4 paranal cells, area posterior to CuA one cell wide for first 2 cells, then increasing to 2 cells for a distance of 2 cells, then decreasing to 1 cell; antenodal crossveins on FW 14/14, on HW 9/9, first and fifth thickened in all wings; postnodal crossveins on FW 7/7, on HW 8/8; basal subcostal crossvein present in all wings; triangles 3-celled and subtriangles 2-celled in all wings.

Abdomen. S1−2 mostly dark brown, S1 lacking a midventral tubercle, becoming paler below; auricles dark brown externally, pale green internally, bearing minute denticles on posterior margin; S3−7 with a dark brown ring at 1/2, overall coloration light brown in the anterior 3/5, remainder dark brown (broken between S6−7); S8 mostly dark brown, becoming brown below; S9 dorsally dark brown, brown laterally becoming black toward venter, with a black spot on each medio-anterior side; S10 mostly brown, with a black anterodorsal stripe. Posterior hamuli stocky, with a thick well-developed hook bearing 5 small basoventral tubercles in a straight row, overall coloration mostly brown with basal paler areas, apex of hook black.

Anal appendages. Cercus with a pronounced basal externo-lateral dilatation, bearing a tooth with acute apex, obliquely oriented; inferior carina of cercus curved, with a row of several minute blunt denticles. Epiproct forcipate, supero-external tooth with blunt and rounded apex; tip of epiproct not bifid, with 3 (left) and 4 (right) blunt rounded teeth.

Measurements. TL 41.5; AL 29.6; FW 22.2; HW 21.1; Pt 2.9.

Remarks. *P. dorsopallidus* (Figure 4) fits best in the *guyanensis* Group, proposed by Belle (1990), by having cerci with a sharply pointed basal externo-lateral dilatation (Figure 5), and can be separated from its congeners by the following character combination: in lateral view, cercus (Figure 5) with a pronounced basal externo-lateral dilatation bearing several minute blunt denticles (shared with *P. mexicanus*, and *P. amarillus*), not so pronounced in the other species; supero-external tooth of epiproct forceps with blunt and rounded apex, bearing 3 or 4 blunt rounded teeth (Figure 6), and a stocky hamule with a thick developed hook. The epiproct structure of *P. dorsopallidus* (Figure 7) resembles those of *P. mexicanus*, and they can be separated mainly by their size (reaching 1/2 of cerci in *P. mexicanus*, 3/4 of cerci in *P. dorsopallidus*), tip of supero-external tooth is acute in *P. mexicanus*,

Table 1. Odonata species recorded for Paraiba State, Brazil. The term "Not informed" was used for records without information about municipality.

Scientific name	Municipality	References
ANISOPTERA		
Libellulidae		
Anatya guttata (Erichson in Schomburgk, 1848)	Santa Rita	**This study**
Brachymesia furcata (Hagen, 1861)	Boa Vista, Cabaceiras, Campina Grande	**This study**
Brachymesia herbida (Gundlach, 1889)	Lucena	**This study**
Diastatops obscura Fabricius, 1775	Santa Rita	Bastos *et al.* 2019; **This study**
Eryhtrodiplax umbrata (Linnaeus, 1758)	Campina Grande	**This study**
Erythemis carmelita Williamson, 1923	Tacima	**This study**
Erythemis credula (Hagen, 1861)	Campina Grande	**This study**
Erythemis haematogastra Burmeister, 1839	João Pessoa	Bastos *et al.* 2019; Pinto 2013
Erythemis mithroides (Brauer, 1900)	João Pessoa	Pinto 2013
Erythemis peruviana (Rambur, 1842)	Cabaceiras, João Pessoa	Pinto 2013; **This study**
Erythemis plebeja (Burmeister, 1839)	Araruna, Areia, Tacima, João Pessoa	Carvalho & Bravo 2014; Pinto 2013; **This study**
Erythemis vesiculosa (Fabricius, 1775)	Campina Grande, João Pessoa	Pinto 2013; **This study**
Erythrodiplax avittata Borror, 1942	Araruna, Cabaceiras, Campina Grande, Santa Rita, Tacima	**This study**
Erythrodiplax basalis (Kirby, 1897)	Areia	Carvalho & Bravo 2014
Erythrodiplax fusca (Rambur, 1842)	Cabaceiras	**This study**
Erythrodiplax leticia Machado 1996	Araruna, Campina Grande, Cajazeiras, Santa Rita	Machado 1995; Nobre 2016; **This study**
Erythrodiplax media Borror, 1942	Santa Rita	**This study**
Macrothemis griseofrons Calvert, 1909	Boa Vista, Cabaceiras, Campina Grande	**This study**
Miathyria marcella (Selys in Sagra,1857)	Areia, Cabaceiras, Caiçara, Campina Grande, Lucena, Tacima	Carvalho & Bravo 2014; **This study**
Micrathyria catenata Calvert, 1909	Not informed	Costa *et al.* 2002
Micrathyria hesperis Ris, 1911	Cabaceiras, Caiçara, Campina Grande	**This study**
Micrathyria ocellata Martin, 1897	Araruna, Cabaceiras, Campina Grande, Lucena	**This study**
Oligoclada aff. *borrori* Santos, 1945	Lucena	**This study**
Orthemis aequilibris Calvert, 1909	Araruna, Lucena	**This study**
Orthemis discolor (Burmeister, 1839)	Campina Grande, Tacima	**This study**
Pantala flavescens (Fabricius, 1798)	Araruna, Cabaceiras, Campina Grande	**This study**
Perithemis tenera (Say, 1840)	Araruna, Boa Vista, Cabaceiras, Caiçara, Campina Grande, Tacima	Costa *et al.* 2006, **This study**
Tramea cophysa Hagen, 1867	Boa Vista, Cabaceiras, Tacima	**This study**
Tramea darwini Kirby 1889	Campina Grande	**This study**
Uracis imbuta (Burmeister, 1839)	Santa Rita	**This study**
Zenithoptera lanei Santos, 1941	Not informed	Pinto 2021
Gomphidae		
Phyllocycla brasilia Belle, 1975	Areia	Carvalho & Bravo 2014
Phyllogomphoides annectens (Selys, 1869)	João Pessoa	St Quentin 1973
Progomphus dorsopallidus Byers, 1934	Cabaceiras	**This study**
Zonophora calippus Selys, 1869	João Pessoa	Belle 1983
ZYGOPTERA		
Calopterygidae		
Hetaerina sp	Santa Rita	**This study**
Coenagrionidae		
Acanthagrion gracile (Rambur, 1842)	Areia, Araruna, Santa Rita	Carvalho & Bravo 2014; **This study**
Argia aff. *reclusa* Selys, 1864	Santa Rita	This study
Enallagma novaehispaniae (Calvert,1907)	Areia, Araruna, Santa Rita	Carvalho & Bravo 2014; **This study**

Continue...

Continuation...

Ischnura capreolus (Hagen, 1861)	Areia, Araruna, Cabaceiras, Caiçara, Lucena, Santa Rita, Tacima	Carvalho & Bravo 2014; Pinto 2021; Takyia *et al.* 2016; DSEC; **This study**
Ischnura fluviatilis Selys, 1876	Areia, Cabaceiras, Campina Grande, Lucena	Carvalho & Bravo 2014; **This study**
Phoenicagrion flammeum (Selys 1876)	Areia	Machado 2010
Telebasis corallina (Selys, 1876)	Campina Grande, João Pessoa	Pinto 2021; Pinto & Carvalho 2012; **This study**
Telebasis filiola (Perty, 1834)	Areia, Araruna, Cabaceiras, Caiçara, Campina Grande, João Pessoa	Carvalho & Bravo 2014; Pinto 2021, Pinto & Carvalho 2012; **This study**
Mecistogaster kesselringi Soldati & Machado, 2019	João Pessoa, Mamanguape	Lacerda & Machado 2019
Mecistogaster mielkei Soldati & Machado, 2019	João Pessoa	Lacerda & Machado 2019
Mecistogaster nordestina Soldati & Machado, 2019	João Pessoa	Lacerda & Machado 2019, DSEC
Heteragrionidae		
Heteragrion sp.	João Pessoa	DSEC
Lestidae		
Lestes forficula Rambur, 1842	Areia, Campina Grande, Tacima	Carvalho & Bravo 2014; **This study**

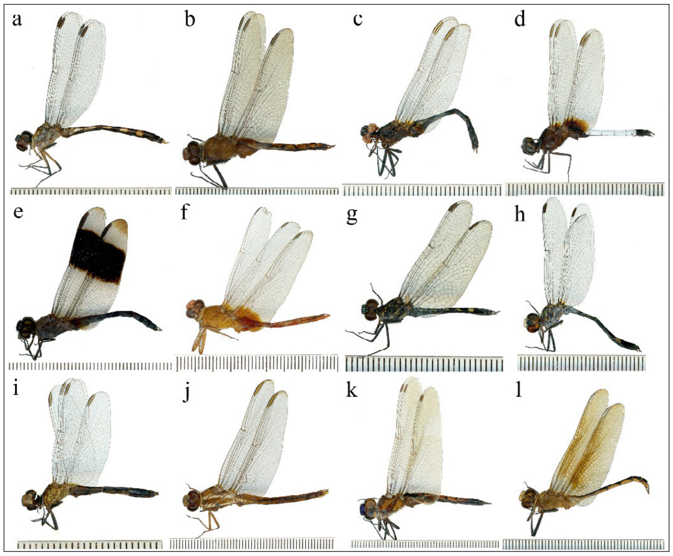

Figure 2. Examples of dragonflies (Odonata:Anisoptera) collected in Paraiba State, Brazil. (a) *Anatya guttata*; (b) *Brachymesia furcata*; (c) *Erythemis credula*; (d) *Erythrodiplax media*; (e) *Erythrodiplax umbrata*; (f) *Erythemis carmelita*; (g) *Micrathyria hesperis*; (h) *Micrathyria ocellata*; (i) *Oligoclada* cf. *borrori*; (j) *Orthemis aequilibris*; (k) *Tramea cophysa*; (l) *Brachymesia herbida*.

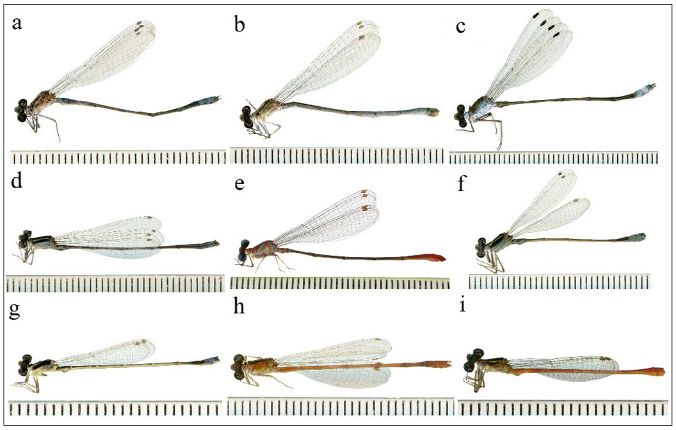

Figure 3. Examples of damselflies (Odonata:Zygoptera) collected in Paraiba State, Brazil. (a) *Enallagma novaehispaniae* - male; (b) *Enallagma novaehispaniae* - female; (c) *Lestes forficula*; (d) *Acanthagrion gracile*; (e) *Phoenicagrion flammeum*; (f) *Ischnura fluviatilis*; (g) *Ischnura capreolus*; (h) *Telebasis corallina*; (i) *Telebasis filiola*.

blunt in *P. dorsopallidus*, and the tip of epiproct ends in 3 or 4 blunt rounded teeth in *P. dorsopallidus*, whereas in *P. mexicanus* it ends in two teeth. It should be added that the two species (*P. dorsopallidus* and *P. mexicanus*) are far separated in distribution.

Habitats, biology and conservation. *P. dorsopallidus* has a wide distribution range in south America, mainly concentrated in coastal regions, where it occurs, for instance, in the states of Ceará and Espírito Santo (Montes-Fontalvo et al. 2021). Due to its large distribution and its occurrence in protected areas, it has been assessed as LC (least concern) by IUCN, which means that the species is not under threat of extinction (Montes-Fontalvo et al. 2021). This species inhabits streams in semi- or open areas and is not found inside forested areas (De Marmels 2005). In Paraíba state, we also found this species in a stream located in an open area, thus corroborating the literature record.

Additions to the female description of *Macrothemis griseofrons* Calvert, 1909

(Figures 8-10)

Material examined. 4♀, Brazil, Paraíba State, Cabaceiras, Lagoas PB-160 Road (-7.3653, -36.2432), 25-27.vi.2020, R. Koroiva & V.G.N. Gomes-Koroiva leg.; 2♀, Brazil, Paraíba State, Cabaceiras, Estacionamento Saca-de-lã (-7.3760, -36.3222), 27.vi.2020, R. Koroiva

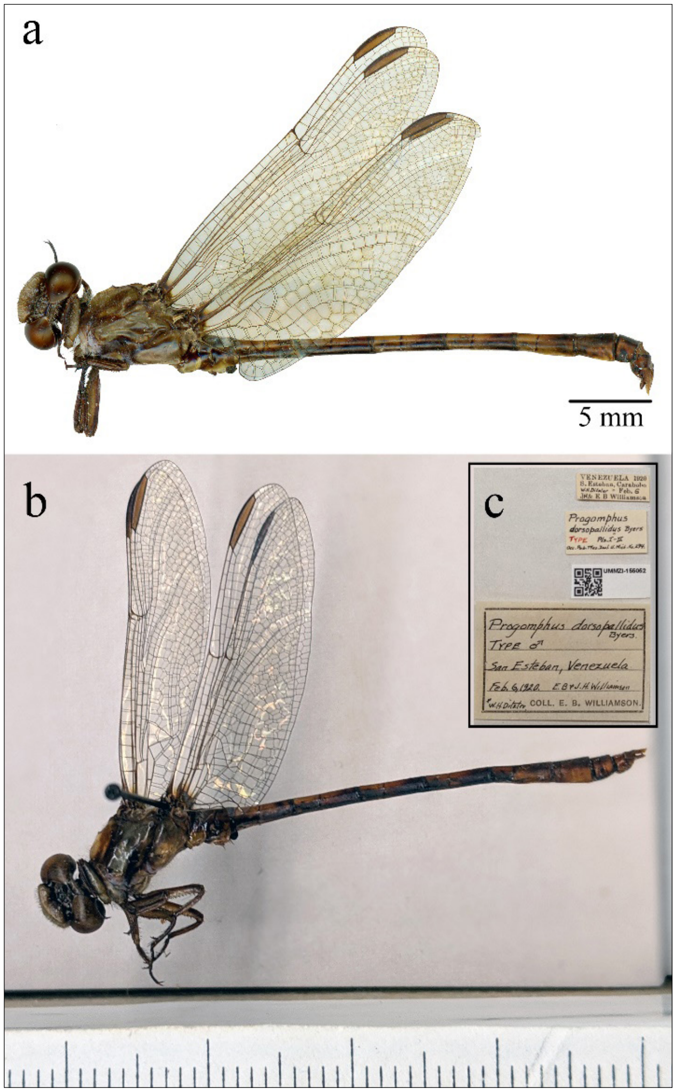

Figure 4. *Progomphus dorsopallidus*: lateral view of habitus; (a) male from Cabaceiras, Paraíba State; (b) Holotype from San Esteban, Venezuela.

& V.G.N. Gomes-Koroiva leg.; 1♀, Brazil, Paraíba State, Cabaceiras, Represa Casa do Pai Mateus (-7.3792, -36.3002), 25-27.vi.2020, R. Koroiva & V.G.N. Gomes-Koroiva leg.; 1♀, Brazil, Paraíba State, Boa Vista, Lagoa entre Lajedos (-7.3697, -36.3089), 27.vi.2020, R. Koroiva & V.G.N. Gomes-Koroiva leg.

Head. Mouthparts pale colored; eyes dark; antenna dark brown, dorsal portion of scape brown, remainder black (Figure 8); postclypeus, antefrons, postfrons brown/dark grey; vertex dark brown; occiput dark brown; posterior area of head with a diffuse brown/pale coloration as in Figure 9.

Thorax. Overall coloration brown (varying as in Figure 10), with a pale oblique lateral stripe (roughly similar to the male) and with two thin stripes parallel to middorsal carina; darker brown stripes on the following areas: a thick humeral stripe, covering most of the mesepisternum; a thick stripe covering the lower portion of mesepisternum, surpassing the suture and covering the upper half of mesepimeron; a stripe covering the lower half of metepisternum; legs light brown, with 6+1 spines on metafemur.

Wings. Hyaline with a circular infumated spot on each FW reaching from postnodal 1/4 until the tip of the wings, and a small brown spot on the HW base, not reaching Ax 1 level; Mspl in FW distinct; FW triangle crossed, subtriangle with 3 cells; arculus proximal to Ax 2 in FW and HW; 13 Ax in FW, 10 in HW; 8 Px in FW, 8 in HW.

Abdomen. Overall coloration of S1-7 brown, with lateral darker coloration; S8-10 dark brown, dorsally black; cerci dark brown, as long as 1.5x the S10 length; vulvar lamina 'U' shaped, with blunt edges.

Measurements. TL 39.2; AL 27.8; FW 33.1; HW 31.8; Pt 2.6.

Remarks. The female of *M. griseofrons* can be distinguished by other female congeners by the following character combination: a circular infumated spot on each FW tip (basal spot in *M. absimile*, hyaline in *M. calliste*), a pale oblique lateral thoracic stripe (absent in *M. absimile* and *M. calliste*), vulvar lamina 'U' shaped, with blunt edges (with a small median excision in *M. absimile*, and a larger median excision in *M. calliste*).

Habitats, biology and conservation. *M. griseofrons* occurs in the states of Bahia, Ceará and Pernambuco (Santos 1946, Nobre and Carvalho 2014). However, there are only four known records to this species so far, being three of these very old, dating before 1945. Current distribution of this species is currently unknown and it was assessed as DD (data deficient) by IUCN (Vilela & Guillermo-Ferreira 2021), which means that the amount of recent records are insufficient to perform a proper assessment, pending on new literature records such as the one we present here. *M. griseofrons* was collected in lentic habitats, where it was found perching on the riparian vegetation.

Discussion

1. *Species list*

The 49 species listed in the state of Paraíba represent about 6.54% of the known species in Brazil (749 species). With the results presented in this study, the state of Paraíba is the third in number of species in the northeast region of Brazil, behind Ceará (73 species; Takiya et al. 2016) and Bahia (54 species; Firme et al. 2019). In relation to other states of Brazil, the number is still far from the number registered to Amazonas (335 species; Koroiva et al. 2020b) and Minas Gerais (308 species; Vilela 2021). Overall, 40 (82%) of the species recorded to Paraíba state fall under the LC category of conservation by IUCN, meaning widespread species with several literature records and that occurs in protected areas. Two species (*M. griseofrons* and *P. brasilia*, 4%) were assessed as DD, with insufficient assessment data, and five species (*M. kesselringi*, *M. mielkei*, *M. nordestina*, *O. borrori*, and *Telebasis filiola*, 10%) were never assessed for its conservation status. None of the species recorded so far to Paraíba state are endemic. The samples in the state are mainly concentrated close to municipalities with the presence of important universities and research institutes such as João Pessoa, Campina Grande and Areia. Similar as evidenced by Koroiva et al. (2020a) for the State of Amazonas, it is necessary to carry out more field samples for the interior of Paraíba, which should provide new records to this list.

2. *Taxonomic notes*

About *P. dorsopallidus*, the most interesting feature about the epiproct structures observed here is the variation of the blunt rounded teeth on the right and left forceps. On the holotype, the left and right forceps has two blunt teeth (Figure 6). On the examined male, there is one variation: left forceps with three blunt teeth (Figure 6) and the right with two, as in the holotype. The same occurred with two additional

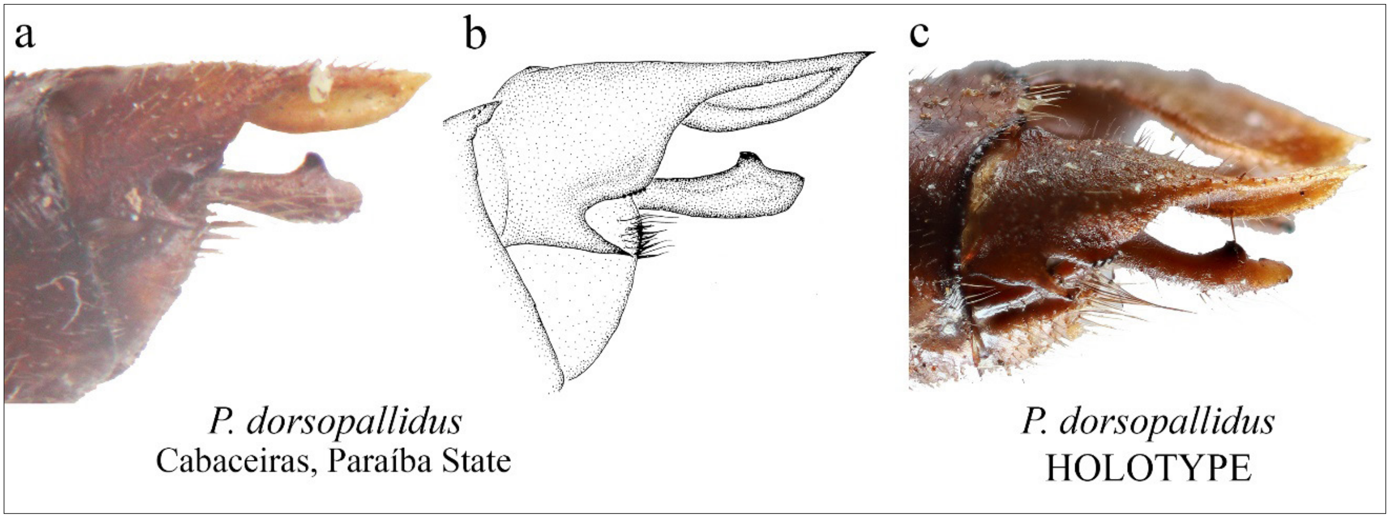

Figure 5. *Progomphus dorsopallidus*: lateral view of anal appendages; (a–b) male from Cabaceiras, Paraíba State; (c) Holotype from San Esteban, Venezuela.

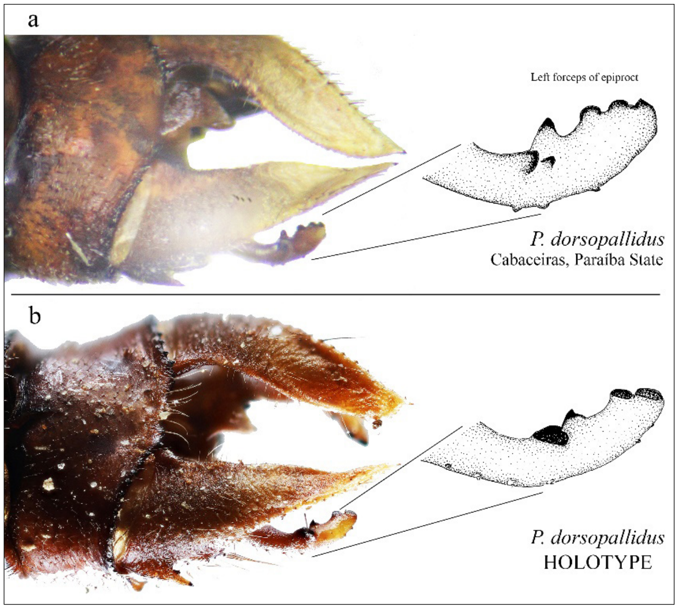

Figure 6. *Progomphus dorsopallidus*: dorsolateral view of anal appendages, showing the left epiproct forceps in detail; (a) male from Cabaceiras, Paraíba State; (b) Holotype from San Esteban, Venezuela.

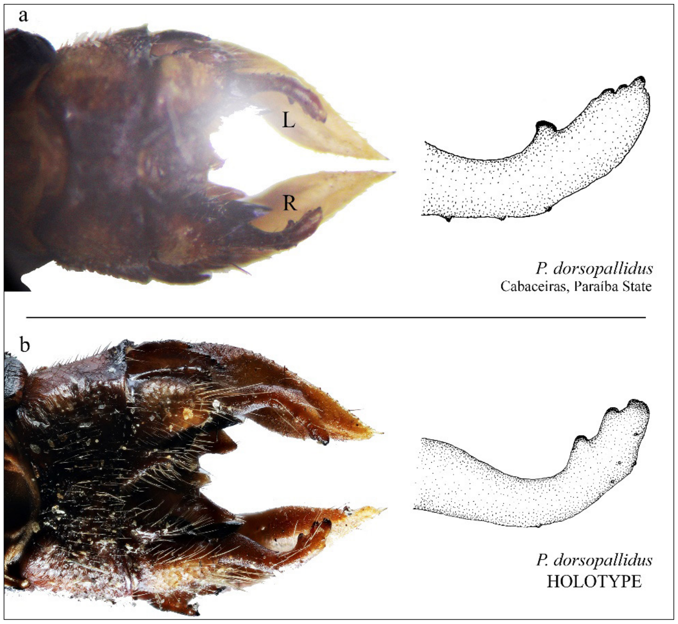

Figure 7. *Progomphus dorsopallidus*: ventral view of anal appendages, showing both epiproct forceps's in detail; (a) male from Cabaceiras, Paraíba State; (b) Holotype from San Esteban, Venezuela.

males that we examined but were not available to include in this study, and one additional male photographed by Dr. Jurg DeMarmels (pers. comm.). At first, we thought our male to be a new species, because cerci and epiproct structures differed greatly from the other species of *Progomphus*, drawn by Belle (1973, 1994) and other authors. Comparing our specimen with the original description by Byers (1934), thoracic coloration patterns and hamuli are very similar to our specimen; however the drawings of the appendages drove our attention away, because they are very different from the actual structure. Anyway, we asked for photographs of the holotype, which were kindly provided by Dr. Erika Tucker, the Insect Collection Manager from the University of Michigan. Comparing our specimen with the holotype, we had no doubt that our specimen represents *P. dorsopallidus* due to cerci and epiproct morphology, in addition to the coloration patterns.

On the account of *M. griseofrons*, after Calvert's description of the species in 1909, Navás (1916) described *Cendra cearana*, which later was synonymized with *M. griseofrons* by Santos (1946). The female was never treated by Calvert and Santos, but was treated by Navás's study in Latin. He never figured the female structures and our study brings additional information on *Macrothemis* females, which are often difficult to identify in the absence of males (Garrison et al. 2006). Also, by adding a new record to the literature (which includes a record within a protected area), we may help future assessments by IUCN to determine the current conservation status of this species.

Final Considerations

The knowledge about the Odonata order has had a unique improvement in the last 10 years in Northeastern Brazil. The presence of specialists and new expeditions demonstrate the importance of participation and exchange between researchers for the taxonomic improvement on insects. Despite

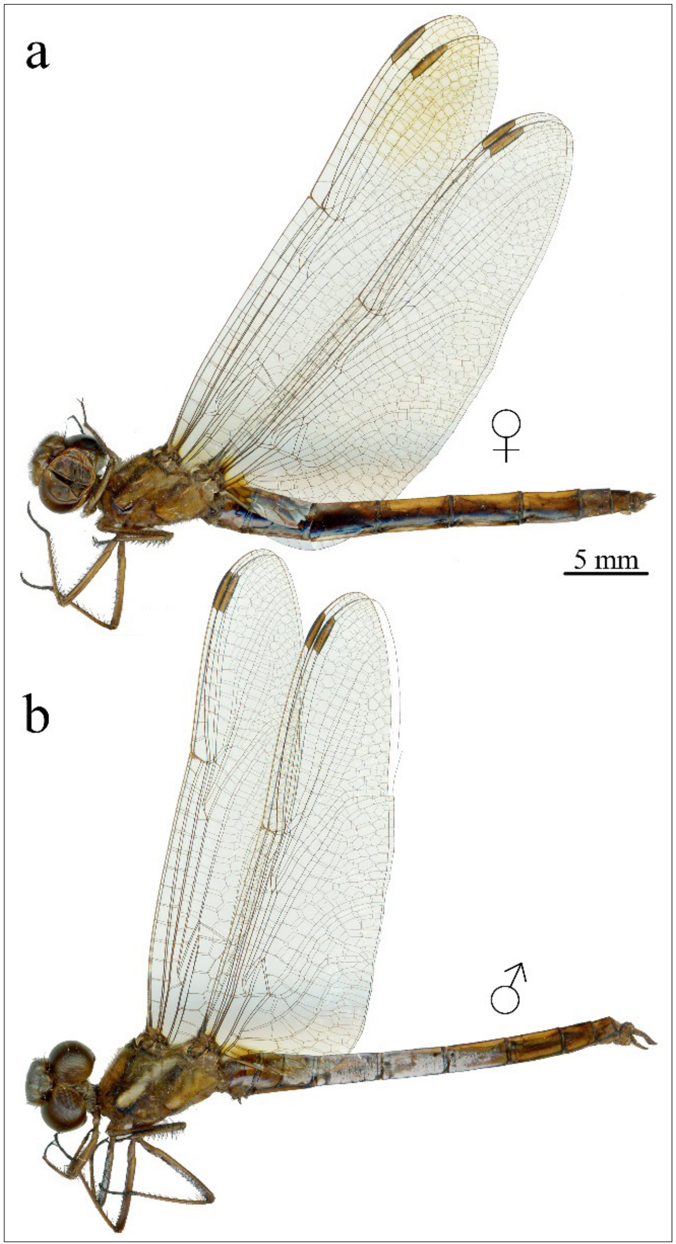

Figure 8. *Macrothemis griseofrons:* lateral view of habitus; (a) female and (b) male from Cabaceiras, Paraíba State.

these advances, until now, this and other studies published have not carried out a wide sampling in these states, which indicates that these numbers are still quite underestimated. Keeping in mind the importance of the correct species identification, the taxonomic notes presented for *Progomphus dorsopallidus* Byers, 1934 and *Macrothemis griseofrons* Calvert, 1909 highlight the need for improvements of descriptions and revisions even for species with wide distribution. In this sense, the increase in taxonomic research and samplings in northeastern Brazil plays a key role in improve knowledge about the diversity of odonatan species, not exclusively for this region, but for the entire Neotropical area.

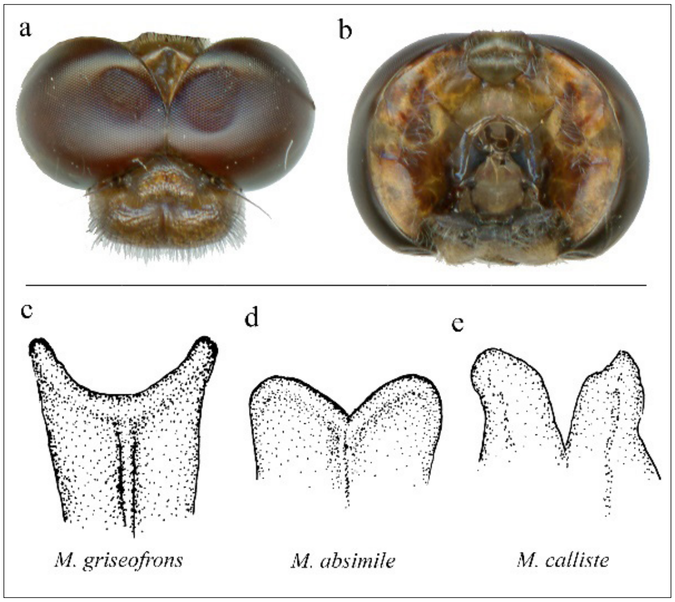

Figure 9. *Macrothemis griseofrons*: dorsal (a) and posterior (b) views of female head. Ventral view of vulvar lamina of M. *griseofrons* (c), M. *absimile* (d) and *M. calliste* (e).

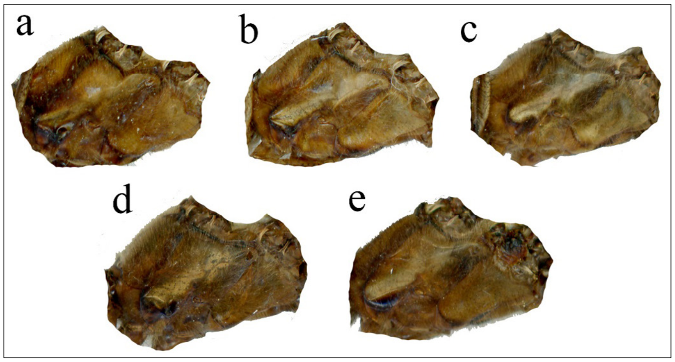

Figure 10. *Macrothemis griseofrons*: color variation on female thoracic pattern.

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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.

Alessandre Pereira-Colavite: Contribution to data collection. Contribution to critical revision, adding intellectual content.

Fabiane Rabelo da Costa Batista: Contribution to manuscript preparation. Contribution to critical revision, adding intellectual content.

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 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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Plant galls recorded from Guanacaste Conservation Area-Costa Rica as an integrated concept of a biological database

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Abstract: Galling insects are specialist herbivorous that have the ability of manipulating plant tissue to form complex biological structures called galls. Even though different organisms have the ability to induce galls in plants, insect galls have the highest degree of structural complexity. The main goal of this study was to obtain a preliminary systematic record of plant gall morphotypes from the Guanacaste Conservation Area in Costa Rica and integrate the information into a biological database. Plant gall morphotypes were recorded, characterized and deposited into a specialized herbarium established as a reference for the inventory. Moreover, organisms associated with gall morphotypes were included in the inventory when it was possible to obtain and identify them. Galls were collected in the rainy season over a period of three years. In total, we recorded forty-four families, seventy genera, and eighty-seven host plant species. One hundred thirty-one morphotypes of plant galls were identified in the Guanacaste Conservation Area. The family with the highest number of gall morphotypes was Fabaceae (8.4%). Leaves were the organ with the largest number of galls (71%), followed by stems (17.6%), and apical buds (6.9%). The predominant gall shape was globular (25.2%), followed by discoid (18.3%). Fifty-nine percent of the galls had a glabrous texture, which was most common on leaves, with 77%. One hundred twenty of our field records (91.6%) of plant galls were new morphotypes not only for Costa Rica but also the world. As a consequence of this research and considering the prospect of future increases in new gall records (and associated organisms), we proposed having the biological entities resulting from the inventory placed in a cecidiarium. This repository represents a standardized and comprehensive way to manage the data and biological materials associated with the plant galls. We also suggest a nomenclature for standardizing gall morphotype registries and identifications. This work is the first and most detailed inventory of plant galls carried out thus far in the Guanacaste Conservation Area.
Keywords: *Plant gall, morphotype, tropical dry forest, biological database, cecidiarium.*

Registro de galhas em plantas da Área de Conservação Guanacaste, Costa Rica, como conceito integrado de um banco de dados biológico

Resumo: Os insetos galhadores são herbívoros especializados, que têm a habilidade de manipular os tecidos vegetais, formando uma complexa estrutura biológica. Diferentes organismos têm a capacidade de induzir galhas, porém as de insetos têm maior grau de complexidade estrutural. O principal objetivo desse estudo foi realizar um levantamento sistemático preliminar das galhas de insetos na Área de Conservação Guanacaste, na Costa Rica, e inserir as informações em uma base de dados biológicos. Os morfotipos de galhas foram registrados, caraterizados e depositados em um herbário estabelecido como base de referência deste inventário. Além disso, quando foi possível obter e identificar os organismos associados a cada morfotipo de galha, eles foram incluídos no inventário. As amostras de galhas foram coletadas na estação chuvosa, durante três anos. No total, foram registradas 44 famílias, 70 gêneros e 87 espécies de plantas hospedeiras. Cento e trinta e um morfotipos de galhas foram identificados na Área de Conservação de Guanacaste. A família com o maior número de morfotipos de galhas foi Fabaceae (8.4%). Os órgãos vegetais com o maior número de galhas foram as folhas (71,0%), seguidas dos caules (17,6%), e das gemas apicais com 6,9%. A forma predominante das galhas foi globoide (25,2%), seguida da lenticular (18,3%) e 59% das galhas apresentaram textura glabra, observada mais frequentemente folhas (77%). Cento e vinte morfotipos de galhas (91.6%) representaram novos registros não só na Costa Rica como também no mundo. Como consequência desta pesquisa e considerando as perspectivas de aumentos futuros de novos registros de galhas (e organismos associados), nós propomos que as entidades biológicas resultantes deste inventário sejam depositadas em um cecidiário. Este repositório representa uma maneira padronizada e abrangente de gerenciar e integrar os dados e os materiais biológicos associados às galhas das plantas. Também sugerimos uma terminologia para padronizar os registros e identificações dos morfotipos de galhas. Este inventário de galhas em plantas é o primeiro e o mais detalhado já realizado na Área de Conservação Guanacaste.

Palavras-chave: *morfotipo, floresta seca tropical, banco de dados biológicos, cecidiarium.*

Introduction

Plant galls are atypical plant tissue structures induced by the action and activity of a foreign organism. Although several organisms have the ability to induce galls in plants, the most diverse and complex galls are formed by insects (Shorthouse & Rohfritsch 1992). Gall-inducing insects are highly specialized sedentary herbivores, which feed specifically on certain specialized cells that are found within the plant structure whose formation they have induced (Shorthouse & Rohfritsch 1992, Tooker et al. 2008, Raman 2011).

Gall-inducing insects generally have specific host plants (Cuevas-Reyes et al. 2014). Gall biology is closely associated with the respective inducing insect, in such a way that galls induced by a particular insect species are basically always the same shape and can differ distinctly from others induced by related species. On the other hand, there are some gall morphotypes induced by different species of insects that present similar shapes (Raman 2011). Distinctive characteristics of each type of gall are probably due to slight variations in the way that each insect species stimulates the development of the gall in the corresponding plant tissue (Shorthouse & Rohfritsch 1992). Li et al. (2017) suggested that gall development is influenced by the gall-inducing insects as well as by the tissue developmental stage and plant genotypes.

The use of gall morphotypes is a commonly used and reliable parameter because evidence indicates that each gall is unique to a particular gall-inducing insect (Stone and Schönrogge 2003), and each galling species is specific to a particular host plant (Abrahamson et al. 1998). According to Isaias et al. (2013), a gall morphotype could be defined as a characteristic phenotypic variation in a neo-formed plant organ, which is produced by the species-specific interaction between the inducing organism and a specific host plant. Due to the fact that each gall inducer is able to alter the morphogenesis in a predetermined organ (Rohfritsch 1992), and because specificity of galler taxa is strongly linked to an appropriate oviposition site in the host plant (Eigenbrode & Jetter 2002), gall morphotype is widely used as a way to refer to types of plant galls. The vast majority of gall-inducing arthropods are restricted to a single host plant species, thus corroborating the idea that the gall morphotype can be used as reliable substitute of gall-inducing species. In addition, gall polymorphism, which could lead to failures in the identification of galls, appears to be a rather rare phenomenon (Carneiro et al. 2009).

Thousands of gall-inducing insects have been identified around the world, for the most part belonging to the orders Thysanoptera, Hemiptera, Lepidoptera, Coleoptera, Diptera, and Hymenoptera (Rohfritsch & Shorthouse 1982, Leitch 1994, Williams 1994, Hanson & Gómez-Laurito 2005, Espírito-Santo & Fernandes 2007, Ansaloni et al. 2018). Gall-inducing insects induce the formation of galls in leaves, buds, flowers, stems, roots and other organs of the plant, depending on the gall-inducing species. A growing number of studies on the diversity and abundance of plant gall morphotypes, and their respective inducing insects, allowed us to build upon the existing information. With a certain regularity reports are made of records and descriptions of new species of gall-inducing insects (Ronquist & Liljeblad 2001, Dalbem & Mendonça 2006, Güçlü et al. 2008, Coelho et al. 2009, Maia & Oliveira 2010, Maia et al. 2010a, Maia et al. 2010b, Medianero et al. 2010, Sano et al. 2011, Santos et al. 2011a, Maia 2014, De Araújo 2017, Bergamini et al. 2017, Coelho et al., 2017, Martins et al. 2018, Ley-López et al. 2019).

Inventories of biological specimens are an important tool to know and preserve biological diversity. To date, for tropical regions, detailed inventories on the occurrence and diversity of gall morphotypes are scarce and incomplete. In the Neotropical Region, the majority of plant gall morphotype records are from Brazil (Urso-Guimarães & Scarelli-Santos 2006, Saito & Urso-Guimarães 2012, Isaias et al. 2013, Carvalho-Fernandes et al. 2016, Urso-Guimarães et al. 2017, Araújo 2017, Liu et al. 2018, Flor et al. 2018, Ascendino & Maia 2018, Vieira et al. 2018, Silva et al. 2018, Araújo et al. 2019, Ribeiro et al. 2019, among others) and some of them were conducted in different types of tropical dry forests or semi-arid ecosystems (Coelho et al. 2009, Santos et al. 2011b, Maia & Souza 2013, Costa & Araújo 2019). Likewise, other reports have been done for the Mexican dry forest (Cuevas-Reyes et al. 2004, Cuevas-Reyes et al. 2014). For the Costa Rican flora there are no systematic and detailed records of plant galls for specific regions or ecosystems. Studies are restricted to sporadic or general reports (Gómez & Kisimova-Horovitz 1997, Hanson & Gómez-Laurito 2005, Retana-Salazar & Nishida 2007, Retana-Salazar & Sánchez-Chacón 2009, Hanson et al. 2014). Hanson et al. (2014) reported 1,100 morphospecies of gall-inducers, distributed in six orders of insects, from Costa Rica. Nevertheless, this survey was restricted to the identification of the insect gall inducers and their associated parasitoids, using plant gall morphotypes as indirect indicators of insect morphospecies, and therefore lacking detailed descriptions of the gall morphotypes found, usually without associated images. The work carried out by Ley-López et al. (2019) in the area of Sarapiquí, in northern Costa Rica provides primarily a checklist of the native vascular plants found to harbor galls.

The Guanacaste Conservation Area (Área de Conservación Guanacaste, ACG for its acronym in Spanish) is located in the northwest region of Costa Rica, in the life zone categorized as tropical dry forest (Holdridge & Tosi 1967). ACG is a conglomeration of several national parks and other natural areas (sectors), among which are Santa Rosa National Park, Guanacaste National Park, Rincón de la Vieja National Park, Murciélago Sector, among others (SINAC 2014). ACG protects the most emblematic tropical dry forest in Central America (Quirós-Arias 2017). This Costa Rican national park was created to favor the restoration process of old pasture areas into the primary and secondary forest through natural succession. Since 1999 it it has been proclaimed a World Heritage Site by UNESCO (Quirós-Arias 2017).

The present work is a first attempt to establish a detailed record and inventory of plant gall morphotypes and their associated organisms in the Guanacaste Conservation Area utilizing an integrated approach consisting of a biological database with a specialized herbarium (cecidiarium).

Materials and Methods

1. *Study area*

Fieldwork and sample collection were carried out predominantly in the Pacific area of Guanacaste Conservation Area (Área de Conservación Guanacaste, ACG), Guanacaste province, Costa Rica, located in the northwest region of the country (10.839366, -85.618176, administrative area) (Figure 1A). Plants and gall morphotypes were collected in different ecosystems in ACG. The Guanacaste Conservation Area is characterized by having a long dry season, generally from late November to mid-May, with a rainy season from mid-May to November (Borchert 1994, Lobo-Segura 2019). The sampled sites are located in the tropical dry forest ecosystem, as well as areas in the premontane wet transition, according to the Holdridge & Tosi (1967) classification. In the last decades, ACG has been affected by long periods of drought, being one of the areas most affected by the *El Niño* phenomenon and climate change projections (Quirós-Arias 2017).

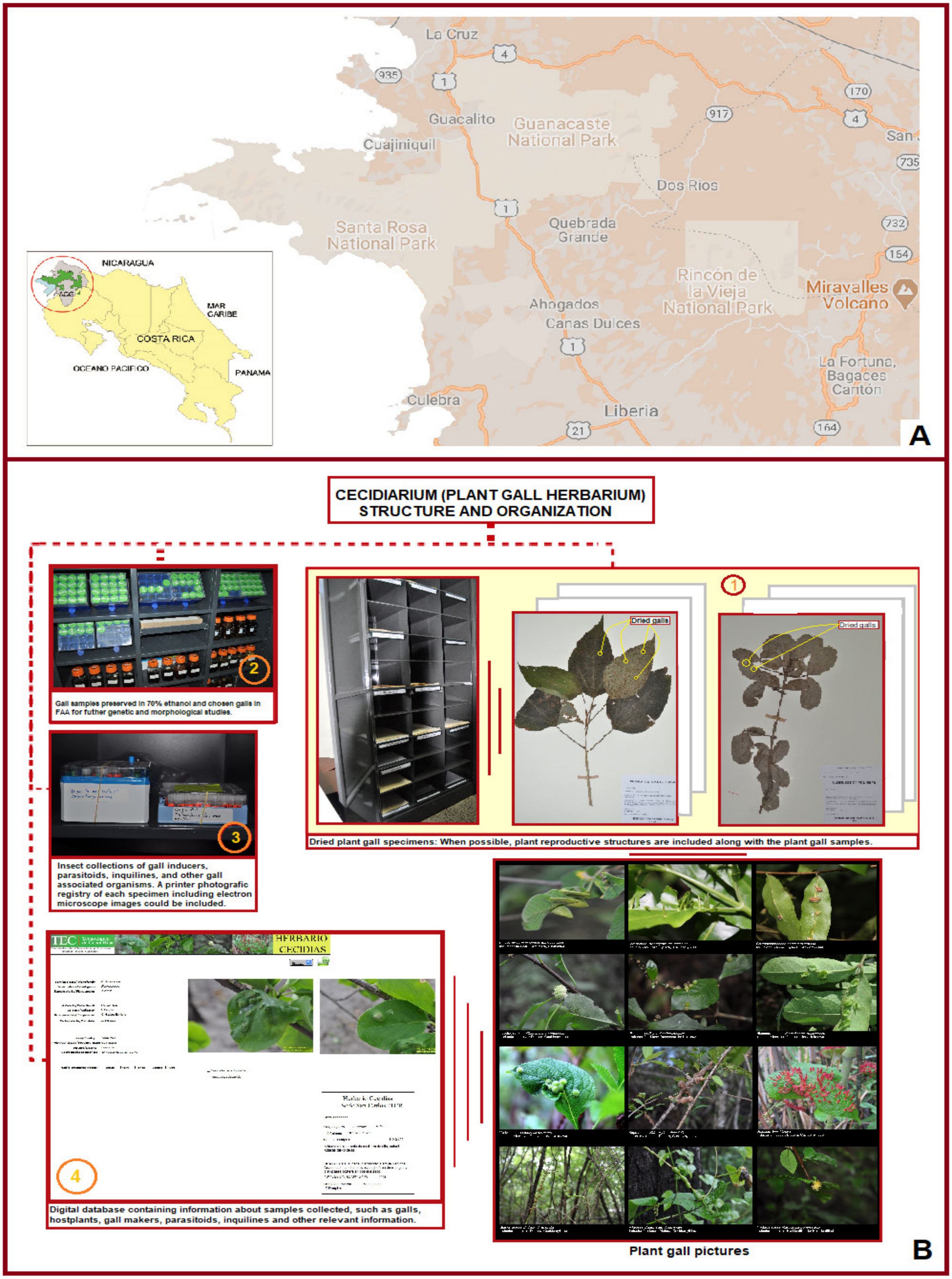
The Guanacaste Conservation Area includes 296,526 acres on land and 106,255 acres of marine habitats. Approximately 65% of all Costa Rican species are present in this area, representing 2.6% of the world's biodiversity (SINAC 2014).

2. *Field and laboratory work for gall morphotypes inventory and sampling associated insects*

Galls were sampled by randomly walking the trails and examining the vegetation along the pathways by two people searching simultaneously on both sides of the road. All plants and their aerial organs were observed to a maximum height of approximately 3 meters. Each gall and host plants found were collected and then packed in plastic bags for further processing. The photographic record of each gall morphotype, when possible, was made directly in the field. Randomized trials that were perpendicular to existing trails were used occasionally for sampling galls, with distances varying from 50 to 400 meters, but without a pre-established experimental design.

Plant galls were collected and processed from May 2010 to December 2012 in different types of vegetation that comprised the ACG biome. Field sampling was carried out every 3 or 4 months per collection season, for a period of three days each, covering approximately 6-8 hours of field work per day. Sampling was conducted especially during the rainy season, when there is a greater probability of finding leaves on the plants, due to the marked dry season and a predominantly deciduous forest. Gall samples were collected mainly at lower-medium altitudes of 0 to 1100 m above sea level (m.a.s.l.): Santa Rosa Sector (La Casona area), Murciélago Sector, Santa Elena Sector, Pocosol Sector (Góngora Area, road to Cacao Volcano), and Rincón de la Vieja National Park. Moreover, gall samples and their corresponding host plants were collected mostly from deciduous plant species typical of non-riparian environments as well as near sites with original-natural forest with evergreen species. More typical riparian sites or similar environments followed comparable field zonification criteria of Frankie et al. (1974) and Borchert (1994). Two *Bosque Viejo* (Old Forest) patches were sampled: close to La Casona (near the administrative area of Santa Rosa National Park) and from the route to Playa Naranjo Sector. The *Bosque Viejo* patches are considered remnants of the original forest with little human disturbance and is characterized by an abundance of evergreen plant species.

Specimens of each plant harboring galls were prepared for reference as herbarium vouchers to be identified later. Plant gall specimens with floral or fruit parts for host identification were dried when possible, otherwise the insects obtained, and relevant gall samples were preserved in 70% ethanol. Since gall traits changed in dried samples, especially their morphology and color, a printed photographic registry of each specimen is included in the inventory. All samples were deposited at the cecidiarium (specialized herbarium) established at the facilities of Technological Institute of Costa Rica (Instituto Tecnológico de Costa Rica, Campus Tecnológico Local San Carlos, Escuela de Ciencias Naturales y Exactas). Also, some selected gall samples were preserved in FAA (formalin, acetic acid, alcohol) for later morphological studies. Collected galls were classified according to place of origin, family, genus, and species of the host plant, and according to the basic morphological type. Sampling site description was registered for all samples, but when there were more than two accessions of plant materials in the inventory, only one description of the sampling site for each morphotype was included here. Collected samples were geo-referenced by Global Positioning System (GPS). Each gall morphotype location was geo-referenced using the Decimal Degrees (DD) format. A map to show the reference morphotypes collected per site at ACG was made with QGIS version 3.10.5 (QGIS.org 2020) Development Team and using the following layers from Atlas Digital CR 2008-2014: Conservation Areas (AConservacionSINAC2014; SINAC 1998), Wild Protected Areas (Areassilvestresprotegidas2014crtm05; SINAC 1999), elevation level (Relieve 2008crtm05; CATIE N.D.), Rivers (Rios150000crtm05; Soto-Montoya 2007), and land cover (Cober2005crtm05; Earth Observation System Laboratory et al. 2006). To facilitate visualization of geographical location, some neighboring galls collected from nearby areas (i.e., spaced between 5 m to 400 m linear meters) were considered as a cluster, depending on the geographic characteristics of the site; for these clusters the same geographic position was assigned.



Gall samples preserved in 70% ethanol and chosen galls in FAA for futher genetic and morphological studies.

Insect collections of gall inducers, parasitoids, inquilines, and other gall associated organisms. A printer photografic registry of each specimen including electron microscope images could be included.

Dried plant gall specimens: When possible, plant reproductive structures are included along with the plant gall samples.

Digital database containing information about samples collected, such as galls, hostplants, gall makers, parasitoids, inquilines and other relevant information.

Figure 1. 1A) Guanacaste Conservation Area (Área de Conservación Guanacaste, ACG) map showing the Santa Rosa National Park, Guanacaste National Park, and Rincón de la Vieja National Park sectors. Taken and modified from Área de Conservación Guanacaste- SINAC (https://www.acguanacaste.ac.cr/index.php), and Google Earth®. 1B) Plant Gall Herbarium (cecidiarium) organization. 1) Dried plant gall specimens, 2) Plant gall samples preserved in 70% ethanol and FAA, 3) Insect collection of gall inducers, parasitoids, and inquilines preserved in 70% ethanol vials, 4) Digital database containing information about gall morphotypes, host plants, gall makers, associated organisms, sampling sites, etc.

In addition to the list of host plants harboring galls, the morphological characterization of all gall morphotypes found is provided. Gall morphotypes were used to register plant galls, as well as a reference for the galling insect collection, assuming that each morphotype is unique and each galling species is specific to its host plant (Espírito-Santo & Fernandez 2007, Abrahamson et al. 1998, Carneiro et al. 2009). The morphological characteristics used in gall differentiation were basic gall form, external color and epidermial structure. Morphotype shape was established according to the most usual morphological classifications found in the literature on this topic (Maia 2001, Urso-Guimarães et al. 2003, Carneiro et al. 2009, Santos et al. 2011a, Saito & Urso-Guimarães 2012, Isaias et al. 2013). Since these classification criteria could be ambiguous, we classified galls based on their basic general shapes considering that gall morphology could be a mixture of different shapes.

Gall morphotypes were named according to the two first letters from the binomial scientific name, followed by the numerical order of appearance in each plant species, and if necessary, the third letter of the specific epithet might also be used. We propose this nomenclature designation to avoid confusion in the registry of gall morphotypes. Moreover, only detailed literature descriptions with photographs were considered for previous records of plant gall morphotypes.

Adult stages of the gall-inducers and their parasitoids were obtained by rearing galls in plastic bags until the adult emerged. Gall inducers, parasitoids, and inquilines were preserved in plastic vials containing 70% ethanol and deposited in the cecidiarium. Roberto Espinoza carried out the taxonomic identification of the host plants, and the inductor insects were identified by Paul Hanson as much as possible.

Data from external gall epidermis lignification and trichome-covered galls from deciduous forest areas and evergreen tree areas such as *Bosque Viejo* were statistically analyzed by a Chi-square test.

3. *Gall morphotype inventory and collection of associated organisms in a specialized herbarium as an integrated biological database*

Inventories of biological specimens are a valuable tool to know and preserve biological diversity; for plant specimens, for instance, a traditional herbarium is an appropriate way to carry out this task. A specialized herbarium of plant galls was created to become a reference collection for Costa Rican plant galls. This herbarium began operating in 2012 and currently has around 400 sample accessions. The collection started with plant galls from the Guanacaste Conservation Area. To date, the herbarium is made up of four basic units: the plant gall collection of dried specimens, selected gall samples preserved in 70% ethanol (some of them stored at -70ºC), associated insects preserved in 70% ethanol, and a digital database with all the collected information (Figure 1B). Due to the fact that gall traits change in dried samples, a printed photographic registry of each specimen is included in the collection, and for further morphological studies, a collection of selected galls in FAA (formalin-acetic acid-alcohol) is expected to be included in the future. A database with plant gall data and photographs, as well as information related to their associated organisms, is expected to be available using FileMaker-Pro software or another similar program. This specialized herbarium functions according to appropriated technical standard and collections are maintained in a controlled environment at 20 C° with relative humidity between 40-60%.

Results

A total of eighty-seven species, in seventy genera and forty-four families, of plants that host galls were recorded in the Guanacaste Conservation Area (Table 1). We found one hundred thirty-one morphologically distinct types of plant galls in ACG. The plant families with the highest number of gall morphotypes were Fabaceae (8.4%), Rubiaceae (7.6%), Malvaceae (6.1%), Sapindaceae (5.3%), Boraginaceae (4.6%), and Nyctaginaceae with 4.6% (Table 2). Sixty plant species harbored one gall morphotype, fifteen had two associated morphotypes, six plant species harbored three gall morphotypes, two species contained four gall morphotypes and three species harbored five morphotypes. The species with the greatest number of galls were *Acalypha diversifolia* (Euphorbiaceae) and *Psychotria horizontalis* (Rubiaceae) with four gall morphotypes, as well as *Pisonia macranthocarpa* (Nyctaginaceae), *Sideroxylon obtusifolium* (Sapotaceae), and *Stegnosperma cubense* (Stegnospermataceae) with five morphotypes each.

Some gall samples were so rare that there were not enough to obtain insects, but in many cases, although we had enough plant material, it was not possible to obtain adult insects for identification purposes. Gall-inducer identification to family level was possible in many cases based on the larval stages encountered during the dissections of some selected galls when enough material was available. Nevertheless, even when adult stages were obtained, identification of most insects beyond the family level was complicated by the lack of appropriate taxonomic references, a limitation described by Hanson et al. (2014). Therefore, most of the collected insects remain as unidentified species. The inducing insects that were identified belong to the family Cecidomyiidae (Diptera). Some parasitoids/inquilines (all belonging to the order Hymenoptera) were identified to the family, subfamily or genus level.

Plant gall morphotype description, name and characteristics are presented below under host plant families, genera and species in alphabetical order. They included gall morphology classification, color, epidermial structure, organs attacked, associated organisms as well as host plant description, location and geographical coordinates.

Acanthaceae

Aphelandra scabra (Vahl) Sm. Morphotype Ap_sc_1 (Figure 2A). Gall description: Irregular shape, white, induced on bud, hairy epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 2 m tall, on top of rock by the river. Location: Guanacaste, Liberia, Curubandé. Guanacaste National Park, Las Pailas Area, gallery forest with remnant trees. Coordinates/Altitude: 10,7749444 N 85,35025 W, 955 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Avicennia germinans L. Morphotype Av_ge_1 (Figure 2B). Gall description: Discoid shape, green or yelowish-brown, induced on leaves and veins, glabrous epidermis, protruding on both surfaces of the leaf. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 3 m tall, barren. Location: Guanacaste, Liberia, Nacascolo. Guanacaste National Park, Naranjo Beach Area, mangrove and beach area, coastal area in dry-forest. Coordinates/Altitude: 10,78335 N 85,6644861 W, 14 m. Registry comments: Gall morphotype resembles the one described by Oliveira dos Santos et al. (2013).

Table 1. Number of gall morphotypes per plant family in ACG (Guanacaste, Costa Rica).

PLANT FAMILY	NUMBER OF GALL MORPHOTYPES	PLANT FAMILY	NUMBER OF GALL MORPHOTYPES
Acanthaceae	2	Nyctaginaceae	6
Anacardiaceae	2	Ochnaceae	1
Annonaceae	2	Olacaceae	2
Apocynaceae	1	Phytolaccaceae	1
Asteraceae	3	Picraminiaceae	2
Bignoniaceae	4	Piperaceae	3
Boraginaceae	6	Poaceae	1
Burseraceae	1	Polygonaceae	2
Chrysobalanaceae	1	Primulaceae	3
Erythoroxylaceae	2	Rubiaceae	10
Euphorbiaceae	4	Rutaceae	1
Fabaceae	11	Sabiaceae	1
Fagaceae	2	Salicaceae	2
Hippocrateaceae	3	Sapindaceae	7
Krameriaceae	1	Sapotaceae	5
Lauraceae	3	Simaroubaceae	1
Malpighiaceae	3	Smilacaceae	1
Malvaceae	8	Solanaceae	1
Melastomataceae	1	Stegnospermataceae	5
Meliaceae	1	Urticaceae	1
Moraceae	5	Verbenaceae	3
Myrtaceae	3	Vitaceae	3
	Total		131

Table 2. Number of gall morphotypes on each plant organ in ACG (Guanacaste, Costa Rica).

PLANT ORGAN	N° GALL MORPHOTYPES	%
Bud	9	6.87
Fruit	1	0.76
Inflorescence	1	0.76
Leaf midvein	5	3.82
Leaf midvein and petiole	1	0.76
Leaf veins	4	3.05
Leaves	80	61.07
Leaves and buds	2	1.53
Leaves and petiole	1	0.76
Petiole	4	3.05
Stem	23	17.56
Total	**131**	**100**

Anacardiaceae

Astronium graveolens Jacq. Morphotype As_gr_1 (Figure 2C). Gall description: Globular shape, yellowish green to brown at maturity, induced on leaves, lignified epidermis. Glabrous, on the adaxial surface of the leaves. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Sapling, nearly 5 m tall, barren. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, Bosque Viejo Area between the entrance of the park and *La Casona*. Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m. Registry comments: Gall recorded by Hanson & Nishida (2014).

Spondias mombin L. Morphotype Sp_mo_1 (Figure 2D). Gall description: Globular shape, green galls, brown at maturity, located on the adaxial surface of the leaf. Glabrous and lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Tree, nearly 4 m tall. Location: Guanacaste, La Cruz. Cañas Castilla Country Estate, along the Sonzapote riverside, area of farms and gallery forests. Coordinates/Altitude: 11,11379167 N 85,57459722 W, 200 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although two galls induced on this plant species by Cecidomyiidae were reported, without a reference image, by Medianero et al. (2010).

Annonaceae

Guatteria diospyroides Baill. Morphotype Gu_di_1 (Figure 2E). Gall description: Fusiform shape, brown, induced on stem, lignified epidermis. On the steam nearly the leaf. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 1.5 m tall, barren. Alternate leaves, elongated (linear in shape), Woody

Figure 2. Plant Gall morphotypes recorded in Área de Conservación Guanacaste (ACG), Guanacaste, Costa Rica. 2A) Gall induced in *Aphelandra scabra* (Vahl) Sm., morphotype Ap_sc_1, 2B) Gall induced in *Avicennia germinans* L., morphotype Av_ge_1, 2C) Gall induced in *Astronium graveolens* Jacq., morphotype As_gr_1, 2D) Gall induced in *Spondias mombin* L., morphotype Sp_mo_1, 2E) Gall induced in *Guatteria diospyroides* Baill., morphotype Gu_di_1, 2F) Gall induced in *Sapranthus palanga* R.E.Fr., morphotype Sa_pa_1, 2G) Gall induced in Sapranthus palanga R.E.Fr., morphotype Sa_pa_1, 2H) Gall induced in *Koanophyllon albicaule* (Sch. Bip. ex Klatt) R.M. King & H. Rob., morphotype Ko_al_1, 2I) Gall induced in *Porophyllum punctatum* (Mill.) S.F. Blake, morphotype Po_pu_1, 2J) Gall induced in *Wedelia* sp. Jacq., morphotype We_sp_1, 2K) Gall induced in *Arrabidaea patellifera* (Schltdl.) Sandwith, morphotype Ar_pa_1, 2L) Gall induced in *Cydista diversifolia* (Kunth) Miers, morphotype Cy_di_1, 2M) Gall induced in *Cydista diversifolia* (Kunth) Miers, morphotype Cy_di_2, 2N) Gall induced in *Pleonotoma variabilis* (Jacq.) Miers, morphotype Pl_va_1, 2O) Gall induced in Cordia alliodora (Ruiz & Pav.) Oken., morphotype Co_al_1, 2P) Gall induced in *Cordia alliodora* (Ruiz & Pav.) Oken., morphotype Co_al_2.

stemleaves, and hardened, lustrous dark green in color. Location: Guanacaste, Liberia, Curubandé. Rincón de la Vieja National Park, road to active crater, Los Gemelos Area, rainforest zone. Coordinates/ Altitude: 10,80032 N 85,35 W, 1000 m; 10,93202778 N 85,46 W, 1421 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Sapranthus palanga R.E.Fr. Morphotype Sa_pa_1 (Figure 2F). Gall description: Spherical shape, green and yellow, induced on leaves, hairy epidermis. Yellowish green galls on the leaf underside, with trichomes, brown at maturity. Gall inducer: unknown. Parasitoids/ Inquilines: unknown. Plant description: Small tree, 4 m tall, barren. Location: Guanacaste, Liberia, Nacascolo. Lookout point between the main entrance of Santa Rosa National Park and *La Casona*, old secondary forest area. Coordinates/Altitude: 10,85648 N 85,6106 W, 623 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Apocynaceae

Forsteronia spicata (Jacq.) G. Mey. Morphotype Fo_sp_1 (Figure 2G). Gall description: Irregular shape, green to yellowish at maturity, induced on leaves, glabrous epidermis, protruding on the surface of the leaves. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Semi-scandent shrub, nearly 5 m tall, barren. Woody stem. Opposite leaves, orbicular to ovate in shape. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, Santa Rosa area, between the Inter-American highway and *La Casona*, secondary oak forest area. Coordinates/Altitude: 10,86577222 N 85,60990278 W, 290 m; 10,83581 N 85,62347 W, 306 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Asteraceae

Koanophyllon albicaule (Sch. Bip. ex Klatt) R.M. King & H. Rob. Morphotype Ko_al_1 (Figure 2H). Gall description: Conical shape, green, induced on leaves, glabrous epidermis. Wider at the middle, green, and protruding from the midvein. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 3 m tall, barren, acuminated leaves. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, Bosque Viejo Area between the entrance of the park and *La Casona.* Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Porophyllum punctatum (Mill.) S.F. Blake. Morphotype Po_pu_1 (Figure 2I). Gall description: Globulous shape, green, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 50 cm tall, white flowers. Opposite simple leaves, 1-1.5cm in length. Location: Guanacaste, La Cruz, Santa Elena. Santa Rosa National Park, Nancite Beach Area, open area over a serpentinite rock. Coordinates/Altitude: 10,80485833 N 85,69909167 W, 10 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Wedelia sp. Jacq. Morphotype We_sp_1 (Figure 2J). Gall description: Discoid shape, greenish or yellow, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Herbaceous plant, nearly 0.75 m tall, pistillate yellow flowers, leaves with serrate margin. Location: Guanacaste, La Cruz. Guanacaste National Park, on the way to the Maritza Biological Station, secondary growth open area, near high-voltage towers. Coordinates/Altitude: 10,95072222 N 85,59705556 W, 272 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Bignoniaceae

Arrabidaea patellifera (Schltdl.) Sandwith. Morphotype Ar_pa_1 (Figure 2K). Gall description: Conical shape, elongated galls, green, induced on leaves, pubescent epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Vine, barren. Bifoliate leaves with cuspidate apex. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, Bosque Viejo Area between the entrance of the park and *La Casona.* Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m; 10,83581 N 85,62347 W, 306 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world. However, one gall induced by Cecidomyiidae on this plant species was reported, without a reference image, by Medianero et al. 2010.

Cydista diversifolia (Kunth) Miers. Morphotype Cy_di_1 (Figure 2L). Gall description: Fusiform shape, green or yellow, green to brown color at maturity. Induced on stem, lignified and glabrous epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Understory vine. Leaves with acute apex, bifoliate. Location: Guanacaste, Liberia, Mayorga. Santa Rosa National Park, Bosque Viejo Area between the main entrance of the park and *La Casona*. Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m; 10,85648 N 85,6106 W, 323 m; 10,95072222 N 85,59705556 W, 272 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall induced by Cecidomyiidae on this plant species was reported, without a reference image, by Medianero et al. (2010).

Cydista diversifolia (Kunth) Miers. Morphotype Cy_di_2 (Figure 2M). Gall description: Discoid shape, yellow and red, yellowish spots, brown center, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Understory vine. Leaves with acute apex, bifoliate. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, start of the road to Naranjo Beach, old secondary growth area with clearings. Coordinates/Altitude: 10,83581 N 85,62347 W, 306 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall induced by Cecidomyiidae on this plant species was reported, without a reference image, by Medianero et al. (2010).

Pleonotoma variabilis (Jacq.) Miers. Morphotype Pl_va_1 (Figure 2N). Gall description: Globular shape, yellowish, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub of 2 m tall. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park between the Inter-American highway and *La Casona*, secondary oak forest area. Coordinates/Altitude: 10,86577222 N 85,60990278 W, 290 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Boraginaceae

Cordia alliodora (Ruiz & Pav.) Oken. Morphotype Co_al_1 (Figure 2O). Gall description: Spherical shape, green, induced on leaves, hairy epidermis. Tomentose, on the surface of the leaf, brownish. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: *Cecidellis* (Pteromalidae); Entedoninae (Eulophidae). Plant description: Shrub, nearly 0,30m-2.5 m tall, barren. Alternate, simple leaves, lanceolate and pubescent. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, start of the road to Naranjo Beach, old secondary growth area with clearings. Coordinates/Altitude: 10,83581 N 85,62347 W, 306 m; 10,89222222 N 85,47077778 W, 701 m; 10,92638889 N 85,7292 W, 45 m; 10,83422222 N 85,6115 W, 324 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall induced by Cecidomyiidae on this plant species has been reported, without a reference image, by Medianero et al. (2010), Cuevas et al. (2014), and Ley-López et al. (2019).

Cordia alliodora (Ruiz & Pav.) Oken. Morphotype Co_al_2 (Figure 2P). Gall description: Spherical shape, green and brown, induced on bud, hairy epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: *Cecidellis* (Pteromalidae); Entedoninae (Eulophidae). Plant description: Shrub, nearly 0,30m -2.5 m tall, barren. Alternate, simple leaves, lanceolate and pubescent. Location: Guanacaste, Liberia, Nacascolo. Guanacaste Conservation Area, Santa Rosa National Park, monument to the heroes of 1856. Coordinates/Altitude: 10,83422222 N 85,6115 W, 324 m. Registry comments: Gall morphotype resembles the one described by Medianero et al. (2010).

Cordia collococca L. Morphotype Co_co_1 (Figure 3A). Gall description: Irregular shape, yellow or white, induced on bud, glabrous epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Tree, nearly 15 m tall, discoid green fruits. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Góngora, roadside to the Cacao Volcano. Coordinates/Altitude: 10,88683333 N 85,47311111 W, 597 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Cordia collococca L. Morphotype Co_co_2 (Figure 3B). Gall description: Discoid shape, green (brown at maturity), induced on leaves, glabrous epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Tree, nearly 15 m tall, discoid green fruits. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, Cacao Biological Station. Coordinates/Altitude: 10,92658333 N 85,47 W, 1129 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Cordia collococca L. Morphotype Co_co_3 (Figure 3C). Gall description: Globular shape, green, induced on petiole, glabrous epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Tree, nearly 15 m tall, discoid green fruits. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, Cacao Biological Station. Coordinates/Altitude: 10,92658333 N 85,47 W, 1129 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Cordia sp. L. Morphotype Co_sp_1 (Figure 3D). Gall description: Conical shape, green, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Tree, nearly 15 m tall, discoid green fruits. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Góngora, roadside to the Cacao Volcano. Coordinates/Altitude: 10,88683333 N 85,47311111 W, 597 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Burseraceae

Bursera graveolens (Kunth) Triana & Planch. Morphotype Bu_gr_1 (Figure 3E). Gall description: Cylindrical shape, greenish or yellow-brown, yellow apex, brownish black at senescence, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 1 m tall, procumbent branches, and barren. Location: Guanacaste, La Cruz, Santa Elena. Guanacaste Conservation Area, Murciélago Sector, El Hachal Bay, rocky beach and dry-forest area. Coordinates/Altitude: 10,93408333 N 85,73 W, 15 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Chrysobalanaceae

Hirtella racemosa Lam. Morphotype Hi_ra_1 (Figure 3F). Gall description: Cylindrical shape, yellow and red, induced on leaves, soft spines covered with hairs epidermis. With white appendages, reddish pilosity, on the upper or lower surface of the leaf. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, 2,5-3 m tall, by the side of the road. Alternate leaves, with cuspidate apex and entire margin, pilose stipules. Location: Guanacaste, Liberia, Nacascolo. Entrance to the old forest (*Bosque Viejo*) between the welcome booth and *La Casona* at Santa Rosa National Park. Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m; 10,85245 N 85,600727 W, 335 m; 10,85072 N 85,60796 W, 321 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Erythoroxylaceae

Erythroxylum macrophyllum Cav. Morphotype Er_ma_1 (Figure 3G). Gall description: Spherical shape, beige, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 2m tall, barren. Leaves with acute apex and entire margin. Location: Guanacaste, Liberia, Curubandé. Guanacaste National Park, Las Pailas Area, in the old secondary forest after the pasture, on the way to the crater. Coordinates/Altitude: 10,78427778 N 85,3484167 W, 955 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall on this plant species was reported, without a reference image, by Ley-López et al. (2019).

Erythroxylum macrophyllum Cav. Morphotype Er_ma_2 (Figure 3H). Gall description: Spherical shape, white-yellow, induced on the upper and lower surface of leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 2m tall, barren. Leaves with acute apex and entire margin. Location: Guanacaste, Liberia, Curubandé. Guanacaste National Park, Las Pailas Area, in the old secondary forest after the pasture, on the way to the crater. Coordinates/Altitude: 10,78427778 N 85,3484167 W, 955 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Euphorbiaceae

Acalypha diversifolia Jacq. Morphotype Ac_di_1 (Figure 3I). Gall description: Irregular shape, greenish and yellow, induced on leaves, more or less terminal on branch, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 1.70-2,5 m tall, barren, with scandent branches, in understory, barren. Leaves with cuspitade apex and crenate margin. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation

Figure 3. Plant Gall morphotypes recorded in Área de Conservación Guanacaste (ACG), Guanacaste, Costa Rica. 3A) Gall induced in *Cordia collococca* L., morphotype Co_co_1, 3B) Gall induced in *Cordia collococca* L., morphotype Co_co_2, 3C) Gall induced in *Cordia collococca* L., morphotype Co_co_3, 3D) Gall induced in *Cordia* sp. L., morphotype Co_sp_1, 3E) Gall induced in *Bursera graveolens* (Kunth) Triana & Planch., morphotype Bu_gr_1, 3F) Gall induced in *Hirtella racemosa* Lam., morphotype Hi_ra_1, 3G) Gall induced in *Erythroxylum macrophyllum* Cav., morphotype Er_ma_1, 3H) Gall induced in E*rythroxylum macrophyllum* Cav., morphotype Er_ma_2, 3I) Gall induced in *Acalypha diversifolia* Jacq., morphotype Ac_di_1, 3J) Gall induced in *Acalypha diversifolia* Jacq., morphotype Ac_di_2, 3K) Gall induced in *Acalypha diversifolia* Jacq., morphotype Ac_di_3, 3L) Gall induced in Acalypha diversifolia Jacq., morphotype Ac_di_4, 3M) Gall induced in *Haematoxylum brasiletto* H. Karst., morphotype Ha_br_1, 3N) Gall induced in *Inga* punctata Willd., morphotype In_pu_1, 3O) Gall induced in *Inga* sp. Mill., morphotype In_sp_1, 3P) Gall induced in Inga sp. Kunth, morphotype In_sp_2.

Area, Góngora, roadside to the Cacao Volcano. Coordinates/Altitude: 10,88683333 N 85,47311111 W, 597 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, alhtough a gall on this plant species was reported, without a reference image, by Ley-López et al. (2019).

Acalypha diversifolia Jacq. Morphotype Ac_di_2 (Figure 3J). Gall description: Globular shape, yellow and red, induced on bud, glabrous epidermis. Red-yellowish inflorescense galls. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 1.70-2,5 m tall, barren, with scandent branches, in understory, barren. Leaves with cuspitade apex and crenate margin. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Góngora, roadside to the Cacao Volcano. Coordinates/Altitude: 10,88683333 N 85,47311111 W, 597 m; 10,89222222 N 85,47077778 W, 701 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall on this plant species was reported, without a reference image, by Nieves-Aldrey et al. (2008).

Acalypha diversifolia Jacq. Morphotype Ac_di_3 (Figure 3K). Gall description: Spherical shape, greenish and yellow, induced on leaves, hairy epidermis. Galls with spiny projections, green to brownish at senescence, Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 1.70-2,5 m tall, barren, with scandent branches, in understory, barren. Leaves with cuspitade apex and crenate margin. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Góngora, road to the Cacao Volcano, secondary rainforest area, next to the road. Coordinates/Altitude: 10,89222222 N 85,47077778 W, 701 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Acalypha diversifolia Jacq. Morphotype Ac_di_4 (Figure 3L). Gall description: Globular shape, green, induced on stem, soft spines epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 1.70-2,5 m tall, barren, with scandent branches, in understory, barren. Leaves with cuspitade apex and crenate margin. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Góngora, road to the Cacao Volcano, secondary rainforest area, next to the road. Coordinates/Altitude: 10,89222222 N 85,47077778 W, 701 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Fabaceae

Haematoxylum brasiletto H. Karst. Morphotype Ha_br_1 (Figure 3M). Gall description: Conical shape, red, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: *Torymus* (Torymidae); Pteromalidae. Plant description: Woody sapling, nearly 5 m tall. Location: Guanacaste, La Cruz, Santa Elena. Santa Rosa National Park, Nancite Beach Area, serpentinite rock. Coordinates/Altitude: 10,80485833 N 85,69909167 W, 10 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Inga punctata Willd. Morphotype In_pu_1 (Figure 3N). Gall description: Globular shape, brown, induced on stem, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: Pteromalidae. Plant description: Tree, nearly 10 m tall, barren. Leaves elliptic in shape. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, pasture area next to the forest, start of the trail to the biological station. Coordinates/Altitude: 10,92286111 N 85,46375 W, 1018 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Inga sp. Mill. Morphotype In_sp_1 (Figure 3O). Gall description: Elliptical shape, green and brown, induced on leaf midvein, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 4 m tall, barren. Location: Guanacaste, Liberia, Curubandé. Rincón de la Vieja National Park, road to active crater, Los gemelos Area, forest zone. Coordinates/Altitude: 10,80032 N 85,35 W, 1000 m; 10,78427778 N 85,3484167 W, 955 m. Registry comments: Gall morphotype resembles the one described by Rodriguez et al. (2014).

Inga sp. Kunth. Morphotype In_sp_2 (Figure 3P). Gall description: Spherical shape, brown, induced on the adaxial surface of the leaf, hairy epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 4 m tall, barren. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, pasture area next to the forest and start of the trail to the biological station. Coordinates/Altitude: 10,92286111 N 85,46375 W, 1018 m; 10,78427778 N 85,3484167 W, 955 m. Registry comments: Gall morphotype resembles the one described by Rodriguez et al. (2014).

Lonchocarpus felipei N. Zamora. Morphotype Lo_fe_1 (Figure 4A). Gall description: Cylindrical shape, green and yellowish, induced on leaves, glabrous epidermis. Protruding on the underside, densely covering the entire leaf. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Sapling, nearly 4 m tall, barren. Opposite and ovated in shape, with glabrous underside and pubescent surface. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, entrance to the lookout point of Naranjo Beach, Bosque Viejo Area. Coordinates/Altitude: 10,80586111 N 85,64 W, 250 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Lonchocarpus felipei N. Zamora. Morphotype Lo_fe_2 (Figure 4B). Gall description: Cylindrical shape, green and yellowish, induced on leaves, hairy epidermis. Protruding on the underside, densely covering the entire leaf. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Sapling, nearly 4 m tall, barren. Opposite and ovated in shape, with glabrous underside and pubescent surface. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, Bosque Viejo Area between the park entrance and *La Casona*. Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Lonchocarpus paviflorus Benth. Morphotype Lo_pa_1 (Figure 4C). Gall description: Discoid shape, green and yellowish, induced on leaves, hairy epidermis. Truncated at apex, pilose, on the underside of the leaf. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 2 m tall, barren. Imparipinnate, opposite compound leaves. Location: Guanacaste, Liberia, Nacascolo. Guanacaste National Park, Santa Rosa area, entrance to the lookout point of Naranjo Beach, secondary forest area. Coordinates/Altitude: 10,80586111 N 85,64 W, 250 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Lonchocarpus phaseolifolius Benth. Morphotype Lo_pha_1 (Figure 4D). Gall description: Discoid shape, green, induced on leaves, hairy

Figure 4. Plant Gall morphotypes recorded in Área de Conservación Guanacaste (ACG), Guanacaste, Costa Rica. 4A) Gall induced in *Lonchocarpus felipei* N. Zamora, morphotype Lo_fe_1, 4B) Gall induced in *Lonchocarpus felipei* N. Zamora, morphotype Lo_fe_2, 4C) Gall induced in *Lonchocarpus paviflorus* Benth., morphotype Lo_pa_1, 4D) Gall induced in *Lonchocarpus phaseolifolius* Benth., morphotype Lo_pha_1, 4E) Gall induced in *Lonchocarpus phlebophyllus* Standl & Steyerm., morphotype Lo_phl_1, 4F) Gall induced in *Lonchocarpus sp.* Kunth, morphotype Lo_sp_1, 4G) Gall induced in *Senegalia tenuifolia* (L.) Britton & Rose., morphotype Se_te_1, 4H) Gall induced in *Quercus oleoides* Schltdl. & Cham., morphotype Qu_ol_1, 4I) Gall induced in Quercus oleoides Schltdl. & Cham., morphotype Qu_ol_2, 4J) Gall induced in *Semialarium mexicanum* (Miers) Mennega, morphotype Se_me_1, 4K) Gall induced in *Semialarium mexicanum* (Miers) Mennega, morphotype Se_me_2, 4L) Gall induced in *Semialarium mexicanum* (Miers) Mennega, morphotype Se_me_3, 4M) Gall induced in *Krameria revoluta* O. Berg, morphotype Kr_re_1, 4N) Gall induced in *Belischmiedia costaricensis* (Mez & Pittier) C.K. Allen, morphotype Be_co_1, 4O) Gall induced in Belischmiedia costaricensis (Mez & Pittier) C.K. Allen, morphotype Be_co_2, 4P) Gall induced in *Nectandra salicina* C.K Allen, morphotype Ne_sa_1.

epidermis. Truncated at apex, pilose, on the underside of the leaf. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Tree, nearly 20 m tall, fallen, racemes with green fruits, unripe fruits. Location: Guanacaste, La Cruz, Santa Elena. Guanacaste Conservation Area, Murciélago Sector, old secondary growth, road between El Hachal Bay and Murciélago Station. Coordinates/Altitude: 10,92638889 N 85,7292 W, 45 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Lonchocarpus phlebophyllus Standl & Steyerm. Morphotype Lo_phl_1 (Figure 4E). Gall description: Irregular shape, green, induced on leaves, hairy epidermis. Flat on the underside of the leaf. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Tree, nearly 4 m tall, by the side of the river. Location: Guanacaste, La Cruz, Santa Elena. Guanacaste National Park, in the Murciélago Sector, old secondary forest area. Coordinates/Altitude: 10,89686111 N 85,7301111 W, 126 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Lonchocarpus sp. Kunth. Morphotype Lo_sp_1 (Figure 4F). Gall description: Globular shape, yellow and brown, induced on leaf midvein, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Sapling, nearly 1 m tall, barren. Leaves with cuspidate apex. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, pasture area next to the forest and start of the trail to the biological station. Coordinates/Altitude: 10,92286111 N 85,46375 W, 1018 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall on this plant species was reported, without a reference image, by Cuevas et al. (2014) and de Souza Mendoca et al. (2014).

Senegalia tenuifolia (L.) Britton & Rose. Morphotype Se_te_1 (Figure 4G). Gall description: Irregular shape, brown, induced on apical buds, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Herbaceous plants, nearly 0.4 m tall, barren. Paripinnate, compound leaves. Location: Guanacaste, Liberia, Nacascolo. Guanacaste Conservation Area, Santa Rosa National Park, roadside near the *Bosque Viejo*, next to the park entrance. Coordinates/Altitude: 10,85263889 N 85,607472 W, 310 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Fagaceae

Quercus oleoides Schltdl. & Cham. Morphotype Qu_ol_1 (Figure 4H). Gall description: Irregular shape, green, yellow at maturity, induced on leaaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 5 m tall, by the side of the road. Alternate, simple leaves, with entire margin, underside heavily pubescent. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, between the Inter-American highway and *La Casona*, secondary oak forest area. Coordinates/Altitude: 10,86577222 N 85,60990278 W, 290 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall on this plant species was reported, without a reference image, by Pascual-Alvarado et al. (2017).

Quercus oleoides Schltdl. & Cham. Morphotype Qu_ol_2 (Figure 4I). Gall description: Globular shape, orange and brown, induced on the underside of the leaf, hairy epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 5 m tall, by the side of the road. Alternate, simple leaves, with entire margin, underside heavily pubescent. Location: Guanacaste, Liberia, Nacascolo. Lookout point between the main entrance of the Santa Rosa National Park and *La Casona*, old secondary forest area. Coordinates/Altitude: 10,85648 N 85,6106 W, 623 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall on this plant species was reported, without a reference image, by Pascual-Alvarado et al. (2017).

Hippocrateaceae

Semialarium mexicanum (Miers) Mennega. Morphotype Se_me_1 (Figure 4J). Gall description: Discoid shape, light green, induced on the underside of the leaf, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: Pteromalidae, Tetrastichinae Eulophidae), *Torymus* (Torymidae). Plant description: Shrub, nearly 3 m tall, barren. Location: Guanacaste, Liberia, Nacascolo. Guanacaste National Park, Santa Rosa Area, entrance to the lookout point of Naranjo Beach, secondary forest area. Coordinates/Altitude: 10,81105556 N 85,64 W, 246 m; 10,80485833 N 85,69909167 W, 10 m; 10,86577222 N 85,60990278 W, 290 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Semialarium mexicanum (Miers) Mennega. Morphotype Se_me_2 (Figure 4K). Gall description: Discoid shape, green, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: Pteromalidae, Tetrastichinae (Eulophidae) *Torymus* (Torymidae). Plant description: Shrub, nearly 3 m tall, barren. Location: Guanacaste, Liberia, Nacascolo. Guanacaste National Park, Santa Rosa area, entrance to the lookout point of Naranjo Beach, secondary forest area. Coordinates/Altitude: 10,81105556 N 85,64 W, 246 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Semialarium mexicanum (Miers) Mennega. Morphotype Se_me_3 (Figure 4L). Gall description: Discoid shape, green, induced on the underside of the leaf, like a shell, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: Pteromalidae, Tetrastichinae (Eulophidae) *Torymus* (Torymidae). Plant description: Shrub, nearly 3 m tall, barren. Location: Guanacaste, La Cruz, Santa Elena. Santa Rosa National Park, Nancite Beach Area, serpentinite rock. Coordinates/Altitude: 10,80485833 N 85,69909167 W, 10 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Krameriaceae

Krameria revoluta O. Berg. Morphotype Kr_re_1 (Figure 4M). Gall description: Elliptical shape, green and brown, induced on stem, hairy epidermis. Gall inducer: unknown. Parasitoids/Inquilines: Tetrastichinae Entedoninae (Eulophidae). Plant description: Herbaceous plant, 30 cm tall, lilac flowers with white filaments. Alternate, simple leaves, heavily pubescent, approx. 1 cm in legth. Small lilac flowers. Location: Guanacaste, La Cruz, Santa Elena. Santa Rosa National Park, Nancite Beach Area, open area over a serpentinite rock. Coordinates/Altitude: 10,80485833 N 85,69909167 W, 10 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Laureaceae

Belischmiedia costaricensis (Mez & Pittier) C.K. Allen. Morphotype Be_co_1 (Figure 4N). Gall description: Spherical shape, yellowish and brown, induced on the underside of the leaf, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Sapling, nearly 1.70 m tall, barren, alternate leaves with entire margin. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, pasture area next to the forest, start of the trail to the biological station. Coordinates/Altitude: 10,92286111 N 85,46375 W, 1018 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Belischmiedia costaricensis (Mez & Pittier) C.K. Allen. Morphotype Be_co_2 (Figure 4O). Gall description: Conical shape, yellow or brown, induced on the underside of the leaf, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Sapling, nearly 1.70 m tall, barren. Alternate leaves with entire margin. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, pasture area next to the forest, start of the trail to the biological station. Coordinates/Altitude: 10,92286111 N 85,46375 W, 1018 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Nectandra salicina C.K. Allen. Morphotype Ne_sa_1 (Figure 4P). Gall description: Discoid shape, yellowish in the centre and green on the borders, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: Braconidae, Entedoninae (Eulophidae). Plant description: Shrub, nearly 1.5 m tall, barren. Location: Guanacaste, Liberia, Curubandé. Guanacaste National Park, Las Pailas Area, in the forest after the pasture, on the way to the crater. Coordinates/Altitude: 10,76955556 N 85,34519444 W, 744 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Malpighiaceae

Banisteriopsis cornifolia (Kunth) C.B. Rob. Morphotype Ba_co_1 (Figure 5A). Gall description: Discoid shape, yellowish, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 3 m tall, with procumbent branches, barren. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, Bosque Viejo Area between the entrance of the park and *La Casona*. Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Banisteriopsis cornifolia (Kunth) C.B. Rob. Morphotype Ba_co_2 (Figure 5B). Gall description: Elliptical shape, green or yellowish, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 3 m tall, with procumbent branches, barren. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, Bosque Viejo Area between the entrance of the park and *La Casona*. Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Byrsonima crassifolia (L.) Kunth. Morphotype By_cr_1 (Figure 5C). Gall description: Conical shape, green or yellowish, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 2m tall, barren. Opposite, simple leaves, medium size, with trichomes on the underside. Location: Guanacaste, La Cruz. Guanacaste National Park, on the way to the Maritza Biological Station, secondary growth area along side the river. Coordinates/Altitude: 10,88683333 N 85,47311111 W, 272 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Malvaceae

Guazuma ulmifolia Lam. Morphotype Gu_ul_1 (Figure 5D). Gall description: Globular shape, yellow and brown, induced on bud, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: *Sycophila*, "*Eurytoma*" (Eurytomidae), Tetrastichinae (Eulophidae). Plant description: Sapling, nearly 3 m tall, barren. Ovate leaves with dentate margin. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Góngora, roadside to the Cacao Volcano. Coordinates/Altitude: 10,88683333 N 85,47311111 W, 597 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Guazuma ulmifolia Lam. Morphotype Gu_ul_2 (Figure 5E). Gall description: Irregular shape, green and yellow, distributed on the glabrous adaxial surface of the leaf, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Sapling, nearly 3 m tall, barren. Ovate leaves with dentate margin. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Góngora, roadside to the Cacao Volcano. Coordinates/Altitude: 10,88683333 N 85,47311111 W, 597 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall on the same plant organ for this plant species was reported, without a reference image, by Coelho et al. (2014) but gall description doesn't match.

Guazuma ulmifolia Lam. Morphotype Gu_ul_3 (Figure 5F). Gall description: Globular shape, green, induced on stem, hairy epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Sapling, nearly 3 m tall, barren. Ovate leaves with dentate margin. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Góngora, roadside to the Cacao Volcano. Coordinates/Altitude: 10,89222222 N 85,47077778 W, 701 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Hampea appendiculata (Donn. Sm.) Standl. Morphotype Ha_ap_1 (Figure 5G). Gall description: Irregular shape, yellow, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Sapling, nearly 1.5 m tall, barren. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, pasture area next to the forest and start of the trail to the biological station. Coordinates/Altitude: 10,92286111 N 85,46375 W, 1018 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Malvaviscus arboreus Dill. ex Cav. Morphotype Ma_ar_1 (Figure 5H). Gall description: Spherical shape, green, induced on leaves, hairy epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines:

Figure 5. Plant Gall morphotypes recorded in Área de Conservación Guanacaste (ACG), Guanacaste, Costa Rica. 5A) Gall induced in *Banisteriopsis cornifolia* (Kunth) C.B. Rob., morphotype Ba_co_1, 5B) Gall induced in *Banisteriopsis cornifolia* (Kunth) C.B. Rob., morphotype Ba_co_2, 5C) Gall induced in *Byrsonima crassifolia* (L.) Kunth, morphotype By_cr_1, 5D) Gall induced in *Guazuma ulmifolia* Lam., morphotype Gu_ul_1, 5E) Gall induced in *Guazuma ulmifolia* Lam., morphotype Gu_ul_2, 5F) Gall induced in *Guazuma ulmifolia* Lam., morphotype Gu_ul_3, 5G) Gall induced in *Hampea appendiculata* (Donn. Sm.) Standl., morphotype Ha_ap_1, 5H) Gall induced in *Malvaviscus arboreus* Dill. ex Cav., morphotype Ma_ar_1, , 5I) Gall induced in *Malvaviscus arboreus* Dill. ex Cav., morphotype Ma_ar_2, 5J) Gall induced in *Ochroma pyramidale* (Cav. ex Lam.) Urb., morphotype Oc_py_1, 5K) Gall induced in *Waltheria indica* L., morphotype Wa_in_1, 5L) Gall induced in *Miconia sp.* Ruiz & Pav., morphotype Mi_sp_1, 5M) Gall induced in Guarea glabra Kunth. , morphotype Gu_gl_1, 5N) Gall induced in *Brosimum alicastrum* Swartz, morphotype Br_al_1, 5O) Gall induced in *Ficus croata* (Miq.) Miq., morphotype Fi_cr_1, 5P) Gall induced in *Ficus ovalis* Desf. ex Willd., morphotype Fi_ov_1.

unknown. Plant description: Shrub, 1.5 m tall, red flowers, on top of rock by the river. Location: Guanacaste, Liberia, Curubandé. Guanacaste National Park, Las Pailas Area, in the forest after the fumaroles. Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Malvaviscus arboreus Dill. ex Cav. Morphotype Ma_ar_2 (Figure 5I). Gall description: Globular shape, brown, induced on stem, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, 1.5 m tall, red flowers, on top of rock by the river. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, around *La Casona* at Santa Rosa National Park. Coordinates/Altitude: 10,76955556 N 85,34519444 W, 745 m; 10,77722222 N 85,35025 W, 955 m; 10,88683333 N 85,47311111 W, 597 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Ochroma pyramidale (Cav. ex Lam.) Urb. Morphotype Oc_py_1 (Figure 5J). Gall description: Irregular shape, reddish-brown on the adaxial surface of the leaf and white on the underside of the leaf, induced on leaves, hairy epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 1.7 m tall, barren. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Góngora, roadside to the Cacao Volcano, next to the Góngora River. Coordinates/Altitude: 10,83422222 N 85,6115 W, 569 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall on this plant species was reported, without a reference image, by Ley-López et al. 2019.

Waltheria indica L. Morphotype Wa_in_1 (Figure 5K). Gall description: Globular shape, green galls, yellowish/redish at maturity, brown, on the underside of the leaf and petiole, hairy epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 5 m tall, by the side of the road. Location: Guanacaste, La Cruz. Guanacaste National Park, on the way to the Maritza Biological Station, secondary growth open area, near high-voltage towers. Coordinates/Altitude: 10,95072222 N 85,59705556 W, 272 m. Registry comments: Gall recorded by Figueiredo et al. 2014.

Melastomataceae

Miconia sp. Ruiz & Pav. Morphotype Mi_sp_1 (Figure 5L). Gall description: Irregular shape, green and brown, induced on bud and leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: *Torymus* (Torymidae), Eupelmidae, Pteromalidae. Plant description: Shrub, nearly 2.5 m tall, barren. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, pasture area next to the forest, start of the trail to the biological station. Coordinates/Altitude: 10,93202778 N 85,46 W, 1277 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall on this plant species has been reported, without a reference image, by De Souza (2014), Medianero et al. (2014), and Ley-López et al. (2019).

Meliaceae

Guarea glabra Kunth. Morphotype Gu_gl_1 (Figure 5M). Gall description: Cylindrical shape, green, on adaxial and abaxial surface of the leaf, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 4 m tall, barren. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Góngora, road to the Cacao Volcano, secondary rainforest area, next to the road. Coordinates/Altitude: 10,89222222 N 85,47077778 W, 701 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Moraceae

Brosimum alicastrum Swartz. Morphotype Br_al_1 (Figure 5N). Gall description: Cylindrical shape, yellowish and brown, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 3 m tall, barren. Location: Guanacaste, Liberia, Nacascolo. Guanacaste National Park, Santa Rosa area, entrance to the lookout point of Naranjo Beach, secondary forest area. Coordinates/Altitude: 10,85072 N 85,60796 W, 292 m; 10,80586111 N 85,64 W, 250 m; 10,85072 N 85,60796 W, 321 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall on this plant species has been reported, without a reference image, by Cuevas et al. (2004), Cuevas et al. (2014), and Ley-López et al. (2019).

Ficus croata (Miq.) Miq. Morphotype Fi_cr_1 (Figure 5O). Gall description: Discoid shape, yellowish or red, induced on leaves, glabrous epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Tree, nearly 15 m tall, barren. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, around the historic *Hacienda La Casona*, isolated trees alongside the old corral. Coordinates/Altitude: 10,83382 N 85,61269 W, 307 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Ficus ovalis Desf. ex Willd. Morphotype Fi_ov_1 (Figure 5P). Gall description: Globular shape, green, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Tree, nearly 15 m tall, pedunculated infructescence, yellow, one or more by leaf bud. Alternate leaves, in several different sizes. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, around the historic *Hacienda La Casona*, isolated trees alongside the old corral. Coordinates/Altitude: 10,83382 N 85,61269 W, 307 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Pseudolmedia glabrata (Liebm.) C.C. Berg. Morphotype Ps_gl_1 (Figure 6A). Gall description: Conical shape, green and yellow, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 3 m tall, milky secretion, barren. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, next to the road. Coordinates/Altitude: 10,88683333 N 85,47311111 W, 597 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Pseudolmedia mollis (Liebm.) C.C. Berg. Morphotype Ps_mo_1 (Figure 6B1/6B2). Gall description: Globular shape, green on the adaxial surface of the leaf, greenish-white and pilose on the abaxial surface of the leaf, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Sapling, nearly 3 m tall, with milky secretion, barren. Location: Guanacaste, Liberia, Mayorga.

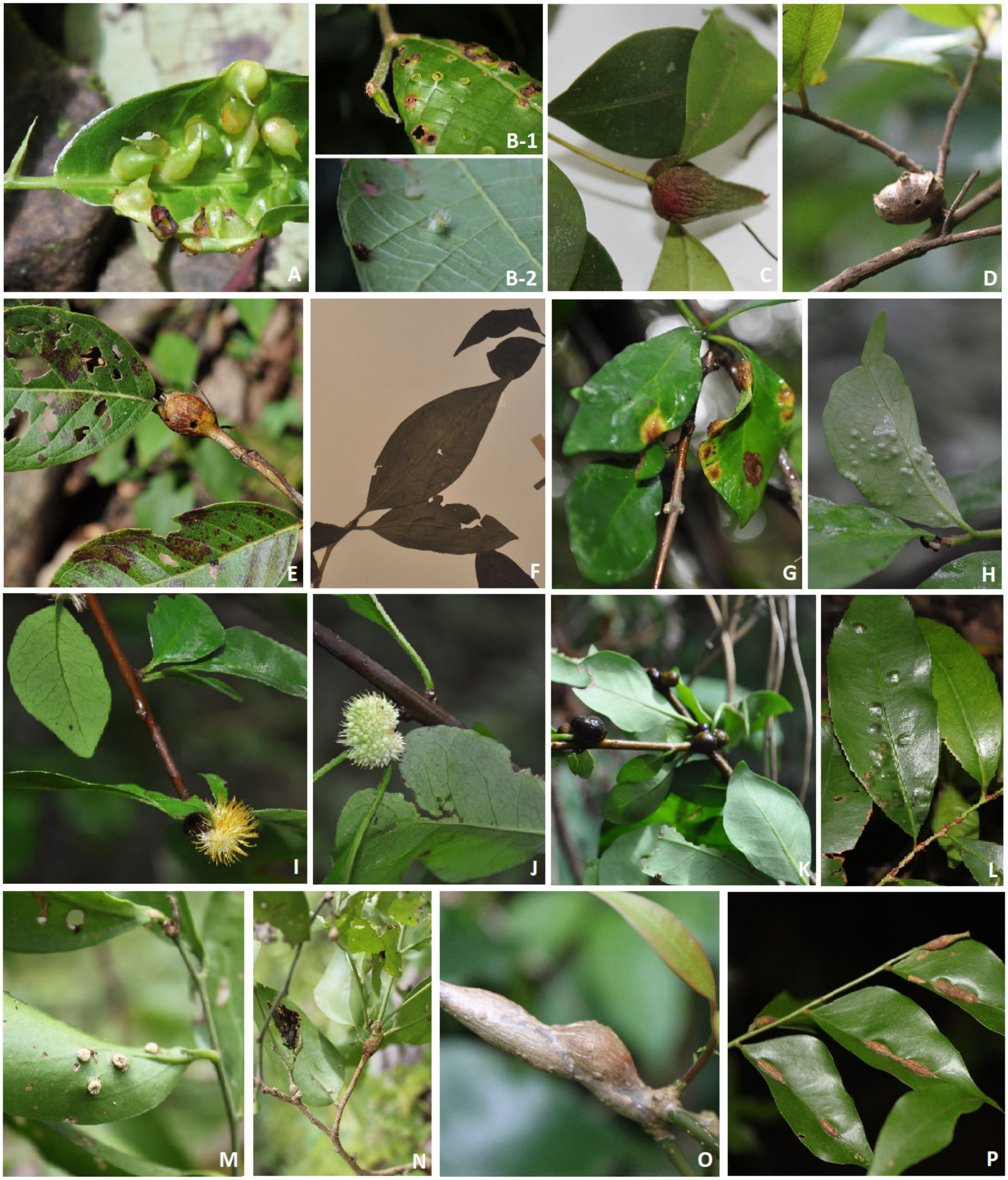


Figure 6. Plant Gall morphotypes recorded in Área de Conservación Guanacaste (ACG), Guanacaste, Costa Rica. 6A) Gall induced in *Pseudolmedia glabrata* (Liebm.) C.C. Berg, morphotype Ps_gl_1, 6B1/6B2) Gall induced in *Pseudolmedia mollis* (Liebm.) C.C. Berg, morphotype Ps_mo_1, 6C) Gall induced in *Eugenia* sp. (Miq.) Miq., morphotype Eu_sp_1, 6D) Gall induced in *Myrcia splendens* (Sw.) DC., morphotype My_sp_1, 6E) Gall induced in *Psidium guajava* L., morphotype Ps_gu_1, 6F) Gall induced in sp. Ruiz & Pav., morphotype Ne_sp_1, 6G) Gall induced in *Pisonia macranthocarpa* (Donn. Sm.) Donn. Sm., morphotype Pi_ma_1, 6H) Gall induced in *Pisonia macranthocarpa* (Donn. Sm.) Donn. Sm., morphotype Pi_ma_2, 6I) Gall induced in *Pisonia macranthocarpa* (Donn. Sm.) Donn. Sm., morphotype Pi_ma_3, 6J) Gall induced in *Pisonia macranthocarpa* (Donn. Sm.) Donn. Sm., morphotype Pi_ma_4, 6K) Gall induced in *Pisonia macranthocarpa* (Donn. Sm.) Donn. Sm., morphotype Pi_ma_5, 6L) Gall induced in Ouratea lucens (Kunth.) Engl., morphotype Ou_lu_1, 6M) Gall induced in *Schoepfia schreberi* J.F. Gmel., morphotype Sc_sc_1, 6N) Gall induced in *Schoepfia schreberi* J.F. Gmel., morphotype Sc_sc_2, 6O) Gall induced in *Trichostigma polyandrum* (Loes.) H. Walter, morphotype Tr_po_1, 6P) Gall induced in *Picramnia antidesma* Sw., morphotype Pi_an_1.

Guanacaste Conservation Area, Cacao Volcano Sector, pasture area next to the forest, start of the trail to the biological station. Coordinates/Altitude: 10,92286111 N 85,46375 W, 1018 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Myrtaceae

Eugenia sp. (Miq.) Miq. Morphotype Eu_sp_1 (Figure 6C). Gall description: Conical shape, greenish and reddish, induced on stem, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 0,5 m tall, barren. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, Cacao Mountain range. Coordinates/Altitude: 10,93202778 N 85,46 W, 1421 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Myrcia splendens (Sw.) DC. Morphotype My_sp_1 (Figure 6D). Gall description: Globular shape, brown, induced on stem, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 2 m tall, barren. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Góngora, road to the Cacao Volcano, sedimentary rock area next to the Góngora River. Coordinates/Altitude: 10,83422222 N 85,6115 W, 629 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall on this plant species was reported, without a reference image, by Ley-López et al. (2019).

Psidium guajava L. Morphotype Ps_gu_1 (Figure 6E). Gall description: Elliptical shape, brown, induced on stem, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Sapling, nearly 0.5 m tall, barren. Location: Guanacaste, La Cruz. Guanacaste National Park, on the way to the Maritza Biological Station, secondary growth open area, near high-voltage towers. Coordinates/Altitude: 10,95072222 N 85,59705556 W, 272 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall on this plant species was reported, without a reference image, by Maia (2012).

Nyctaginaceae

Neea sp. Ruiz & Pav. Morphotype Ne_sp_1 (Figure 6F). Gall description: Fusiform shape, green, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shurb, nearly 1.5 m tall, barren. Location: Guanacaste, Liberia, Curubandé. Rincón de la Vieja National Park, forest area on the way to active crater. Coordinates/Altitude: 10,78427778 N 85,3484167 W, 955 m. Registry comments: Similar to gall recorded by Maia (2014).

Pisonia macranthocarpa (Donn. Sm.) Donn. Sm. Morphotype Pi_ma_1 (Figure 6G). Gall description: Irregular shape, yellow and brown, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 2.5 m tall, barren. Location: Guanacaste, La Cruz, La Cruz. Guanacaste National Park, on the way to the Maritza Biological Station, secondary growth area alongside the river. Coordinates/Altitude: 10,95072222 N 85,59705556 W, 272 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Pisonia macranthocarpa (Donn. Sm.) Donn. Sm. Morphotype Pi_ma_2 (Figure 6H). Gall description: Irregular shape, green, induced on leaves, glabrous epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 4 m tall, unripe fruit are light green. Location: Guanacaste, La Cruz, La Cruz. Guanacaste National Park, on the way to the Maritza Biological Station, secondary growth area along the river. Coordinates/Altitude: 10,95072222 N 85,59705556 W, 272 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Pisonia macranthocarpa (Donn. Sm.) Donn. Sm. Morphotype Pi_ma_3 (Figure 6I). Gall description: Spherical shape, yellow, induced on bud, soft spines on epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 2 m tall, barren. Location: Guanacaste, La Cruz, La Cruz. Guanacaste National Park, on the way to the Maritza Biological Station, secondary growth area along the river. Coordinates/Altitude: 10,95072222 N 85,59705556 W, 272 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Pisonia macranthocarpa (Donn. Sm.) Donn. Sm. Morphotype Pi_ma_4 (Figure 6J). Gall description: Globular shape, white, induced on bud, soft spines on epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 2 m tall. Location: Guanacaste, La Cruz. Guanacaste National Park, on the way to the Maritza Biological Station, secondary growth area alongside the river. Coordinates/Altitude: 10,95072222 N 85,59705556 W, 272 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Pisonia macranthocarpa (Donn. Sm.) Donn. Sm. Morphotype Pi_ma_5 (Figure 6K). Gall description: Globular shape, brownish, induced on stem, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 2 m tall. Location: Guanacaste, La Cruz. Guanacaste National Park, on the way to the Maritza Biological Station, secondary growth area along the river. Coordinates/Altitude: 10,95072222 N 85,59705556 W, 272 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Ochnaceae

Ouratea lucens (Kunth.) Engl. Morphotype Ou_lu_1 (Figure 6L). Gall description: Discoid shape, green (concolorous) to brownish yellow galls on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Understory sapling, with red stipules. Location: Guanacaste, Liberia, Nacascolo. Entrance to the old forest (*Bosque Viejo)*, between the welcome booth and *La Casona* at Santa Rosa National Park. Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m. Registry comments: Similar to gall recorded by Bergamini et al. (2017).

Olacaceae

Schoepfia schreberi J.F. Gmel. Morphotype Sc_sc_1 (Figure 6M). Gall description: Discoid shape, white, induced on leaves, glabrous epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Shrub, 3 m tall, by the side of the road. Location: Guanacaste, Liberia, Nacascolo. Entrance to the old forest (*Bosque Viejo*), between the welcome booth and *La Casona* at Santa Rosa National Park. Coordinates/Altitude: 10,8336278 N 85,6132333 W, 292 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Schoepfia schreberi J.F. Gmel. Morphotype Sc_sc_2 (Figure 6N). Gall description: Elliptical shape, brown, induced on stem, lignified-glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, 3 m tall, by the side of the road. Location: Guanacaste, Liberia, Nacascolo. Entrance to the old forest (*Bosque Viejo*), between the welcome booth and *La Casona* at Santa Rosa National Park. Coordinates/Altitude: 10,8336278 N 85,6132333 W, 292 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Phytolaccaceae

Trichostigma polyandrum (Loes.) H. Walter. Morphotype Tr_po_1 (Figure 6O). Gall description: Fusiform shape, brown, induced on stem, lignified, and glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 1.5 m tall, procumbent branches, reddish petioles, and barren. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Góngora, road to the Cacao Volcano, side the road, next to the Góngora River. Coordinates/Altitude: 10,83422222 N 85,6115 W, 569 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Picraminiaceae

Picramnia antidesma Sw. Morphotype Pi_an_1 (Figure 6P). Gall description: Fusiform shape, brown, induced on leaves, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, barren. Alternate leaves, with entire margin. Location: Guanacaste, Liberia, Nacascolo. Entrance to the old forest (*Bosque Viejo*), between the welcome booth and *La Casona* at Santa Rosa National Park. Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Picramnia antidesma Sw. Morphotype Pi_an_2 (Figure 7A). Gall description: Globular shape, brown, induced on stem, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, barren. Alternate leaves, with entire margin. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, *Bosque Viejo* area between the park entrance and *La Casona* Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Piperaceae

Piper sp. L. Morphotype Pi_sp_1 (Figure 7B). Gall description: Spherical shape, green and yellowish on the surface, whitish pubescence, on petiole and leaf rachis. On abaxial or abaxial leaf position, hairy epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Herbaceous plant, nearly 1m tall, by the side of the road. Location: Guanacaste, Liberia, Nacascolo. Entrance to the old forest (*Bosque Viejo*), between the welcome booth and *La Casona* at Santa Rosa National Park. Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m. Registry comments: Gall morphotype resembles the one described by Maia & Mascarenhas (2017) on *P. richardiifolium*.

Piper sp. L. Morphotype Pi_sp_2 (Figure 7C). Gall description: Spherical shape, green and yellow, induced on Petiole, hairy epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Herbaceous plant, nearly 1m tall, by the side of the road. Location: Guanacaste, Liberia, Nacascolo. Entrance to the old forest (*Bosque Viejo*), between the welcome booth and *La Casona* at Santa Rosa National Park. Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m. Registry comments: Gall morphotype resembles the one described by Bergamini et al. (2017) on *Piper arboreum* Aubl.

Piper yucatanense C. DC. Morphotype Pi_yu_1 (Figure 7D). Gall description: Globular shape, green, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Herbaceous plant, nearly 1 m tall, barren. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, pasture area next to the forest, start of the trail to the biological station. Coordinates/Altitude: 10,92286111 N 85,46375 W, 1018 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Poaceae

Paspalum sp. L. Morphotype Pa_sp_1 (Figure 7E). Gall description: Globular shape, brown, on the inflorescense, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Herbaceous plants, nearly 50 cm tall, by the side of the road, purple glumes. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, between the Inter-American highway and *La Casona*, secondary oak forest area. Coordinates/Altitude: 10,86577222 N 85,60990278 W, 290 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Polygonaceae

Coccoloba tuerckheimii Donn. Sm. Morphotype Co_tu_1 (Figure 7F). Gall description: Globular shape, orange and brown, induced on on the underside of the leaf, hairy epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 3 m tall, spiral leaves at the end of the branch, barren. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Góngora, road to the Cacao Volcano, secondary forest area, next to the road. Coordinates/Altitude: 10,89222222 N 85,47077778 W, 701 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall induced on this plant species was reported, without a reference image, by Ley-López et al. 2019.

Coccoloba venosa L. Morphotype Co_ve_1 (Figure 7G). Gall description: Cylindrical shape, Yellow/brown, induced on the adaxial and abaxial surface of the leaf, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 1.5 m tall, on rocky area, flowers with yellow petals and white

Figure 7. Plant Gall morphotypes recorded in Área de Conservación Guanacaste (ACG), Guanacaste, Costa Rica. 7A) Gall induced in *Picramnia antidesma* Sw., morphotype Pi_an_2, 7B) Gall induced in *Piper* sp. L., morphotype Pi_sp_1, 7C) Gall induced in *Piper* sp. L., morphotype Pi_sp_2, 7D) Gall induced in *Piper yucatanense* C. DC., morphotype Pi_yu_1, 7E) Gall induced in *Paspalum* sp. L., morphotype Pa_sp_1, 7F) Gall induced in *Coccoloba tuerckheimii* Donn. Sm, morphotype Co_tu_1, 7G) Gall induced in *Coccoloba venosa* L., morphotype Co_ve_1, 7H) Gall induced in *Ardisia compressa* Schltdl., morphotype Ar_co_1, 7I) Gall induced in *Ardisia compressa* Kunth, morphotype Ar_co_2, 7J) Gall induced in *Ardisia revoluta* Kunth, morphotype Ar_re_1, 7K) Gall induced in *Psychotria deflexa* DC., morphotype Ps_de_1, 7L) Gall induced in *Psychotria horizontalis* Sw., morphotype Ps_ho_1, 7M) Gall induced in *Psychotria horizontalis* Sw., morphotype Ps_ho_2, 7N) Gall induced in *Psychotria horizontalis* L., morphotype Ps_ho_3, 7O) Gall induced in *Psychotria horizontalis* Sw., morphotype Ps_ho_4, 7P) Gall induced in *Psychotria quinqueradiata* Pol., morphotype Ps_qu_1.

anthers. Location: Guanacaste, Liberia, Nacascolo. Guanacaste National Park, Santa Rosa Area, old secondary forest area, road to Naranjo Beach. Coordinates/Altitude: 10,79383333 N 85,66 W, 15 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Primulaceae

Ardisia compressa Schltdl. Morphotype Ar_co_1 (Figure 7H). Gall description: Discoid shape, green, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, 2 m tall, barren. Location: Guanacaste, Liberia, Curubandé. Guanacaste National Park, *Las Pailas* Sector, in the forest after the pasture, on the way to the crater. Coordinates/Altitude: 10,78427778 N 85,3484167 W, 955 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Ardisia compressa Kunth. Morphotype Ar_co_2 (Figure 7I). Gall description: Discoid shape, green, brown, and red at maturity, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: *Torymus* (Torymidae). Plant description: Small tree, 2 m tall, barren. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, Cacao mountain range. Coordinates/Altitude: 10,93202778 N 85,46 W, 1421 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Ardisia revoluta Kunth. Morphotype Ar_re_1 (Figure 7J). Gall description: Fusiform shape, green, induced on leaf midvein, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 4m tall, barren. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, *Bosque Viejo* area between the entrance of the park and *La Casona*. Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Rubiaceae

Psychotria deflexa DC. Morphotype Ps_de_1 (Figure 7K). Gall description: Conical shape, green and yellow, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 1m tall, barren. Location: Guanacaste, Liberia, Curubandé. Guanacaste National Park, *Las Pailas* Sector, in the old secondary forest after the pasture, on the way to the crater. Coordinates/Altitude: 10,78427778 N 85,3484167 W, 955 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Psychotria horizontalis Sw. Morphotype Ps_ho_1 (Figure 7L). Gall description: Fusiform shape, brown, induced on stem, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Herbaceous plant, nearly 50 cm tall, by the side of the road, greenish unripe fruits. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, between the Inter-American highway and *La Casona*, secondary oak forest area. Coordinates/Altitude: 10,86577222 N 85,60990278 W, 290 m. Registry comments: Gall morphotype resembles the one described by Bergamini et al. (2017) on a Rubiaceae sp.

Psychotria horizontalis Sw. Morphotype Ps_ho_2 (Figure 7M). Gall description: Spherical shape, green, induced on leaves, presence of trichomes epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Herbaceous plant, nearly 50 cm tall, by the side of the road, greenish unripe fruits. Location: Guanacaste, Liberia, Curubandé. Guanacaste National Park, Las Pailas Sector, in the old secondary forest after the pasture, on the way to the crater. Coordinates/Altitude: 10,78427778 N 85,3484167 W, 955 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Psychotria horizontalis Sw. Morphotype Ps_ho_3 (Figure 7N). Gall description: Globular shape, brown, induced on stem, corrugated and lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 1.5 m tall, barren. Location: Guanacaste, LaCruz. Parque Nacional Guanacaste, on the way to the Maritza Biological Station, secondary growth area along the river. Coordinates/Altitude: 10,95072222 N 85,59705556 W, 272 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Psychotria horizontalis Sw. Morphotype Ps_ho_4 (Figure 7O). Gall description: Globular shape, green, induced on petiole, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 2.5 m tall, barren. Location: Guanacaste, Liberia, Curubandé. Guanacaste National Park, Las Pailas Sector, in the old secondary forest after the pasture, on the way to the crater. Coordinates/Altitude: 10,76955556 N 85,34519444 W, 744m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Psychotria quinqueradiata Pol. Morphotype Ps_qu_1 (Figure 7P). Gall description: Fusiform shape, brown, induced on stem, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 1 m, greenish fruits Location: Guanacaste, Liberia, Curubandé. Guanacaste National Park, *Las Pailas* Sector, in the old secondary forest after the pasture, on the way to the crater. Coordinates/Altitude: 10,78427778 N 85,3484167 W, 955 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Psychotria valerioana Standl. Morphotype Ps_va_1 (Figure 8A). Gall description: Globular shape, green, induced on leaves and buds, glabrous epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: Entedoninae (Eulophidae). Plant description: Shrub, nearly 1 m tall, greenish fruit, white flowers. Location: Guanacaste, Liberia, Curubandé. Guanacaste National Park, Las Pailas Sector, in the old secondary forest after the pasture, on the way to the crater. Coordinates/Altitude: 10,78427778 N 85,3484167 W, 955 m; 10,80669 N 85,35 W, 1074 m; 10,80032 N 85,35 W, 1000 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Psychotria valerioana Standl. Morphotype Ps_va_2 (Figure 8B). Gall description: Conical shape, green on the base and the apex, yellowish in the middle, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 1 m tall, greenish fruit, white flowers. Location: Guanacaste, Liberia, Curubandé. Rincón de la Vieja National Park, road to active crater, Los gemelos Sector, forest zone. Coordinates/Altitude: 10,80669 N 85,35 W, 1074 m; 10,92286111 N 85,46375 W, 1018 m.

Figure 8. Plant Gall morphotypes recorded in Área de Conservación Guanacaste (ACG), Guanacaste, Costa Rica. 8A) Gall induced in *Psychotria valerioana* Standl., morphotype Ps_va_1, 8B) Gall induced in *Psychotria valerioana* Standl., morphotype Ps_va_2, 8C) Gall induced in *Psychotria valerioana* Standl., morphotype Ps_va_3, 8D) Gall induced in *Randia monantha* Benth., morphotype Ra_mo_1, 8E) Gall induced in *Zanthoxylum sp.* L., morphotype Za_sp_1, 8F) Gall induced in *Meliosma glabrata* (Liebm.) Urb., morphotype Me_gl_1, 8G) Gall induced in *Casearia arguta* Kunth, morphotype Ca_ar_1, 8H) Gall induced in *Casearia arguta* Kunth, morphotype Ca_ar_2, 8I) Gall induced in *Allophylus racemosus* (Sw.), morphotype Al_ra_1, 8J) Gall induced in *Allophylus racemosus* (Sw) , morphotype Al_ra_2, 8K) Gall induced in *Allophylus racemosus* (Sw) , morphotype Al_ra_3, 8L) Gall induced in Paullinia cururu L., morphotype Pa_cu_1, 8M) Gall induced in *Serjania pyramidata* Radlk., morphotype Se_py_1, 8N) Gall induced in Serjania schiedeana Schltdl., morphotype Se_sc_1, 8O) Gall induced in *Thouinidium decandrum* (Hump & Band), morphotype Th_de_1, 8P) Gall induced in *Sideroxylon obtusifolium* (Roem & Schult), morphotype Si_ob_1.

Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Psychotria valerioana Standl. Morphotype Ps_va_3 (Figure 8C). Gall description: Globular shape, greenish and brown, induced on leaf midvein, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 1 m tall, greenish fruit, white flowers. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, pasture area next to the forest and start of the trail to the biological station. Coordinates/Altitude: 10,92286111 N 85,46375 W, 1018 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Randia monantha Benth. Morphotype Ra_mo_1 (Figure 8D). Gall description: Irregular shape, yellowish green (concolorous) on the surface, pale green on the underside, near veins on the underside, protruding from the abaxial surface, hairy epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 6 m tall, barren. Location: Guanacaste, Liberia, Nacascolo. Entrance to the old forest (*Bosque Viejo*), between the welcome booth and *La Casona* at Santa Rosa National Park. Coordinates/Altitude: 10,85072 N 85,60796 W, 321 m; 10,83581 N 85,62347 W, 306 m; 10,83382 N 85,61269 W, 307 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Rutaceae

Zanthoxylum sp. L. Morphotype Za_sp_1 (Figure 8E). Gall description: Irregular shape, green and yellow, induced on leaves, bulging on the leaf border, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Tree, nearly 3 m tall, barren, and fallen. Location: Guanacaste, Liberia, Curubandé. Rincón de la Vieja National Park, road to active crater, Los Gemelos Sector, forest zone. Coordinates/Altitude: 10,80032 N 85,35 W, 1000 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Sabiaceae

Meliosma glabrata (Liebm.) Urb. Morphotype Me_gl_1 (Figure 8F). Gall description: Discoid shape, green and yellow, induced on leaves, sometimes with black dots, rough, on both the surfaces of the leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Sapling, nearly 1.5 m tall, barren. Oblong shaped leaves, with cuspidate apex. Location: Guanacaste, Liberia, Curubandé. Rincón de la Vieja National Park, road to active crater, Los gemelos Sector, forest zone. Coordinates/Altitude: 10,80032 N 85,35 W, 1000 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall on this plant species was reported, without a reference image, by Ley-López et al. (2019).

Salicaceae

Casearia arguta Kunth. Morphotype Ca_ar_1 (Figure 8G). Gall description: Irregular shape, green, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: Entedoninae (Eulophidae). Plant description: Sapling, nearly 4 m tall, barren. Alternate, simple leaves, with crenate margin. Location: Guanacaste, Liberia, Curubandé. Rincón de la Vieja National Park, road to active crater, Los Gemelos Sector, forest zone. Coordinates/Altitude: 10,80669 N 85,35 W, 1074 m; 10,92286111 N 85,46375 W, 1018 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Casearia arguta Kunth. Morphotype Ca_ar_2 (Figure 8H). Gall description: Elliptical shape, light brown mixed with green, induced on stem, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: Entedoninae (Eulophidae). Plant description: Sapling, nearly 4 m tall, barren. Alternate, simple leaves, with crenate margin. Location: Guanacaste, Liberia, Curubandé. Rincón de la Vieja National Park, road to active crater, Los Gemelos Sector, forest zone. Coordinates/Altitude: 10,80669 N 85,35 W, 1074 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Sapindaceae

Allophylus racemosus Sw. Morphotype Al_ra_1 (Figure 8I). Gall description: Globular shape, green-white, induced on leaves, hairy epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 4 m tall, barren. Location: Guanacaste, La Cruz, Santa Elena. Guanacaste Conservation Area, Murciélago Sector, old secondary growth, road between *El Hachal* bay and *Murciélago* Station. Coordinates/Altitude: 10,92638889 N 85,7292 W, 45 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Allophylus racemosus Sw. Morphotype Al_ra_2 (Figure 8J). Gall description: Spherical shape, green or yellowish, induced on leaf midvein and petiole, hairy epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 2.5 m tall, barren. Location: Guanacaste, La Cruz, La Cruz. Guanacaste National Park, on the way to the Maritza Biological Station, secondary growth area along the river. Coordinates/Altitude: 10,95072222 N 85,59705556 W, 272 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Allophylus racemosus Sw. Morphotype Al_ra_3 (Figure 8K). Gall description: Globular shape, green and yellowish, induced on petiole, hairy epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 4 m tall, barren. Location: Guanacaste, La Cruz, La Cruz. Guanacaste National Park, on the way to the Maritza Biological Station, secondary growth area along the river. Coordinates/Altitude: 10,95072222 N 85,59705556 W, 272 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Paullinia cururu L. Morphotype Pa_cu_1 (Figure 8L). Gall description: Discoid shape, green-yellowish and brown, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Understory, scandent, herbaceous plant, nearly 3 m tall. Location: Guanacaste, Liberia, Curubandé. Guanacaste National Park, Las Pailas Sector, in the forest after the fumaroles. Coordinates/Altitude: 10,76955556 N 85,34519444 W, 744 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall on this plant species was reported, without a reference image, by Cuevas et al. (2014).

Serjania pyramidata Radlk. Morphotype Se_py_1 (Figure 8M). Gall description: Globular shape, brown, induced on stem, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Vine, barren. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, between the Inter-American highway and *La Casona*, secondary oak forest area. Coordinates/Altitude: 10,86577222 N 85,60990278 W, 290 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Serjania schiedeana Schltdl. Morphotype Se_sc_1 (Figure 8N). Gall description: Discoid shape, yellow or brown, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Sapling, nearly 25 cm tall, barren. Rhomboid shaped leaves, with cuspidate apex and denticulate margin, trifoliate/ternate leaves. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, next to the research laboratories, old secondary forest area. Coordinates/Altitude: 10,83926 N 85,61808 W, 310 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Thouinidium decandrum Hump & Band. Morphotype Th_de_1 (Figure 8O). Gall description: Discoid shape, green to black, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 3 m tall, barren. Imparipinnate, alternate, compound leaves, with slightly serrate margin. Location: Guanacaste, Liberia, Nacascolo. Guanacaste National Park, Naranjo Beach Area, mangrove and beach area, coastal area at dry-forest. Coordinates/Altitude: 10,77928 N 85,6654 W, 14 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Sapotaceae

Sideroxylon obtusifolium (Humb. ex Roem. & Schult.) T.D. Penn. Morphotype Si_ob_1 (Figure 8P). Gall description: Fusiform shape, brown, induced on stem, lignified epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 3 m tall, simple axillary white flowers, unripe fruits (green). Location: Guanacaste, La Cruz, Santa Elena. Guancaste National Park, Murciélago Sector, old secondary forest area, on serpentinized peridotite on the edge of the Murciélago River. Coordinates/Altitude: 10,89686111 N 85,7301111 W, 126 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Sideroxylon obtusifolium (Humb. ex Roem. & Schult.) T.D. Penn. Morphotype Si_ob_2 (Figure 9A). Gall description: Irregular shape, green, induced on leaves (midvein), glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 3 m tall, simple axillary white flowers, unripe fruits (green). Location: Guanacaste, La Cruz, Santa Elena. Guanacaste National Park, Murciélago Sector, old secondary forest area, on serpentinized peridotite on the edge of the Murciélago River. Coordinates/Altitude: 10,89686111 N 85,7301111 W, 126 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Sideroxylon obtusifolium (Humb. ex Roem. & Schult.) T.D. Penn. Morphotype Si_ob_3 (Figure 9B). Gall description: Conical shape, green and yellowish, induced on fruit, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 3 m tall, simple axillary white flowers, unripe fruits (green). Location: Guanacaste, La Cruz, Santa Elena. Guancaste National Park, Murciélago Sector, old secondary forest area, on serpentinized peridotite on the edge of the Murciélago River. Coordinates/Altitude: 10,89686111 N 85,7301111 W, 126 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Sideroxylon obtusifolium (Humb. ex Roem. & Schult.) T.D. Penn. Morphotype Si_ob_4 (Figure 9C). Gall description: Elliptical shape, brown and yellow-green, induced on stem, bulging galls on thorns, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: *Cecidellis* (Pteromalidae). Plant description: Small tree, nearly 3 m tall, simple axillary white flowers, unripe fruits (green). Location: Guanacaste, La Cruz, Santa Elena. Guancaste National Park, Murciélago Sector, old secondary forest area, on serpentinized peridotite on the edge of the Murciélago River. Coordinates/Altitude: 10,89686111 N 85,7301111 W, 126 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Sideroxylon obtusifolium (Humb. ex Roem. & Schult.) T.D. Penn. Morphotype Si_ob_5 (Figure 9D). Gall description: Globular shape, green, induced on inflorescence, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 3 m tall, simple axillary white flowers, unripe fruits (green). Location: Guanacaste, La Cruz, Santa Elena. Guancaste National Park, Murciélago Sector, old secondary forest area, on serpentinized peridotite on the edge of the Murciélago River. Coordinates/Altitude: 10,89686111 N 85,7301111 W, 126 m. Registry comments: Gall morphotype resembles the one described by Rodrigues et al. (2014).

Simaroubaceae

Simarouba glauca DC. Morphotype Si_gl_1 (Figure 9E). Gall description: Irregular shape, green and yellowish, induced on leaves (foliar midrib), glabrous epidermis. Sometimes twisting the leaf. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small tree, nearly 4 m tall, barren. Location: Guanacaste, Liberia, Mayorga. Santa Rosa National Park, lookout point between the main entrance of the park and *La Casona*. Coordinates/Altitude: 10,85648 N 85,6106 W, 323 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Smilacaceae

Smilax spinosa Mill. Morphotype Sm_sp_1 (Figure 9F). Gall description: Discoid shape, green and yellowish, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: Eurytomidae. Plant description: Vine on shrubs, barren. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Cacao Volcano Sector, Cacao Mountain range. Coordinates/Altitude: 10,93202778 N 85,46 W, 1421 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Solanaceae

Lycianthes multiflora. Morphotype Ly_mu_1 (Figure 9G). Gall description: Fusiform shape, brown, induced on leaf veins, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Herbaceous vine on shrub. Alternate leaves. Location:

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Figure 9. Plant Gall morphotypes recorded in Área de Conservación Guanacaste (ACG), Guanacaste, Costa Rica. 9A) Gall induced in *Sideroxylon obtusifolium* (Roem & Schult), morphotype Si_ob_2, 9B) Gall induced in *Sideroxylon obtusifolium* (Roem & Schult), morphotype Si_ob_3, 9C) Gall induced in *Sideroxylon obtusifolium* (Humb. ex Roem. & Schult.) T.D. Penn., morphotype Si_ob_4, 9D) Gall induced in *Sideroxylon obtusifolium* (Humb. ex Roem. & Schult.) T.D. Penn., morphotype Si_ob_5, 9E) Gall induced in *Simarouba glauca* DC, morphotype Si_gl_1, 9F) Gall induced in *Smilax spinosa* Mill., morphotype Sm_sp_1, 9G) Gall induced in *Lycianthes multiflora*, morphotype Ly_mu_1, 9H) Gall induced in Stegnosperma cubense A. Rich, morphotype St_cu_1, 9I) Gall induced in Stegnosperma cubense A. Rich, morphotype St_cu_2, 9J) Gall induced in Stegnosperma cubense A. Rich, morphotype St_cu_3, 9K) Gall induced in Stegnosperma cubense A. Rich, morphotype St_cu_4, 9L) Gall induced in *Stegnosperma cubense* A. Rich, morphotype St_cu_5, 9M) Gall induced in *Urera simplex* Wedd., morphotype Ur_si_1, 9N) Gall induced in *Lippia oxyphyllaria* (Donn. Sm.) Standl., morphotype Li_ox_1, 9O) Gall induced in *Rehdera trinervis* (S.F. Blake) Moldenke, morphotype Re_tr_1, 9P) Gall induced in *Rehdera trinervis* (S.F. Blake) Moldenke, morphotype Re_tr_2.

Guanacaste, Liberia, Curubandé. Rincón de la Vieja National Park, road to active crater, Los Gemelos Sector, rainforest zone. Coordinates/Altitude: 10,80032 N 85,35 W, 1000 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world, although a gall induced on this plant species was reported, without a reference image, by Ley-López et al. (2019).

Stegnospermataceae

Stegnosperma cubense A. Rich. Morphotype St_cu_1 (Figure 9H). Gall description: Fusiform shape, grayish, induced on stem, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Decumbent shrub, nearly 2.5 m and 1m tall, barren. Location: Guanacaste, Liberia, Nacascolo. Guanacaste National Park, Naranjo Beach Area, mangrove and area, coastal area in dry-forest. Coordinates/Altitude: 10,7791389 N 85,66594444 W, 14 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Stegnosperma cubense A. Rich. Morphotype St_cu_2 (Figure 9I). Gall description: Discoid shaped galls, green, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: Eulophidae. Plant description: Decumbent shrub, nearly 2.5 m and 1m tall, barren. Location: Guanacaste, Liberia, Nacascolo. Guanacaste National Park, Naranjo Beach Area, mangrove and beach area, coastal area in dry-forest. Coordinates/Altitude: 10,77928 N 85,6654 W, 14 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Stegnosperma cubense A. Rich. Morphotype St_cu_3 (Figure 9J). Gall description: Globular shape, light green, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Decumbent shrub, nearly 2.5 m and 1m tall, barren. Location: Guanacaste, Liberia, Nacascolo. Guanacaste National Park, Naranjo Beach Area, mangrove and beach area, coastal area in dry-forest. Coordinates/Altitude: 10,7791389 N 85,66594444 W, 14 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Stegnosperma cubense A. Rich. Morphotype St_cu_4 (Figure 9K). Gall description: Discoid shape, yellow to greenish, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Decumbent shrub, nearly 2.5 m and 1m tall, barren. Location: Guanacaste, La Cruz, Santa Elena. Guanacaste Conservation Area, Murciélago Sector, old secondary growth, road between El Hachal Bay and Murciélago Station. Coordinates/Altitude: 10,92638889 N 85,7292 W, 45 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Stegnosperma cubense A. Rich. Morphotype St_cu_5 (Figure 8L). Gall description: Globular shape, white to greenish, induced on the underside of the leaf, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Decumbent shrub, nearly 2.5 m and 1m tall, barren. Prominent globularl galls,. Location: Guanacaste La Cruz, Santa Elena. Guanacaste Conservation Area, Murciélago Sector, old secondary growth, road between El Hachal Bay and Murciélago Station. Coordinates/Altitude: 10,92638889 N 85,7292 W, 45 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Urticaceae

Urera simplex Wedd. Morphotype Ur_si_1 (Figure 9M). Gall description: Irregular shape, green and yellow, induced on leaves, distributed throughout the upper leaf surface and underside, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Shrub, nearly 3 m tall, inflorescence with white stamens, pink petals and pedicels. Location: Guanacaste, Liberia, Curubandé. Rincón de la Vieja National Park, road to active crater, Los gemelos Area, rainforest zone. Coordinates/Altitude: 10,80032 N 85,35 W, 1000 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Verbenaceae

Lippia oxyphyllaria (Donn. Sm.) Standl. Morphotype Li_ox_1 (Figure 9N). Gall description: Spherical shape, light green, induced on leaves (midvein or secondary veins), hairy epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Herbaceous plant or shrub, up to 2 m tall, barren. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, Santa Rosa Area, between the entrance of the Inter-American highway and *La Casona*, secondary oak forest area. Coordinates/Altitude: 10,86577222 N 85,60990278 W, 290 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Rehdera trinervis (S.F. Blake) Moldenke. Morphotype Re_tr_1 (Figure 9O). Gall description: Elliptical shape, green and brown, induced on leaf midvein, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small woody sapling, nearly 3 m tall, strong secondary growth. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park between the Inter-American highway and *La Casona*, secondary oak forest area. Coordinates/Altitude: 10,86577222 N 85,60990278 W, 290 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Rehdera trinervis (S.F. Blake) Moldenke. Morphotype Re_tr_2 (Figure 9P). Gall description: Discoid shape, green and yellowish, induced on leaves, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Small woody sapling, nearly 3 m tall, strong secondary growth. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park between the Inter-American highway and *La Casona*, secondary oak forest area. Coordinates/Altitude: 10,86577222 N 85,60990278 W, 290 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Vitaceae

Cissus fuliginea Croat. Morphotype Ci_fu_1 (Figure 10A). Gall description: Fusiform shape, green to yellowish green, induced on stem and leaf veins, hairy epidermis. Gall inducer: Cecidomyiidae. Parasitoids/Inquilines: unknown. Plant description: Vine, near by the mud pits. Tropical dry forest area. Trifoliate leaves with serrate margin and tendrils. On top of *Sweetenia*, barren. Location: Guanacaste, Liberia, Nacascolo. Administrative area of the National Park. Coordinates/Altitude: 10,83694444 N 85,62 W, 406 m; 10,76955556 N 85,34519444 W, 744 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

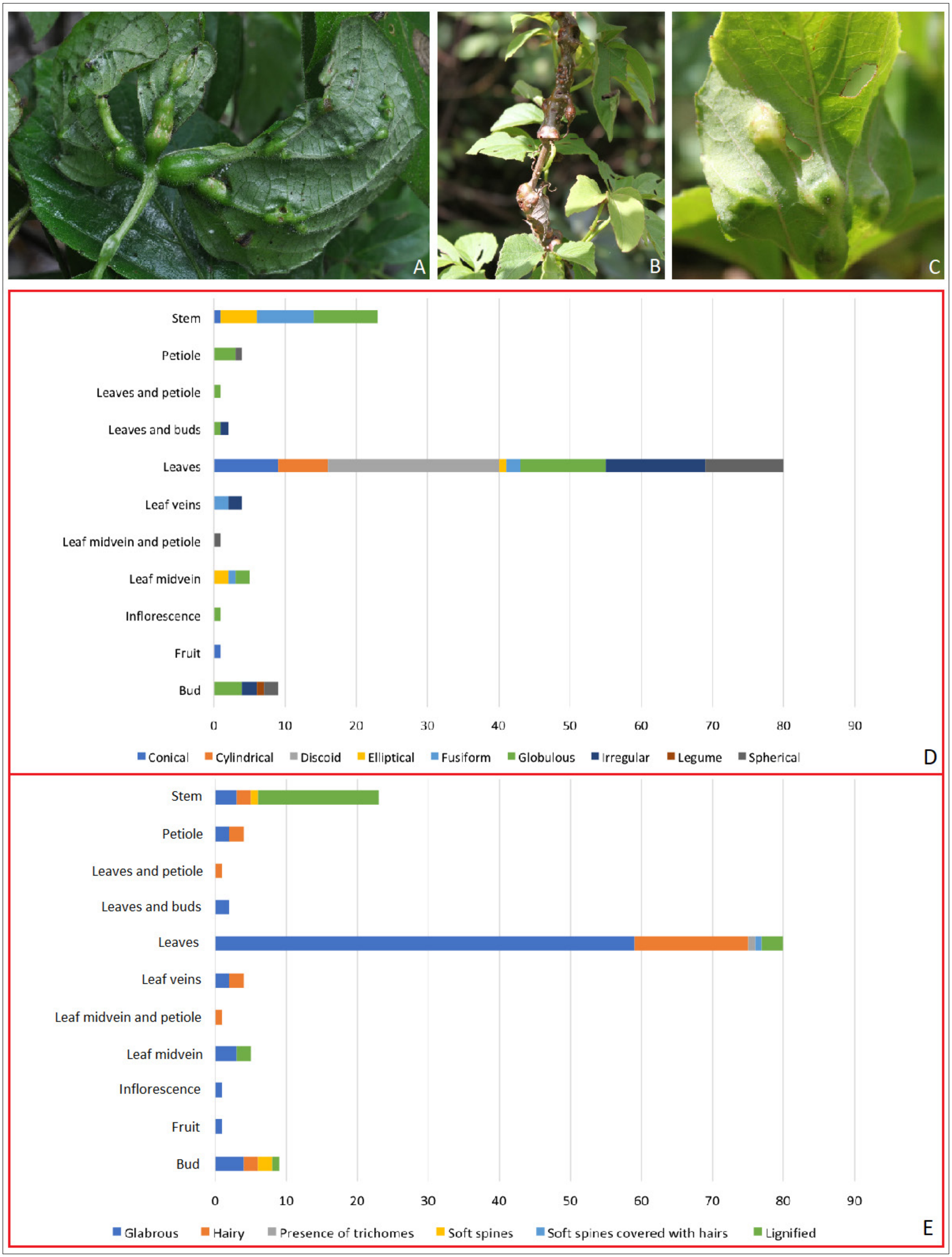

Figure 10. Plant Gall morphotypes recorded in Área de Conservación Guanacaste (ACG), Guanacaste, Costa Rica. 10A) Gall induced in *Cissus fuliginea* (Croat.), morphotype Ci_fu_1, 10B) Gall induced in *Cissus fuliginea* (Croat.), morphotype Ci_fu_2, 10C) Gall induced in *Cissus fuliginea* (Croat.), morphotype Ci_fu_3, 10D) Gall morphology vrs incidence in plant organs, 10E) Gall epidermis texture and their incidence by plant organ. For 10D and 10E, the values on the X-axis represent the total number of morphotypes.

Cissus fuliginea Croat. Morphotype Ci_fu_2 (Figure 10B). Gall description: Fusiform shape, reddish-brown or green, induced on stem, lignified epidermis. Gall inducer: unknown. Parasitoids/Inquilines: unknown. Plant description: Vine, near by the mud pits. Tropical dry forest area. Trifoliate leaves with serrate margin and tendrils. On top of *Sweetenia*, barren. Location: Guanacaste, Liberia, Mayorga. Guanacaste Conservation Area, Góngora, road to the Cacao Volcano, sedimentary rock area next to the Góngora River. Coordinates/Altitude: 10,83422222 N 85,6115 W, 569 m; 10,76955556 N 85,34519444 W, 744 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

Cissus fuliginea Croat. Morphotype Ci_fu_3 (Figure 10C). Gall description: Irregular shape, green to yellowish green, induced on leaf veins, glabrous epidermis. Gall inducer: unknown. Parasitoids/Inquilines: Tetrastichinae (Eulophidae). Plant description: Vine, near by the mud pits. Tropical dry forest area. Trifoliate leaves with serrate margin and tendrils. On top of *Sweetenia*, barren, exposed. Location: Guanacaste, Liberia, Nacascolo. Santa Rosa National Park, start of the road to Naranjo Beach, old secondary growth area with clearings. Coordinates/Altitude: 10,83581 N 85,62347 W, 306 m; 10,83422222 N 85,6115 W, 569 m. Registry comments: First gall morphotype record for Guanacaste Conservation Area, Costa Rica, and the world.

From the 131 gall morphotypes recorded, the leaves were the organ with the largest number of galls with sixty-one percent (n=80), followed by stems (17.6%), and apical buds (6.9%) (Figure 10D). Eight different morphotype forms of galls were identified: conical, cylindrical, discoid, elliptical, fusiform, globular, irregular, and spherical. The most frequent gall shape was globular (*globulous*) (25.2%), followed by discoid (18.3%), irregular (14.5%), spherical (11.5%) and conical with 8.4%. The greatest number of gall shapes on leaves were discoid (30%), followed by irregular (17.5%), globular (15%), and spherical (14%) (Figure 10D). We also described six different types of gall epidermal texture: hairy, presence of trichomes, glabrous, soft spines, soft spines covered with hairs, and lignified. Fifty-nine percent of galls were glabrous, twenty-one percent were hairy and eighteen were lignified, which were among the most abundant. The most common epidermal texture on leaves was glabrous (77%), as well as hairy about 61%). Lignified epidermis (74% prevalence) was the most frequent texture on stems (Figure 10E). Green was the predominant color of galls, with 27%.

Except for 11 records, 120 of all recorded galls are new records for ACG, Costa Rica and the world. The collected plant gall morphotypes and their associated organisms from the Guanacaste Conservation Area, were characterized and recorded in a biological database within a specialized herbarium. We named this integrated herbarium a cecidiarium.

When we compare trichome-like structures and lignified external texture in the recorded gall morphotypes between the deciduous and evergreen forest (*Bosque Viejo*), 55% of the total morphotypes exhibit trichome-like structures and 43.5% has lignified texture in the evergreen forest. The chi-square test did not show significant statistical differences between the two types of forest for these two phenotypic variables ($p>0.05$, $\chi^2_{(\alpha=0,.05,\ df=1)=}$ 3.84).

Discussion

A large number of galling insects have been described in recent years and estimates clearly suggest that the number of species yet to be described could significantly exceed the number of known species (Espírito-Santo & Fernandes 2007). New gall morphotypes have been reported continuously, especially from Brazil, mainly as a consequence of an active community of researchers in that country.

Based on the reviewed literature, it appears that 120 morphotypes described and registered in this study are new records, not only for Costa Rica, but also for the world. Although samples were collected in the rainy season, when plants have a greater amount of green biomass, we estimate that the galls recorded here represent a small portion of the total plant galls present in the Guanacaste Conservation Area. This is based on the higher plant diversity and topographic characteristics of the AGC, as well as the difficulties in searching and obtaining samples from the canopy, particularly in tall trees like those in the *Bosque Viejo* (old forest). The canopy is the forest stratum with the greatest active growth, and so this is an area where it would be more probable to find galls. Additionally, many galls are hidden inside fruits and other plant organs such as roots (Ley-López et al. 2019), and the high plant density interferes with searching for and finding galls.

Most of the galling species in the Mexican tropical dry forest, for instance, occurred on trees and shrubs, with fewer on herbs and climbing plants (Cuevas-Reyes et al. 2014). For the ACG tropical dry forest, the panorama was similar, based on our results. Moreover, in the tropical dry forest of the Caatinga (Pernambuco, Brazil), most galls were induced on leaves (73.44%), stems (20.31%), and on apical buds (6.25%) (Santos et al. 2011b). These results were similar to data obtained for ACG, where 61% of galls were formed on leaves, followed by stems (17.6%), and on apical buds (6.9%) (Figure 10D). In contrast to the Caatinga, where the most frequent gall shape was spheroid (32.81%), followed by discoid with 25% (Santos et al. 2011b), for ACG the most frequent gall shape was globular (25.2%), but, the percentage of discoid galls was similar with 18.3% (the second one in frequency). Furthermore, glabrous epidermis shows the highest frequency in both tropical dry forests, with 78% for the Caatinga and 77% for the ACG, surprisingly similar values. Additionally, green was the predominant surface color of galls with 27% for ACG, while it was 73% for the Caatinga (Santos at al. 2011b). Moreover, as in the ACG, for the tropical dry forest of Parque da Sapucaia-Brazil (Costa & Araújo 2019), the plant family with the greatest richness of gall morphotypes was Fabaceae. Similarly, the most affected plant organ was the leaf (82.2%). Otherwise, globular (20.6%) and discoid (13.7%) were the most abundant gall shapes in the aforementioned study, which are comparable with the values for ACG (globular 25.2% and discoid with 18.3%). Glabrous was the predominant external texture with 82.7% and green the most frequent gall color (44.8%) in the tropical dry forest of Parque da Sapucaia, while in the ACG 59% of the galls were glabrous and 27% were green.

The presence of trichomes on gall epidermis ("hairy" or pilose) could be important due to the known properties of these anatomical structures in protecting plants against insect attack (especially the phytophagous insects), temperature regulation, and drought resistance by reducing water loss and moisture retention. Moreover, accumulated evidence suggests that trichomes can absorb UV radiation and reduce the damage by UV-B to photosystem II, preventing stomatal closure (Xiao et al. 2017). Lignins have been associated with plant mechanical support, growth, resistance to insect pests, temperature regulation, and drought tolerance, among other functions (Liu et al.2018). Leaving aside the hypothesis that tissue lignification protects the plant against natural enemies, in galls lignification has also been associated with water conduction (Guedes et al. 2019), as well as protection from UV and oxidative damages generated by excess light exposure and water deficiency (Detoni et al. 2011, Arriola et al. 2018). Our data from ACG shows that only 21% of morphotypes exhibit trichomes on the epidermis while 17.6% of gall morphotypes were lignified, which represents less than expected according to the adaptive advantages attributed to both phenotypic traits. Nevertheless, the lignified epidermis was the most frequent texture in stem galls with 74% (Figure 10E). Given the function that both anatomical traits could have as a selective response to abiotic conditions, when we compare the deciduous and evergreen forest (e.g. *Bosque Viejo*), our results contrast with what might be expected, since in the evergreen forest 55% of the total morphotypes showed trichome-like structures and 43.5% of all galls exhibit lignified external texture ($p>0.05$, $\chi^2_{(\alpha =0,.05,\ df=1)} = 3.84$). Hence, the values for these two phenotypic variables did not show significant statistical differences between the two types of forest. The role of lignified and trichome-covered galls in different biomes of the tropical dry forest are still open questions that should be studied in greater detail.

The low success rate in obtaining adult gall-inducers from a given sample can be explained by the lack of knowledge of insect and gall phenologies. The most practical way of increasing the success rate of rearing adults is probably by collecting the same gall morphotype throughout the year since many galls are seasonal. Furthermore, multiple samples would be needed from each plant species, a task that is frequently not possible because of the time and resources required.

In recent years new gall morphotypes are being reported continuously (Nieves-Aldrey et al. 2008, Hanson et al. 2014), Goetz et al. 2018, Araújo et al. 2019, Costa & Araújo 2019). The evidence from these new reports suggests that gall diversity is directly correlated with the richness of plant species in the areas under study (Cuevas-Reyes et al. 2014, Araújo 2017, Coelho et al. 2017). Thus, the previous assumption that gall diversity in tropical regions is less than that in xeric temperate regions is not sustainable considering the biodiversity in tropical ecosystems and the results of the latest studies on the diversity of galls in tropical regions. Cuevas-Reyes et al. (2004) found a significant positive correlation between gall-inducing insect species richness and plant species abundance in a Mexican tropical dry forest.

Given the above evidence that future inventories in tropical regions will continue to discover an increasing diversity of gall morphotypes, we proposed organizing the plant galls and associated organisms in a specialized herbarium. This allowed us to have wet and dry collections of plant samples, and preserved specimens of the organisms associated with the galls, in combination with physical records and digital databases providing detailed information about the collected morphotypes, including proper image registration. A detailed repository for the inventory will avoid failures in gall descriptions as well as prevent mixing samples and information from plant galls with other unrelated data. For instance, Ley-López et al. (2019), reported that around 25% of plant specimens previously recorded with galls in the herbarium were ambiguous as to whether the tissue alteration was a gall or not. The specialized herbarium established as a direct consequence of this research represents a unique kind of biological collection different from a traditional plant herbarium, and for this reason the name cecidiarium was suggested as a general concept for summarizing these types of biological records. Considering the diversity of plant galls, this effort represents an important reservoir of germplasm that should be conserved under proper conditions.

Despite the increasing number of new gall morphotypes being reported, some problems still remain beforeachieving a standardized classification. Problems include poor gall morphotype characterization, lack of referenced photos or poor quality images, and the non-existence of a standardized nomenclature. Here, we propose a standardized codification system for plant gall morphotype classification, with the aim of avoiding confusion in the registry of these structures. Gall morphotypes were named using the two first letters from the binomial scientific name of the host plant, followed by the numerical order in which they were discovered (Figures 2-10).

Detailed maps with geographic coordinates, altitudinal distribution, forest cover, and other data are useful tools for understanding the ecological context of gall occurrence. Therefore, georeferenced maps with an appropriate data will allow us to pinpoint and contrast host plant distribution with insect-inducer distribution and habitat (Figure 11).

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Author Contributions

Omar Gätjens-Boniche: substantial contribution in the concept and design of the study; contribution to data collection; contribution to data analysis and interpretation; contribution to the data registration and processing; obtained the financial support and wrote the article.

Paul Hanson: contribution in the concept and design of the study; contribution to critical revision, adding intellectual content; contribution to manuscript preparation; contribution to identify the inductor and insects associated with plant galls.

Marilyn Sanchez-Valverde: contribution to the data registration and processing; contribution to manuscript preparation.

Carla Trejos-Araya: contribution to data analysis and interpretation; contribution to critical revision; contribution to manuscript preparation.

Roberto Espinoza: substantial contribution in the taxonomic identifications of the host plants.

Adrian Pinto-Tomás: 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 article.

Ethics

Host plants and their galls were collected under the permission of the Comisión Nacional para la Gestión de la Biodiversidad (CONAGEBIO) of Costa Rica.

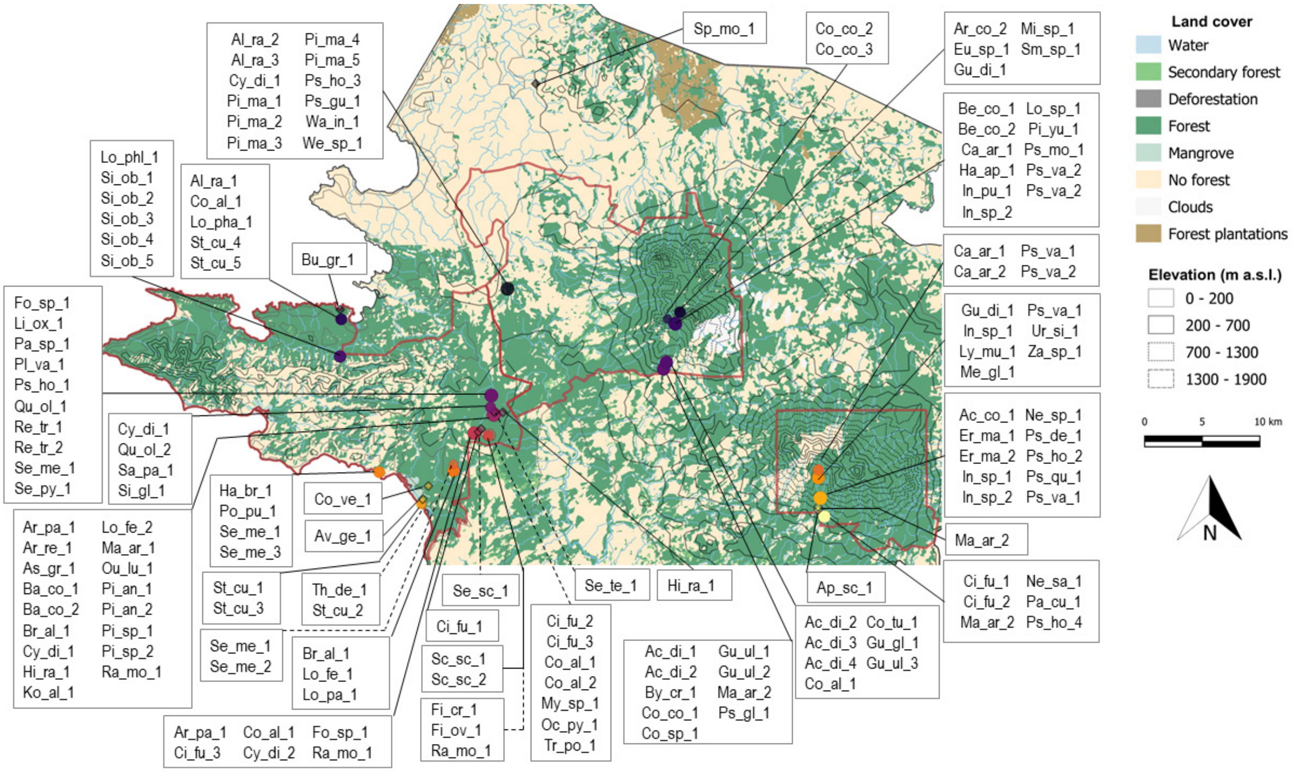

Figure 11. Spatial distribution of gall morphotypes collected in Área de Conservación Guanacaste (ACG), Guanacaste province, northwest region of Costa Rica. Diamond symbols represent sites were only one gall morphotype was collected. Circle symbols represent cluster sites where two or more gall morphotypes were found; circle diameters vary according to the number of gall morphotypes collected in this area. Larger circles mean that more gall morphotypes were found at a specific area. Cluster size varies between 5-400 linear meters.

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Long-term monitoring of marine turtle nests in northeastern Brazil

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Abstract: This study monitored marine turtle nests in a region known as the Potiguar Basin, which stretches from the northern region of Rio Grande do Norte State (5°4'1.15" S, 36°4'36.41" W) to eastern Ceará State (4°38'48.28" S, 37°32'52.08" W) in Brazil. We collected data from January 2011 to December 2019 to identify species of sea turtles that spawn in the basin, to analyze the nesting spatial-temporal pattern and nests characteristics, and to record effects of environmental and anthropic factors on nests. A field team examined sea turtle tracks and nests signs. Turtle clutches were monitored daily until hatchings emerged from the nests. We monitored nests of hawksbill (*Eretmochelys imbricata*; n = 238) and olive Ridley turtles (*Lepidochelys olivacea*; n = 103). The nesting season for *E. imbricata* occurred between December and May and for *L. olivacea* from March to August. Hawksbills had clutch size, incubation time, number of unhatched eggs, and dead hatchlings higher than olive Ridley turtles; nevertheless, they presented lower hatching success. Precipitation between 0 and 22 mm and relative humidity (RH) higher than 69% increased the hatching success rate for *E. imbricata*; however, rainfall above 11 mm and RH 64% had the same effect for *L. olivacea*. Signs of egg theft and human presence (e.g. vehicle traffic and plastic residues on the beach) were recorded and are considered threats to nests. The results of our long-term monitoring study in the Potiguar Basin provide basis for the implementation of mitigation measures and adoption of management policies at nesting beaches in this Brazilian region.

Keywords: *Eretmochelys imbricata; Lepidochelys olivacea; spawn; hatching success; threats.*

Monitoramento de longo prazo de ninhos de tartarugas marinhas no nordeste do Brasil

Resumo: Este estudo permitiu o monitoramento de ninhos de tartarugas marinhas em uma região conhecida como Bacia Potiguar, que se estende da região norte do Estado do Rio Grande do Norte (5 ° 4'1,15 "S, 36 ° 4'36,41" W) até o leste do Estado do Ceará (4 ° 38'48,28 "S, 37 ° 32'52,08" W), no Brasil. Coletamos dados de janeiro de 2011 a dezembro de 2019 com o objetivo de identificar as espécies de tartarugas marinhas que desovam na bacia, analisar o padrão espaço-temporal de nidificação, as características dos ninhos, e registrar os efeitos de fatores ambientais e antrópicos. Uma equipe de campo examinou rastros de tartarugas marinhas e sinais de ninhos. As ninhadas das tartarugas foram monitoradas diariamente até que os filhotes emergissem dos ninhos. Monitoramos ninhos de tartarugas-de-pente (*Eretmochelys imbricata*; n = 238) e tartarugas-oliva *(Lepidochelys olivacea*; n = 103). A época de nidificação para *E. imbricata* ocorreu entre dezembro e maio e para *L. olivacea* de março a agosto. Tartarugas-de-pente apresentaram maior tamanho das ninhadas, tempo de incubação, número de ovos não eclodidos e número de filhotes mortos quando comparado com tartarugas-oliva; no entanto, apresentaram menor sucesso de eclosão. Precipitação entre 0 e 22 mm e umidade relativa (UR) maior que 69% aumentaram a taxa de sucesso de eclosão para *E. imbricata*; entretanto, chuvas acima de 11 mm e UR 64% tiveram o mesmo efeito para *L. olivacea*. Sinais de roubo de ovos e presença humana (por exemplo, tráfego de veículos e resíduos de plástico na praia) foram registrados e são considerados ameaças aos ninhos. Os resultados do nosso estudo de monitoramento de longo prazo na Bacia Potiguar fornecem base para a implementação de medidas de mitigação e adoção de políticas públicas em praias de desova nesta região brasileira.

Palavras-chave: *Eretmochelys imbricata; Lepidochelys olivacea; spawn; hatching success; threats.*

Introduction

Sea turtle species are distributed around the globe throughout tropical, subtropical, and temperate oceans, migrating to and from their nesting beaches. There are seven sea turtles species and five of which are found in Brazil, namely hawksbill turtle (*Eretmochelys imbricata*: Linnaeus 1766), olive Ridley turtle (*Lepidochelys olivacea*: Eschscholtz 1829), loggerhead turtle (*Caretta caretta*: Linnaeus 1758), leatherback turtle (*Dermochelys coriacea*: Linnaeus 1766), and green turtle (*Chelonia mydas*: Linnaeus 1758) (Santos et al. 2011). According to the Red List of Threatened Species of the International Union for Conservation of Nature, sea turtles are classified as critically endangered (*E. imbricata*), vulnerable (*L. olivacea*, *C. caretta* and *D. coriacea*), and endangered (*C. mydas*) (Seminoff 2004, Abreu-Grobois & Plotkin 2008, Mortimer & Donnelly 2008, Wallace et al. 2013, Casale & Tucker 2017).

Sea turtles face many threats, and urban development and fisheries on the coast pose as the main ones, a condition that has continuously increased in last two decades (Carvalho et al. 2016). Incidental capture occurs in many fisheries in Brazil, leading to high mortality of adult females around nesting areas (Castilhos et al. 2011, Santos et al. 2011, Guebert et al. 2013). In the past, the hunting of females during nesting and the collection of turtle eggs for food reduced populations of hawksbill and olive Ridley sea turtles. For the hawksbill turtle, carapace commerce was the main threat (Castilhos et al. 2011, Marcovaldi et al. 2011).

In Brazil, sea turtles species use many important nesting areas. Hawksbill turtle nests mainly on the eastern coast of Rio Grande do Norte (RN) and the northern coast of Sergipe and Bahia. Olive Ridley turtle spawns on the southern coast of Alagoas and on the northern coast of Bahia. Loggerhead turtle nests on the coast in Sergipe and the northern coast of Bahia, Espírito Santo, and Rio de Janeiro. Leatherback turtle spawns on the coast of Piauí and the northern coast of Espírito Santo (Marcovaldi et al. 2007, Silva et al. 2007, Marcovaldi et al. 2011, Santos et al. 2011, Santana et al. 2016). Green turtles make their nests kilometers off the coast, on the Island of Trindade/Espírito Santo, Atol das Rocas Biological Reserve/Rio Grande do Norte, and Fernando de Noronha Archipelago/Pernambuco (Moreira et al. 1995, Bellini & Sanches 1996, Grossman et al. 2003).

Research conducted in different sites, considering regional environmental conditions and anthropogenic interaction, has revealed variation in nesting ecology, such as nesting season, clutch frequency, remigration intervals, size of nesting females, clutch size, incubation time, and hatching success (Richardson et al. 1999, Dornfeld et al. 2014, Santos et al. 2016, Chatting et al. 2018). In Brazil, studies have been carried out in the eastern portion of the coast of Rio Grande do Norte State (RN) to investigate the life cycle and nesting of sea turtles (Marcovaldi et al. 2007, Santos 2008, Santos et al. 2013, Santos et al. 2016). However, knowledge on nesting of sea turtles on the northern coast of RN is scarce, as previous studies focused on the breeding activity of hawksbill and olive Ridley sea turtles (Souza-Junior 2014, Costa et al. 2016).

Knowledge on the nesting ecology of sea turtles is useful for their conservation (e.g. beach coverage, monitoring of nesting females and their nests). This study aimed to: (1) survey sea turtle species that nest on the northern coast of RN and eastern coast of Ceará, (2) analyze the spatial-temporal pattern of nesting and characteristics of nests, and (3) record the effects of environmental and anthropic factors on the nesting of species that spawn in the region.

Materials and Methods

1. Study site

This study was carried out on the coastal region in the Brazilian northeast, between the municipalities of Caiçara do Norte, Rio Grande do Norte (RN) (5°4'1 .15" S, 36°4'36.41" W) and Icapui, Ceará (CE) (4°38'48.28" S and 37°32'52.08" W), a region known as the Potiguar Basin (Figure 1). The study site comprises crystalline basement rocks (Soares et al. 2003) and sand beaches, with different geomorphological and environmental characteristics along the extension monitored (approximately 300 km long). The main economic activities in Icapuí are tourism, artisanal fishing, and saliniculture, while in Caiçara do Norte, artisanal or professional fishing (depending on the beach), wind energy, and gas/petroleum exploration are the main economic activities. The climate in the region is semi-arid with varied humidity, low rainfall, and two well-defined seasons: dry (between June and January), with strong winds, and rainy (from February to May) (Jimenez et al. 1999, Testa & Bosence 1999, Souto 2009).

Since 2010, the Projeto Cetáceos da Costa Branca - Universidade do Estado do Rio Grande do Norte (PCCB-UERN) has conducted the Beach Monitoring Project in the Potiguar Basin (Projeto de Monitoramento de Praias da Bacia Potiguar – PMP-BP). The PMP-BP is part of an environmental constraint compliance enforced by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis - IBAMA (Brazilian Institute of the Environment and Renewable Natural Resources) for oil exploration by PETROBRAS (Petróleo Brasileiro S.A.; agreement number 2500.005657510.2).

2. Nesting ecology

We evaluated breeding biology and spatial-temporal distribution of nests by the number of nests and the turtle eggs recorded between January 2011

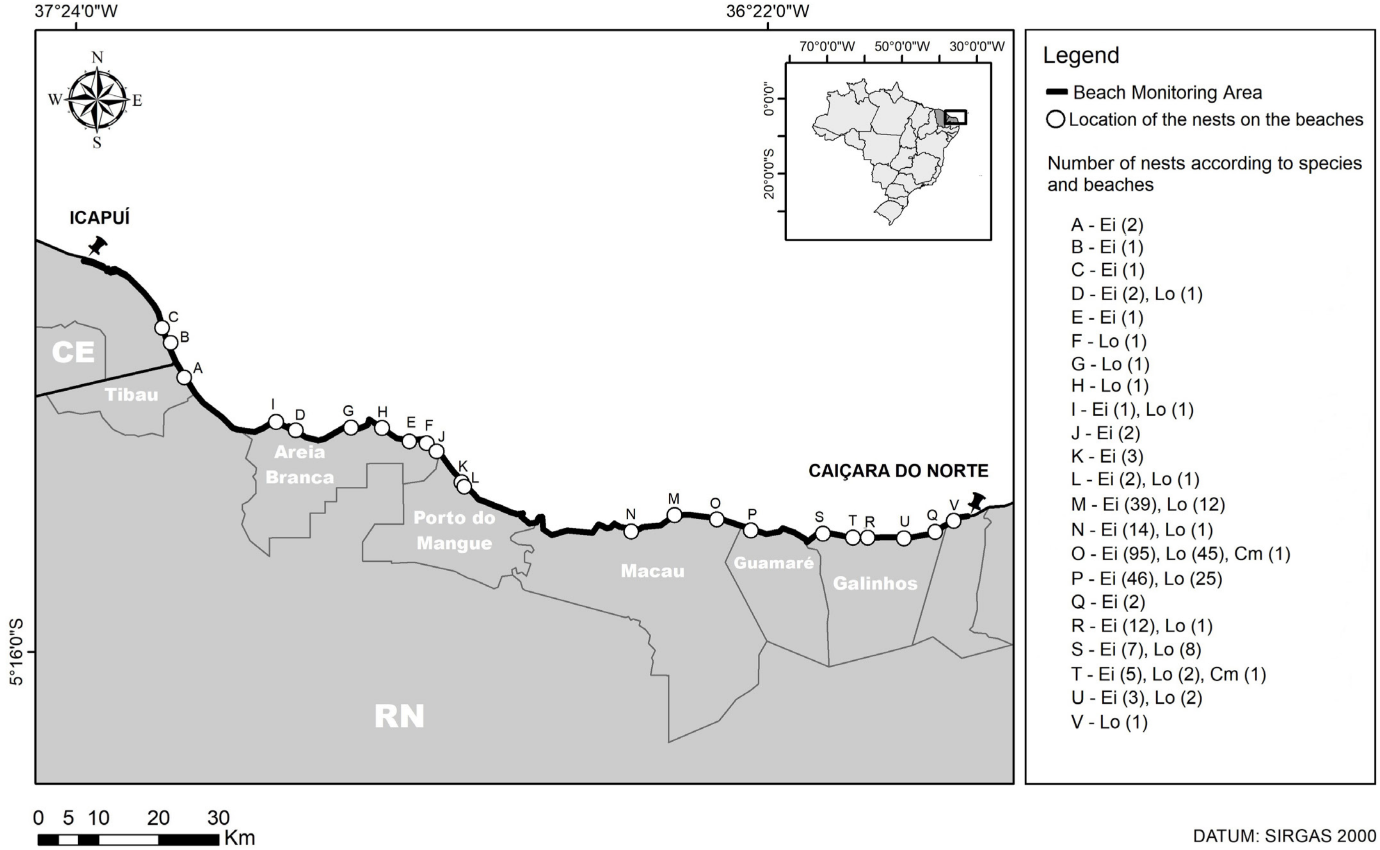

Figure 1. Geographic distribution of the study site, Brazilian northeastern coast. (Ei) *Eretmochelys imbricata*, (Lo) *Lepidochelys olivacea*, (Cm) *Chelonia mydas*, (A) Emanuelas Beach, (B) Manibu Beach, (C) Peixe Gordo Beach, (D) Baixa Grande Beach, (E) Mel de Baixo Beach, (F) Ponta do Mel Beach, (G) Redonda Beach, (H) São Cristóvão Beach, (I) Paraíso Beach, (J) Pedra Grande Beach, (K) Porto do Mangue Beach, (L) Rosado Beach, (M) Costa da Ponta do Tubarão, (N) Pontal dos Anjos Beach, (O) Restinga de Diogo Lopes, (P) Minhoto Beach, (Q) Fazenda Beach, (R) Dunas Beach, (S) Galinhos Beach, (T) Galos Beach, (U) Catavento Beach, (V) Caiçara do Norte Beach.

and December 2019. During the daily monitoring, our field team examined sea turtle tracks, and if the place looked like a nest, the site was excavated to determine presence of a turtle clutch. The static function of GPS was used to determine the nest position and a wood stake was fixed next to each nest to indicate its location. Daily monitoring was carried out to record possible damage to nests caused by human and erosion or stake loss. Eggs from some nests were excavated and moved to other sites to protect from vehicles and high tides. The nests were opened after incubation time (approximately 60 days) or when the field team found hatchling tracks on the beach. Species were identified according to Pritchard & Mortimer (2000). In this study, we analyzed characteristics of nests, types of nest site, nests depth, and distance from the highest tide line.

Characteristics of nests (from 2011 to 2019) adapted from Miller (1999): (a) clutch size: total number of eggs laid by turtles; (b) incubation time: from the day of egg laying until emergence of hatchlings, when we found tracks of hatchlings on the beach; (c) unhatched eggs: total number of unhatched eggs with no obvious embryo + unhatched eggs with obvious embryo; (d) dead hatchlings: total number of dead hatchlings found in nests; (e) live hatchlings: total number of live hatchlings found in nests + number of empty shells counted (>50% complete); and (f) hatching success = (total number of live hatchlings / clutch size) × 100.

Types of nest site (data from 2018 to 2019): defined as the distance of 50 cm from the nest center. The types were classified into three categories according to Santos et al. (2016): (a) vegetation, areas with herbaceous species; (b) open sand, presence of fine granular sand soil without any vegetation; and (c) sand slope, formations of sandbanks.

Nest depth (data from 2016 to 2019): measured at the bottom of the egg chamber after removal of nest contents according to Miller (1999).

Distance from the highest tide line (data from 2015 to 2019): measured according Santos et al. (2016) and defined as the distance from the nest to the mark of the highest tide, visualized as a line of marine detritus on the beach.

3. *Weather data*

Data on precipitation, relative humidity and air temperature for the study period was obtained from INMET (National Institute of Meteorology) (http://www.inmet.gov.br/portal/index.php?r=bdmep/bdmep accessed 13 Feb 2020).

4. *Anthropogenic interaction with nests and nesting activity*

We collected information on threats for 108 months considering the observations during the monitoring of PCCB-UERN, which included signs of egg theft. We also monitored light pollution, defined as the introduction of artificially produced light into nesting areas, and signs of human presence (e.g. vehicle traffic, plastic residue found on the beach) according to Lopez et al. (2015) and Fernandes et al. (2016).

5. *Statistical analyses*

Komolgorov-Smirnov and Levene tests were performed to verify distribution and homocedasticity, respectively. The Mann-Whitney test was used to compare results between *E. imbricata* and *L. olivacea* in terms of clutch size, incubation time, unhatched eggs, dead hatchlings, live hatchlings, and hatching success. Kruskal-Wallis and Bonferroni tests were applied to analyze spatial-temporal variations in the number of recorded nests.

The Kruskal-Wallis test was used to analyze the hatching success and incubation time during the months of the breeding season. The ANOVA and Kruskal-Wallis tests were performed to compare hatching success and incubation time between the nest sites. The Spearman rank correlation was used to correlate hatching success and incubation time with (1) depth nest, and (2) nest distance to the highest tide. We calculated the equation that represents the relation between hatching success and weather data (precipitation, relative humidity, and air temperature). The analyses were performed using IBM SPSS Statistics (version 20) and the results were considered significant at P-value < 0.05.

Results

1. *Spatial-temporal distribution and characteristics of the examined nests*

We recorded 692 nests during 108 months (January 2011- December 2019), namely 238 of *E. imbricata* (34.39%), 103 of *L. olivacea* (14.88%), two of *C. mydas* (0.29%), and 349 of species that could not be identified (50.43%). The non-identification occurred due to presence of unhatched eggs, egg removal by humans, erosion resulting in loss of nests, loss of wood stake fixed next to each nest to indicate its location, and absence of live or dead hatchlings whose could allow the species identification. Nests of green sea turtles, nests of non-identified species, and the nests transferred to protected areas accounted for 58.67% of the nests examined (406/692) and were excluded from the statistical analyses. Most nests of *E. imbricata* and *L. olivacea* were recorded between Macau/RN (207/341; 60.70%) and Guamaré/RN (71/341; 20.82%) along 46 km (Figure 2). There was significant statistical difference between the municipalities (Kruskal-Wallis test, *H*7 = 42.476, *P* < 0.001) and the number of nests in Macau differed from other municipalities, except from Guamaré (Bonferroni test). The nests of *C. mydas* were recorded in Restinga de Diogo Lopes, Macau/RN, on May 3, 2015 (70 eggs, incubation time = 48 days, and hatching success = 81.43%) and in Galos Beach, Galinhos/RN, on March 21, 2017 (74 eggs, incubation time = 58 days, and hatching success = 21.62%). Details of all data are shown in Table 1.

There was significant statistical difference in number of nests of *E. imbricata* (Kruskal-Wallis test, *H*11 = 51.021, *P* < 0.001) and *L. olivacea* (Kruskal-Wallis test *H*11 = 38.323, *P* < 0.001) between the months. The nesting season occurred between December and May with a peak of the nesting activity recorded in March for *E. imbricata* (n = 88, 36.97%) and from March to August for *L. olivacea* (n = 33, 32.04%; Figure 3), with higher nesting activity in May.

Only the nests kept *in situ* and that completed the incubation time were included in the statistical analyses (n = 278). *Eretmochelys imbricata* had higher clutch size (Mann-Whitney U test, *U* = 3.537, N1 = 184, N2 = 92, *P* < 0.001), incubation time (Mann-Whitney U test, *U* = 4.404, N1 = 165, N2 = 84, *P* < 0.001), number of unhatched eggs (Mann-Whitney U test, *U* = 5.671, N1 = 184, N2 = 92, *P* < 0.001), and dead hatchlings (Mann-Whitney U test, *U* = 6.876, N1 = 184, N2 = 91, *P* = 0.034) compared to *L. olivacea*. The number of live hatchlings was similar between these species (Mann-Whitney U test; *U* = 6.895, N1 = 183, N2 = 91, *P* = 0.064) and hatching success for *E. imbricata* was lower than for *L. olivacea* (Mann-Whitney U test; *U* = 9.324.5, N1 = 183, N2 = 92, *P* = 0.043; Table 1).

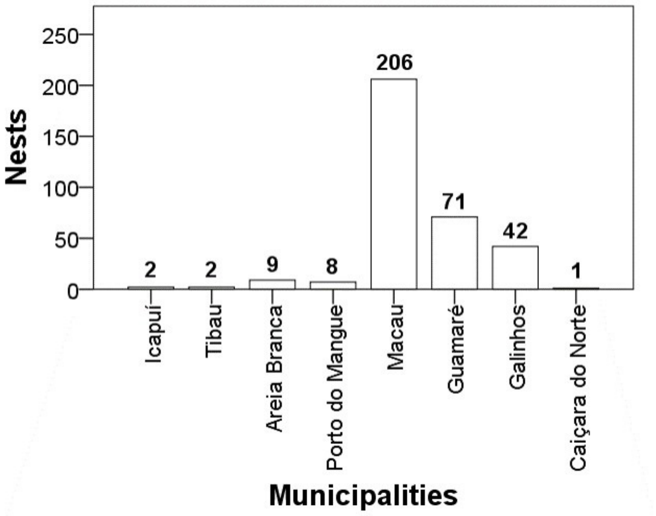

Figure 2. Number of nests of sea turtles (*Eretmochelys imbricata* and *Lepidochelys olivacea*) registered by municipalities in the Potiguar Basin, January 2011 – December 2019.

2. *Hatching success*

The highest hatching success rate was recorded in December for *E. imbricata* (67.07 ± 27.95%, n = 7) and in June for *L. olivacea* (79.17 ± 21.69%, n = 14). There was no statistical difference (Kruskal-Wallis test, *E. imbricata H*5 = 4.066, *P* = 0.540; *L. olivacea H*5 = 6.778, *P* = 0.238; Table 2).

The highest hatching success rate was recorded on sand slope for *E. imbricata* (62.82 ± 11.94%, n = 3) and under vegetation for *L. olivacea* (84.28 ± 20.89%, n = 4; Table S1). The ANOVA and Mann-Whitney U tests revealed similarity of the hatching success rate between nest sites of *E. imbricata* and *L. olivacea*: *F* (2, 26) = 0.145, *P* = 0.865; *U* = 73.000, *N*1 = 24, *N*2 = 4, *P* = 0.110, respectively.

Nests 30-39 cm deep presented higher hatching success rate (*E. imbricata* 58.22 ± 29.25%, n = 22; and *L. olivacea* 56.28 ± 29.53%, n = 20). There was no correlation between nest depth and hatching success rate (Spearman rank correlation, *E. imbricata* rs = 0.163, *N* = 60, *P* = 0.201; *L. olivacea* rs = -0.018, *N* = 33, *P* = 0.922). All results on nest depth are shown in Table S2.

Nests found between 49 and 70 m from the highest tide line presented higher hatching success rate for *E. imbricata* (57.78 ± 37.09%, n = 4; Spearman rank correlation, rs = -0.014, *N* = 71, *P* = 0.908) and between 5-25 m for *L. olivacea* (62.51 ± 31.77%, n = 40; Spearman rank correlation, rs = 0.055, *N* = 47, *P* = 0.712) (Table S3).

3. *Incubation time*

January represented the highest incubation time for *E. imbricata* (58.94 ± 2.14 days, n = 16), and March for *L. olivacea* (59.5 ± 0.71

Table 1. Characteristics of nests of hawksbill (Eretmochelys imbricata), olive Ridley (Lepidochelys olivacea), and green (Chelonia mydas) sea turtles according to our results and previous studies. n.r: not reported. *standard error.

Species	Clutch size	Incubation time	Unhatched eggs	Dead hatchlings	Live hatchlings	Hatching success rate	Refererence
	Mean ± Standard deviation; Median (Q1; Q3); Sample size (Range)						
Eretmochelys imbricata	121.75 ± 45.03; 127.0 (96; 154); 184 (2−222)	57.66 ± 3.36; 59.0 (55; 60); 165 (40−64)	36.14 ± 39.91; 20.0 (7; 58); 184 (0−160)	8.26 ± 17.32; 2.0 (0; 8); 184 (0−153)	68.41 ± 53.59; 63.0 (0; 113); 183 (0−183)	53.43 ± 33.81; 61.54 (17.91; 85); 183 (0−100)	Our study
	118.3 ± 23.6; n.r (n.r; n.r); 38 (70−196)	58.3 ± 3.3; n.r (n.r; n.r); 26 (50−63)	n.r	7 ± 11.7; n.r (n.r; n.r); n.r (n.r)	n.r	78.3 ± 18.7; n.r (n.r; n.r); 38 (14.3−98)	Camillo et al. (2009)
	144.77 ± 38.11; n.r (n.r; n.r); 9 (108−231)	54 ± n.r; n.r (n.r; n.r); 9 (50−58)	34.11 ± 28.20; n.r (n.r; n.r); 9 (3−100)	1.33 ± 1.93; n.r (n.r; n.r); 9 (0−6)	76.22 ± 48.25; n.r (n.r; n.r); 9 (17−161)	51.88 ± 27.36; n.r (n.r; n.r); 9 (94.73−12.4)	Simões et al. (2014)
	113.8 ± n.r; n.r (n.r; n.r); 356 (69−227)	55 ± n.r; n.r (n.r; n.r); 201 (40−67)	n.r	n.r	77.7 ± n.r; n.r (n.r; n.r); n.r (n.r)	65.6 ± n.r; n.r (n.r; n.r); n.r (45.9–68.6)	Moura et al. (2012)
	143 ± 27.6; n.r (n.r; n.r); 83 (41−207)	58 ± 3; n.r (n.r; n.r); 41 (51−66)	n.r	n.r	n.r	57.6 ± 31; n.r (n.r; n.r); 76 (0−97.4)	Santos (2008)
Lepidochelys olivacea	80.80 ± 31.69; 85.0 (60.5; 105); 92 (1−146)	55.19 ± 4.31; 54.0 (52; 60); 84 (43−63)	17.02 ± 22.65; 8.0 (2; 26); 92 (0−121)	5.89 ± 14.79; 1.0 (0; 4); 91 (0−91)	52.60 ± 34.42; 52.5 (24.5; 75); 91 (0−124)	61.55 ± 31.76; 71.3 (30.76; 91.09); 92 (0−100)	Our study
	100.1 ± 0.29*; 102 (n.r; n.r); 6,480 (4−182)	50.6 ± 0.1*; n.r (n.r; n.r); 453 (41−72)	n.r	n.r	n.r	80.2 ± 0.7*; 88.7 (n.r; n.r); 1,034 (0−100)	Silva et al. (2007)
	111.6 ± 26.38; n.r (n.r; n.r); 31 (n.r)	n.r	n.r	n.r	n.r	n.r	Marcovaldi & Laurent (1996)
	87.5 ± 33.6; n.r (n.r; n.r); 160 (n.r)	49.1 ± 3.6; n.r (n.r; n.r); 125 (n.r)	n.r	n.r	n.r	78.5 ± 23.4; n.r (n.r; n.r); 143 (n.r)	Dornfeld et al. (2014)
	98.5 ± 26.5; n.r (n.r; n.r); 38 (46−149)	n.r	n.r	n.r	n.r	81.7 ± 22.1; n.r (n.r; n.r); 26 (8.9−98.5)	Whiting et al. (2007)
Chelonia mydas	72 ± 2.83; n.r (n.r; n.r); 2 (70−74)	53 ± 7.07; n.r (n.r; n.r); 2 (48−58)	32.5 ± 27.58; n.r (n.r; n.r); 2 (13−52)	3 ± 4.24; n.r (n.r; n.r); 2 (0−6)	36.5 ± 28.99; n.r (n.r; n.r); 2 (16−57)	51.53 ± 42.29; n.r (n.r; n.r); 2 (21.62−81.43)	Our study
	111 ± 14.53; n.r (n.r; n.r); 3 (96−125)	51 ± 1.41; n.r (n.r; n.r); 2 (50−52)	n.r	n.r	n.r	85.4 ± 8.28; n.r (n.r; n.r); 3 (76−91.7)	Camillo et al. (2009)
	127.8 ± 28.19; n.r (n.r; n.r); 25 (n.r)	n.r	n.r	n.r	n.r	n.r	Marcovaldi & Laurent (1996)
	121.5 ± 28; 121 (n.r; n.r); 426 (19−211)	n.r	n.r	n.r	n.r	n.r	Bellini et al. (2013)
	n.r	53 ± n.r; n.r (n.r; n.r); n.r (n.r)	n.r	n.r	n.r	80.2 ± n.r; n.r (n.r; n.r); n.r (n.r)	Bellini & Sanches (1996)

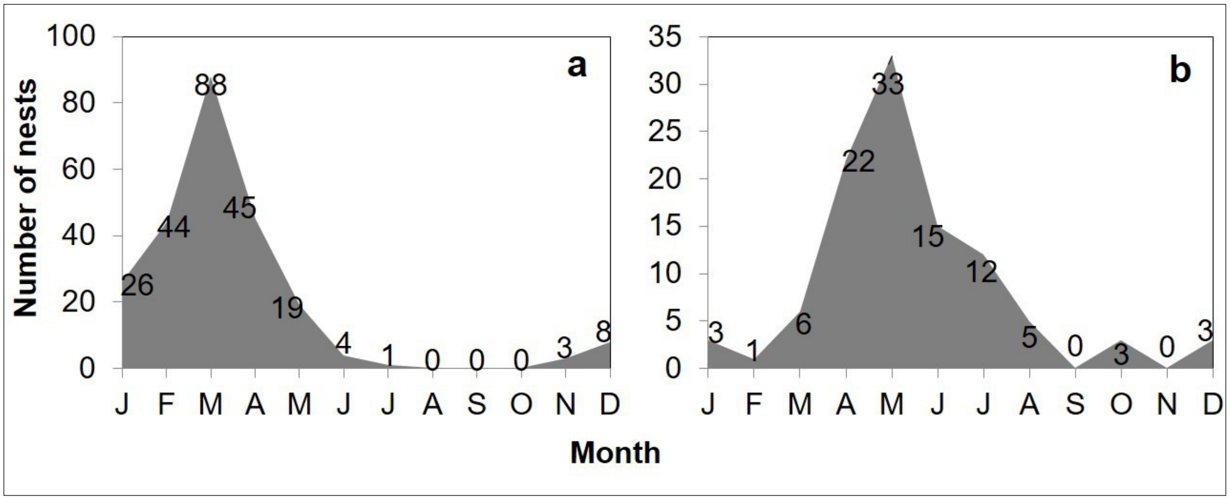

Figure 3. Number of nests of *Eretmochelys imbricata* (a) and *Lepidochelys olivacea* (b) recorded by months in the Potiguar Basin, January 2011 – December 2019.

Table 2. Hatching success rate and mean incubation time along the nesting season of hawksbill (Eretmochelys imbricata) and olive Ridley (Lepidochelys olivacea) sea turtles in the Potiguar Basin, January 2011 – December 2019.

Species	Month	Hatching success (%)			Incubation time (days)		
		Mean	Range	n	Mean	Range	n
Eretmochelys imbricata	December	67.07 ±27.95	17.56−96.11	7	55.86 ±4.38	50−62	7
	January	43.78 ±35.33	0.00−93.57	19	58.94 ±2.14	55−64	16
	February	56.87 ±32.59	0.00−100	36	57.67 ±3.32	48−63	33
	March	54.07 ±33.52	0.00−100	66	57.6 ±3.33	44−60	65
	April	48.17 ±35.64	0.00−98.41	37	57.48 ±2.74	52−61	31
	May	62.22 ±32.98	0.00−94.44	11	54.17±7.36	40−61	6
Lepidochelys olivacea	March	40.82 ±25.49	11.9−60	3	59.5 ±0.71	59−60	2
	April	61.39 ±30.90	0.00−100	18	54.65 ±4.91	44−60	17
	May	61.74 ±31.67	10.00−100	33	54 ±4.06	43−61	32
	June	79.17 ±21.69	30.26−99.2	14	56.62 ±2.90	53−62	13
	July	58.81 ±33.16	16.13−96.97	11	54.22 ±3.9	49−60	9
	August	63.13 ±30.57	17.5−94.23	5	54.2 ±5.4	49−63	5

days, n =2) (Table 2). The analysis revealed no statistical difference (Kruskal-Wallis test, *E. imbricata* $H5 = 4.076$, $P = 0.539$; *L. olivacea* $H5 = 6.818$, $P = 0.235$) between the monitored months (Table 2). Sand slope was the nest site with higher incubation time for *E. imbricata* (60 days for each three nests) and vegetation for *L. olivacea* (56.67 ± 3.06 days, n = 3). There was no statistical difference of nest sites for *E. imbricata* (Kruskal-Wallis test, $H2 = 0.384$, $P = 0.825$), and *L. olivacea* (Mann-Whitney U test, $U = 37.000$, $N1 = 23$, $N2 = 3$, $P = 0.880$). All results according to nest sites are shown in Table S1.

The highest incubation time was recorded in nests with 20-29 cm depth for *E. imbricata* (60 days for each nine nests) and between 40-49 cm depth for *L. olivacea* (60.5 ± 0.71 days, n = 2) (Table S2). There was no correlation between nest depth and incubation time (Spearman rank correlation, *E. imbricata* rs = 0.054, $N = 59$, $P = 0.606$; *L. olivacea* rs = 0.001, $N = 33$, $P = 0.997$). Nests found between 49-70 m from the highest tide line presented the highest incubation time for *E. imbricata* (59.75 ± 0.5 days, n = 4; Spearman rank correlation, rs = -0.041, $N = 70$, $P =$ 0.661) and between 26-46 m for *L. olivacea* (56.2 ± 4.15 days, n = 5; Spearman rank correlation, rs = -0.119, $N = 47$, $P = 0.427$) (Table S3).

4. *Weather data*

High precipitation and air relative humidity were recorded from January to May, with the highest value in February and March (2.27 ± 7.13 mm; 72.98 ± 7.17%, respectively). The warm season was between September and May and the highest temperatures were recorded in December (28.56 ± 0.72 °C) and January (28.54 ± 0.87 °C) (Figure 4).

Precipitation between 0 and 22 mm and humidity higher than 69% increased hatching success; however, its decrease was recorded over 22 mm (inflection point) and from 40% to 69% for *E. imbricata*. Regarding air temperature, hatching success increased between 28.5 °C and 31 °C (Figure 5a, b, c). For *L. olivacea*, the highest hatching success rate was recorded about 11 mm of rainfall and 64% of RH, with a decrease between 0-11 mm and at lower humidity (50%-64%). Temperatures

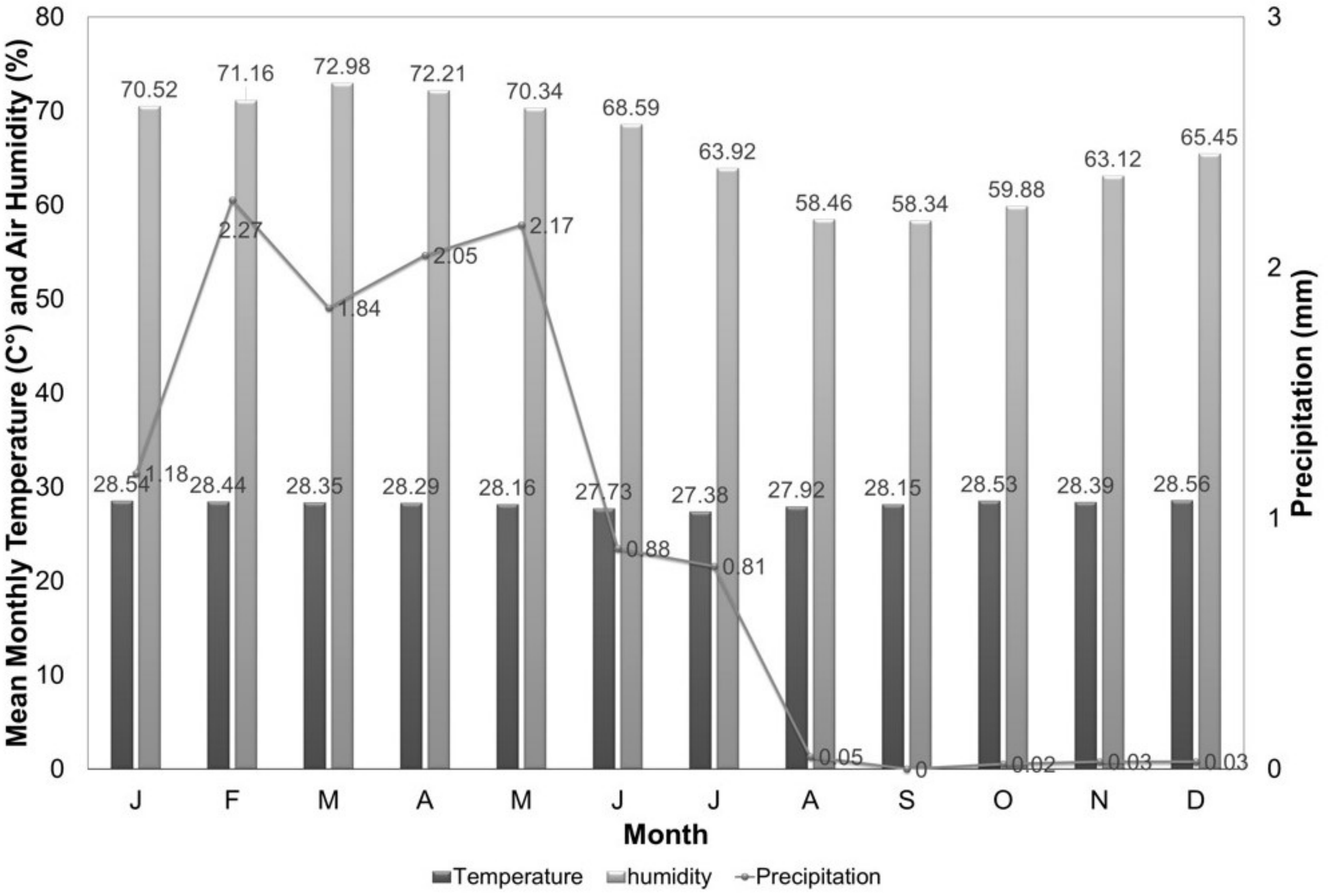

Figure 4. Monthly means of climatic conditions in the Potiguar Basin, January 2011 – December 2019. **Precipitation (mm), air humidity (%), and air temperature (°C).**

between 25 °C and 28 °C increased hatching success (with a decrease above 28 °C) (Figure 5d, e, f).

5. *Threats*

We recorded 16 nests with signs of eggs collection (egg theft). Two nests of olive Ridley and 14 of non-identified species, because the nests were totally empty (Figure 6a). High human predation was recorded during the five first years of our survey (68.75%; 11/16) with a decrease in the following years, probably due to the daily monitoring and environmental education carried out by PCCB-UERN. Non-formal environmental education campaigns have been carried out involving people who live in the study site in order to raise public awareness of sustainable interaction between human population and nature, under nature conservation perspective including subjects such as marine ecosystem and anthropogenic interactions.

The field team also found dead or alive hatchlings (Figure 6b), which were disoriented due to artificial lights in the nesting grounds due to the growing coastal development. Live and healthy hatchlings were delivered to the sea. The frequent presence of human on nesting grounds causes other threats, which were noted during monitoring, such as tracks of hatchlings associated to the vehicle tyre tracks on the sand, especially in Galinhos Beach (RN) (Figure 6c) and hatchlings tangled in nets or plastic residues (Figure 6d).

Discussion

Nests of *E. imbricata* and *L. olivacea* were not distributed uniformly along the coastal municipalities monitored and nests were deposited mainly on the beaches of Macau/RN and Guamaré/RN, with greater emphasis on the former. Areas of these municipalities are included in the Ponta do Tubarão State Sustainable Development Reserve (RDSEPT), which covers an area of 12,946.03 ha, 95% of its territory belonging to Macau and 5% to Guamaré. The RDSEPT comprises the estuarine system of the Tubarão River, Ponta do Tubarão, and the sandbank adjacent to the districts of Diogo Lopes and Barreiras, located in Macau (Dias & Salles 2006). Disposition of these environmental elements makes the coastal environment more protected, therefore we believe that the largest number of nests in this area is due to the absence of artificial lighting, as light pollution affects the spawning activity of marine turtles (Raymond 1984, Witherington 1992, Witherington & Frazer 2003, Brei et al. 2016, Sforza et al. 2017).

The reproductive season of *E. imbricata* in the Potiguar Basin was similar to that recorded on the coast of Bahia, Pernambuco, and eastern coast of the state of Rio Grande do Norte (Marcovaldi et al. 2007, Camillo et al. 2009, Moura et al. 2012, Simões et al. 2014). The reproductive season of *L. olivacea* lasted from March to August, with a peak in May, different from records from the coast of Sergipe and Bahia States (Silva et al. 2007), the region with most nests of this species in

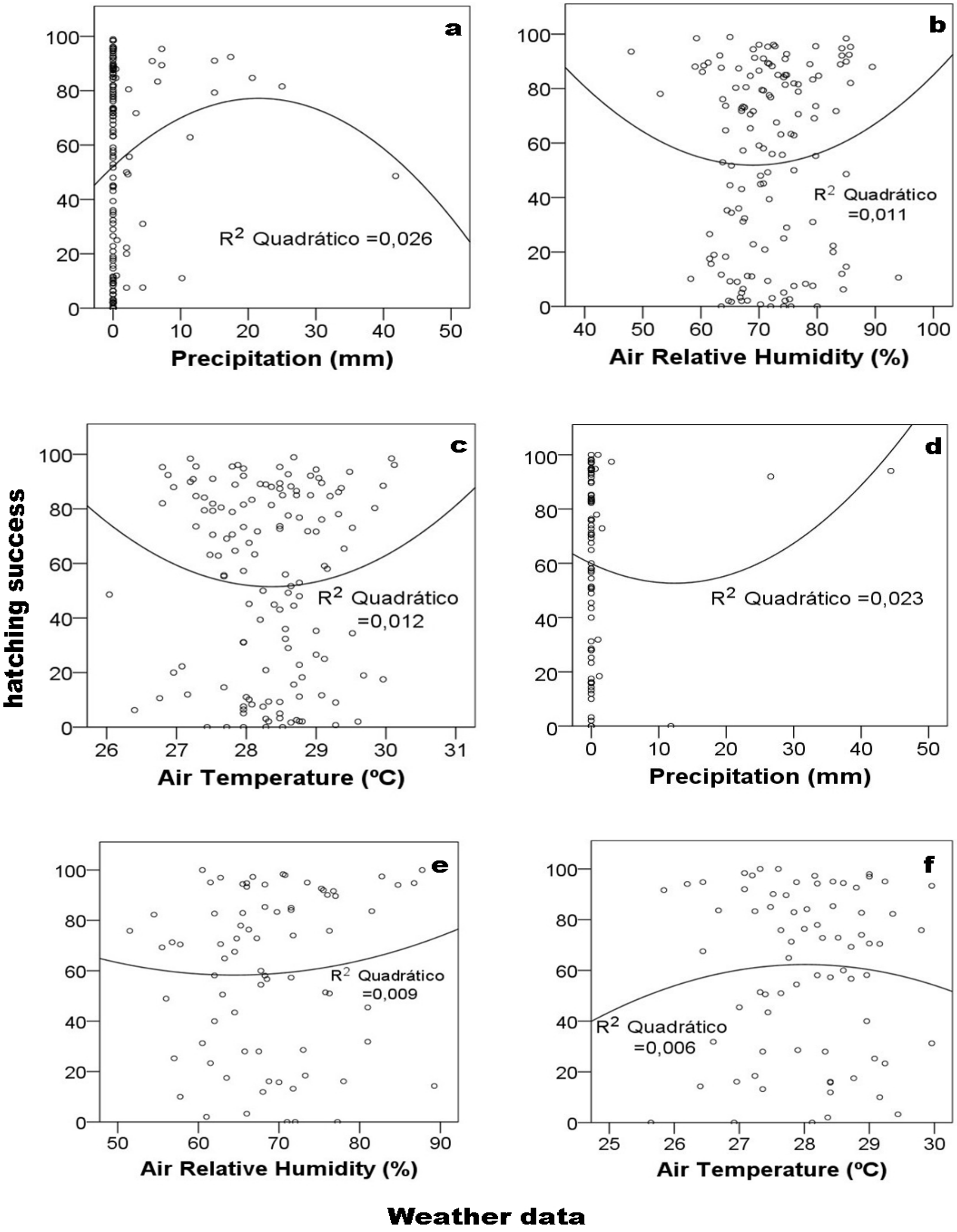

Figure 5. Means of precipitation, relative humidity, and air temperature in the Potiguar Basin, in 2011–2019, regarding hatching success of clutches of *Eretmochelys imbricata* (a, b, c) and *Lepidochelys olivacea* (d, e, f).

Brazil, where spawning begins in September and ends in March, peaking in December. This difference may be explained by the adaptation of *L. olivacea* to minimize interspecific competition in the same spawning area of *E. imbricata* by means of temporal displacement during the nesting season. A similar result was observed for the species *E. imbricata* and *C. caretta* on the southern coast of Bahia (Camillo et al. 2009).

Our results show that the hawksbill turtles that spawned in the Potiguar Basin had lower clutch size compared to results in previous

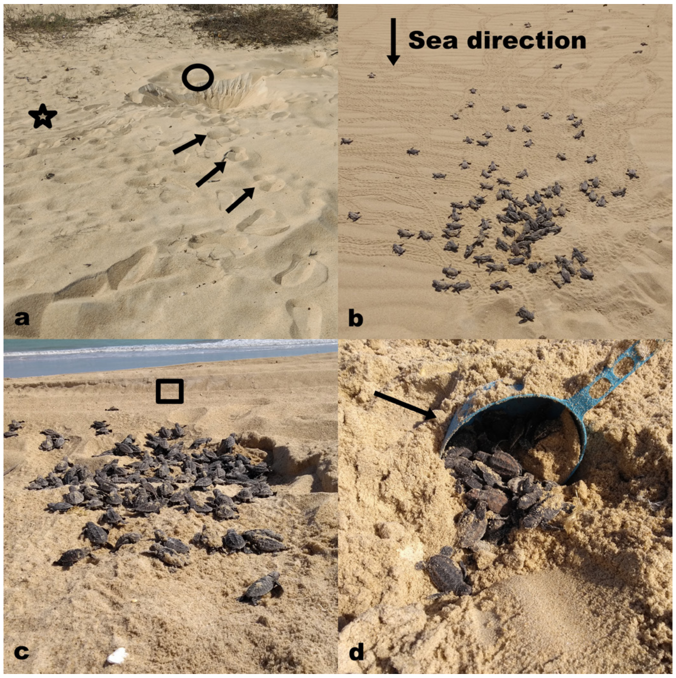

Figure 6. Threats to sea turtle nests and hatchlings in the Potiguar Basin, Brazil. (a) Nest registered on Aug 16, 2017, at Galinhos Beach, municipality of Galinhos/RN, with evidence of human predation: human footprints (arrows), sea turtle trail (star), and nest excavated for theft the eggs (circle), with only one egg left in place. (b) Disoriented hatchlings and in a direction contrary to the sea, registered on Feb 4, 2019, at Catavento Beach, municipality of Galinhos/RN. (c) Vehicle trail (square) as an obstacle/threat to hatchlings, registered on Feb 09, 2019, at Fazenda Beach, municipality of Galinhos/RN. (d) Hatchlings trapped in a domestic sieve registered on Dec 1, 2017, at Dunas Beach, municipality of Galinhos/RN.

studies on the eastern coast of RN and in Pernambuco (Santos 2008, Simões et al. 2014). On the other hand, hawksbill turtles showed higher clutch size compared to females that spawned on the southern coast of Bahia (Camillo et al. 2009). Nests of *E. imbricata* in the Potiguar Basin have more unhatched eggs and dead hatchlings and fewer live hatchlings when compared to nests monitored on the coast of Pernambuco (Simões et al. 2014, Moura et al. 2012). The incubation time was shorter than that found on the eastern coast of RN and southern Bahia (Santos 2008, Camillo et al. 2009).

Sea turtles of species *L. olivacea* that spawned in the Potiguar Basin had lower clutch size when compared to females that spawned in the states of Sergipe and Bahia in Brazil, in Playa Grande in Costa Rica, and in Cape Van Diemen in Australia (Marcovaldi & Laurant 1996, Silva et al. 2007, Whiting et al. 2007, Dornfeld et al. 2014). This species has two types of reproductive behavior. One is the independent (solitary) behavior and the other is called *arribada*, in which females behave in a synchronized and massive way (Dornfeld et al. 2014). Most studies have focused on nesting beaches with *arribada* behavior, even though the solitary behavior is the most common. Few studies evaluated the nesting of *L. olivacea* in Brazil, where independent reproductive behavior occurs, whose importance is evidenced for species conservation (Dornfeld et al. 2014).

The average hatching success rate recorded in the Potiguar Basin for *E. imbricata* and *L. olivacea* was lower than that obtained elsewhere in Brazil and in the world (Silva et al. 2007, Whiting et al. 2007, Santos 2008, Camillo et al. 2009, Moura et al. 2012, Dornfeld et al. 2014), indicating the vulnerability of these species in our study site. This may be related to environmental characteristics during the incubation period, which mainly influence temperature and humidity inside the nest (Ackerman 1997, Ferreira Jr 2009). Wave disturbances in the Campo dos Alísios (Pertubações Ondulatórias no Campo dos Alísios - POA) are important in the total rainfall of RN. The POA waves primarily affect the eastern coast of the Brazilian northeast. Therefore, the northern coast rarely has rain associated with this phenomenon and when precipitation occurs, it is much lower than that on the eastern coast, as the POA hit the eastern coast first, lose humidity, and only after, they reach the northern coast (Diniz & Pereira 2015). Sea and land breezes play an important role in the increase of total rainfall on the eastern coast of RN and have great importance to inhibit rainfall on the northern coast. On the northern coast, land breeze comes from the south, southeast, or southwest, and is responsible to push rain clouds off the coast, causing rains to fall on the Atlantic; thus, this portion of the RN coast is the driest stretch of the entire Brazilian coast (Diniz & Pereira 2015). Low rainfall in the region contributes to lower humidity and higher temperature, which can affect the hatching success rate of sea turtle nests.

The hawksbills monitored had larger clutch size, incubation time, number of unhatched eggs, and dead hatchlings compared to olive Ridley sea turtles. However, variation in clutch size, clutch frequency, breeding frequency, and remigration intervals have been observed in individuals of the same species, as recorded for loggerhead sea turtles that lay their eggs on the same beach, but use different foraging grounds with varied food availability (Hatase et al. 2013). Thus, differences in clutch size between the species of sea turtles could be explained by genetic characteristics of females and variation of their habitats (Tiwari & Bjorndal 2000, Gillis et al. 2008, Grayson et al. 2011). In addition, the clutch size is strongly associated with the body size of females, which varies between species and between populations (Van Buskirk & Crowder 1994, Broderick et al. 2003). Our results are in line with this knowledge, considering that hawksbills turtles have a larger body size when compared to the olive Ridley, as reported in previous studies (Marcovaldi et al. 1999, Silva et al. 2007).

Nest site types, depth, and distance from the highest tide line of hawksbill sea turtles nests did not differ statistically, although the nests on sand slope, 30-39 cm deep and 49-70 m from the highest tide line presented a higher hatching success rate. Other studies have also shown that nest depth of hawksbill turtles and green turtles does not influence the hatching success of these species (Zárate et al. 2013, Defever 2019). On the other hand, some studies reported an influence on hatchling and hatchery survival due to the relationship between nest temperature and egg chamber depth (Sarahaizad & Shahrul-Anuar 2014, Hill et al. 2015, Tomillo et al. 2017). We recorded hawksbill turtles spawning at a greater distance from the highest tide line (68 m) than on the eastern coast of RN (31 m; Santos et al. 2016) and in Barbados (22.5 m; Horrocks & Scott 1991). We found more nests of *E. imbricata* deposited in areas with open sand, corroborating previous studies on the eastern coast of RN (Santos et al. 2016); however, differing from the results obtained in the Caribbean, which showed more nests in an area with vegetation cover (Kamel & Mrosovsky 2006a, b). Nevertheless, open sand nests may be more exposed to the sun, leading to decreased hatching success. We recorded longer incubation periods in the nests located in the sand slope, which favors the development of embryos, despite the action of high tides (Marcovaldi et al. 2014).

Olive Ridley sea turtles nests on vegetation, with 30-39 cm deep and found between 5-25 m from the highest tide line, presented higher hatching success rate. However, we recorded a larger number of nests in open sand at 30-39 cm deep, similar to results reported in another study in Costa Rica (Drake et al. 2003). The spawning site has a major influence on the hatching success of turtles (Mrosovsky 1980). Comparisons between leatherback, green, and olive Ridley sea turtles revealed greater thermal stability for deeper leatherback nests (Tomillo et al. 2017). In our study, we observed that *L. olivacea* nests at 5-25 m from the highest tide line showed a tendency of greater hatching success, similar to observations of López-Castro et al. (2004), whose hatching success was greater for nests deposited between 10-30 m far from the high tide line.

Nests of *E. imbricata* showed greater hatching success and shorter incubation time at the beginning of the reproductive season (December), when precipitation is lower and humidity and air temperature is higher. On the other hand, nests of *L. olivacea* with the greatest hatching success were recorded in June, the end of the reproductive season and the period with the highest precipitation and humidity and lowest air temperature. Reproductive success and incubation duration for species that bury eggs, such as sea turtles, may vary depending on variations in ambient temperature, rainfall, relative humidity, sand particle size, and CO_2 and O_2 concentrations that act directly on the development of neonates (Webb & Cooper-Preston 1989, Ackerman 1997, Ferreira Jr et al. 2003, Ferreira Jr 2009, Tomillo et al. 2012).

Regarding the climatic conditions, we recorded an increase in the hatching success between 0 mm and 22 mm of precipitation for hawksbill sea turtles, while *L. olivacea* showed a higher hatching success from 11 mm onward. Our results corroborate with a previous study, whose results demonstrated that low rainfall was harmful for egg incubation and for hatchlings emerging from leatherback sea turtles nests (Tomillo et al. 2012). However, studies carried out in a hatchery in Playa Grande, Costa Rica, found a more prolonged effect of shading than water in reducing the temperature of *D. coriacea* nests (Hill et al. 2015). The hatching success was greater under relative humidity equals to or higher than 69% for *E. imbricata* and from 64% onward for *L. olivacea*. A similar result was obtained for nests of *C. caretta* in Florida (USA) (Lolavar & Wyneken 2020). We recorded an increase in hatching success from the inflection point of 28.5 °C to 31 °C for *E. imbricata* and between 25 °C and 28 °C for *L. olivacea*. However, from 28 °C onward, there was a decrease in the hatching success of eggs of Ridley sea turtles, differing from studies conducted in Costa Rica, which registered reductions from 31 °C and 32 °C onward (Dornfeld et al. 2014, Tomillo et al. 2017). Environment and nest temperatures are closely correlated (Márquez 1990); therefore, population resilience to climate warming may depend on the balance between temperatures to generate offspring also the temperature that reduces their survival.

Sea turtles, their nests, and their offspring are often exposed to different threats, such as urban development on the coast (Kamrowski et al. 2014, Lopez et al. 2015), pollution, (Farias et al. 2019, Soares et al. 2020), climate change (Tomillo et al. 2015, Reneker & Kamel 2016), and interaction with fishing (Castilhos et al. 2011, Guebert et al. 2013). Theft of eggs is an old threat and it still occurs today, as observed in our study site. The coastal development did not aggravate the old threats (e.g. egg poaching), but it has triggered new problems (Lopez et al. 2015). Currently, light pollution is one of the greatest threats to the survival of sea turtle hatchlings, especially in more densely populated areas. Artificial lights can disrupt the behavior of turtles to find the direction toward the sea, making them more susceptible to mortality due to exhaustion, dehydration, and predation (Kamrowski et al. 2014, Lopez et al. 2015). As stated by Santos et al. (2011), the vehicles can compact the sand where sea turtles laid their eggs hampering hatchlings out of the nests, and the vehicle trails make difficult the movement of the hatchlings to the sea become them more vulnerable to predation. Plastic waste on the beach and in the sea also interfere the hatchlings survival once they can trapped in this kind of residue, including fragments of fishing nets (Santos et al. 2011). In our study, many hatchlings were found under these conditions. To a lesser extent, we found offspring tracks associated to vehicle tracks on the beaches, as well as newborns entangled in fragments of fishing nets or plastic waste.

Intensive development in the coastal zones poses a risk to sea turtle populations when physical characteristics of the sea turtle spawning sites are modified by sand removal and beach nourishment. This affects egg chambers, hinders water absorption and the movement of newborns in the nests, changes the incubation temperature and gas exchange rates, interferes with sex ratio, and compromises the survival of eggs and hatchlings (Santos et al. 2011, Lopez et al. 2015). Such changes can turn the beach unfeasible for egg laying by females reducing the number of nesting sites, as mentioned by the National Action Plan for Sea Turtles Conservation (Plano de Ação Nacional para Conservação das Tartarugas Marinhas), (Santos et al. 2011).

Non-formal environmental education campaigns carried out by PCCB-UERN during the study period resulted in a decrease of egg removal by human after five years of our survey. According to Bizzo (2009), daily knowledge is considered during the teaching-learning process once people learn about this knowledge since they are very young. Therefore, activities involving all people (local residents, tourists and entrepreneurs) with different ages became necessary, especially in the areas of high relevance.

Our study revealed spawning of *E. imbricata* and *L. olivacea* in the Potiguar Basin and the municipalities of Macau/RN and Guamaré/RN were the prevailing breeding areas for these species. Successful incubation of sea turtles is important for the survival of these vulnerable species; thus, evaluation of factors related to the hatchlings survival in the study site are extremely important. Theft of eggs, light pollution, vehicle traffic, and plastic waste on the beaches are anthropic activities that influence the survival of hatchlings in the spawning sites. In addition, the distance traveled by the turtles for spawning is also critical information for the adoption of measures to protect the nesting sites. Therefore, protection of nesting sites increases genetic variability of populations and contributes to the conservation of sea turtles. Measures must be adopted to protect nesting habitats in the Potiguar Basin through effective coastal zone management plans that limit the use of artificial lights, buildings, and intense human presence in areas that overlap beaches with spawning sites of sea turtles in the basin studied. In addition, we suggest (1) a continuous environmental education program to raise public awareness (local residents, tourists and entrepreneurs) focused on beach conservation to ensure the nesting activities of sea turtles, and (2) a continuous monitoring program for the protection of females and hatchlings in order to reduce impacts on populations of hawksbill and olive Ridley sea turtles.

Supplementary material

The following online material is available for this article:

Table S1 - Hatching success rate and mean incubation time of hawksbill (*Eretmochelys imbricata*) and olive Ridley (*Lepidochelys olivacea*) sea turtles according to nest sites in the Potiguar Basin, January 2018 – December 2019.

Table S2 - Hatching success rate and mean incubation time according to the depth of nests of hawksbill (*Eretmochelys imbricata*) and olive Ridley (*Lepidochelys olivacea*) sea turtles in the Potiguar Basin, January 2016 – December 2019.

Table S3 - Hatching success rate and mean incubation time of nests of hawksbill (*Eretmochelys imbricata*) and olive Ridley (*Lepidochelys olivacea*) sea turtles according to the distance from the highest tide line in the Potiguar Basin, January 2015 – December 2019.

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Author Contributions

Aline da Costa Bomfim: 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.

Daniel Solon Dias de Farias: substantial contribution in the concept and design of the study; contribution to data collection; contribution to data analysis and interpretation; contribution to manuscript preparation.

Flávio José de Lima 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.

Silmara Rossi: contribution to data analysis and interpretation; contribution to manuscript preparation; contribution to critical revision, adding intellectual content.

Simone Almeida Gavilan: substantial contribution in the concept and design of the study; contribution to data collection; contribution to data analysis and interpretation; contribution to manuscript preparation.

Vinícius Gabriel da Silva Santana: contribution to data analysis and interpretation; contribution to manuscript preparation.

Cibele Soares Pontes: contribution to data analysis and interpretation; contribution to manuscript preparation; contribution to critical revision, adding intellectual content.

Conflicts of Interest

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

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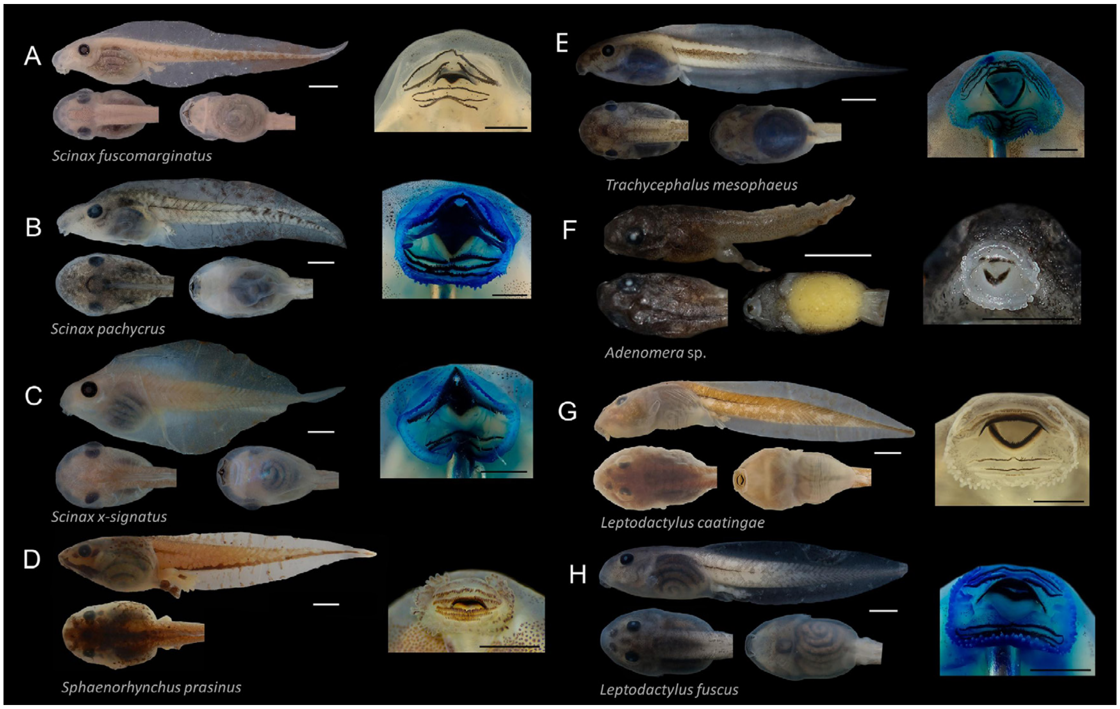
Erratum

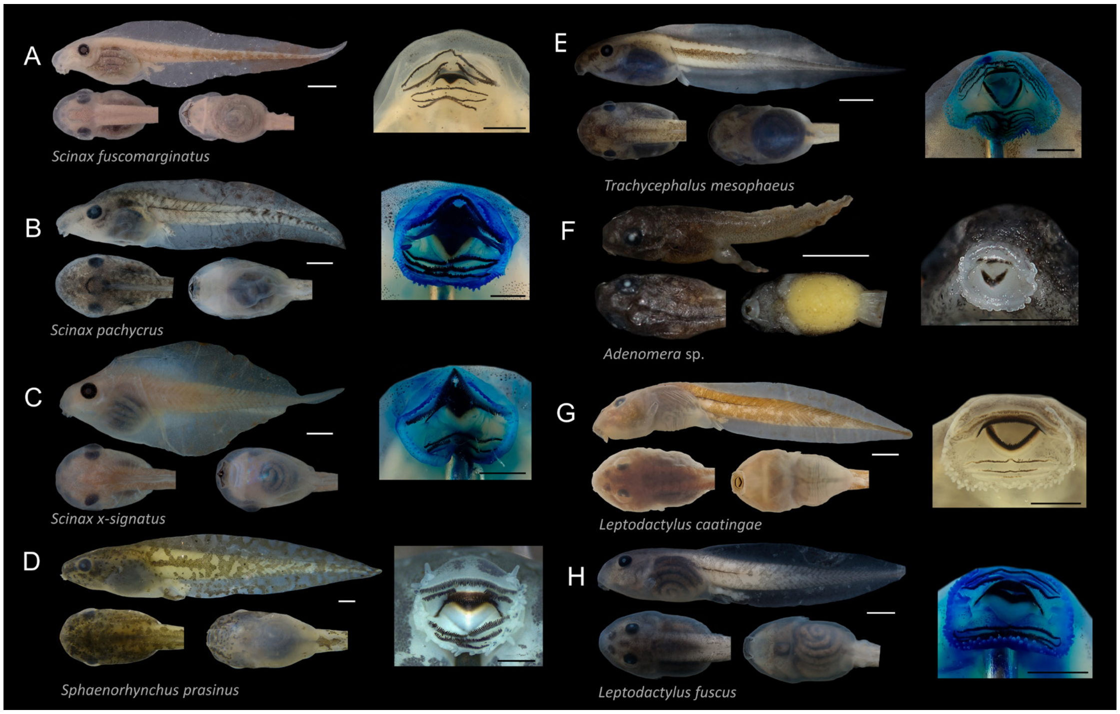
Erratum: Morphological characterization and taxonomic key of tadpoles (Amphibia: Anura) from the northern region of the Atlantic Forest

In the article “Morphological characterization and taxonomic key of tadpoles (Amphibia: Anura) from the northern region of the Atlantic Forest”, with the DOI code number: https://doi.org/10.1590/1676-0611-BN-2018-0718, published at Biota Neotropica 20(2): e20180718:

On page 10, where it was shown *Sphaenorhynchus prasinus* in Fig. 7D



Should see:



On page 11, where it was written:

Specimens examined. *Sphaenorhynchus prasinus*: MZUESC (these tadpoles were obtained in a recent sampling, right on with the closing of Universities during COVID-19 pandemic, preventing us from getting voucher numbers for these specimens, n =10, stages 33–38), municipality of Ilhéus, state of Bahia, Brazil.

Characteristics: Body ovoid in dorsal view, triangular-depressed in lateral view. Snout rounded in dorsal view, sloped in lateral view. Nostrils reniform, closer to tip of snout than to eyes. Eyes lateral. Oral disc anteroventral, not emarginate. Marginal papillae arranged ventrolaterally, with a wide dorsal gap, few large marginal papillae (highlighted papillae) on the anterolateral and posterolateral margins (large papillae about twice the size of the small papillae and alternating among them). LTRF 2(2)/3(1). Spiracle sinistral. Vent tube medial. Dorsal fin originating at tail-body junction, dorsal fin parallel to longitudinal axis of tail and ventral fin slightly arched. Tail length about 60% of total length, tail tip acute.

Should read:

Specimens examined. *Sphaenorhynchus prasinus*: MZUESC (these tadpoles were obtained in a recent sampling, right on with the closing of Universities during COVID-19 pandemic, preventing us from getting voucher numbers for these specimens, n =1, stage 36), municipality of Ilhéus, state of Bahia, Brazil.

Characteristics: Body elliptical-elongated in dorsal view, triangular-depressed in lateral view. Snout rounded in dorsal view, sloped in lateral view. Nostrils reniform, anteriorly positioned, much closer to tip of snout than to eyes. Eyes lateral. Oral disc anterior, not emarginate. Marginal papillae arranged ventrolaterally, with a wide dorsal gap, few large marginal papillae (highlighted papillae) on the anterolateral and posterolateral margins (large papillae about twice the size of the small papillae and alternating among them). LTRF 2(2)/3(1). Spiracle sinistral. Vent tube medial. Dorsal fin originating at tail-body junction, dorsal fin slightly arched and ventral fin parallel to longitudinal axis of tail. Tail length about 60% of total length, tail tip acute.

On page 17, where it was written:

24a. (23b) Presence of long marginal papillae interspersed by conical shorter ones (Fig. 11w), body ovoid in dorsal view (Fig. 2c), vent tube medial (Fig. 11ah) .... ***Sphaenorhynchus prasinus*** (Fig. 7d)
24b. Marginal papillae with similar size and shape, body elliptical or elliptical-elongated in dorsal view (Figs. 2a or 2b), vent tube dextral (Fig. 11ag) .... ***Scinax*** 25

Should read:

24a. (23b) Presence of long marginal papillae interspersed by conical shorter ones (Fig. 11w), vent tube medial (Fig. 11ah) ...***Sphaenorhynchus prasinus*** (Fig. 7d)
24b. Marginal papillae with similar size and shape, vent tube dextral (Fig. 11ag) .... ***Scinax*** 25

In Supplementary Material 2, where it was written:

24a. (23b) Presença de papilas marginais longas intercaladas por papilas mais curtas e cônicas (Fig. 11w), corpo ovóide em vista dorsal (Fig. 2c), tubo cloacal mediano (Fig. 11ah)... ***Sphaenorhynchus prasinus*** (Fig. 7d)
24b. Papilas marginais com tamanho e formato semelhantes, corpo elíptico ou elíptico-alongado em vista dorsal (Figs. 2a ou 2b), tubo cloacal destral (Fig. 11ag) .... ***Scinax*** 25

Should read:

24a. (23b) Presença de papilas marginais longas intercaladas por papilas mais curtas e cônicas (Fig. 11w), tubo cloacal mediano (Fig. 11ah) .... ***Sphaenorhynchus prasinus*** (Fig. 7d)
24b. Papilas marginais com tamanho e formato semelhantes, tubo cloacal destral (Fig. 11ag) .... ***Scinax*** 25

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Article

Diversity of longhorned beetles (Coleoptera: Cerambycidae) in the Caribbean region of Colombia: temporal variation between two fragments of tropical dry forest

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Abstract: The tropical dry forest is under constant threat from many anthropic activities which are conducted indiscriminately, modifying the forest, and therefore, affecting species that are closely related to its phenology, such as longhorned beetles (Cerambycidae). The spatio-temporal variation of the cerambycid diversity in two fragments of tropical dry forest (Reserva Campesina la Montaña and La Flecha) in the Caribbean region of Colombia was analyzed. At each locality, four squared plots were delimited, and the beetles were collected with fruit traps, beating sheets and manual capture, and with light traps in the center. Five hundred eighty-seven specimens representing 128 species were collected, of which members of the tribe Ectenessini (Cerambycinae) were the most abundant. At the subfamily level, Cerambycinae was the most abundant (465 specimens) and diverse (73 species), followed by Lamiinae and Prioninae. The highest values of richness (110 species), abundance (428), biomass (21.18 g), and as well as the highest values of true diversity (1D= 73.44, 2D= 34.30) were found during the first precipitations. Regarding beta diversity, temporal variation was determined and mainly explained by a high percentage of turnover (> 70%). Lastly, the high diversity of Cerambycidae was associated with high values of relative humidity and canopy cover during the rainy season. This showed that the structure of the cerambycid community in the tropical dry forest of the Caribbean region of Colombia depends on these variables, which are closely related to precipitation.
Keywords: *Abundance; biomass; cerambycid; Neotropical; richness, structure.*

Diversidade de besouros serra-pau (Coleoptera: Cerambycidae) na região caribenha da Colômbia: variação temporal entre dois fragmentos de floresta seca tropical

Resumo: A floresta seca tropical está sob constante ameaça devido às muitas atividades antrópicas que são realizadas indiscriminadamente, modificando a floresta e, portanto, afetando espécies que se encontram muito relacionadas com a sua fenologia, tais como os besouros serra-pau (Cerambycidae). Foi analisada a variação espaço-temporal da diversidade de cerambícidos em dois fragmentos de floresta seca tropical (“Reserva campesina La Montaña e La Flecha”) na região caribenha da Colômbia. Em cada localidade, quatro quadrantes foram delimitados e os besouros foram coletados usando armadilhas com isca de fruta, guarda-chuva entomológico, captura manual e armadilhas de luz. Quinhentos e oitenta e sete espécimes, de 128 espécies foram coletados, sendo os membros da tribo Ectenessini (Cerambycinae) os mais abundantes. Ao nível de subfamília, Cerambycinae foi a mais abundante (465 espécimes) e diversa (73 espécies), seguida de Lamiinae e Prioninae. Os valores mais altos de riqueza (110 espécies), abundância (428) e biomassa (21.18 g) foram encontrados durante as primeiras chuvas, assim como os valores mais altos de diversidade verdadeira (1D= 73.44, 2D= 34.30). Em relação à diversidade beta, a variação temporal foi determinada e principalmente explicada por uma alta porcentagem de substituição (> 70%). Por último, uma alta diversidade de Cerambycidae foi associada com altos valores de humidade relativa e cobertura vegetal durante a temporada de chuva, mostrando que a estrutura da comunidade de Cerambycidae na floresta seca tropical da Colômbia depende dessas variáveis, as quais são muito relacionadas com a precipitação.
Palavras-chave: *Abundância; biomassa; cerambicídeos; Neotropical; riqueza; estrutura.*

Introduction

Originally in Colombia, the tropical dry forest (TDF) was very extensive, but today it has been reduced to less than 10% of its original area, of which only about 5% is under protection (Rodríguez et al. 2012, Pizano & García 2014). The departments with the highest TDF coverage in Colombia are in the Caribbean region (Acevedo 2016), where Atlántico and Bolívar stand out with the highest percentages (5,7% and 4,1%, respectively) (Otero et al. 2006, Pizano & García 2014). Tropical dry forest in these departments is represented by small fragments isolated from each other, surrounded by agricultural ecosystems, pastures, living fences, paths, and plantations (Otero et al. 2006, Rangel & Martínez 2017). However, these fragments provide habitat, resources, and specific environmental conditions for native fauna, constituting an important refuge and biodiversity reserve (Kattan & Álvarez-López 1996, Otero et al. 2006, Rangel & Martínez, 2017).

In order to conserve this ecosystem it is critical to know the temporal dynamics of the diversity of groups of great importance such as the longhorned beetles (Coleoptera: Cerambycidae), due to their high sensitivity to the changes in the floristic composition caused by the alteration of environmental variables, such as temperature, thermal radiation, and relative humidity (Bouget 2005, Baselga 2008), from one season to another. This sensitivity results from a decrease in the availability of host plants for cerambycid species, as well as a reduction in resources and reproduction sites (Hjältén et al. 2012) negatively altering the distribution, taxonomic composition, and diversity of the family (Maeto et al. 2002). Lastly, factors such as climate change, which is constantly affecting the TDF in the Caribbean region of Colombia (Miles et al. 2006), produces high mortality of cerambycid larvae and decreases species diversity (Haack et al. 2017). Also, it is important to know the dynamics of these beetles as they perform ecological functions such as secondary pollination (Maeto et al. 2002) and decomposition of senescent and dead trees, contributing to the cycle of minerals and nutrients into the soil (Martínez 2000, Noguera 2014).

The structure and spatial variation of the cerambycid community is not expected to change because tropical dry forest in most of the Caribbean region of Colombia are very similar in their general characteristics (Otero et al. 2006), and offer a vegetal diversity favorable to the development of these beetles, which are closely related to the type of the forest and the size, development, and composition of the vegetation in a delimited area (Meng et al. 2013, Sataral et al. 2015, Sugiarto et al. 2016).

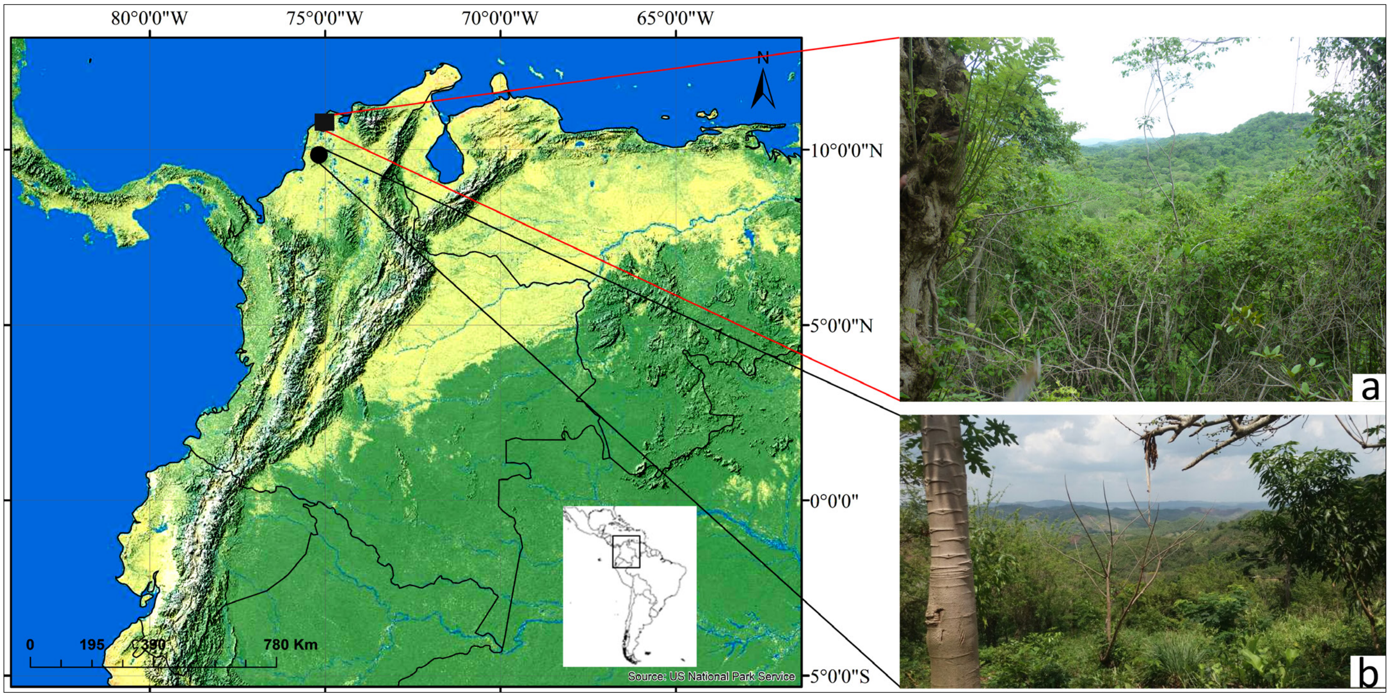
Accordingly, our hypothesis for this study was that the community structure should present a marked seasonality due to the close relationship between Cerambycidae and the phenology of TDF in the Caribbean region of Colombia. To test our hypothesis we analyzed the temporal variation of the community of longhorned beetles in two fragments of TDF (Reserva Campesina La Montaña and Reserva La Flecha) in the Caribbean region of Colombia.

Materials and Methods

1. Study area

Two fragments of TDF in the Caribbean of Colombia were chosen: Reserva Campesina la Montaña (RCM), located in the department of Atlántico, and Reserva La Flecha (RLF), in the department of Bolívar (Figure 1).

The RCM is located around the coordinates 10° 46' 2.6" N, 75° 0.2' 34" W, at an altitude between 150 and 260 m (Vargas et al. 2015). The average temperature is 27°C and the relative humidity around 62% (García-Atencia & Martínez-Hernández 2015). The rainy season runs from April to November and the dry season from December to March (Rangel-Ch & Carvajal-Cogollo 2012). This fragment comprises 47 ha (Figure 1a) that are surrounded by farms, felling activities and controlled burning, which have disturbed the original forest cover in recent years (García-Atencia & Martínez-Hernández 2015). According to Holdridge's (1978) classification, the vegetation is hygrotrophophytic, losing most of the canopy layer during the dry season.



Source: US National Park Service

Figure 1. Study Area. a. Reserva Campesina la Montaña (RCM), Atlántico (square); b. Reserva La Flecha (RLF), Bolívar (circle). Adapted from García-L, Nascimento & Martínez-Hernández (2019).

The RLF is located at the median part of the Caribe plain, around the coordinates 09° 51' 12.4" N, 75° 10' 41.4" W, at an altitude between 324 and 500 m. The average temperature is 25°C and the relative humidity 75%. The rainfall regime is bimodal, with a period of intense drought between December and March, and the rainy season from April to June and from August to November (approx. 25 mm/month) (Rangel-Ch & Carvajal-Cogollo 2012). This fragment comprises 149 ha (Figure 1b) and is also surrounded by pastures, annual and perennial crops, and plant succession areas. These activities, such as burning, cutting trees and livestock grazing have caused a decrease of this forest, making this region a priority to become a protected area (Pizano & García 2014). According to Holdridge's (1978) classification, the vegetation is subhigrophic, whereby the evergreen vegetation is present (Villareal et al. 2019).

2. *Sampling design*

At each fragment, we performed four samplings: two during the dry season (0 mm/month), one in February and the second one in March, and two in the rainy season (150-280 mm/month), one in April/May and the second one in June. Each sampling lasted eight days, four days in one locality, and the next four days in the other. At each locality, four squared plots of 50x50 m were delimited, 350 m from each other (Figure 2). A point was placed on each vertex of the square plot (four points/plot), where the Cerambycidae were collected with fruit-baited traps (F.T), beating sheet (B.S) and manual capture (M.C). In the center, a fifth point was marked, where a light trap (L.T) was installed.

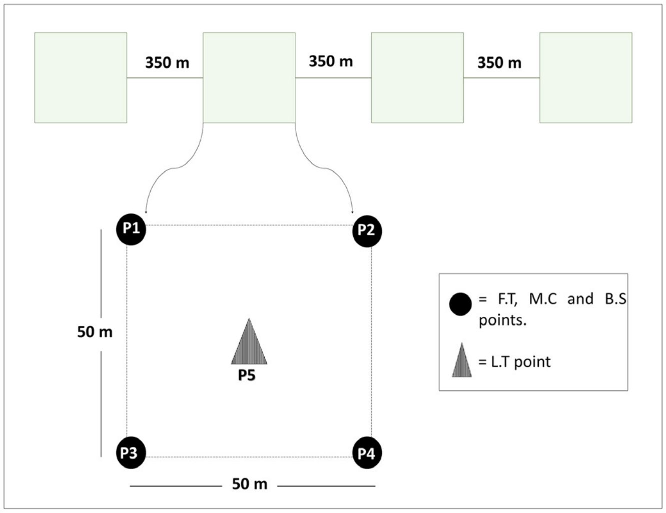


Figure 2. Sampling design and position of each technique point.

The F.T consisted of a cylindrical receptacle with two plastic funnels (diameter: 6 cm) positioned on the lateral margin of the trap, projected inward (Supplementary Material 1A). Inside the receptacle, an attractant (fermenting fruit) was included, which contained ripe banana (from the plant *Musa paradisiaca* L.), red wine, vanilla essence, and raw cane sugar. The F.T were placed at an elevation between 2-4 m, remained in the field for 48 hours, and were checked every 24 hours. The B.S was conducted with a wooden mallet and a fabric sheet (diameter: 80 cm, depth: 13 cm) (Supplementary Material 1B). This technique was performed with an intensity of 80 beats per point, at a distance of 10 m from the central point. The B.S sampling was conducted during the day, focusing on bushes, flowers, and small trees. The M.C sampling was conducted during the day and night, with an intensity of 20 minutes per point (Supplementary Material 1C), focusing on foliage, bark of trees, wood, flowers, and fruits. The L.T consisted of a rectangular acrylic sheet (30x50 cm), with a lamp on each side (two plots with white lights, and two with UV lights). A collection receptacle was placed under the acrylic sheet with a solution of alcohol (70%), salt and detergent (Supplementary Material 1D). The L.T were turned on at 6 pm, only on new moon nights.

The environmental parameters were measured with an Extech (RHT10) datalogger placed at the center of each square plot (to record ambient temperature and relative humidity), and a Hellman rain meter at each sampling site to register daily precipitation (mm^3) at each season. The canopy cover was measured with a spherical crown densitometer, according to Valdez et al. (2006).

The specimens are deposited in the entomological collection of the Universidad del Atlántico, Colombia (UARC), of the Pontificia Universidad Javeriana (MPUJ) and the Museu de Zoologia da Universidade de São Paulo, Brazil (MZSP).

3. *Data analysis*

Cerambycid richness was calculated as the number of species captured by season and fragment. Abundance was determined as the number of individuals of each species. For biomass analysis, 10 random individuals of each species were selected. These were dried for 20 days under an incandescent lamp (Cancino et al. 2014). Later, we calculated the average weight of one individual with a portable electronic scale (Model Ohaus Adventurer of 220 g ± 0.00001) and multiplied by the total number of specimens per species to obtain biomass data.

These variables were compared, between localities and seasons, with the non-parametric analysis Kruskal-Wallis and a Mann-Whitney pairwise comparison to calculate the statistical significance *a posteriori*. This analysis was conducted with the software PAST version 2.17 b (Hammer et al. 2001). To represent richness, equitability, and relative abundance by season and fragment, a range-abundance curve was developed (Whittaker 1965). The biomass was also included in this curve (Trapero & Reyes 2017). These analyses were performed with the software PRIMER 6.0 (Clarke & Gorley 2006) and MS Excel.

Alfa diversity was estimated as "true diversity" using the effective numbers of species, according to the diversity orders *sensu* Jost (2006) (^0D, ^1D and ^2D). This analysis was performed with the software iNEXT version 1.3.0 (Chao et al. 2014). Following Baselga (2010), the proportion of the components of *beta* diversity (B_{sor}): nestedness (B_{nes}) and turnover (B_{sim}), between season-fragments, were calculated with the software *Betapart package* (Baselga & Orme 2012).

We also conducted a non-metric multidimensional scaling analysis (*nMDS*) to explore spatial and temporal patterns of the community (Bray & Curtis 1957, Meng et al. 2013). Previously, data were transformed into $\log_e (x+1)$ and a Bray-Curtis similarity matrix was produced. To establish if the patterns obtained in the *nMDS* were significant, an ANOSIM test ($p < 0.05$) was performed (Meng et al. 2013). These statistics were generated with the software PRIMER 6.0 (Clarke & Gorley 2006). Lastly, a Canonical Correspondence Analysis (CCA) (Ter-Braak 1986) was performed to determine the relation between the relative abundance of each species and the environmental variables. The singleton specimens were eliminated to increase precision. This analysis was performed with the software R and the packages MASS (Venables & Ripley 2002) and VEGAN (Oksanen et al. 2017).

Results

1. Composition of Cerambycidae species

A total of 587 specimens from three subfamilies, 30 tribes and 128 morpho-species were collected, of which 115 were identified to species, eight to generic level, and 5 to tribal level (Supplementary Material 2). At the RCM we collected 81 species from 22 tribes, and at the RLF we collected 78 species from 23 tribes. The subfamily Cerambycinae was the most abundant and rich, representing 79.22% of the total number of specimens and 57.03% of the species, followed by Lamiinae with 19.6% of the abundance and 39.85% of the richness, and lastly the subfamily Prioninae, with just 1.19% of the abundance and 3.12% of the total amount of species.

In Cerambycinae, the highest number of species and specimens were registered for Elaphidiini, followed by Hexoplonini, Eburiini and Neoibidionini. In Lamiinae, the most represented tribes were Acanthoderini and Acanthocinini. In the subfamily Prioninae, all four species belong to Macrotomini (Supplementary Material 2).

2. Richness, abundance and biomass of Cerambycidae

During the rainy season, the highest value of richness (S= 110) was registered, very distinct from the dry season (S= 30). The Kruskal-Wallis test determined that there is statistical significance in the richness between seasons, and the Mann-Whitney test allowed us to establish that these differences are mainly between the rainy season in the RCM and the dry season in both fragments (Supplementary Material 2). Regarding the abundance, in the RCM we collected 328 specimens (114 during the dry season and 214 during the rainy season), while in the RLF we registered 259 specimens (45 in dry season and 214 during the rainy season). Lastly, the highest biomass value was found in the RLF during the rainy season, and the lowest value during the dry season in both fragments. According to the Kruskal-Wallis test and the Mann-Whitney test, there is no statistical difference ($p>0.05$) in the abundance nor in biomass by fragment and season (Supplementary Material 2).

3. Dominance, evenness, and relative abundance of Cerambycidae species

The highest dominance was registered during the dry season in the RCM, where Ectenessini sp. was the most dominant (N= 89), and the common species were *Lissonotus corallinus* Dupont, 1836 (N= 6), *Ysachron pilosus* (N= 4), and *Diploschemopsis howdeni* (Martins & Monné, 1980) (N= 3) (Figure 3a). Additionally, we found nine more species represented by one or two specimens. Regarding the rainy season of this particular fragment, *Sphaerion costae* García & Nascimento, 2020 was the dominant species (N= 41), *Psiloibidion boteroi* García, 2019, and *Neocompsa glaphyra* Martins, 1970 were registered as common species with 21 and 18 specimens respectively (Figure 3a). In addition, in this sampling we found 69 species with less than 10 specimens.

The highest evenness was registered in the RLF during the rainy season (Figure 3a), where the abundance was distributed in five species: *Diasporidion duplicatum* (Gounelle, 1909) (N= 17), *Tropidion litigiosum* Martins, 1968 (N= 15), *Sphaerion costae* (N= 15), *Limernaea ochracea* (Fisher, 1927) (N= 14), and *Piola colombica* Martins & Galileo, 1999 (N= 12). In addition to these species, 56 rare species were added, in which 64.3% were registered with only one or two specimens. Lastly, during the dry season in this fragment, we found the lowest richness and abundance of species overall (Figure 3a). Moreover, the most abundant species had less than 10 individuals *Ysachron pilosus* García, Botero & Santos-Silva, 2021, and the common species (*Ectenessa wappesi* Galileo & Santos-Silva, 2016*, Beraba marica* Galileo & Martins, 1999*, Ceragenia insulana* Fisher, 1943, and *Aegomorphus circumflexus* (Jacquelin Duval, 1857)) less than four. Eighteen rare species were registered in this sampling.

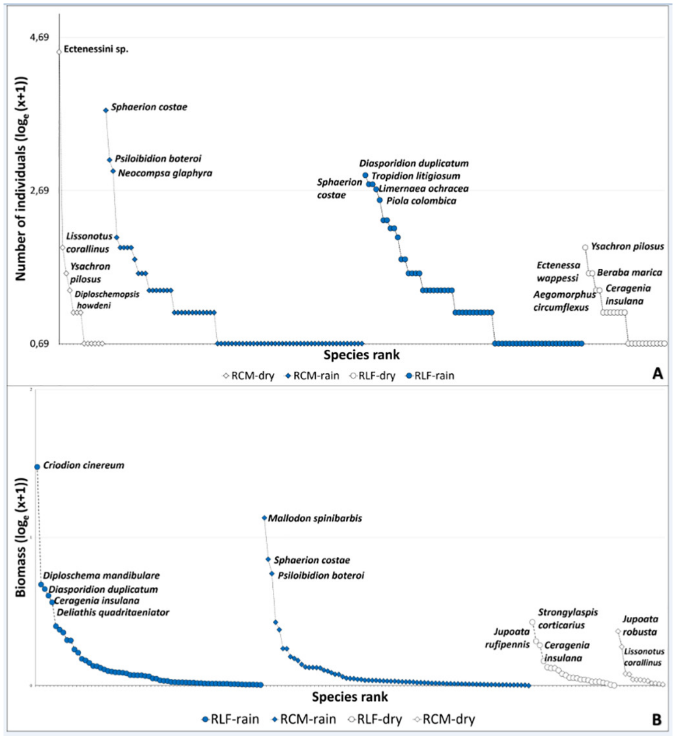


Figure 3. Whittaker plot of abundance (a) and biomass (b) of Cerambycidae species per season on each fragment.

Regarding the biomass, the biggest contribution was during the rainy season (Figure 3b). The highest biomass was registered in the RLF, and *Criodion cinereum* (Olivier, 1795) stood out as the dominant species (N= 3, B= 3.4 g). During the dry season, *Strongylaspis corticarius* (Erichson, 1848) (N= 2, B= 0.53 g), *Jupoata rufipennis* (Gory, 1831) (N= 1, B= 0.35 g), and *Ceragenia insulana* (N= 3, B= 0.31 g) were dominant. As for the RCM, *Mallodon spinibarbis* (Linnaeus, 1758) was the dominant species during the rainy season (N=2, B= 2.1 g). Other species such as *Sphaerion costae* (N= 41, 1.35 g) and *Psiloibidion boteroi* (N= 21, B= 1.13 g) stand out for having a medium size and high abundance making a relevant contribution to biomass. The dry season in general presented low values of biomass; *Jupoata robusta* Martins & Monné, 2002 (N= 1, B= 0.44 g) and *Lissonotus corallinus* (N= 6, B= 0.30 g) were dominant species.

4. α diversity

A total of 128 species were collected, of which a significant amount was registered during the rainy season (Supplementary Material 2).

The lowest value of the effective number of species (0D, 1D, 2D) was registered in the RCM during the dry season. Seventy-two species were registered in the RCM, and 61 in the RLF. Regarding the diversity order ^{1}D, 47 species were registered, mainly during the rainy season, 39 in the RLF and 35 in the RCM. Lastly, *alfa* diversity of abundant species (^{2}D) was higher in the RLF during the rainy season; for the dry season in the RLF and rainy season in the RCM, the same values were registered (S= 16).

4. *β diversity*

A total of 31 species were registered as shared between fragments, 50 exclusive for the RLF and 47 for the RCM. Regarding the seasons, a low number of shared species were registered (S= 12), and the rainy season had the highest value of exclusive species (S= 98), very different from the dry season (S= 18). The *beta* diversity values were high and explained mainly by turnover. According to the estimation (Jaccard dissimilarity), turnover exceeds 70% in all the cases, hitting 87% when comparing the rainy season in the RCM with the dry season in the RLF (Figure 4). Percentages of nestedness are under 14% in all the cases, and the highest value (13.2%) was obtained when comparing the dry with the rainy season in the RCM (Figure 4).

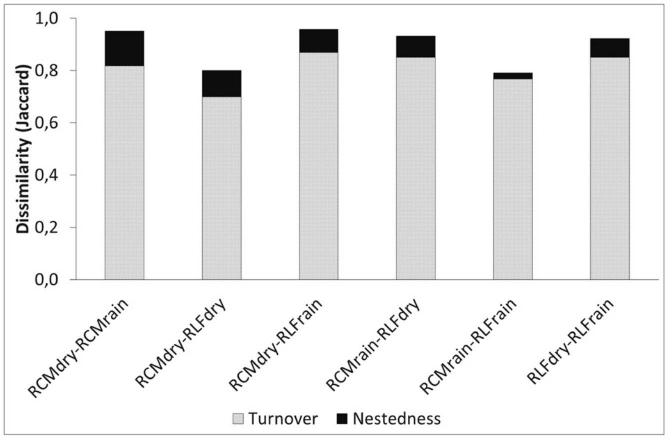


Figure 4. Variation of *beta* diversity in Cerambycidae community, with percentage of turnover and nestedness in the study area, according to Jaccard dissimilarity index.

4. *Spatio-temporal variation of the Cerambycidae community*

The non-metric multidimensional scaling analysis (*nMDS*) showed that the composition and structure of cerambycid species between fragments form two separate groups, and it can be said that the groups are mainly for the seasons (dry and rainy) rather than the fragments (Figure 5). The results observed on the *nMDS* agree with the analysis of similarities (ANOSIM), which determined statistical significances in the structure of the community (R= 0.345, p= 0.001). In this case, the differences were registered in different seasons between the same or different fragments, and when both fragments were compared at the same season there were no differences (RCM-Dry vs RLF-Dry 0.065 and RCM-Rain vs RLF-Rain 0.054) (Table 1).

5. *Relation of environmental variables and canopy cover with variation of the Cerambycidae community*

Regarding the environmental variables, we measured ambient temperature (AT), relative humidity (RH), canopy cover (CC) and precipitation (prec), as seen in Supplementary Material 3.

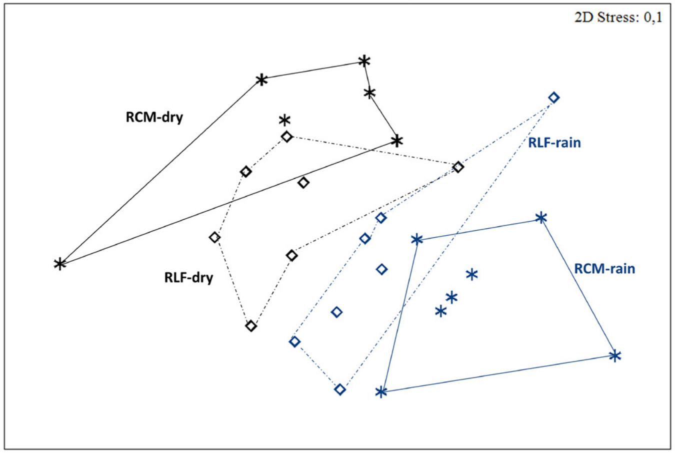


Figure 5. Non-metric multidimensional scaling analysis (*nMDS*) based on a Bray-Curtis dissimilarity matrix, which describes the spatio-temporal variation of the Cerambycidae community in the study area.

Table 1. Comparisons of the structure of the Cerambycidae community by seasons and fragments using the analysis of similarities (ANOSIM).

Groups	R	Significance level
RCM-Dry vs RCM- Rain	0.451	0.002
RCM-Dry vs RLF-Dry	0.177	0.065*
RCM-Dry vs RLF-Rain	0.53	0.001
RCM-Rain vs RLF-Dry	0.471	0.003
RCM-Rain vs RLF-Rain	0.138	0.054*
RLF-Dry vs RLF-Rain	0.327	0.01

* Do not have statistical significance

The first two axes of the CCA explained 71% of the variation of the data and was shown to be statistically significant ($p < 0.05$) (Table 2), registering the highest value (0.91) on the first axis. The variables that contributed the most to this variation were canopy cover (CC), precipitation (Prec) and relative humidity (RH) on the first axis, and ambient temperature (AT) on the second. Also, we observed there is a higher concentration of species when the CC and RH increases, which occurred when the highest precipitation was registered, however then the AT increases, and we observed a lower quantity of species (Figure 6).

The abundance of species such as *Diploschemopsis howdeni*, Ectenessini sp., *Compsibidion paradoxum* Martins, 1971, *Ysachron pilosus* and *Protumida insularis* Monné & Wappes, 2014, exclusive for dry season, presented a directly proportional relation to AT and inversely proportional to RH and CC. Furthermore, other species were associated with high values of RH and CC, and inversely proportional to AT, such as *Stizocera geniculata* (Pascoe, 1866)*, Gnomidolon bellus* Martins & Galileo, 2002*, Lepturges* (*Lepturges*) *elegantulus* Bates, 1863*, Coleoxestia rubromaculata* (Gounelle, 1909)*, Mimasyngenes icuapara* Galileo & Martins, 1996*, Beraba piriana* Martins, 1997, and *B. anae* García, Botero & Martínez, 2019.

Discussion

On account of the constant threat from many anthropic activities TDF fragments face in the Caribbean of Colombia and the lack of information on the diversity of Cerambycidae, this research represents the first ecological study of the family in Colombia, serving as a pioneer

Table 2. Percentage of explained variation for each axis in the canonical correspondence analysis (CCA). AT: Ambient temperature; RH: Relative humidity; Prec: Precipitation; CC: canopy cover. Variables that contribute the most to the diversity variation in bold.

Variables/ Axes	**CCA1**	**CCA2**	**CCA3**	**CCA4**
Eigenvalue	0,9122	0,514	0,3303	0,2518
Explained variation (%)	45,42 (F=3,1568; p= 0,001)	25,59 (F=1,7787; p= 0,014)	16,45 (F=1,143; p= 0,523)	12,5 (F=0,8714; p= 0,657)
Accumulated variation (%)	45,42	71,01	87,46	100
AT	-0,3464	**0,70443**	-0,5676	-0,24828
RH	**0,6214**	-0,68843	0,351	-0,12939
CC	**0,9604**	0,04455	0,2589	-0,09276
Prec	**0,9094**	-0,38883	-0,1407	0,0442

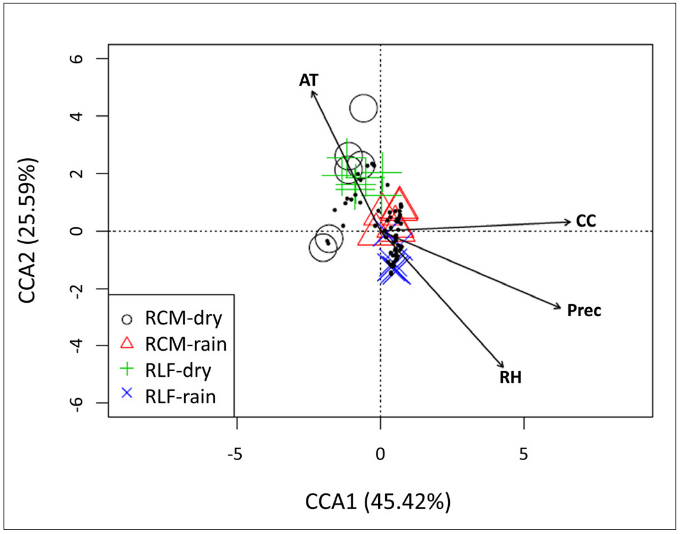


Figure 6. Graphic representation of the canonical correspondence analysis (CCA) based on the interaction of environmental variables (AT: Ambient temperature; RH: Relative humidity; Prec: Precipitation) and canopy cover (CC) with Cerambycidae diversity.

investigation on the region, making contributions to the taxonomy, ecology, and biology of this group. First of all, with this research we were able to identify the cerambycid fauna associated with TDF in the Caribbean region of Colombia, adding 18 new species and 32 new distribution records for Colombia, which are currently published or *in press* (e.g. García et al. 2019, García 2019, García & Nascimento 2020). Additionally, 49 species were registered for the first time for Bolívar, and 56 for Atlántico departments. Also, this research demonstrated that the structure of the cerambycid community of TDF, in the Caribbean region of Colombia, presents ecological patterns associated with the vegetation structure and environmental variables determined by seasonal ecosystem conditions.

The highest diversity and abundance of Cerambycinae coincides with the research of Noguera et al. (2002, 2007, 2009, 2012, 2017), who reported this subfamily as dominant in Mexican TDF. In addition, Gutiérrez et al. (2014) mentioned that Cerambycinae is the most common subfamily in dry forest, even though Lamiinae is the most abundant in most of the world and in rain forests. It is not clear what factors act on the differences registered in the pattern of richness of Cerambycinae and Lamiinae between rain and dry forest. Gutiérrez et al. (2014) suggested that these differences could be due to a sampling effect, because most of the Cerambycinae species exhibit diurnal activity and frequent flowers, making their capture easy during the flowering season, especially in dry forests where the trees have an average height of 10 m. However, the rain forest has taller trees, making capture more difficult. Lastly, Prioninae was the least common subfamily in this research, coinciding with the findings of Martínez (2000) and Botero (2018), who mentioned it as the least diverse of the subfamilies found in our study.

Tribes with a great diversity (e.g. Acanthoderini, Acanthocinini, Mallodonini) can be explained by the presence of some of their host plants, in and around the sampling plots, plant species that had been registered in TDF fragments of the Caribbean of Colombia according to Mendoza (1999), Rodríguez et al. (2012), Pizano & García (2014), and Herazo-Vitola et al. (2017). For example, the presence of *Lepturges* Bates, 1863, and *Urgleptes* Dillon, 1956 species (Acanthocinini) is explained by their association with plant species of the genus *Acacia* (Martius, 1829) (Romero et al. 2007), present in the study area; *Steirastoma histrionicum* White, 1855 (Acanthoderini) has been associated with plant species such as *Ceiba pentranda* (L.) Gaertner, and *Sterculia apetala* Druce (Vitali et al. 2006), plants characteristic from the sampled fragments; and *Mallodon dasystomus dasystomus* (Say, 1824), and *M. spinibarbis,* (Mallodonini) have *Bursera simaruba* (L.) Sarg., and species of the genus *Ficus* L. as their host plants (Maes et al. 2010), which are also present in the study area.

Regarding the seasons, during the rainy season we observed the highest values of abundance, richness, and biomass of Cerambycidae in the adult stage due to the changes in the dry forest phenology in the area. Due to their sapro-xylophagous behavior, during the dry season the larvae feed on the great quantity of dead wood available (Noguera et al. 2012) and when the rain comes, the resources increase in the forest and so does the activity of the adults of many cerambycid species to feed and mate (Sugiarto et al. 2016, Noguera et al. 2017). These results coincide with Noriega et al. (2007), who did a research on Coleoptera in the Colombian Amazonian, and found that herbivorous beetles (including Cerambycidae), were more abundant during the rainy season. Also, Noguera et al. (2002, 2012, 2017) found a higher richness and abundance of Cerambycidae during the rainy season on Mexican TDF, where 75% of the registered longhorn beetles were exclusive to this season.

The unevenness registered is mainly because of a high frequency of *singletons* and *doubletons*, a characteristic occurrence of arthropods in Neotropical ecosystems (Cava et al. 2015). The high dominance of Ectenessini sp. during the dry season in the RCM and *Ysachron pilosus* in the RLF, is due to the small size of these species (< 10 mm), which are characterized for having a high number of individuals, because the larvae are able to develop in small logs, frequent in TDF forest, unlike bigger species which could have different microhabitat requirements (Sataral et al. 2015). However, there might be a sampling effect, too, because both species were collected with light trap, which is an active collection method. The even dominance of *Diasporidion duplicatum, Tropidion litigiosum, Sphaerion costae, Limenaea ochracea* and *Piola colombica* during the rainy season in the RLF, might indicate a preference of these species for the characteristics of this forest during the rain, however, further studies are necessary to clarify this finding.

The highest values of biomass during the rainy season in the RLF can be explained because during the rainy season we registered the lowest temperatures, which allows larger species to thermo-regulate because the surface/volume ratio decreases and consequently, the energy expenditure (Amat 2007). This is very important because thermoregulation in herbivorous insects is essential for controlling the energy expenditure on digestion and absorption of nutrients (Fuentes-Rodríguez et al. 2017). Lastly, a higher biomass during the rainy season is also due to the biggest individuals belonging to the subfamily Prioninae, in which almost all species are nocturnal and crepuscular, and are easily attracted to artificial lights such as the ones we used in our sampling (Švácha & Lawrence 2014).

The lowest biomass during the dry season is mainly because of the high frequency of small cerambycid species (less than 0.5 g each). These values are important because they allowed us to recognize which species contribute the most in the primary production of the ecosystem, participating in the reallocation of nutrients (Noriega et al. 2012), and influencing the TDF services and functionality.

Alfa diversity for all three orders (^{0}D, ^{1}D, ^{2}D) is similar, when comparing the sampling places, probably because both forests have similar vegetation structure, containing host plants of many Cerambycidae species, so it is expected that both places will have a similar diversity of Cerambycidae as well, as the species will have enough resources in either of them. This pattern concurs with the research of Noguera et al. (2017), who showed a close relationship between the richness of plants and the richness of Cerambycidae in the Mexican TDF. Additionally, the highest diversity during the rainy season is because precipitation brings about changes in the foliage, a higher availability of habitats and flowering of many vegetal species (Pizano & García 2014), which are key to developmental activities such as reproduction of these beetles (Švácha & Lawrence 2014), and a greater availability of resources for the posterior development of the larvae. In this case, some species appear to co-evolve with their host plants (Farrell & Mitter 1998), synchronizing the adult stage with the season that offers more and better resources (Noguera et al. 2017).

We registered a high *beta* diversity mainly explained seasonally, which indicates a high environmental heterogeneity (Morrone & Escalante 2016). High levels of environmental heterogeneity are an answer to a well-marked seasonality of TDF in the Caribbean region of Colombia, influencing the recorded *beta* diversity by three mechanisms. The first mechanism are the ambient conditions which change from dry season to rainy season on each fragment, this implies that there is a separation of species with different physiological characteristics, which allows them to have niche difference between seasons on each place; the second one depends on the configuration of the environment, because the dry forest seasonality causes a low similarity within the same locality because of the environment heterogeneity; the third one depends on the capacity of dispersion of the species, because many species are not able to disperse for the barriers created by the environmental heterogeneity between both localities (Martínez et al. 2010, Pizano & García 2014, Villareal et al. 2019). Also, taking into account the geological history of TDF in Colombia, its original extension was reduced due to geological and climatic processes, and recently for anthropic interference (Kattan et al. 2019, Suarez & Vargas 2019).

The high *beta* diversity due to turnover can be explained spatially: the deforested areas between the forest fragments, which possibly were a continuum of TDF in the Caribbean of Colombia, represent a geographic barrier for those species closely related to their host plants (Pérez & Zaragoza 2015). In addition, turnover is also a result of the geographic size of forest fragments and habitat restriction (Harrison et al. 1992, Morrone & Escalante 2016), because the species are specific in their requirements, so their distribution is also restricted, forming groups with greater differences between each other (Rodríguez et al. 2003, Morrone & Escalante 2016).

Moreover, the low nestedness registered in this research is due to differentiation on the composition of species by the presence of barriers or patterns of selective differentiation between both localities, so they were not found in a wide range of environmental variation or geographic distribution (Baselga 2010). The above is because the composition of the communities between both localities are not a subgroup of richer communities in terms of species (Calderón-Patrón et al. 2012). Lastly, is important to take into account that the preferences of each species for its habitat or certain environmental conditions are not only for the advantage these factors offers for survival, but it is also probable that is an evolutionary component, to co-exist and decrease competition, throughout the processes of speciation. In this way, it is proposed as hypothesis that those macroecological causes also models the high *beta* diversity founded in this study (Morrone & Escalante 2016).

The highest diversity of Cerambycidae associated with high values of canopy cover (93.21% ± 2.07) during the rainy season could be explained by the fact that some beetles have adapted to microclimatic changes of vegetation and the availability of resources which proliferate in the canopy and soil, as explained for Onciderini (Cerambycidae, Lamiinae) (Paro et al. 2014) and even for Scarabaeidae (Martínez et al. 2010). This finding concurs with Sugiarto et al. (2016) and Gatti et al. (2018), who reported a higher diversity and dominance of Cerambycidae when canopy cover is higher. Furthermore, the close relation of high relative humidity (79.1% ± 1.92) and high cerambycid diversity, can be explained by how this variable influences wood decomposition, main food source of Cerambycidae larvae (Toledo et al. 2014, Noguera et al. 2017), coinciding with Noguera et al. (2017) study, who reported that Cerambycidae adults use death matter for larvae development, and this resource is derived from branches on the ground which could fell off for the increase of weight caused by high humidity.

The low quantity of cerambycid species related to high temperature is because this variable has a negative effect on certain functions performed by the beetles, such as wood degradation (Noriega et al. 2007). In addition, it also produces dehydration and loss of the forest canopy, decreasing the quantity of available resources for Cerambycidae (Martínez et al. 2010).

These results demonstrate that there is a temporal variation of the structure of the cerambycid community in the study area, in which the abundance, richness, and biomass are higher during the rainy season, mainly explained by the high turnover of species from one season to another. Therefore, we conclude that TDF represents an ecosystem with a high cerambycid diversity, especially during the rainy season. It is critical to monitor these populations to evaluate the impact of anthropic activities on these remaining fragments in the Caribbean region of Colombia. This study also represents a practical approach to the study of diversity patterns of understudied groups in TDF such as the Cerambycidae in Colombia.

Supplementary Material

The following online material is available for this article:

Supplementary material 1 - Sampling techniques used; fruit-bated trap (a), beating sheet (b), manual capture (c), light trap (d).

Supplementary material 2 - Richness (S), abundance (N) and biomass (in parenthesis) of Cerambycidae species registered in the study area. RCM-d: Reserva Campesina la Montaña, dry season; RCM-r: Reserva Campesina la Montaña, rainy season; RLF-d: Reserva La Flecha, dry season; RLF-r: Reserva La Flecha, rainy season; S.T: Sampling technique; MC: Manual capture; FT: Fruit-bated trap; BS: Beating sheet; WLT: White light trap; UVLT: UV light trap. *Singletone, **Doubletones.

Supplementary material 3 - Variation of temperature (a), relative humidity (b), canopy cover (c) and precipitation (d) between the sampling seasons on both fragments. Bars indicate CI.

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Author Contributions

Kimberly García: contributed with the material preparation, data collection, identification, statistical analysis and interpretation, the manuscript preparation, and read and approved the final manuscript.

Neis Martinez: contributed with the study conception and design, statistical analysis and interpretation, the manuscript preparation, and read and approved the final manuscript.

Juan Pablo Botero: contributed with the identification, the manuscript preparation, and read and approved the final 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

Leguminosae tree species diversity in coastal forests of Rio de Janeiro, Brazil

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Abstract: This study investigated the current Leguminosae tree species composition in coastal forests over lithosoil soil or sandy plains in the eastern and central portion of Rio de Janeiro state, Brazil. A comparative study between the Atlantic Forest areas of the Southeast Region of Brazil was conducted to evaluate the influence of environmental variables on floristic differentiation. A total of 34 areas of the Southeast Region was selected from the NeoTropTree platform and the Leguminosae species in these areas were the basis for a similarity analysis. The Jaccard Similarity Index and the UPGMA method were applied for grouping analysis. The relationships between the Leguminosae species composition and the environmental variables were investigated via Cannonical Correspondance Analysis (CCA). The cluster analysis showed that the Leguminosae tree species group of this portion of Rio de Janeiro coastline share floristic affinity with seasonal forests, a result confirmed by CCA. This floristic differentiation is sustained by an exclusive group of Leguminosae species established over lithosoils or sandy plains, and signals that the extent of dry forests in Rio de Janeiro state might be larger than currently stated. The results justify distinct conservation actions in view of the floristic singularities of these areas.

Keywords: *Diversity; dry forest; endemism; Fabaceae; floristic similarity.*

Diversidade de espécies de Leguminosae arbóreas nas florestas costeiras do Rio de Janeiro, Brasil

Resumo: O presente trabalho investigou a composição de espécies arbóreas de Leguminosae presentes em florestas litorâneas, estabelecidas sobre solos litólicos ou planície arenosa, na porção Central e Leste do estado do Rio de Janeiro, Brasil. Foi realizado um estudo comparativo entre áreas de Floresta Atlântica no Sudeste brasileiro para avaliar a influência de variáveis ambientais nas diferenciações florísticas. Foram elencadas 34 áreas da Região Sudeste na plataforma NeoTropTree e tabuladas as espécies de Leguminosae dessas áreas para análise de similaridade. Foi utilizado o índice de similaridade de Jaccard e o método UPGMA para as análises de agrupamento. As relações entre a composição de espécies de Leguminosae e as variáveis ambientais foram investigadas através da análise de Correspondência Canônica (CCA). A análise de agrupamento mostrou que o conjunto de espécies de Leguminosae arbóreas dessa porção do litoral fluminense possui afinidade florística com as florestas estacionais, resultado igualmente corroborado pela CCA. Essa diferenciação florística é sustentada por um conjunto exclusivo de espécies de Leguminosae, estabelecidas nessas florestas sobre solos litólicos ou planície arenosa e sinaliza que a extensão de matas secas no estado do Rio de Janeiro pode ser maior que o apresentado atualmente. Este resultado justifica ações diferenciadas em termos de conservação, tendo em vista a singularidade florística apresentada por estas áreas.

Palavras-chave: *Diversidade; Fabaceae; endemismo; matas secas; similaridade florística.*

Introduction

The Atlantic Domain is well known for its great heterogeneity, notably its latitudinal extent and topographic variation (Oliveira-Filho & Fontes, 2000; Joly et al., 2014). The rainfall distribution and temperature fluctuations are the main differentiating factors between seasonal and ombrophilous forests, and strongly control the floristic composition of these different forest types (Oliveira-Filho & Fontes, 2000; Oliveira-Filho et al., 2005; Nettesheim et al., 2010). The overall differentiation between these two floristic blocks is more apparent in the East-West distribution related to gradients in seasonal rainfall according to the distance from the ocean (Salis et al., 1995; Scudeller et al., 2001; Joly et al., 2014), with seasonal forests extending into the Domain's inner boundaries. The climate in the Brazilian Southeastern Region at the central portion of the Atlantic Coast varies drastically, with seasonal forests reaching as far as the Rio de Janeiro northern coastal zone (Oliveira-Filho & Fontes, 2000). This drier coastal climate is caused by the cold oceanic resurgence phenomena in the Região dos Lagos (Araujo, 1997), which spreads in both north and south directions along the Rio de Janeiro coastline (Barbiére, 1984; Oliveira-Filho et al., 2005). In addition, precipitation decreases gradually with the distancing from top of Serra do Mar towards the coast and in the west-east direction, due to less orographic control (Bohrer et al., 2009).

The seasonal forests are currently acknowledged as part of a singular global biome denominated Seasonally Dry Tropical Forests (SDTF), and, in Rio de Janeiro, only 10% of the areas originally covered by these forests remains, most of them (50%) highly fragmented, composed by patches smaller than 100 ha (Fidalgo et al., 2009; Pennington et al., 2009). SDTFs show rainfall of less than 1600mm per year and with periods of at least 5 to 6 months of 100mm. The vegetation is mainly deciduous, the degree of deciduality increases with decreasing rainfall (Mooney et al., 1995; Pennington et al., 2000; 2009). Scarano et al. (2009) point out that these areas are little known regarding their floristic and structural composition, with studies having been centered in the North and Northwestern regions (e.g. Silva & Nascimento 2001; Carvalho et al., 2006; Nascimento & Lima 2008; Dan et al., 2010; Mauad 2010; Abreu et al., 2014; Souza 2015; Fortes et al., 2020); in the Southern Paraiba river basin region (e.g. Peixoto et al., 1995; Bloomfield 1997; Spolidoro 2001; Souza et al., 2007; Fernandes et al., 2012; Freitas & Magalhães 2014; Medeiros et al., 2020); and in the Cabo Frio Plant Diversity Center (CDVCF) (e.g. Sá 1992, 2002, 2006; Araujo et al., 2009; Kurtz et al., 2009; Ribeiro & Lima 2009; Sá & Araujo 2009; Carvalho et al., 2018).

Among the lesser known forest formations in Rio de Janeiro State, the coastal forests mainly stand out for their co-occurrence on lithosoil or over sandy plains (restinga). Although located at the edge of the Dense Ombrophilous Forest (IBGE 2012), they can be distinguished by their microclimate characteristics which feature a brief dry season which is intensified by the soil conditions, since sandy soils generally have low water retention capacity (Scarano 2009). These areas are considered the Atlantic Rain Forest's marginal habitats, upon which environmental factors act and limit species distributions (Scarano 2009; Neves et al., 2017).

This study aimed to compare the Leguminosae tree composition of these forests with other Atlantic Rain Forests in the Southeast Region and to evaluate the influence of environmental variables on floristic differentiation among the forest areas. The hypothesis raised in this study is that the Leguminosae tree composition of coastal forests presents greater floristic affinity with Semi-Deciduous Seasonal Forests due to the occurrence of similar environmental filters. This hypothesis will be tested using the Leguminosae as an indicator for richness and composition evaluation, since it is featured among the five richest in species in Rio de Janeiro state, and is well represented in floristic and phytosociological inventories of different phytophysiognomies (Araujo 2000; Lima 2000; Barros 2008; Ribeiro & Lima 2009; BFG 2015; Coelho et al., 2017; Fortes et al., 2020). Leguminosae is the plant family with the greatest species richness and abundance in the SDTF (DRYFLOR 2016), been used a model family for biogeographic studies of this biome before in South America (e.g. Särkinen et al., 2012).

Although there is already a relatively robust set of floristic data on the SDTF, currently compiled in databases such as NeoTropTree (Oliveira-Filho 2017), the low representativeness of inventories, particularly in the southeastern Atlantic coastal strip, has hampered more comprehensive biogeographic analyzes. Filling this gap is urgent to advance global and local conservation strategies of this biome, which is extremely threatened by its disjunct distribution, high level of threat and low representation in protected areas. In addition, it is expected that the results of this study can support conservation actions of those remaining in the region. The strongholds of Seasonal Forests in the state of Rio de Janeiro are still poorly studied when compared to Ombrophilous Forests and poorly represented in conservation units, especially those of Integral Protection. Improving the knowledge of the distribution of family species on the coast of Rio de Janeiro, understanding issues of diversity and turnover are points that can help in the conservation of dry forests and lead to the improvement of conservation strategies for these remnants.

Material and Methods

A total of 34 areas corresponding to ombrophilous forests, seasonal forests and restinga forests in the Southeast Brazilian Atlantic Rain Forest in the NeoTropTree database were analyzed, of which 21 are in Rio de Janeiro state, six in Minas Gerais, four in Espírito Santo and three in São Paulo (Table 1; Figure 1). The NeoTropTree database (Oliveira-Filho 2017) provides arboreal species lists and environmental variables obtained in sites with a single phytophysiognomy. Thus, a single area can encompass several sites, provided that those sites correspond to different phytophysiognomies (Eisenlohr & Oliveira-Filho 2015).

There are coastal forests encountered in the central and eastern portions of Rio de Janeiro state, including in the areas of Niterói and Maricá (RJnite), Ilha de Marambaia (RJmrbm), Maciço do Itaoca (RJitaoc), Cabo Frio (RJcabo) and Saquarema (RJsaqu). The Leguminosae list for Niterói and Maricá solely gathers species occurring in coastal slopes and lithosoil areas within three Conservation Units in Niterói (Área de Proteção Ambiental do Morro do Morcego, da Fortaleza de Santa Cruz e dos Fortes do Pico e do Rio Branco, Parque Natural Municipal de Niterói and Parque Estadual da Serra da Tiririca) and in four localities of the Refúgio de Vida Silvestre de Maricá (Pedra de Inoã, Pedra de Itaocaia, Pedra do Macaco and Serra do Camburi). Only species in Saquarema with occurrence at the Núcleo Massambaba of the Parque Estadual da Costa do Sol encompassing only Restinga formation were collected.

The Leguminosae species were organized into a binary matrix, revised and complemented by additional data. This complement was based on consulting the collections of FCAB, GUA, HB, HRJ, HUENF, NIT, R, RB, RBR, RFA and RFFP herbaria (acronyms in accordance

Table 1. Environmental variables of the 34 areas of the Southeast Region used in the Canonical Correspondence analysis. Alt (Altitude); DOcean (Distance from Ocean); Soil Salinity; TBS (Soil fertility based on average TBS - % of total base saturation); WDD (Average dry season duration). Phy (phytophysiognomy: Dense Ombrophilous Forest – DOF/Seasonal Semideciduous Forest - SSF/Restinga - RES).

Study area	**Phy**	**Code**	**Coordinates**		**Environmental Variables**				
			Latitude	**Longitude**	**Alt (m)**	**DOcean (Km)**	**Soil Salinity (dS/m)**	**TBS (%)**	**WDD (days)**
Cabo Frio	SSF	RJcabo	-228.644	-420.342	15	2	20	37	70
C. de Macacu, E. Paraíso	DOF	RJcach	-224.772	-426.761	337	55	0	17	60
Cachoeiro de Itapemirim	SSF	ESitpm	-207.422	-413.011	133	56	0	37	110
Campos, Terras Baixas	SSF	RJcamp	-216.529	-414.708	60	47	0	17	115
Carangola	SSF	MGcarg	-206.742	-419.997	890	118	0	17	85
Castelo	SSF	EScast	-20.61	-411.714	133	54	0	37	100
Descoberto	SSF	MGdesc	-214.236	-429.531	752	156	0	17	105
Desengano, Imbé	DOF	RJimb	-218.475	-416.772	314	48	0	17	65
Ilha de Marambaia	RES	RJmrbm	-230.483	-438.694	13	2	15	17	0
Ilha Grande	DOF	RJilha	-231.514	-442.011	825	25	0	17	0
Itatiaia	DOF	RJitat	-224.261	-44.62	1218	65	0	37	45
Juiz de Fora	SSF	MGjuiz	-217.483	-433.181	893	146	0	17	95
Lima Duarte	SSF	MGlima	-218.567	-438.661	768	131	0	17	105
Linhares	SSF	Esrvrd	-191.586	-400.217	50	40	0	17	25
Macaé de Cima	DOF	RJcima	-224.408	-425.694	1424	52	0	37	0
Maciço do Itaoca, Campos	SSF	RJitaoc	-217.936	-414.481	391	45	0	17	85
Maciço da Pedra Branca	DOF	RJpdbc	-229.406	-434.481	456	9	0	17	0
Maciço da Tijuca	DOF	RJtiju	-229.636	-433.014	730	6	0	17	0
Maciço do Tinguá	DOF	RJting	-225.511	-434.131	749	52	0	17	0
Mimoso do Sul	SSF	ESmimo	-210.131	-413.856	348	36	0	17	95
Miraí	SSF	MGmira	-212.447	-426.147	514	158	0	17	115
Muriaé	SSF	MGmrae	-210.803	-424.286	336	151	0	17	120
Natividade	SSF	RJnatv	-210.356	-419.275	470	102	0	17	115
Niterói/Maricá	DOF	RJnite	-229.294	-429.794	123	3	15	17	0
Paraty	DOF	RJpara	-232.972	-447.919	820	3	0	17	0
Petrópolis	DOF	RJpetr	-225.347	-431.581	1203	58	0	17	0
Picinguaba	DOF	SPpic	-233.181	-448.097	305	8	0	17	0
Poço das Antas	DOF	RJpoco	-225.414	-422.867	143	27	0	17	30
S. Francisco de Itabapoana	SSF	RJsaof	-213.933	-410.958	24	10	15	17	90
São José do Barreiro	SSF	SPjjbr	-226.347	-446.569	550	43	0	17	95
Saquarema	RES	RJsaqu	-229.072	-424.914	38	3	15	17	0
Teresópolis	DOF	RJtere	-224.544	-429.503	1180	62	0	37	0
Ubatuba	DOF	SPuba	-233.692	-450.203	525	1	0	17	0
Valença	SSF	RJvale	-223.333	-437.067	638	73	0	17	90

with Thiers 2020). All evaluated materials were identified or revised at species level. A nomenclatural revision was performed based on Flora do Brasil (2020a). The binary matrix gathered a total of 250 species.

The cluster analysis was performed, adopting Unweighted Pair Group Method with Arithmetic Mean (UPGMA) and the Jaccard index (Mueller-Dombois & Ellemberg 1974) as a similarity measure between formations, using the PAST v.2.10 program (Hammer et al., 2001). Venn diagrams were made to visualize legume species shared between distinct groups (Gotelli & Ellison 2016).

A Canonical Correspondence Analysis (CCA) was applied to analyze the correlation between species distribution and environmental variables. A total of 50 environmental variables acquired via the NeoTropTree (Eisenlohr & Oliveira-Filho 2015) database were initially considered. After preliminary CCA, 45 of those slightly correlated or highly redundant variables with high inflation factors in the analysis (ter Braak 1987) were discarded. The final CCA has five variables: altitude (m); DOcean – distance from the ocean (km); Soil Salinity (dS/m); TBS – soil fertility based on the average percentage of Total Base Saturation; WDD – dry season average

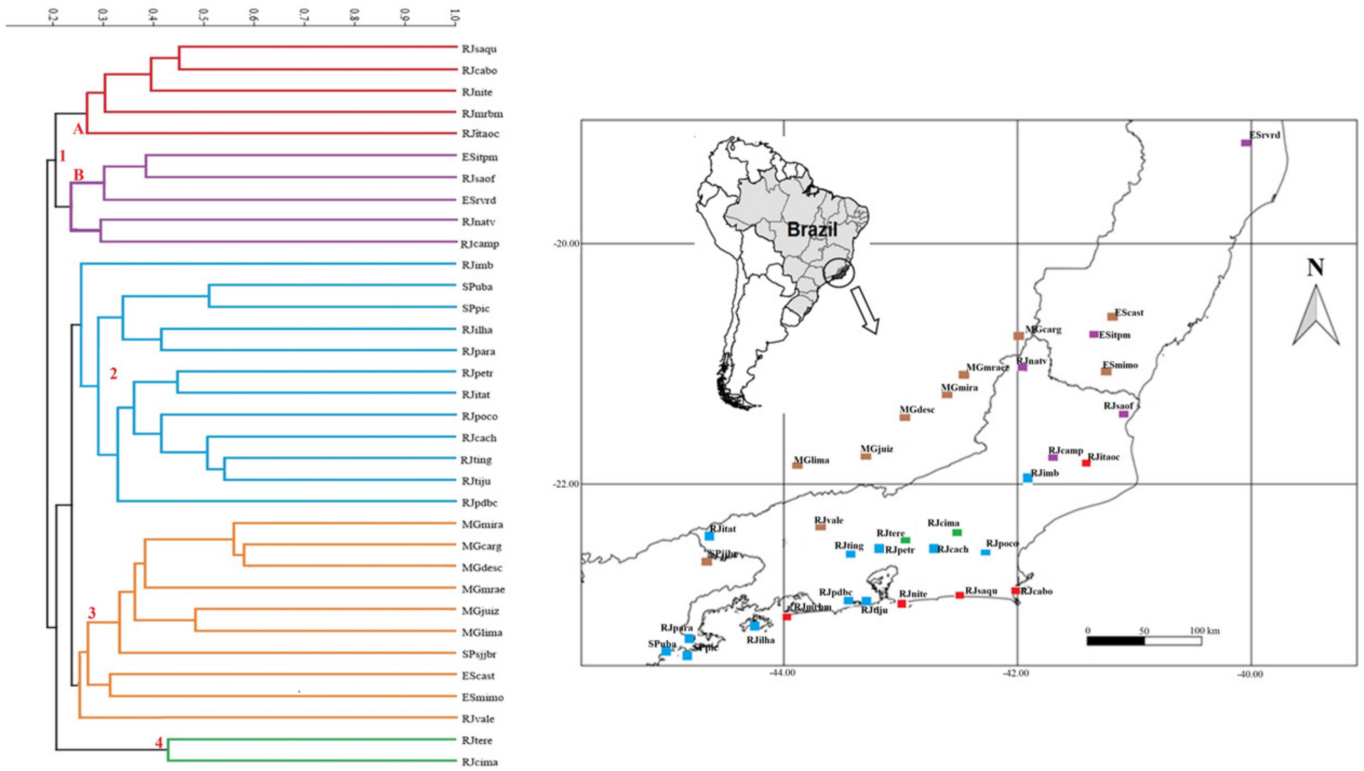

Figure 1. Stretch from the Southeastern Region of Brazil with the 34 areas grouped in the similarity analysis (Cophenetic Correlation Coefficient = 0.7442). Group 1: Seasonal Forests RJ / ES and Coastal Forests inserted in the central and eastern portion / RJ; Group 2: Ombrophilous Forests RJ / SP; Group 3: Seasonal Forests RJ / ES / MG; Group 4: Ombrophilous Forests / RJ. Areas: EScast = Castelo, ESitpm = Itapemirim, ESmimo = Mimoso do Sul, ESrvrd = Linhares/C. Vale do Rio Doce, MGcarg = Carangola, MGdesc = Descoberto, MGjuiz = Juiz de Fora, MGlima = Lima Duarte, MGmira = Miraí, MGmrae = Muriaé, RJcabo = Cabo Frio, RJcach = Cachoeiras de Macacu/Paraíso, RJcamp = Campos dos Goytacazes, RJcima = Macaé de Cima, RJilha = Ilha Grande, RJimb = Desengano/Imbé, RJitaoc = Maciço do Itaoca/Campos, RJitat = Itatiaia, RJmrbm = Ilha de Marambaia, RJnatv = Natividade, RJnite = Niterói/Maricá, RJpara = Paraty, RJpdbc = Maciço da Pedra Branca, RJpetr = Petrópolis, RJpoco = Poço das Antas, RJsaof = São Francisco do Itabapoana/Carvão, RJsaqu = Saquarema, RJtere = Teresópolis, RJtiju = Maciço da Tijuca, RJting = Maciço da Tinguá, RJvale = Valença, SPjjbr = São José do Barreiro, SPpic = Picinguaba, SPuba = Ubatuba.

duration, expressed by the number of days with water deficit (Table 1). The Monte Carlo Permutation Test was applied with 999 permutations in order to evaluate the canonical correlation significance, adopting a 95% significance level ($P<0.05$) (ter Braak 1987; Palmer 1993). The PAST v.2.10 software program was also used for this analysis.

Results

1. *Similarity analysis*

The cluster analyses revealed four well supported (approximately 0.75 of Cophenetic Correlation Coeficient - CCC) groups (Figure 1). The Centre-East Coastal Forests were included in Group 1, together with Rio de Janeiro and Espírito Santo seasonal forests. It was possible to distinguish two subgroups in the similarity variation summarized in the dendrogram for this group (Jaccard index between 0.2 and 0.5), which gathered the coastal forests inserted in Rio de Janeiro's central and eastern (RJsaqu, RJcabo, RJnite, RJmrbm and RJitaoc – Subgrup A) and the forests of the Rio de Janeiro's northern and northwestern regions, as well as the northern and southern regions of Espírito Santo (RJsaof, RJnatv and RJcamp, ESitpm and ESrvrd – Subgroup B).

Another three groups were highlighted in the dendrogram, grouping Dense Submontane Ombrophilous Forest (Group 2), Montane and High Montane forest of Rio de Janeiro state (Group 4) and Seasonal forests of Middle Paraíba in Rio de Janeiro, Minas Gerais and São Paulo States (Group 3). However, the differentiation shown by coastal forests of the central and eastern portions of Rio de Janeiro is highlighted, which have greater Leguminosae species similarity with Seasonal Forests in Rio de Janeiro and Espírito Santo.

2. *Condensed analysis of species sharing*

Of the 250 species selected, 170 were found in the Ombrophilous Forests and 180 in Semi-Deciduous Seasonal Forests. These numbers imply 113 common species, with 57 being species exclusive to Ombrophilous Forests and 67 exclusive to Semi-Deciduous Seasonal Forests (Figure 2). Proportionally, these numbers correspond to 45.2%, 22.8% and 26.8% species in total. Comparing the Leguminosae species composition in Seasonal Forests (n=180) with the central and eastern portion areas of Rio de Janeiro Coastal Forests (n=108) (Figure 2), there are 80 common species, with 100 species exclusive to Semi-Deciduous Seasonal Forests and 28 to Coastal Forests. It appears that few species are shared between these areas when the geographic substitution patterns of Leguminosae species are observed among the five stretches of coastal forests (Figure 3), even among the closest ones.

3. *Environmental variables and species composition*

The CCA results (Table 2) gave eigenvalues of 0.28 (axis 1), 0.22 (axis 2) and 0.14 (axis 3), which were considered low, indicating the existence of short gradients, where only the first axis eigenvalue

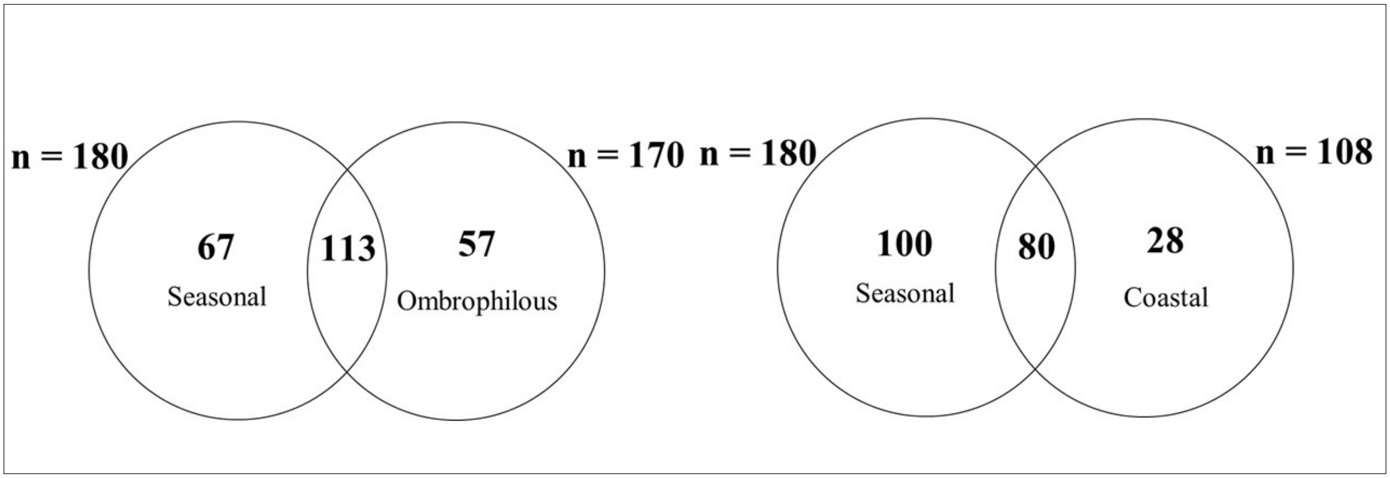

Figure 2. Leguminosae sharing between seasonal and ombrophilous forests and between seasonal and coastal forests inserted in the central and eastern portion of the state of Rio de Janeiro.

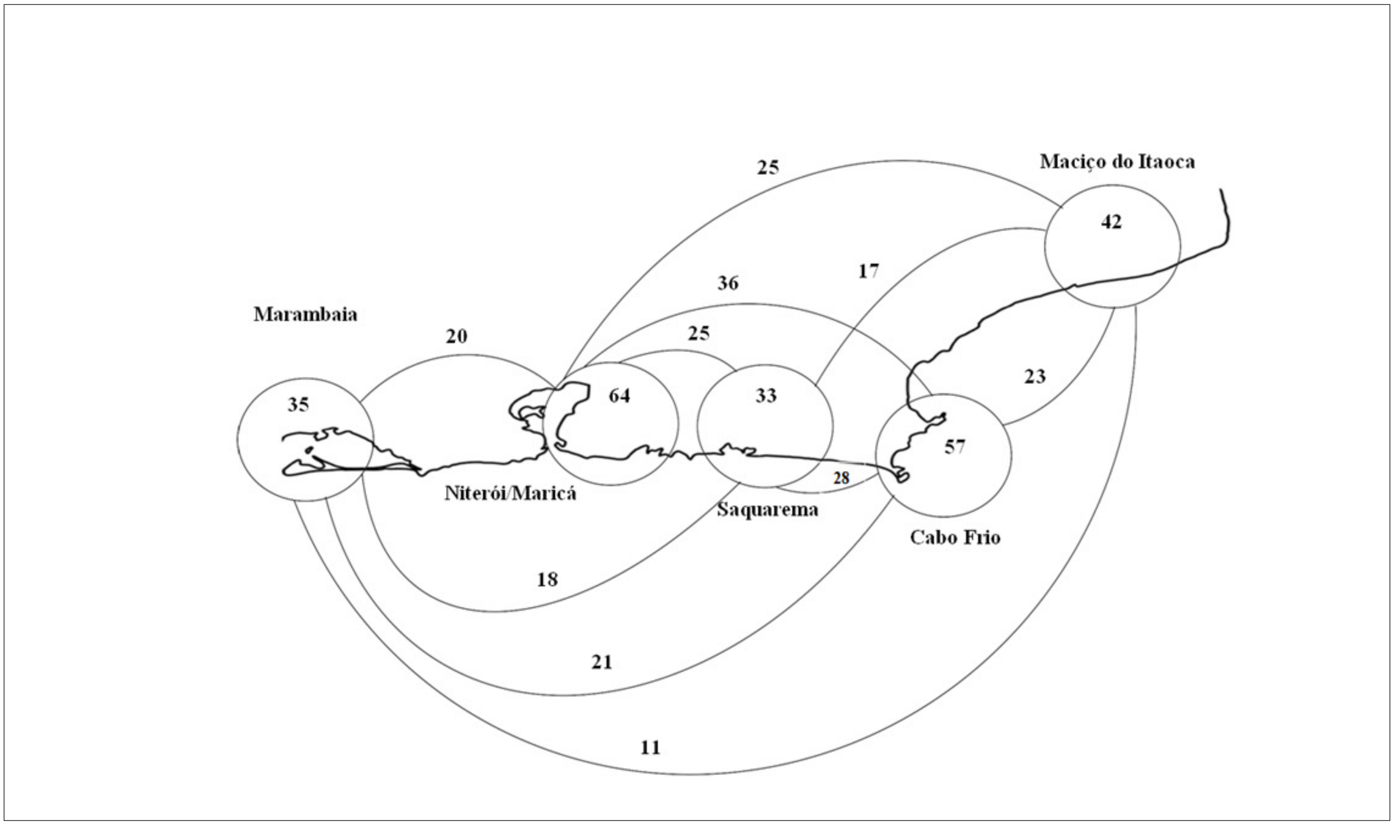

Figure 3. Geographic patterns of Leguminosae species substitution (turnover) among the five coastal forests inserted in the central and eastern portion of the state of Rio de Janeiro grouped in the similarity and CCA analyses. Circles (Leguminosae richness in each area); curves (richness shared between each area).

approaches the limit value (0.3) (ter Braak 1995, Felfili et al., 2011). The three axes explained 85.8% of the total variance, in which the first axis accounted for 37.3%, the second axis accounted for 29.9%, and the third axis 18.6%. The test was effective with P=0.001 and F=1.75, implying significant gradients for the three axes and significant correlations between environmental variables and species distribution. Those with stronger correlation ($r > 0.7$) with the first CCA axis were soil salinity ($r = 0.81$) and altitude ($r = -0.79$). The strongly correlated variables for the second axis were the dry season duration ($r = -0.84$) and DOcean ($r = -0.57$) (Table 3). The CCA clearly shows a five group division (Figure 4), with central and eastern coastal forests included in a distinct group (Group 5), and the RJitaoc and RJsaof areas in an intermediate position between groups 4 and 5 (Interior Seasonal Forests).

Discussion

1. *Leguminosae tree composition in coastal forests in the state of Rio de Janeiro*

Table 2. Estimators of the canonical order axes (CCA analysis) among the 34 analyzed areas and the main environmental variables.

	Axis 1	Axis 2	Axis 3
Eigenvalues	0.280	0.224	0.140
Variance (%)	37.32	29.86	18.61
Monte Carlo test	0.001	0.001	0.001

Table 3. Correlation of the main environmental variables in the two axes of canonical ordering (CCA analysis) among the 34 analyzed areas.

Environmental Variables	Axis 1	Axis 2
Distance from Ocean	-0.519696	-0.565544
Altitude	-0.786054	0.385223
Average dry season duration	0.022908	-0.843088
Soil fertility based on mean TBS (% of total base saturation)	-0.0316089	0.285007
Soil Salinity	0.812388	0.30686

The similarity pattern found in the Leguminosae tree species' composition among different forest sites of Rio de Janeiro, São Paulo, Minas Gerais and Espírito Santo states (Figures 1 and 4) shows great resemblance to previous studies (Oliveira-Filho & Fontes 2000; Oliveira-Filho et al., 2005; Nettesheim et al., 2010), suggesting that floristic differentiation is correlated to altitude and average duration of the dry season. However, coastal forests showed greater correlation with soil salinity in addition to these variables.

The groupings in the present study point to a distinguished aspect from the current Rio de Janeiro Ombrophilous and Seasonal forest formation distribution proposal (Ururahy et al., 1983). The Brazilian Southeastern Ombrophilous Forests in this mapping (IBGE 2012), are associated with the mountain ranges (Serras do Mar and Mantiqueira) and surrounding oceanic slopes and coastal plains, while Seasonal Forests are found inland, yet reach the coastline through the northern stretch of Rio de Janeiro state (Silva & Nascimento 2001; Nascimento & Lima 2008), reaching as far as the Cabo Frio Vegetal Diversity Center (Sá 2006). The lack of Ombrophilous Forests in this region mainly occurs due to the distance from the mountain ranges of the Atlantic coast. This biogeographic discontinuity is known as the "Campos de Goytacazes gap", in which a considerable reduction in humidity through southern São Paulo to northern Rio de Janeiro occurs. The Ombrophilous Forests from this region reappear in Espírito Santo in accordance with an increase in the average annual rainfall and declining seasonality, reaching as far as southern Bahia (Oliveira-Filho & Fontes 2000; Oliveira-Filho et al., 2005).

There is a gradual decrease in rainfall western portion of the study area (Araujo et al., 2009). The climate between Rio de Janeiro city and the Serra do Mato Grosso (border between the municipalities of Maricá and Saquarema) is classified as *Aw* according to the Köppen-Geiger system, being warm and humid with a rainy season in summer and dry in winter (Barbiéri 1984; Araujo et al., 2009). The mountain range and coastal massifs in Rio de Janeiro city approach the coast, forming a natural screen and influence the climate, with increased rainfall to values which can exceed 2,000 mm per annum, as seen in the Tijuca National Park (Costa 1986). Niterói and Maricá are part of the pluviometric transition between the coastal plain and the coastal massif (Barros 2008), with average precipitation values between 1,000 and 1,500 mm.year^{-1} being recorded (Barbiére & Coe-Neto 1999). The precipitation between Saquarema and Cabo Frio drastically decreases to around 800 mm/year with five months of drought (Ribeiro & Lima 2009). The climate in this stretch is classified as *BSh*, a variation of the Köppen-Geiger hot semi-arid climate, and factors such as the relief (distance from the Serra do Mar towards the coast and towards the West-East) and the coastal upwelling of Cabo Frio lead to a decrease in the rainfall in this zone (Araujo et al., 2009; Bohrer et al., 2009).

The State of Rio de Janeiro Bioclimatic Map (Cronemberger et al., 2011) characterized Niterói and Maricá in the Pre-Region of the Lakes with a Tropical Sub-humid to Humid climate based on the Thornthwaite classification, and its vegetation as transitional. This categorization is related to the fact that Niterói and Maricá are inserted in a transitional area of two climatic zones which makes it less rainy than in the capital of Rio de Janeiro, but is also not characterized by the marked water deficit between Cabo Frio and Saquarema (Barros 2008). Nevertheless, part of these forests are on lithosols, with a shallow horizon and part of the crystalline massif, which can generate a "local seasonality" intensified by low water retention, especially in periods of high temperatures, and thereby cause the deciduousness seen in SDTF.

However, the analysis showed that the presence of Seasonal Forests may extend along the coastline beyond the Região dos Lagos and reach the municipalities of Maricá and Niterói, as well as other areas such as Ilha de Marambaia (Figure 1 - subgroup 1a). As highlighted by Scarano (2009), these areas have a transitional nature, sharing a flora derived from the surrounding areas with characteristic elements of rocky environments or outcrops, which are considered peripheral in the Atlantic Forest.

The results also highlighted the group of seasonal forests in the states of Rio de Janeiro and Espírito Santo (Figure 1 - group 1b), and a floristic pattern which has already been pointed out by Rizzini (1963, 1979), Oliveira-Filho & Fontes (2000), Oliveira -Filho et al. (2005), Nascimento & Lima (2008) and Saiter et al. (2016). This high floristic differentiation is often overlooked due to vegetation gradients, but is a very important aspect in the Atlantic Forest's biogeographic history, as some Angiosperm clades are confined to or concentrated in SDTF of the South American tropics (Pennington et al., 2009). This draws attention to this composition of tree species from these coastal forests as relictual elements of dry forests present in these environments. This irradiation is associated with profound changes in temperature and precipitation during the Quaternary period, with possible implications for the current distribution of forest formations (Ledru et al., 1998; Oliveira-Filho & Fontes 2000).

Although grouped with the seasonal formations, the forests on sandy plains and coastal outcrops (Figure 1 - subgroup 1a) showed a high level of dissimilarity (Jaccard Index ≤ 0.4), highlighting the heterogeneity in the composition of Leguminosae species in seasonal environments in the Atlantic Forest of the state of Rio de Janeiro. The coastal vegetation of the Lakes Region has been considered distinct, initially as a vegetative enclave with links to the Caatinga (Ab´Saber 1973, 1977; Ururahy 1987).

Although the forests growing on lithosoils are considered as part of the ombrophilous formations due to the frequent incidence of marine winds and shallow soils, their low physiognomy was classified as a "woody thicket" by Rizzini (1979). The floristic affinity between these coastal formations with the state's forests on Baixada Campista tablelands (Lima 2000; Nascimento

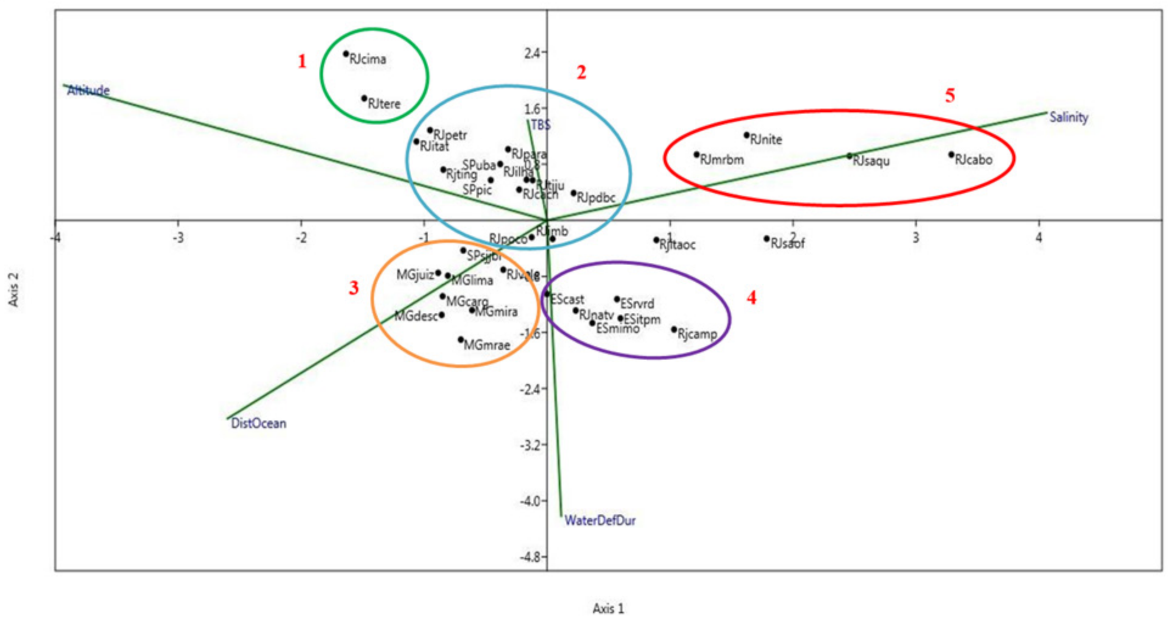

Figure 4. Biplot ordering diagram resulting from the analysis of canonical correspondence with the 34 Atlantic Forest areas of the Southeast analyzed regarding their arboreal Leguminosae composition and the correlated environmental variables. Group 1: Ombrophilous Forests / RJ; Group 2: Ombrophilous Forests RJ / SP; Group 3: Seasonal Forests RJ / ES / MG; Group 4: Seasonal Forests RJ / ES; Group 5: Coastal Forests inserted in the central and eastern portion / RJ. Areas:EScast = Castelo, ESitpm = Itapemirim, ES mimo = Mimoso do Sul, Esrvrd = Linhares/C. Vale do Rio Doce, MGcarg = Carangola, MGdesc = Descoberto, MGjuiz = Juiz de Fora, MGlima = Lima Duarte, MGmira = Miraí, MGmrae = Muriaé, RJcabo = Cabo Frio, RJcach = Cachoeiras de Macacu/Paraíso, RJcamp = Campos dos Goytacazes, RJcima = Macaé de Cima, RJilha = Ilha Grande, RJimb = Desengano/Imbé, RJitaoc = Maciço do Itaoca/Campos, RJitat = Itatiaia, RJmrbm = Ilha de Marambaia, RJnatv = Natividade, RJnite = Niterói/Maricá, RJpara = Paraty, RJpdbc = Maciço da Pedra Branca, RJpetr = Petrópolis, RJpoco = Poço das Antas, RJsaof = São Francisco do Itabapoana/Carvão, RJsaqu = Saquarema, RJtere = Teresópolis, RJtiju = Maciço da Tijuca, RJting = Maciço do Tinguá, RJvale = Valença, SPjjbr = São José do Barreiro, SPpic = Picinguaba, SPuba = Ubatuba.

& Lima 2008; Ribeiro & Lima 2009) was only recently suggested. The variation in Leguminosae species composition in these coastal forest stretches suggests a different floristic pattern than those presented by Barros (2008) and Conde et al. (2005), showing an even greater similarity with Cabo Frio and Saquarema, which are areas highlighted by Sá (2006), Dantas et al. (2009) and Ribeiro & Lima (2009) as having marked seasonality and whose arboreal component is characteristic of these dry forests. This analysis carried out with Leguminosae is a first approach to this discussion, about a floristic differentiation pattern which is more related to seasonal forests.

Although the coastal group is supported by Jaccard values (Figure 1), there is great variation within this group. An exclusive group of Leguminosae species for each of the coastal areas (Figure 3) supports the floristic differentiation which is sometimes established on lithosols, and sometimes grows on a stretch of sandy plains. Although Ilha de Marambaia and Maciço do Itaoca belong to this same coastal group, they showed greater dissimilarity. This result may be related to the geographical distance between these areas and mainly to the effect of the surrounding forest formations, as highlighted by Scarano (2009). In the case of Ilha de Marambaia there is a contribution of species from Ombrophilous Forest and in the case of Maciço do Itaoca from the Semi-Deciduous Seasonal Forest (Conde et al., 2005; Souza 2015). In contrast, Cabo Frio and Saquarema were the most similar areas, which might be related to their greater geographical proximity and to the effects of the soil and salinity.

The presence of these 108 Leguminosae species (Figure 2, Table 4) in Cabo Frio, Maciço do Itaoca, Ilha de Marambaia, Maricá/Niterói and Saquarema highlights the differentiation of coastal forests located in the central and eastern portion of the state of Rio de Janeiro, and shows that they would better be considered seasonal forests among marginal rain forest strongholds. Therefore, the Semi-Deciduous Seasonal Forest area in the state of Rio de Janeiro may be much larger than that referred by to IBGE (2012) and other literature (Sá 2006; Nascimento & Lima 2008; Ribeiro & Lima 2009; Abreu et al., 2014), and reach the south of the state. Lima (2000) argued in his analysis that although there are strong indications of Leguminosae floristic differentiation (coinciding with different altitudinal bands), a continuous pattern was detected along this gradient, which sometimes leads to difficulty in distinguishing the limits of the different forest types adopted in the different Brazilian vegetation classification systems.

Thus, our results suggest that the debate regarding the forests relationships of the of the Atlantic Domain will be resolved as new data on floristic structure and composition are collected, as we have done by filling the gaps in the Rio de Janeiro state inventories.

2. *Richness and sharing of Leguminosae tree species in the coastal forests in the state of Rio de Janeiro*

The listing of 250 Leguminosae tree species in the selected areas (Table 4) confirmed the high representativeness of the family in the forests which was already revealed in several studies about the Atlantic Rain Forest (Leitão-Filho 1986; Oliveira-Filho & Fontes 2000; Lima 2000). The family is virtually found in every plant formation throughout the planet, although the family's endemic center is currently in the Neotropics (Lavin et al., 2004; LPWG 2017). They compose significant elements in species diversity and abundance, ranging from humid tropical forests to dry forests and savannas all over the tropics (LPWG 2017). It is represented by 795 genera and almost 20,000 species, of

Table 4. Brazil Geographic distribution, phytophysiognomy (Dense Ombrophilous Forest - DOF/Seasonal Semideciduous Forest - SSF) and endemism of the Leguminosae tree species of the coastal stretch of Rio de Janeiro. Occurrence in the coastal stretch (IMAR – Ilha de Marambaia; NIT – Niterói and Maricá; SAQ – Saquarema; CBF – Cabo Frio; ITA – Maciço do Itaoca); Distribution in Brazil, State acronyms: Acre – AC; Alagoas – AL; Amapá – AP; Amazonas – AM; Bahia – BA; Ceará – CE; Espírito Santo – ES; Goiás – GO; Maranhão – MA; Mato Grosso – MT; Mato Grosso do Sul – MS; Minas Gerais – MG; Pará – PA; Paraíba – PB; Paraná – PR; Pernambuco – PE; Piauí – PI; Rio de Janeiro – RJ; Rio Grande do Norte – RN; Rio Grande do Sul – RS; Rondônia – RO; Roraima – RR; Santa Catarina – SC; São Paulo – SP; Sergipe – SE; Tocantins – TO). Data (Flora do Brasil 2020a; Lima 2000). *endemic species of Brazil. ** occurrence restricted to the coastal stretch of RJ.

Species	IMAR	NIT	SAQ	CBF	ITA	Distribution (Brazil)	Phytophysiognomy
Abarema cochliacarpos (Gomes) Barneby & J.W. Grimes*	X	X	X	X		Northeast and Southeast (except MA and PI)	DOF, SSF
Abarema langsdorffii (Benth.) Barneby & J.W. Grimes*				X		Southern and Southeastern Regions and BA	DOF, SSF
Acosmium lentiscifolium Schott*		X	X	X	X	BA, ES, MG, RJ	DOF, SSF
Albizia pedicellaris (DC.) L. Rico	X					All Regions (except CE, GO, PI, RS and SC)	DOF, SSF
Albizia polycephala (Benth.) Killip ex Record*	X	X	X	X	X	Midwestern, Northeastern, Southern and Southeastern Regions (except MA)	DOF, SSF
Anadenanthera colubrina (Vell.) Brenan		X		X		Midwestern, Northeastern, Southeastern, Southern (except AL, ES, MA, RS and SC)	DOF, SSF
Anadenanthera peregrina (L.) Speg.					X	Midwestern, AC, AM, BA, MG, PA, PB, PR, RJ, RR and SP	DOF, SSF
Andira anthelmia (Vell.) Benth.*	X			X		Northeastern, Southern and Southeastern Regions (except CE, MA, PI and RS)	DOF
Andira fraxinifolia Benth.*	X	X	X	X		Midwestern, Northeastern, Southern and Southeastern (except MA and MT)	DOF, SSF
Andira legalis (Vell.) Toledo*	X		X	X		BA, ES, MG, PE and RJ	SSF
Apuleia leiocarpa (Vogel) J.F. Macbr.		X		X		All Regions, except AP	DOF, SSF
Barnebydendron riedelii (Tul.) J.H.Kirkbr.					X	AC, BA, ES, RJ and SP	DOF, SSF
Bauhinia albicans Vogel*, **		X		X		RJ	SSF
Bauhinia forficata Link		X			X	Southern, Southeastern and AL, BA and PE	DOF, SSF
Bauhinia longifolia (Bong.) Steud.		X			X	Midwestern and Southeastern Regions, BA, PA, PR and RO	DOF, SSF
Bowdichia virgilioides Kunth				X		All Regions (except AC, SC and RS)	SSF
Calliandra harrisii (Lindl.) Benth.	X			X		RJ and BA	DOF, SSF
Calliandra tweedii Benth.		X				Southern and Southeastern Regions	DOF, SSF
Cassia ferruginea (Schrad.) Schrad. ex DC.		X				All Regions (except AC, AM, AP, MS, RN, RR, SC)	DOF, SSF
Cenostigma pluviosum var. *peltophoroides* (DC.) Gagnon & G.P.Lewis*				X		ES, RJ and BA	SSF
Centrolobium tomentosum Guillem. ex Benth.*		X				Southeastern Region, BA, GO, MT and PR	DOF, SSF
Chamaecrista ensiformis (Vell.) H.S. Irwin & Barneby	X	X		X		Northeastern, Southeastern, GO, PA and TO	DOF, SSF
Chloroleucon tortum (Mart.) Pittier*	X		X	X		Southeastern, BA, MS, GO and TO	SSF
Copaifera langsdorffii Desf.					X	Midwestern, Northeastern, Southeastern Regions, PR, RO, RS and TO	DOF, SSF

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Copaifera lucens Dwyer *	X	X	X	X		Southeastern Region and BA	DOF, SSF
Copaifera trapezifolia Hayne		X	X	X	X	BA, MG, PR, PE, RJ, SC and SP	DOF, SSF
Dahlstedtia grandiflora (A.M.G. Azevedo) M.J. Silva & Azevedo*					X	RJ	DOF, SSF
Erythrina speciosa Andrews*		X				BA, MG, MS, GO, PB, PR, RJ, SC and SP	DOF
Exostyles venusta Schott*		X	X	X	X	BA, ES, RJ and SP	DOF, SSF
Grazielodendron rio-docensis H.C. Lima*				X		BA, ES and RJ	SSF
*Hymenaea aure*a Y.T.Lee & Langenh.*					X	BA, ES and RJ	DOF, SSF
Hymenaea courbaril L.					X	All Regions (except RS and SC)	DOF, SSF
Inga capitata Desv.	X	X	X	X	X	Northeastern, Northern and Southeastern Regions (except AL, CE, PI, RN and TO)	DOF, SSF
Inga congesta T.D. Penn.*		X				BA, ES and RJ	DOF, SSF
Inga cordistipula Mart.*		X		X		Southeastern Region	DOF, SSF
Inga edulis Mart.	X					Northern and Southeastern Regions, BA, MT, PB, PE, PR and SC	DOF, SSF
Inga flagelliformis (Vell.) Mart.		X				AC, AM, AP, BA, ES, MG, PA and RJ	DOF, SSF
Inga lanceifolia Benth.*	X	X				ES, RJ and SP	DOF, SSF
Inga laurina (Sw.) Willd.	X	X	X	X	X	All Regions (except AL, AP, PI, RO, RN, RR, RS, SC, SE and TO)	DOF, SSF
Inga lenticellata Benth.*		X				MG, RJ and SP	DOF, SSF
Inga marginata Willd.		X				All Regions (except RN, RR and SE)	DOF, SSF
Inga maritima Benth.*	X		X	X		RJ	SSF
Inga subnuda subsp. *luschnathiana* (Benth.) T.D.Penn.*	X	X	X	X	X	Southern, Southeastern (except ES and RS)	DOF, SSF
*Inga tenui*s (Vell.) Mart.*					X	BA, ES and RJ	DOF
Inga vera subsp. *affinis* (DC.) T.D.Penn.		X				All Regions (except AL, RN and SE)	DOF, SSF
Libidibia ferrea (Mart. ex Tul.) L.P. Queiroz		X	X	X		All Regions (except MT)	SSF
Lonchocarpus cultratus (Vell.) A.M.G. Azevedo & H.C. Lima			X			Southern and Southeastern Regions, AC, AL, AM, BA, GO, MS, PE, RN, RO and SE	DOF, SSF
Machaerium brasiliense Vogel				X	X	Southeastern Region, AL, AM, BA, GO, MA, MT, PE and PR	DOF, SSF
Machaerium firmum (Vell.) Benth.*, **		X		X		RJ	DOF, SSF
Machaerium hirtum (Vell.) Stellfeld	X	X	X	X	X	All Regions	DOF, SSF
Machaerium incorruptibile (Vell.) Benth.*		X		X	X	BA, ES, RJ and SP	DOF, SSF
Machaerium leucopterum Vogel*				X		BA, MG, PE and RJ	SSF
Machaerium nyctitans (Vell.) Benth.					X	Southern and Southeastern Regions and BA	DOF, SSF
Machaerium obovatum Kuhlm. & Hoehne*, **		X		X		RJ	SSF
Machaerium pedicellatum Vogel*		X	X	X		BA, ES, MG and RJ	DOF, SSF
Machaerium robsonnianum Filardi & H.C. Lima*		X		X	X	ES, MG and RJ	SSF
Machaerium stipitatum Vogel				X	X	Southern and Southeastern Regions, BA, GO and MS	DOF, SSF

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Martiodendron mediterraneum (Mart. ex Benth.) R.C.Koeppen*						MG, RJ, PA, PE, MA, PI and TO	DOF, SSF
Mimosa arenosa (Willd.) Poir. var. *arenosa*		X		X		Northeastern and Southeastern (except ES)	SSF
Mimosa bimucronata (DC.) Kuntze var. *bimucronata*	X	X	X	X		Midwestern, Northeastern, Southern and Southeastern (except MT, PI, PB and RN)	DOF, SSF
Mimosa schomburgkii Benth.		X				AC, AM, BA, ES, MG, PA, PE,RJ and RR	DOF, SSF
Muellera filipes (Benth.) M.J. Silva & A.M.G. Azevedo*	X					RJ and SP	DOF
Muellera virgilioides (Vogel) M.J. Silva & A.M.G. Azevedo*		X	X	X		BA, MG and RJ	SSF
Myrocarpus fastigiatus Allemão*		X		X		AL, BA, ES, MG, PE and RJ	DOF, SSF
Myrocarpus frondosus Allemão	X					Southern and Southeastern Region and BA	DOF, SSF
Ormosia arborea (Vell.) Harms*	X	X	X	X	X	RJ and ES	DOF, SSF
Parapiptadenia pterosperma (Benth.) Brenan*		X	X	X	X	BA, ES, MG and RJ	SSF
Parapiptadenia rigida (Benth.) Brenan					X	Southern Region, MT, MS, RJ and SP	SSF
Paubrasilia echinata (Lam.) Gagnon, H.C. Lima & G.P. Lewis*		X	X	X		AL, BA, ES, PB, PE, RJ, RN and SE	SSF
Peltogyne discolor Vogel*		X		X	X	RJ	SSF
Peltophorum dubium (Spreng.) Taub.		X				Midwestern, Northeastern, Southern, Southeastern (except MA and PI)	DOF, SSF
Piptadenia gonoacantha (Mart.) J.F. Macbr.	X	X			X	All Regions (except AP, MA, PI and RR)	DOF, SSF
Piptadenia paniculata Benth.*		X			X	Southeastern, BA, PR and SC	DOF, SSF
Plathymenia reticulata Benth.					X	Midwestern, Southeastern, BA, CE, MA, PA, PI and PR	DOF, SSF
Platycyamus regnellii Benth.*		X				Southeastern Region, BA, GO and PR	DOF, SSF
Platymiscium floribundum Vogel var. *floribundum**		X	X			BA, CE, MG, PE, PR, RJ and SC	DOF, SSF
Platymiscium floribundum var. *nitens* (Vogel) Klitg.*				X		BA, CE, ES, GO, MG, RJ, PE and PI	SSF
Poecilanthe falcata (Vell.) Heringer*			X	X	X	BA, ES and RJ	SSF
Pseudopiptadenia contorta (DC.) G.P. Lewis & M.P. Lima*	X	X	X	X	X	Northeast and Southeastern Regions (except CE, PI, MA)	DOF, SSF
Pseudopiptadenia inaequalis (Benth.) Rauschert*	X	X	X			RJ	DOF, SSF
Pseudopiptadenia leptostachya (Benth.) Rauschert*	X	X				MG, RJ and SP	DOF, SSF
Pseudopiptadenia schumanniana (Taub.) G.P. Lewis & M.P. Lima*		X			X	ES and RJ	DOF, SSF
Pterocarpus violaceus Vogel	X	X	X	X	X	MS, PR, SC, Southeastern and Northeast Regions (except MA)	DOF, SSF
Pterogyne nitens Tulasne		X				Midwestern, Northeast, Southern, Southeastern and AM	DOF, SSF
Schizolobium parahyba (Vell.) S.F. Blake	X					All Regions (except AP, MA, PB, RN, RR, SE, TO)	DOF, SSF

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Senegalia duartei Seigler & Ebinger*		X		X	X	BA, MG and RJ	SSF
Senegalia grandistipula (Benth.) Seigler & Ebinger*		X				Southeastern Region, AL, BA, GO, PA, PE, PR and SC	DOF, SSF
Senegalia langsdorffii (Benth.) Seigler & Ebinger*			X			BA, CE, ES, GO, MG, MS, PB, PI, RJ and RN	DOF, SSF
Senegalia polyphylla (DC.) Britton & Rose		X	X			All Regions (except AP, PI, RS, SC and SE)	DOF, SSF
Senegalia riparia (Kunth) Britton & Rose ex Britton & Killip		X				Southeastern Region, AM, BA, CE, MT,RN, RR, RS and SC	DOF, SSF
Senna affinis (Benth.) H.S. Irwin & R.C. Barneby*		X		X		Southeastern Region and BA	DOF, SSF
Senna macranthera (DC. ex Collad.) H.S. Irwin & Barneby	X	X				Midwestern, Northeastern, Southern, Southeastern and TO	DOF, SSF
Senna pendula (Humb.& Bonpl. ex Willd.) H.S. Irwin & Barneby	X	X	X	X	X	All Regions	DOF, SSF
Senna silvestris (Vell.) H.S. Irwin & Barneby	X			X		All Regions (except AL, PB, PE, RN, RS and SE)	DOF, SSF
Swartzia apetala Raddi var. apetala*		X	X	X	X	BA, ES, MG and RJ	DOF, SSF
Swartzia apetala var. glabra (Vogel) R.S.Cowan*				X	X	BA, ES, MG, RJ and SE	SSF
Swartzia flaemingii Raddi*			X	X	X	Southeastern Region and AL, BA, CE, MA, PA, PE, PI, SE and TO	DOF, SSF
Swartzia glazioviana (Taub.) Glaz.* , **				X		RJ	SSF
Swartzia langsdorffii Raddi*	X					MG, RJ and SP	DOF, SSF
Swartzia myrtifolia var. *elegans* (Schott) R.S. Cowan*				X		BA, ES, MG and RJ	DOF, SSF
Swartzia simplex var. *grandiflora* (Raddi) R.S. Cowan		X			X	BA, ES, RJ and SP	DOF, SSF
Sweetia fruticosa Spreng.				X		Southeastern Region and BA, MA, MS, MT and PR	SSF
Tachigali denudata (Vogel) Oliveira-Filho*	X					RJ, PR, SC and SP	DOF, SSF
Tachigali paratyensis (Vell.) H.C.Lima*	X					Southeastern Region,BA, PE and PR	DOF, SSF
Tachigali pilgeriana (Harms) Oliveira-Filho*					X	BA, ES, MG and RJ	DOF, SSF
Zollernia glabra (Spreng.) Yakovlev	X	X	X	X	X	BA, ES, RJ and SP	DOF, SSF
Zollernia ilicifolia (Brongn.) Vogel	X					Southeastern, AL, BA, PB, PE, PR, RN, RO, SC and SE	DOF, SSF
Zygia latifolia (L.) Fawc. & Rendle					X	Southeastern Regions, AC, AM, AP, BA, GO, MT, PA, PE, PR, RO and RR	DOF, SSF

which 253 genera and 3033 species occur in Brazil. Of the latter, it is estimated that around 50% are endemic to Brazil (Flora do Brasil 2020b).

The family is morphologically, physiologically and ecologically diverse, representing one of the most spectacular examples of evolutionary diversification in plants (LPWG 2017). The pantropical intercontinental disjunction, observed along the geological scale, is an interesting biogeographic pattern that helps to understand Leguminosae diversification in Angiosperms. It can be explained by the Boreotropic Hypothesis, which postulates an exchange between North America and Eurasia tropical biotic during the beginning of the Tertiary (Schrire et al., 2005). Many taxa (e.g. *Bauhinia*) resulted from the boreotropical flora rupture per climatic cooling after the Paleocene-Eocene Thermal Maximum (PETM) (Lavin & Luckow 1993; Meng et al., 2014). Furthermore, the family's origin was dated via fossil records found in North America, Europe, Africa and Asia up to 60 million years AP in the Eocene at least, with subsequent rapid diversification around the world (Herendeen et al., 1992; Schrire et al., 2005). In the Neotropics, this diversification of Leguminosae can also be understood by historical climate changes, which drove the diversification of SDTF in the Tertiary and Quaternary periods (Pennington et al., 2004; 2009). Other issues contribute to this understanding, such as historical (e.g. rising of the Andes and the Panama's Isthmus) (Fiaschi et al., 2016) and punctual factors involving local climatic and edaphic variations or on a micro-scale with endemism and species with reduced area of occurrence (e.g. Mansano & Tozzi 2001; Morim 2006; Ribeiro & Lima 2009).

The floristic sharing analysis (Figure 2) also showed that although the number of common species between the Ombrophilous and Seasonal Forests is higher (45.2% - 113 species), the species exclusive to the seasonal formations is also relatively high (26.8% - 67 species). This number also stands out when comparing interior and coastal seasonal forests (Figure 2), indicating that there is a distinctive component in these forests. Oliveira-Filho & Fontes (2000) and Oliveira- Filho et al. (2005) argue that a good part of the seasonal forests' arboreal flora is solely composed by the fraction of rain forest flora which is capable of resisting and competing under water stress. However, in testing the limiting characteristics as a function of the floristic component of the Atlantic Forest, Neves et al. (2017) showed that about 45% of all endemic species only occur in areas experiencing more extreme environmental conditions. Although extremely neglected in terms of conservation, they contribute significantly to the richness and diversity of the Atlantic Forest.

The coastal forests on sandy plains and lithosoil showed a high level of floristic heterogeneity as already highlighted in the similarity analysis (Figure 1). Changes in the composition are evident, indicating floristic differentiation even in geographically proximal areas (Figure 3). The connection between Niterói/Maricá and the areas of Cabo Frio and Saquarema is relatively high and supported by sharing of 36 and 25 species respectively, which further supports that the Seasonal Forests' nucleus in the Região dos Lagos extends along the coast to the Guanabara Bay vicinity (Lima 2000).

The species distribution in the group of coastal forest areas showed variations between the amount of exclusive Seasonal Forest floristic components and those shared with Ombrophilous Forests. Although preliminary, the data support the proposal that the distribution of Ombrophilous Forests in the Atlantic Forest is limited by extreme environmental conditions and is replaced by Seasonal Forests (Scarano 2002) where there is a fraction of the flora capable of resisting and competing under water stress (Oliveira-Filho & Fontes 2000; Oliveira-Filho et al., 2005). Recent molecular phylogenetic studies have shown a strong PNC pattern in SDTF plant genealogy (Särkinen et al., 2011), highlighting the importance of old, niche conserved lineages confined to these plant formations. It is likely that this SDTF pattern also explains the floristic differentiation in coastal seasonal forest shelters in southeastern Brazil, but future studies are needed to infer the origin and biogeographic history of plant lineages with a preference for rocky outcrops and sandy coastal plains in the Atlantic Forest.

3. *Anthropic activity and implications for the conservation of coastal seasonal forest remnants in Rio de Janeiro*

The different economic activities developed throughout the state of Rio de Janeiro have resulted in profound environmental changes which have led to a drastic reduction in forest remnants, as well as marked changes in their composition and vegetation structure, which have consequences for the fauna and the environment. Such changes have happened since the arrival of Portuguese settlers with the removal of brazil wood (*Paubrasilia echinata* (Lam.) Gagnon, H.C. Lima & G.P. Lewis) to extract tree`s red dye. Other tree species were intensively logged between the 16th and 19th centuries with the expansion of the naval and timber industry, and are currently categorized under different threat of extinction levels (Fernandez et al., 2018). The planting of sugar cane (*Saccharum officinarum* L.) and coffee (*Coffea arabica* L.) monocultures in several stretches of Dense Ombrophilous Forest and mainly in the Semi-Deciduous Seasonal Forests of the Paraíba River Valley in those same centuries expanded the deforestation (Sales et al., 2018). Other factors such as agricultural expansion, cutting down trees for charcoal production, the installation of urban centers, the construction of road networks, the coastal occupation and the introduction of alien species all contributed to this degradation and suppression process, reducing the Atlantic Forest of Rio de Janeiro to an estimated area of only 917,196 ha (SOS MATA ATLÂNTICA 2019). The studies carried out in coastal forests of the central and eastern portions of Rio de Janeiro (e.g. Sá 1992, 2002, 2006; Conde et al., 2005; Araujo et al., 2009; Barros 2008; Patzlaff 2016; Machado 2018; Barros et al., 2020) show that the forests were affected in different ways by these activities.

The multiple land uses to which coastal forests have been subjected represent a major factor in shaping tree species composition, increasing the occurrence of some species in some places and reducing to rare occurrences or eliminating species in others, while the generalist species and those which are more adapted to disturbances have been able to expand their distribution (e.g. *Anadenanthera colubrina* (Vell.) Brenan, *Piptadenia gonoacantha* (Mart.) J.F.Macbr., *Piptadenia paniculata* Benth., *Pseudopiptadenia contorta* (DC.) G.P.Lewis & M.P.Lima and *Pterogyne nitens* Tul.). The parameters from the phytosociological analyzes carried out in these areas (e.g. Sá 2006; Barros 2008; Patzlaff 2016; Machado 2018) show the contribution of these species to the structure of the sampled forests. In the municipalities of Maricá and Niterói, this was enhanced mainly by the intentional production of charcoal, an activity that was very important for the development of large urban centers, such as Rio de Janeiro and Niterói. What is behind these species and parameters is the current expression of the forests devastated by these human activities (Barros 2008; Patzlaff 2016). Thus, the results indicate that this Leguminosae distribution in Seasonal and Ombrophilous Forests can be influenced by not only geographic and climatic factors, but also by human interventions. As pointed out by Carvalho et al. (2006), these aspects have been little discussed in comparative analyses, but they could lead to new avenues of research in floristic composition and beta-diversity. Regarding the Leguminosae, Ribeiro & Lima (2009) argue that, in addition to its diversification into seasonal environments, the association of the family with nitrogen-fixing bacteria has been identified as an efficient strategy for occupancy in nutrient and regeneration-poor environments, which are common in the Atlantic Forest.

Costa et al. (2009) argue that more than 70% of the original area covered by Semi-Deciduous Forests in Rio de Janeiro state have already been lost and has currently a low coverage of remnants in Conservation Units (CU), especially in the Integral Protection category. This situation harsh is not restricted to the state of Rio de Janeiro, it can be observed throughout the dry forest extension area. Durigan et al. (2000) consider the Semi-Deciduous Forest to be the most rapidly and extensively devastated vegetation throughout its natural occurrence area. This is a critical situation intensified by the high beta-diversity among the remaining Neotropical Seasonal Forest fragments, since 23 to 73% of the species found in each of the areas are exclusive, indicating high levels of endemism (DRYFLOR 2016). Therefore, the most effective strategy to reduce the extinction of these species would be to consider these remnants individually and to adopt less orthodox conservation measures, which include protecting a group of separate areas. This strategy is also supported by the high degree of phylogenetic geographic structure of the SDTF, mainly due to its limited dispersion (Pennington et al., 2009), which further reinforces the urgent conservation priority.

Conservation Units of different categories have already been created in coastal forest stretches located in the central and eastern portion of the state of Rio de Janeiro (Table 5), but the protection of these areas is hardly effective, as most have not been properly implemented and its enforcement is still very precarious. These municipalities cover 6,845 km^2 (Araruama, Armação de Búzios, Arraial do Cabo, Cabo Frio, Campos dos Goytacazes, Mangaratiba, Maricá, Niterói, São Pedro da Aldeia and Saquarema). However, when the extension of these ten municipalities is contrasted with the extension of protected areas, the CUs only cover 312 km^2, i.e., a small extension of areas is really protected. These forests are basically protected by nine CUs, five of which belong to the Integral Protection group, and the other four are in the Sustainable Use category. However, the Environmental Protection Area category stands out in the municipalities of Campos dos Goytacazes and Mangaratiba, while different categories occur in Niterói, Maricá and in the Região dos Lagos, which overlap in certain locations. It can also be observed that only part of the Ilha de Marambaia extension is included in Mangaratiba's Environmental Protection Area, which refers to the island portion.

These ten municipalities are amongst those with the greatest concentration of Rio de Janeiro endemic flora (Table 5). Four Leguminosae tree species are endemic and threatened with extinction (Table 4), being categorized as Vulnerable (*Machaerium firmum* (Vell.) Benth., *M. obovatum* Kuhlm. & Hoehne, *Swartzia glazioviana* (Taub.) Glaz.) or Endangered (*Bauhinia albicans* Vogel). Other Leguminosae species also stand out in the coastal stretch such as *Apuleia leiocarpa* (Vogel) J.F.Macbr. (Vulnerable) and *P. echinata* (Lam.) Gagnon, H.C.Lima & G.P.Lewis (Endangered) (Lima et al., 2013; Lima et al., 2018). Thus, this study used data present in NeoTropTree, but it additionally covered several coastal areas, thereby improving local floristic knowledge by conducting new collections. The study also worked with the collections of Herbaria in the state of Rio de Janeiro, identifying and reviewing collections to expand our dataset.

Table 5. Conservation Units implemented in a coastal forests stretch inserted in the central and eastern portion of the state of Rio de Janeiro. E.S. = Endemic Species and E.S.T.E. = Endemic species threatened with extinction (Rosa et al., 2018). Municipalities area (IBGE, 2020).

Municipality	Area	E.E.	E.E.A.E.	Conservation Unit	Group	Area (ha)	Source
Araruama	638.150	5	2	Costa do Sol State Park	Integral Protection	9,841	INEA 2020
Armação de Búzios	70.978	26	24				
Arraial do Cabo	152.105	29	27				
Cabo Frio	413.575	37	33				
Saquarema	352.130	33	30				
São Pedro da Aldeia	332.922	19	18				
Campos dos Goytacazes	4031.989	27	15	Serra do Itaoca EnvironmentalProtection Area	Sustainable Use	600	Farias et al. 2014
				Taquaruçu State Park	Integral Protection	65	Abreu Filho & Kristosch 2008
Mangaratiba	358.563	27	23	Mangaratiba EnvironmentalProtection Area	Sustainable Use	2,125.43*	INEA 2015
Maricá	361.572	35	32	Serras de Maricá Municipal Wildlife Refuge	Integral Protection	8,938.27	Maricá 2011
Niterói	133.757	51	45	Morro do Morcego, da Fortaleza de Santa Cruz e os Fortes do Pico e do Rio Branco Environmental Protection Area	Sustainable Use	141	Niterói 2018
				Lagunas e Florestas de Niterói Environmental Protection Area	Sustainable Use	5,139**	Niterói 2018
				Serra da Tiririca State Park	Integral Protection	3,493	Niterói 2018
				Nature Municipal Park	Integral Protection	918	Niterói 2018
Total (sq. km2)	6,845.741					312,607	
Total (ha)	684,574.1					31,260.7	

*** The Mangaratiba Environmental Protection Area does not cover the entire length of Marambaia, only the island (hillside forest).**

**** The Environmental Protection Area of the Niterói Lagoons and Forests overlaps with the Serra da Tiririca State Park (PESET).** Thus, the value shown in the table is given by the total area minus the PESET area, so that a value larger than the real one would not be presented.

The results of our analyses reinforce the need to preserve the remaining vegetation of these coastal forests included in the central and eastern portion of Rio de Janeiro state. The floristic differentiation supported by an exclusive group of Leguminosae species shows that the extent of dry forests may be greater than currently acknowledged. The patterns of diversity, endemism and phylogenetic niche conservatism indicate SDTF as a stable biome and limited by dispersion. Such uniqueness justifies conservation action given especially the speed at which these forests have been modified by human activities.

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Author Contributions

Davi Nepomuceno da Silva Machado: Plant collection in forested areas, data analysis, interpretation and manuscript preparation.

Marcelo Trindade Nascimento: Dry Forest floristic data contribution from Southeastern Brazil, data interpretation and critical revision of the manuscript.

Ana Angélica Monteiro de Barros: Contribution to the floristic data, collection of plants from forests of the Niterói and Maricá stretches and critical revision of the manuscript.

Richieri Antônio Sartori: Contributed to data processing in statistical packages and interpretation; critical review of the manuscript.

Cláudio Belmonte de Athayde Bohrer: Contributed to data processing in statistical packages and interpretation; critical review of the manuscript.

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Haroldo Cavalcante de Lima: Contributed to the study concept and design; collected plants in forest areas; data analysis and interpretation, and preparation of the manuscript.

Conflicts of interest

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

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Leaf morphoanatomy of an endemic massaranduba from Chapada Diamantina, Bahia, Brazil

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Abstract: The Sapotaceae family is recognized for its economic importance, presenting food, medicinal and timber potential. *Pouteria andarahiensis* T.D.Penn., popularly known as "massaranduba", is endemic to Chapada Diamantina, Bahia, Brazil, and is currently classified on the IUCN red list as "endangered". *Pouteria andarahiensis* is little studied, highlighting this work as the first anatomical study for the species. Light microscopy and scanning electron microscopy techniques were used to perform anatomical studies. The species showed characters shared with the family (laticifers and malpiguiaceous trichomes), as well as diagnostic characters and associated with xeromorphy. The data obtained from the leaf architecture can assist in the identification of the species in a vegetative state, while the leaf surface provided unpublished data to the species, indicating the presence of a cuticle with complex ornamentation. Stand out as xeromorphic anatomical features, high stomatal density, high number of trichomes per area, sclerenchymatic columns in the mesophyll and a subepidermal sclerenchyma layer connecting the vascular bundles in the mesophyll.
Keywords: *Leaf anatomy; Chrysophylloideae; Xeromorphy.*

Morfoanatomia foliar de uma massaranduba endêmica da Chapada Diamantina, Bahia, Brasil

Resumo: A família Sapotaceae é reconhecida pela sua importância econômica, apresentando potencial alimentício, medicinal e madeireiro. A espécie *Pouteria andarahiensis* T.D.Penn., conhecida popularmente como "massaranduba", é endêmica da Chapada Diamantina, Bahia, Brasil, e atualmente encontra-se classificada na lista vermelha da IUCN como "em perigo". *Pouteria andarahiensis* é pouco estudada, destacando este trabalho como o primeiro estudo anatômico para a espécie. Foram empregadas técnicas de microscopia de luz e de microscopia eletrônica de varredura para a realização dos estudos anatômicos. A espécie apresentou caracteres compartilhados com a família (laticíferos e tricomas malpiguiáceos), assim como, caracteres diagnósticos e associados a xeromorfia. Os dados obtidos da arquitetura foliar podem auxiliar na identificação da espécie em estado vegetativo, enquanto a superfície foliar forneceu dados inéditos a espécie, indicando a presença de uma cutícula com ornamentação complexa. Destacam-se como características anatômicas xeromórficas, alta densidade estomática, alto número de tricomas por área, colunas esclerenquimáticas no mesofilo e uma camada subepidérmica de esclerênquima conectando os feixes vasculares no mesofilo.
Palavras-chave: *Anatomia foliar; Chrysophylloideae; Xeromorfia.*

Introduction

The genus *Pouteria* Aubl. belongs to the subfamily Chrysophylloideae and stands out within the Sapotaceae family for presenting about 200 species, with 128 occurring in Brazil (Carneiro & Almeida Jr. 2010; Carneiro et al. 2015, Alves-Araújo et al. 2020), in which 52 are endemic. *Pouteria andarahiensis* T.D.Penn. is characterized by the shrub or arboreal habit; presence of white latex in the branches, leaves and fruits; petiolate leaves, simple, leathery texture, alternating-spiral, which have ferruginous trichomes; inflorescences with 3-12 flowers, axillary, and unisexual flowers. *Pouteria andarahiensis* can be identified in the presence of its reproductive organs, however, its vegetative characters demonstrate morphological uniformity with other species of the genus, making it difficult to identify sterile species.

Pouteria andarahiensis is endemic to Chapada Diamantina, occurring in regions of caatinga and cerrado, composing the rupestrian field vegetation, being popularly known as "massaranduba" (Pennington 1990). According to the National Flora Conservation Center (CNCFLORA 2020) *Pouteria andarahiensis* occupies an occurrence extension of 46,376.90 km², being protected by the Chapada Diamantina National Park.

However, the area of occurrence of the species has been suffering continuous degradation due to factors that date back to the diamond and gold mines, or even, by the use of fire used to open pastures for cattle breeding, the expansion of agricultural areas and also the demand for wood, which is commonly used for construction (Funch et al. 2005; Nascimento et al. 2010). This reduction in the area of occupation, as well as the use of timber, included *P. andarahiensis* in the red list of the International Union for Conservation of Nature - IUCN (O'Brien 1998), being classified as "endangered" (EN).

The species of the genus *Pouteria* are known for presenting compounds used in medicine and in the production of cosmetics, for the use of their fruits in food, the use of latex in the production of rubber and gum, and for the use of wood in constructions. The realization of morphological studies, mainly that address the internal structure, may indicate whether the species has medicinal, commercial and ecological potential, as observed in other representatives of the genus.

Cabral et al. (2016) consider that the leaves present characteristics as useful for the identification of species as their floral characters and the pollen morphology, while Roth-Nebelsick et al. (2001) consider the architecture of leaf venation an important character for the taxonomic classification. In this context, the morphology and anatomy of *Pouteria andarahiensis* leaves were used to provide distinctive characters for the species in a vegetative state and, consequently, to support its taxonomy and assist in the knowledge of Northeastern flora.

Material and Methods

This work was based on the material collected in the municipality of Morro do Chapéu, as well as analysis of the material deposited in the Herbarium of the State University of Feira de Santana (HUEFS). Samples in good condition and with fully expanded leaf blades were selected.

To obtain the leaf architecture, Strittmatter's (1973) diaphanization technique was used. The samples obtained were stained with 1% aqueous safranin and kept in glass plates with 50% glycerin (Kraus & Arduin 1997). The measurements of the veins were carried out in three regions of the leaf blade (base, middle, apex) through the micrometric eyepiece of the Zeiss Primo Star light microscope in all diaphanized specimens, and for descriptive analysis the terms of classification by Ash et al. (1999) were used.

The study of leaf epidermis was performed using scanning electron microscopy and light microscopy. For analysis in a scanning electron microscope (SEM), segments of the median region of the leaves stored in ethyl alcohol were dried in an oven at 60°C, and then covered with 18k gold powder in a Denton Vacuum IV metallizer. The samples were analyzed using a JSM-6390LV scanning electron microscope. For analysis under a light microscope, the epidermis was obtained using two methodologies, the Foster technique (Macêdo 1997) in whole and fractionated leaves, and the Jeffrey technique (Macêdo 1997) only for whole leaves, verifying the obtainment of the best results in fractional leaves submitted to the Foster technique. The obtained epidermis was stained with 1% aqueous safranin and mounted on semi-permanent slides according to the manual by Kraus & Arduin (1997). The cuticle description viewed through SEM was based on the classification and terminology used by Barthlott et al. (1988) for epicuticular waxes, and the description of the epidermis was based on the terminology used by Solereder (1908). For the metric data of the leaf epidermis, two methods were used. For counting the number of cells, stomata and trichome scars, 20 areas (10 fields on the adaxial face and 10 on the abaxial face) of 5 slides for each specimen were photographed with the aid of a Leica ICC50 W camera attached to the Leica DM500 microscope, being used to *Pouteria andarahiensis* 2 specimens from herbarium and 2 specimens of fresh material.

For the measurements of cells and stomata, the same slides were used to count the number of cells in the Zeiss Primo Star microscope with the aid of the micrometric eyepiece, where 5 cells and 5 stomata (on the abaxial face) were measured for each of the 20 counted fields.

To analyze the internal structure, the material was transversally sectioned by freehand and with a freezing microtome in the base, middle, apex, border and petiole regions (distal, median and proximal regions). For samples sectioned in a freezing microtome, distilled water was used as the inclusion medium. The material was sectioned at 25 µm thick, using the Leica CM1860 cryostat at -26°C. The samples were clarified in commercial sodium hypochlorite, stained with 1% astra blue and 1% safranin in the 9: 1 ratio (Bukatsch 1972), or 1% alcian blue and 1% safranin (Luque et al. 1996), and mounted on semi-permanent slides (Kraus & Arduin 1997). The analysis of the samples was performed in a Zeiss Primo Star light microscope, and the images were obtained with the Leica ICC50W camera coupled to the Leica DM500 microscope. For the metric data of the anatomical samples, 20 fields of 5 slides of each specimen used were counted, made with cross sections of the leaf blade and the petiole, being 10 fields of the adaxial side and 10 of the abaxial side. To determine the degree of cuticle thickness, it was measured using the micrometric eyepiece of the Zeiss Primo Star microscope, using the following classification method: cuticles with 1.0 µm <2.0 µm were considered thin, ≥ 2.0 µm <4.0 µm were considered medium thickness, ≥ 4.0 µm were considered thick. Cross-sectional measurements of the palisade parenchyma cells were also performed. The terminology used in the anatomical descriptions was based on Metcalfe & Chalk (1972); Howard (1979) and Theobald et al. (1979), for leaf shape, petiole and trichomes, respectively.

Results

Pouteria andarahiensis T.D.Penn. has a shrub or arboreal habit and trees up to 6 meters high can be found (Figure 1A), with whitish milky latex common to the family occurring on the trunk, branches, leaves and fruits. The leaves are simple, leathery, alternating spiral, and with non-channeled petiole. The leaf blade has an elliptical to ovate shape, acute to obtuse apex, attenuated base, whole revolute margin (Figure 1B), shows trichomes on both sides in young leaves, and loses these trichomes in adult leaves, being thus considered glabrescent.

The leaves are peninerved, camptodromous of the brochidodromous type, with midrib showing straight development and high caliber gradually tapering towards the apex with a diameter ranging from 1 mm at the base to 0.2 mm at the apex. The secondary veins are presented in eight to ten pairs, which originate from the midrib alternately, with straight development that form arcs at the ends. The intersecondary veins are found in the median region between the secondary veins, developing in parallel and connected to the secondary ribs through the tertiary veins. The tertiary veins are inserted in the secondary veins at straight angles, alternating, forming a sinuous pattern that can present secondary arcs when connected to other tertiary or quaternary veins. Tertiary and smaller caliber ribs are present outside the arches formed by the secondary veins, presenting the same reticulated pattern as the rest of the leaf. It was possible to see veins of up to fifth order and free terminal venules (Figure 1C).

In cross-section, the petiole of the *Pouteria andarahiensis* is biconvex, the cuticle is thick, the epidermis is unistratified and the anticline walls straight, it has six to seven layers of angular collenchyma below the epidermis in the cortical region and the medulla has filling parenchyma (Figure 1D). The central vascular bundle is closed, plane-convex, with the phloem and xylem arranged in parallel rows and the medulla of the vascular bundle is filled with parenchyma (Figure 1E). Accessory bundles may or may not occur and, when present, vary from one to two, anastomosed through the sclerenchyma sheath that surrounds the vascular bundle. Laticifers are seen in the center of the vascular bundle, between the elements of the phloem and throughout the cortical region. There were no differences between the distal, median and proximal regions of the petiole.

The leaf blade of *Pouteria andarahiensis* has a cuticle with complex ornamentation, with platelets covering the stretch marks and guard cells of the stomata, forming slight elevations on the leaf surface (Figure 1F). These platelets are distributed over the guard cells perpendicularly and longitudinally over the stretch marks. These stretch marks can also be viewed under light microscopy, using the extracted epidermis, where it was observed that these stretch marks are less prominent in the costal cells. Through the transverse sections, a thickened cuticle layer about 16-20.8 μm on the adaxial face and 6.4-19.2 μm on the abaxial face, with unistratified epidermis and presenting differentiated cells, was visualized under light microscopy close to the main rib on the adaxial face, being square and smaller and on the rest of the blade elongated and with tabular shape, while in the abaxial face are rounded and uniform (Figure 1G).

Through light microscopy it was found that the intercostal epidermal cells have a rectangular and polygonal shape on both sides, with a larger diameter on the abaxial face, with about 40 μm x 15 μm and about 645 cells per mm², while on the adaxial face, have a smaller diameter and are more numerous, measuring an average of 19.5 μm x 16.6 μm with about 1,908 cells per mm². The costal epidermal cells on the abaxial surface are larger and rectangular, approximately 60 μm x 14.5 μm. The anticline walls are straight (Figure 1H-I).

P. andarahiensis is hypoestomatic, and the stomata are anisocytic type. In cross-section, the stomata are on the same level as the epidermal cells, widely distributed among intercostal cells, with about 61 stomata per mm², and may rarely occur between the costal cells. *Pouteria andarahiensis* presented simple non-glandular trichomes (tectors), in "T" shape, known as malpighiaceous trichomes, on both sides, with greater concentration on the abaxial surface, presenting an average of 26 trichomes per mm², while on the adaxial surface, it presents 5 trichomes per mm² (Figure 1J). These trichomes are distributed over intercostal and costal cells, being more abundant in intercostal cells, with four to five cells at the base.

The mesophyll is dorsiventral, composed of two layers of palisade parenchyma and six to seven layers of spongy parenchyma, the cells of the palisade parenchyma are elongated, juxtaposed transversely to the epidermis and with straight anticline walls. The spongy parenchyma is formed by cells of irregular shape, provided with braciform projections forming intercellular spaces of varying dimensions. On average, the mesophyll is 341.8 μm thick, with the palisade parenchyma about 124.8 μm thick and the spongy parenchyma is about 147.2 μm, where the cells of the palisade parenchyma measure about 56 μm x 14, 4 μm. The vascular bundles present in the mesophyll are accompanied by sclerenchyma cells forming a sheath surrounding these bundles which extends forming a subepidermal layer that connects the lateral bundles (Figure 1K). Laticifers are present in the spongy parenchyma and associated with vascular bundles (Figure 1G-K).

In cross section in the median region of the leaf, the leaf blade exhibits a biconvex shape, being more prominent on the abaxial face. The epidermal cells in the midrib region do not differ when compared to the epidermal cells of the rest of the leaf blade. The cortical region consists of six to seven layers of angular collenchyma on the adaxial surface and eight to nine layers on the abaxial surface. The simple parenchymal tissue fills the entire remaining cortical region, and on the adaxial surface it transitions to the palisade parenchyma when approaching the mesophyll. It is possible to identify laticifers throughout the cortex and idioblasts have been identified in the cortex, on the abaxial face. The vascular system is in the form of a continuous arch, flat-convex, where the phloem and xylem are organized in parallel rows, being able to visualize the presence of laticifers between the phloem elements, and the medulla is filled with parenchymatic tissue that contains laticifers. The vascular system may or may not have accessory bundles, when present they are from one to three anastomosed through the sheath elements of perivascular sclerenchyma cells.

The leaf edge is flexed, the epidermal cells of the adaxial face when viewed in cross section, are rectangular arranged in parallel and are narrowing as they approach the distal portion, on the abaxial face the epidermal cells are polygonal and smaller than on the adaxial face, the palisade parenchyma has two layers of cells arranged in parallel and seven to eight layers of spongy parenchyma with braciform projections. In the distal portion of the border, the parenchyma gradually loses the distinction between palisade and lacunous and appears as a homogeneous tissue with rounded cells, where the presence of laticifers was verified (Figure 1L).

Discussion

Pouteria andarahiensis is a difficult species to identify based only on vegetative characters, because in the absence of fertile material its morphology is very similar to other species of the genus and family.

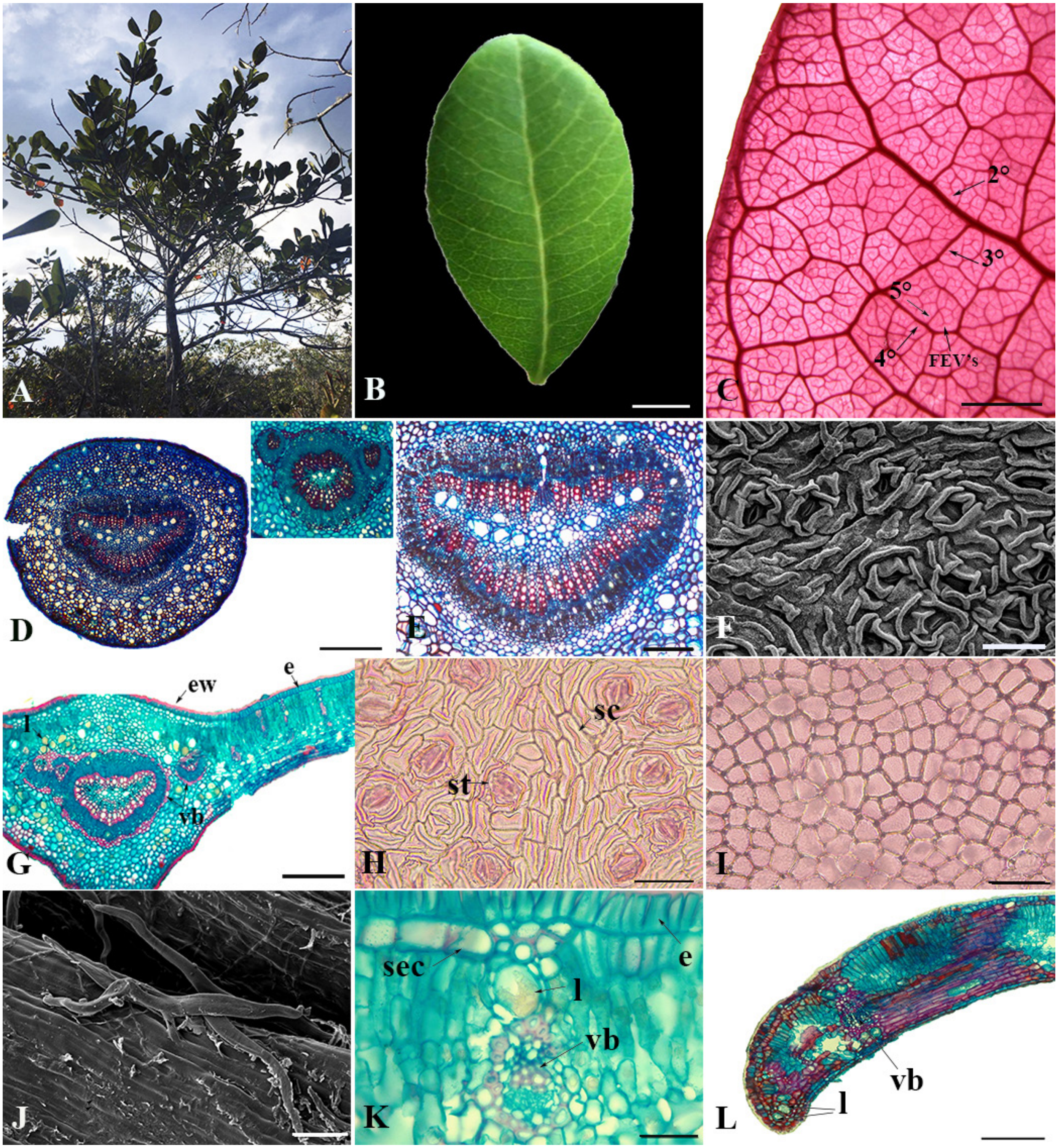

Figure 1. A – Individual of *Pouteria andarahiensis* T. D. Penn. B – Leaf. C - Part of the diaphanized leaf, showing the second to fifth order veins and the free terminal venules (FEV's). D - Cross section of the median region of the biconvex petiole. E - Cross section of the petiole showing the closed vascular bundle. F - Complex cuticle of the abaxial face, composed of streaks and platelets with patterns of organization in scanning electron microscopy. G - Cross section of the median region of the leaf, showing the cuticle (ew), the epidermis (e), the laticifers (l) and the vascular bundles (vb). H - Leaf epidermis of the abaxial face, showing stomata (st) and stretch marks (sc) under light microscopy. I - Leaf epidermis of the adaxial face. J - T-shaped malpiguiaceous trichome in scanning electron microscopy. K - Cross section of the mesophyll, showing the epidermis (e), the laticifers (l), the subepidermal cell layer (sec) and the vascular bundle (vb). L - Transverse section of the border, showing the laticifers (l) in the distal portion, and the vascular bundle (vb). Scale: B 1 cm; C 2 mm; D, G 500 µm; E – L 200 µm; F, H – K 50 µm.

Although identification through reproductive characters is effective for most species, it is extremely important to correctly identify a species based only on vegetative characters. According to Roth-Nelbelsick et al. (2001) it is beneficial to use topological aspects to characterize the patterns of leaf venation, since these are unequivocal, therefore, using the pattern of leaf venation found in *Pouteria andarahiensis* can be considered a reliable method to identify specimens in vegetative state. Schulz & Hilgenfeldt (1994) use the term "dendritic structure" to define the venation pattern found in *Pouteria andarahiensis*. Using the standardization of leaf venation classification by Hickey (1974, 1979), veins were considered up to fifth order, since the simplest venations form reticles that do not allow differentiation in caliber. Although *Pouteria andarahiensis* leaves present many macroscopic differences when compared to other genera of the family, in microscopic character the leaf architecture still manages to present many similarities between them. Studies were carried out that described the leaf venation of *Diploon*'s species (Lima et al. 2019) and of *Manilkara*'s species (Almeida-Jr et al. 2013), where similarities were found with the results of this work. The brochidodromous venation, with single primary vein, secondary veins originating from the primary vein without reaching the margin, with one or more intersecondary veins, were characters of *Pouteria andarahiensis* shared with *Diploon* species. The straight tertiary veins was the only characteristic of *Pouteria andarahiensis* found similar in the species of *Manilkara*. Differently the leaf architecture, the characters found in the petiole of *P. andarahiensis* presented similarities to the results found by Almeida-Jr et al. (2013) for *Manilkara* species, such as, circular shape, the format of the flat-convex vascular bundle and the accessory bundles when present, occurring in number of one or two. However, when compared to the characters found in the petiole in the genus *Diploon* (Lima et al. 2019), similarities were found in the shape of the flat-convex vascular bundle, the occurrence of accessory bundles in number of one or two and the presence of laticifers in the medullary region. The flat-convex vascular bundle shape found in the petiole of *P. andarahiensis* can also be verified in *P. beaurepairei*, however, Monteiro et al. (2007) verified that the vascular bundle shape presents a lot of variation, being able to visualize biconvex, flat-convex, flat and slightly convex vascular bundles for *Pouteria* species from Rio de Janeiro.

The characters used to identify species of the family in a vegetative state described by Solereder (1908) and by Metcalfe & Chalk (1957), are present in *Pouteria andarahiensis*, being easily distinguished by the presence of latex and malpighiaceous trichomes. The thick cuticle in *Pouteria andarahiensis* may be related to the environment in which it is found, as according to Figueiredo et al. (2012) and Gutschick (1999) the thick cuticle helps stomata against water loss in periods of dry and are present in plants with a xeromorphic character, this thick and extremely striated cuticle resembled that found by Monteiro et al. (2007) for *Pouteria ramiflora*, however, it differed from all other *Pouteria* species studied for the Rio de Janeiro state. The similarity found between *Pouteria andarahiensis* and *Pouteria ramiflora* may be related to the environment in which they occur, since both can be found in Cerrado, in regions with sandy soil. The work of Popovkin et al. (2016) for *Pouteria synsepala*, also presented a cuticular pattern similar to that found in *Pouteria andarahiensis*, where the cuticle forms labyrinths around stomata that are at the same level as the cuticle, however, the formation of stretch marks in the cuticle is more evident in *Pouteria andarahiensis*. Barthlott et al. (1998), describe the shape of the platelets as flat crystals, with an entire margin and regular shape, according to him, these platelets may have characteristic orientation patterns. Therefore, when present, these patterns are important to characterize a surface, in *Pouteria andarahiensis* the platelets deposited on the guard cells are oriented perpendicularly to the ostioles and those deposited on the stretch marks are oriented along their length. The pattern of organization of the platelets on the stretch marks can be classified as parallel and those found on guard cells would have a pattern of locally restricted orientation, these patterns can be used as taxonomic markers, since these have remained constant in all specimens analyzed.

Regarding the diagnostic characters of the family, trichomes are numerous in young leaves of *P. andarahiensis*, and according to Press (1999) in hot and arid environments, the main role of trichomes is to decrease leaf temperature and water loss, decreasing the absorption of solar radiation, and hypoestomatic leaves with anisocytic stomata are in accordance with several works for the family and genus (Solereder 1908; Metcalfe & Chalk 1957; Pennington 2004; Monteiro et al. 2007; Leite et al. 2017), these stomata are numerous, which Wilkinson (1979) relates to xerophyte species.

The outline of the anticline walls of the epidermal cells is straight, which corroborates with Santiago et al. (2001) who correlated leaves exposed to the sun to the presence of epidermal cells with straight anticline walls, since *P. andarahiensis* is exposed to frequent sunlight.

The mesophyll with dorsiventral disposition found in *P. andarahiensis* corroborates the description of Metcalfe & Chalk (1957) for the family and with the data found by Monteiro et al. (2007), Almeida Jr. (2013); Leite et al. (2017) and Lima et al. (2019), for other species of Sapotaceae. It is possible to visualize sclerenchyma columns in the mesophyll, these columns together with the thick cuticle, may be related to long periods of drought, strong light and poor nutrient soil (Dickison 2000; Cutler et al. 2011).

Solereder (1908) affirms that the vascular bundles present in the mesophyll can connect vertically through a layer of cells that can be sclerenchymatic or parenchymal, and in the present study it was found that in *P. andarahiensis,* it presents this connection between the columns by a layer sclerenchymatic cells that appear around the vascular bundles and form a layer below the epidermis, connecting to the nearest vascular bundle.

Conclusion

Unpublished data about *P. andarahiensis*, an endemic species of the Chapada Diamantina, were presented, such as platelets with patterns of organization present in the cuticle, subepidermal cell layer, anisocytic stomata and malpiguiaceous trichomes common to the family and sclerenchyma cell sheath that surround the vascular bundles, that can be used for its identification in a vegetative state, in addition, it was possible to verify that the species has mechanisms of adaptation to xeromorphic environments, such as the presence of ornamented cuticle, high stomatal density, high number of trichomes per area and sclerenchyma columns in the mesophyll.

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Author Contributions

Monick Lima Carvalho: 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.

Cláudia Elena Carneiro: 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 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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Amphibians of Serra das Torres Natural Monument: a reservoir of biodiversity in the Atlantic Forest of southeastern Brazil

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Abstract: The Brazilian Atlantic Forest holds a major part of the country's amphibian species richness and high rates of endemism. In this study, we conducted surveys using the Rapid Assessment (RA) method to sample the amphibian fauna of the Serra das Torres Natural Monument (MONAST), an Atlantic Forest remnant in southeastern Brazil. We sampled actively with a 6-10-person team to collect standard samples from 09:00 to 12:00 hours for the daytime period, and from 18:00 to 22:00 hours for the crepuscular/nighttime period, with a total of approximately 1,320 hours of sampling effort. We supplemented these data with 720 hours of passive sampling, using pitfall traps with drift fences (30 bucket-days). We recorded 54 amphibian species (two gymnophionans and 52 anurans), and the species richness estimated by the *Bootstrap* method indicates that a slightly larger number of species (n = 60) may occur in the study area. The most speciose family was Hylidae (n = 21), followed by Brachycephalidae (n = 8). Overall, 25% of the species (n = 13) were recorded only once (singletons) and 15% (n = 8) only twice (*doubletons*). Most amphibians recorded in this study (71%, n = 37 species) were restricted to the Atlantic Forest biome, two species *(Euparkerella robusta and Luetkenotyphlus fredi)* are endemic to the Espírito Santo state, and one of them, the leaf litter species , is endemic to the MONAST. *Euparkerella robusta* is currently listed as Vulnerable by the IUCN and is classified as Critically Endangered in the Espírito Santo State red list, while *L. fredi* has yet to be evaluated due to its recent description. *Thoropa* cf. *lutzi* is currently listed as Endangered (EN) by both the IUCN and in the State list. Nine species are listed as Data Deficient (DD) and populations of 13 species are considered to be declining by the IUCN. We extend the geographical distribution of two anuran species (*Hylodes babax and Phasmahyla lisbella*) and fill an important gap in the distribution of *Siphonops hardyi*. Amphibians associated with the forest floor represented 42% of the species richness from MONAST, and 43% of these species inhabit the leaf litter exclusively. Our study revealed that Serra das Torres preserves a considerable diversity of Atlantic Forest amphibians, which reinforces the need for the conservation of this forest remnant.

Keywords: *Distribution extension, Filling gaps; Gymnophiona; Inventory; Leaf litter frogs; Rapid Assessment Method.*

Anfíbios do Monumento Natural Serra das Torres: um reservatório da biodiversidade da Mata Atlântica no sudeste do Brasil

Resumo: A Mata Atlântica brasileira guarda importante porção da riqueza de anfíbios e altas taxas de endemismos. Neste estudo, nós realizamos pesquisas usando o Método de Avaliação Rápida (RA) com o objetivo de inventariar a fauna de anfíbios de um remanescente da Mata Atlântica no sudeste do Brasil, o Monumento Natural Serra das Torres (MONAST). Amostramos ativamente com uma equipe de 6 a 10 pessoas para coletar amostras padronizadas entre 09:00 e 12:00 horas durante o período diurno e entre 18:00 e 22:00 durante o período crepuscular/noturno, totalizando aproximadamente 1320 horas de esforço amostral. Complementamos estes dados com 720 horas de amostragem passiva usando armadilhas de queda com cercas-guia (30 dias de balde). Registramos 54 espécies de anfíbios (dois gimnofionos e 52 anuros) e a riqueza de espécies estimada pelo *Bootstrap* indicou um número relativamente maior de espécies (n = 60). A família mais especiosa foi Hylidae (n = 21), seguida por Brachycephalidae (n = 8). No geral, 25% das espécies (n = 13) foram registradas apenas uma vez - (*singletons*) e 15% (n = 8) apenas duas vezes (*doubletons*). A maioria dos anfíbios registrados neste estudo (71%, n = 37 espécies) esteve restrita ao bioma Mata Atlântica, duas espécies (*Euparkerella robusta* e *Luetkenotyphlus fredi*) são endêmicas do estado do Espírito Santo, sendo uma delas, a espécie de serapilheira *E. robusta*, endêmica do MONAST. *Euparkerella robusta* está atualmente listada como Vulnerável pela IUCN e classificada como Criticamente Ameaçada na lista vermelha do estado do Espírito Santo, enquanto *L. fredi* ainda não foi avaliada devido a sua descrição ser muito recente. *Thoropa* cf. *lutzi* está atualmente listada como Ameaçada (EN) pela IUCN e na lista estadual. Nove espécies estão listadas como Deficiente de Dados (DD) e as populações de 13 espécies são consideradas em declínio pela IUCN. Estendemos a distribuição geográfica de duas espécies de anuros (*Hylodes babax e Phasmahyla lisbella*) e preenchemos uma importante lacuna na distribuição de *Siphonops hardyi*. Os anfíbios associados ao chão da floresta representaram 42% das espécies do MONAST e 43% destas espécies habitavam exclusivamente a serapilheira. Nosso estudo revelou que a Serra das Torres preserva diversidade considerável de anfíbios da Mata Atlântica, o que reforça a necessidade de conservação desse remanescente florestal.

Palavras-chave: *Anfíbios do folhiço; Distribuição geográfica; Gymnophiona; Inventário; Método de Avaliação Rápida.*

Introduction

Brazilian amphibians are among the world's most diverse, with approximately 1136 recognized species (Segalla et al. 2019). The Atlantic Forest is home of an important portion of this richness (around 600 species) and most species are found in ombrophilous forest vegetation, which has high rates of endemism, in just over half (approximately 52%) of the species (Rossa-Feres et al. 2017). The heterogeneity of Atlantic Forest habitats is probably one of the factors that have led to this high amphibian diversity (Carnaval et al. 2009, Bastazini et al. 2007, Oliveira et al. 2017), once it provides several favorable microhabitats for anuran development that contribute, for example, to species specificity and endemism (Sá 2013). Although considerable knowledge exists on the amphibian diversity of the Atlantic Forest, it is assumed that many species have yet to be discovered (Pimm et al. 2010) and new species are described every year (e.g., Ferreira et al. 2015, Baêta et al. 2016, Maciel et al. 2019). In addition, the amphibian fauna of many forest remnants is still under-sampled or completely unknown (Silvano & Segalla 2005). The state of Espírito Santo, in southeastern Brazil, is located entirely within the Atlantic Forest biome (IBGE 2004), although the state's forest cover has been reduced to only 483,087 hectares (SOS Mata Atlântica/INPE 2017/2018), even though 85% of its 46,000 km^2 area was originally covered with forest (Atlas dos Ecossistemas do Espírito Santo 2008). Several forest remnants in the Espírito Santo state are still poorly sampled, mainly within the ombrophilous forest vegetation, which implies a persistent knowledge bias regarding the composition of the amphibian communities of many areas (Almeida et al. 2011).

In this study, we surveyed a major forest remnant of the Atlantic Forest biome in southeastern Brazil, in southern Espírito Santo state. We evaluated parameters of species richness and abundance, spatial distribution, and habitat use by the amphibians of the Serra das Torres Natural Monument. We also add range extensions and fill gaps for three amphibian species.

Material and Methods

1. Study site

We collected samples at the Serra das Torres Natural Monument (Monumento Natural Serra das Torres – MONAST: -21.0209°, -41.2378°, WGS84 datum), which is located in the southern portion of the Espírito Santo state, in the municipalities of Atílio Vivacqua, Mimoso do Sul, and Muqui in southeastern Brazil (Figure 1). The MONAST encompasses the largest complex of forest remnants in southern Espírito Santo, with approximately 10,450 hectares of Atlantic Forest. The habitats of this remnant include mountains that rise to more than 1,000 m asl at their highest point, and are covered by seasonal forest, semi-deciduous forest, dense rainforest, and dense submontane rainforest (Magnago et al. 2008). Several rocky outcrops (*inselbergs*) covered with tank bromeliads are found in the MONAST, many of which are relatively prominent, with steep slopes (Figure 2). The mean annual temperature of the study area is approximately 24.5ºC and the mean annual rainfall is around 1290 mm (Oliveira et al. 2013). The area surrounding the MONAST is occupied by private properties with extensive areas of farmland, primarily coffee and banana plantations.

2. Amphibian survey

We used the Rapid Assessment (RA) method to assess the species richness and abundance of amphibians during three months of the rainy season of 2018. The RA is an effective sampling method that permits the collection of reliable and replicable data over a short period of time (Patrick et al. 2014). We did not include acoustic records in the assessment of the species richness and abundance data.

We surveyed the MONAST over 10 consecutive days in each of the three municipalities in which the protected area is located, with a total of 30 sampling days: Atílio Vivacqua (January 2018), Mimoso do Sul (February 2018), and Muqui (March 2018). The survey was conducted by a team of six to 10 people, at 19 different sample sites (Figure 1). We conducted time-limited active searches (Crump & Scott Jr. 1994), from 09:00 to 12:00 in daytime period, and from18:00 to 22:00 in crepuscular/nighttime period, with a total sampling effort of approximately 1320 hours (considering variation in team members and sampling hours per day). We conducted the active searches in preserved fragments of forest that were located as far as possible from areas of anthropogenic impact at altitudes from ca. 600 m to 1000 m asl. We installed all transects at least one kilometer from the nearest trail to avoid pseudo-replication, and to sample the largest possible area of forest.

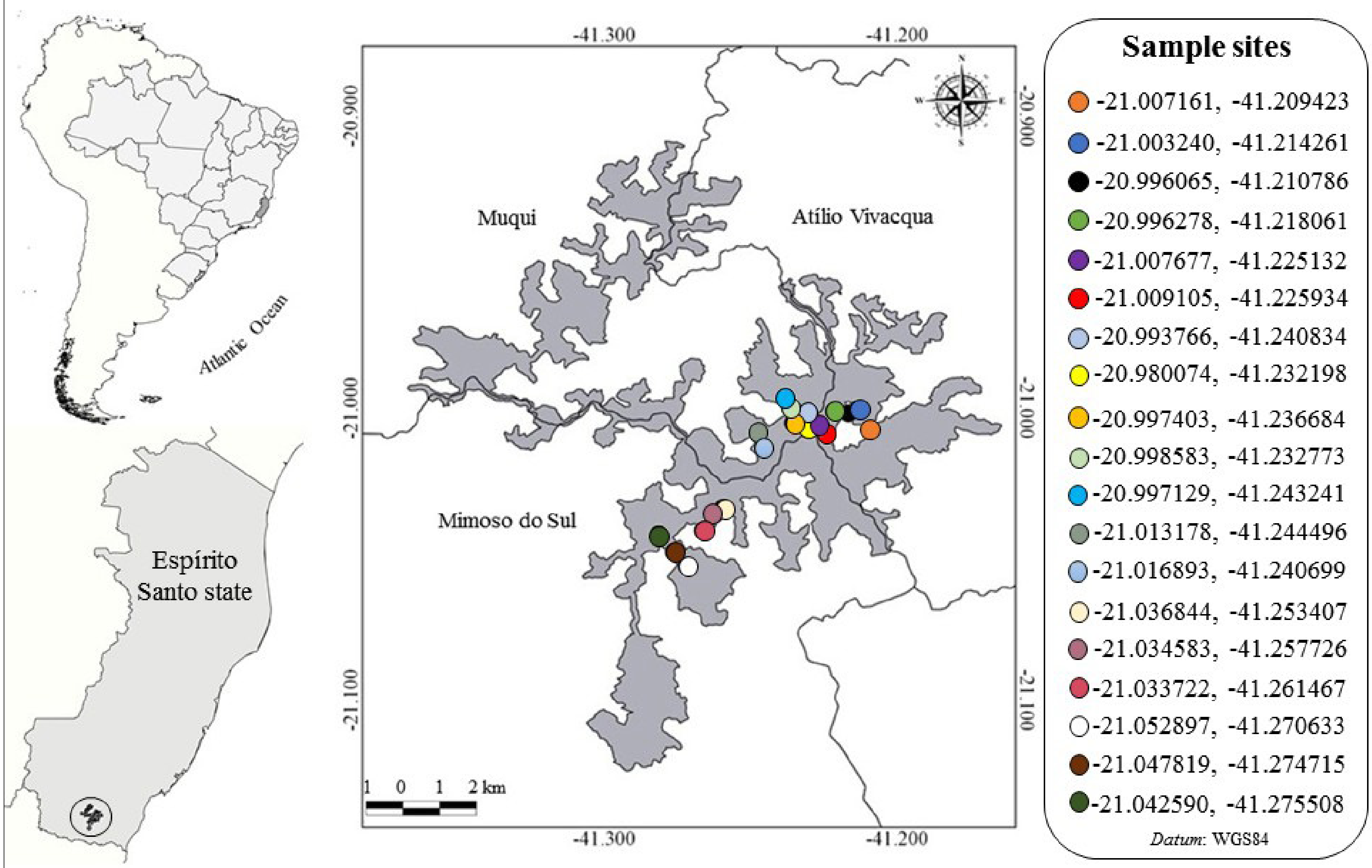

Figure 1. Points sampled in the Serra das Torres Natural Monument (MONAST) in the Brazilian state of Espírito Santo (black dots), southeastern Brazil. The enlarged figure to the right shows the limits of the MONAST in relation to the three municipalities in which it is located (Atílio Vivacqua, Mimoso do Sul, and Muqui).

We also used four systems of pitfall traps with drift fences (Corn 1994), each consisting of 40 buckets (20 L each), arranged in a line within each study area. We placed the pitfall traps in the best-preserved habitats at different forest fragments and altitudes and, as far as possible from each other. We installed the traps three days prior to the sampling period, with all the buckets remaining open until the 10th consecutive day of sampling. We removed the buckets and fences from each forest at the end of the sampling period, and we then moved them to the next sampling area. The overall sampling effort of the pitfall traps was approximately 720 hours.

We collected data on the microhabitats used by the amphibians encountered during the active search (e.g., leaf litter, streams, trees, ponds, and bromeliads). We also recorded the height above ground (cm) which each individual was encountered in the microhabitat. In the case of species associated with streams, we also measured the distance (cm) between the individual and the stream, together with the depth (cm), width (cm), and temperature (°C) of the stream at the point closest to the location of the sampled individual.

Voucher specimens were collected under the authorization of SISBIO/RAN Nº 57085-6 and the Espírito Santo State Environment Institute (IEMA), license number 033-2017. The specimens were deposited in the following Brazilian collections (Table 1): Museu Nacional (MNRJ) in Rio de Janeiro state, Museu Paraense Emílio Goeldi (MPEG), Pará state and, Museu de Biologia Professor Mello Leitão (MBML), Espírito Santo state.

3. *Data analysis*

We compiled a species accumulation curve based on the cumulative number of species (*S*) recorded during the RA, as a function of sampling effort (n_days). We estimated species richness by the Bootstrap method, for which we considered the diversity index best suited to our data (Magurran 2004). Species recorded opportunistically during fieldwork were included in the richness counts but were not used to plot the accumulation curve or to quantify abundance. We analyzed the abundance data using Whittaker plots (Whittaker 1960), which rank the log abundance of each species (Krebs 1999). We assessed the vertical distribution of the species in the habitat using bloxplots. We analyzed the Whittaker plots in PAST 2.17 (Hammer et al. 2011). The species accumulation and rarefaction curves were plotted in EstimateS 8.0 (Colwell 2005).

Figure 2. Sampling areas in the Serra das Torres Natural Monument (MONAST), Espírito Santo state, southeastern Brazil. (A) Forests in the municipality of Atílio Vivácqua (Photograph: Pedro Fatorelli); (B) Rocky outcrop in the municipality of Muqui (Photograph: Pedro Fatorelli); (C) Bromeliad *Aechmea flavorosea* on a rocky outcrop in the municipality of Atílio Vivacqua (Photographs: Marcelo Simonelli); (D) Forest on the municipal limits of Atílio Vivácqua and Muqui (Photograph: Jane C. F. Oliveira); (E) Stream in in the municipality of Atílio Vivacqua (Photograph: Pedro Fatorelli), (F) Forests in the municipality of Atílio Vivácqua (Photograph: Jane C. F. Oliveira).

Results

We recorded 495 individuals belonging to 54 amphibian species distributed in two orders (Gymnophiona = two species; Anura = 52 species) (Table 1; Figures 3, 4 and 5). The cumulative species curves did not reach the asymptote (Figure 6), and species richness estimated by the Bootstrap procedure (*S* = 61 species) was higher than that recorded in the active searches (*S* = 54).

We extended the known geographical distribution of two anuran species, *Hylodes babax* and *Phasmahyla lisbella* (Figure 7). *Hylodes babax* was previously known from its type locality (Caparaó National Park) Serra do Brigadeiro State Park, and Uaimií State Forest, in the southern Espinhaço mountain range (Pirani et al. 2010), all in the state of Minas Gerais, and from Santa Teresa municipality, in Espírito Santo state (Table 2, Figure 7). The record of *H. babax* in the MONAST extends the known geographic range of this species by approximately 86 km from the nearest locality, in the Caparaó National Park. *Phasmahyla lisbella* was recently described from Ventania Environmental Protection Area, in the Miracema municipality, Rio de Janeiro state (Pereira et al. 2018), and here we extend its known geographic range in Brazil by approximately 110 km to the north. We also filled a distributional gap in the known range of *Siphonops hardyi*, for which no records are available from northern Rio de Janeiro or southern Espírito Santo states (Table 2, Figure 7).

Hylidae was the anuran family with the highest species richness (n = 21), followed by the Brachycephalidae (n = 9), whereas Odontophrynidae was represented by only a single species. The caecilian species were relatively rare, with *Luetkenotyphlus fredi* being represented by only three individuals, and *Siphonops hardyi* by a single specimen (Table 1). *Haddadus binotatus* was the most abundant species (n = 117 individuals; 26% of total sample), followed by *Thoropa miliaris* (n = 67; 15%), and *Hylodes lateristrigatus* (n = 35; 8%). Overall, 40% of the species were recorded only once (13 species) or twice (8 species). The best-fitting Whittaker abundance model for the MONAST amphibian community was the logarithmic series model (Figure 8).

Most amphibians recorded in the MONAST (72%; n = 38 species) are endemic to the Atlantic Forest biome. Two of them, *Luetkenotyphlus fredi* and *Euparkerella robusta*, are endemic to Espírito Santo state, in which, the frog *E. robusta* is endemic to the MONAST and listed as Critically Endangered (CR) in the Espírito Santo state red list (Ferreira et al. *in press*) and Vulnerable (VU) by the IUCN (2020). The gymnophionan *L. fredi* was described during this study, based on specimens collected by us from this study site, and this species is endemic to the Espírito Santo state. Furthermore, the frog *Thoropa* cf. *lutzi* is listed as Endangered (EN) in the Espírito Santo

Table 1. Amphibian species recorded in the Serra das Torres Natural Monument (MONAST) in Espírito Santo state, southeastern Brazil, showing abundance (number of records), voucher number in herpetological collections, endemism (End/AF = endemic to the Atlantic Forest; End/ES = endemic to Espírito Santo state), and conservation status of each species based in global (The IUCN Red List, IUCN 2020), national (Ministério do Meio Ambiente, ICMBio 2018) and Espírito Santo state lists (Lista Vermelha do Espírito Santo - ES, Ferreira et al. in press). * = secondary data (Oliveira et al. 2013). Conservation status: CR = Critically Endangered; DD = Data Deficient; EN = Endangered; LC = Least Concern; VU = Vulnerable. MBML = Museu de Biologia Mello Leitão; MPEG = Museu Paraense Emílio Goeldi; MNRJ = Museu Nacional, Rio de Janeiro.

					Conservation status			
	Voucher	**Abundance (%)**	**End/ AF**	**End/ ES**	**Global**	**National**	**ES**	**Population trend (IUCN)**
ORDEM GYMNOPHIONA								
Family Siphonopidae								
Luetkenotyphlus fredi Maciel, Castro, Sturaro, Silva, Ferreira, Santos, Risse-Quaioto, Barboza, Oliveira, Sampaio & Schneider, 2019	MBML 11620	3 (0.6)	x	x	–	–	–	–
Siphonops hardyi Boulenger, 1888	MPEG 41563	1 (0.2)	x	–	LC	LC	DD	Stable
ANURA								
Family Bufonidae								
Rhinella crucifer (Wied-Neuwied, 1821)	MNRJ 93680-1	18 (3.6)	x	–	LC	LC	LC	Decreasing
Rhinella granulosa (Spix, 1824)	MNRJ 93672	7 (1.4)	–	–	LC	LC	LC	Stable
Family Leptodactylidae								
Leptodactylus fuscus (Schneider, 1799)	MNRJ 93768	7 (1.4)	–	–	LC	LC	LC	Stable
Leptodactylus latrans (Steffen, 1815)	MNRJ 93760	2 (0.4)	–	–	LC	LC	LC	Stable
Leptodactylus mystacinus (Burmeister, 1861)	MNRJ 93769	1 (0.2)	–	–	LC	LC	LC	Stable
Family Leptodactylidae (Leiuperinae)								
Adenomera bokermanni (Heyer, 1973)*	MNRJ 66710	–	x	–	LC	LC	LC	Stable
Physalaemus crombiei Heyer & Wolf, 1989	MNRJ 93802-6	1 (0.2)	x	–	LC	LC	LC	Decreasing
Physalaemus cuvieri Fitzinger, 1826	MNRJ 93801-2	3 (0.6)	–	–	LC	LC	LC	Stable
Family Brachycephalidae								
Ischnocnema abdita Canedo & Pimenta, 2010	MNRJ 93775-8	16 (3.2)	x	–	–	LC	LC	–
Ischnocnema cf. *izecksohni* (Caramaschi & Kisteumacher, 1989)	MNRJ 93697	13 (2.6)	–	–	–	–	–	–
*Ischnocnema verrucosa (*Reinhardt & Lütken, 1862)	MNRJ 93689	7 (1.4)	x	–	DD	LC	LC	Unknown
Brachycephalus didactylus (Izecksohn, 1971)	MNRJ 58974	1 (0.2)	x	–	LC	LC	DD	Decreasing
Ischnocnema bolbodactyla (Lutz, 1925)	MNRJ 66698	17 (3.4)	x	–	LC	LC	LC	Decreasing
Ischnocnema parva (Girard, 1853)	MNRJ 66699	3 (0.6)	x	–	LC	LC	LC	Decreasing
Ischnocnema sp.	MNRJ 93717	1 (0.2)	–	–	–	–	–	–
Ischnocnema cf. *guentheri* (Steindachner, 1864)	MNRJ 93701	3 (0.6)	–	–	–	–	–	–

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Family Hylidae								
Aplastodiscus arildae (Cruz & Peixoto, 1987)	MNRJ 93780	2 (0.4)	x	–	LC	LC	LC	Stable
Boana sp.	MNRJ 93715	4 (0.8)	–	–	–	–	–	–
Boana aff. *polytaenia* (Cope, 1870)	MNRJ 93682	2 (0.4)	x	–	–	–	–	–
Boana albomarginata (Spix, 1824)	MNRJ 93710	3 (0.6)	x	–	LC	LC	LC	Stable
Boana albopunctata (Spix 1824)	MNRJ 93779							
Boana crepitans (Wied-Neuwied, 1824)	MNRJ 93696	1 (0.2)						
Boana faber (Wied-Neuwied, 1821)	MNRJ 93674-8	17 (3.4)	–	–	LC	LC	LC	Stable
Boana pardalis (Spix, 1824)	MNRJ93762	3 (0.6)	x	–	LC	LC	LC	Stable
Bokermannohyla caramaschii (Napoli, 2005)	MNRJ93699, 93702, 93703	3 (0.6)	x	–	LC	LC	LC	Unknown
Dendropsophus bipunctatus (Spix 1824)	MNRJ93761	13 (2.6)	x	–	LC	LC	LC	Stable
Dendropsophus elegans (Wied-Neuwied, 1824)	MNRJ93711	7 (1.4)	x	–	LC	LC	LC	Stable
Dendropsophus minutus (Peters, 1872)	MNRJ93673	10 (2.0)	–	–	LC	LC	LC	Stable
Dendropsophus sp.	MNRJ93685-6, 93708, 93814	5 (1.0)	–	–	–	–	–	–
Fritziana ohausi (Wandolleck, 1907)	MNRJ93687	1 (0.2)	x	–	LC	LC	LC	Stable
Ololygon argyreornata (Miranda-Ribeiro, 1926)	MNRJ93690-5	13 (2.6)	x	–	LC	LC	LC	Stable
Scinax cf. *belloni* (Faivovich, Gasparini & Haddad, 2010)								–
Ololygon gr. *perpusilla*	MNRJ 93791-2	1	–	–	–	–	–	–
Ololygon cf. *tripui* (Lourenço, Nascimento & Pires, 2010)	MNRJ 93818	5 (1.0)	x	–	–	–	DD	–
Phasmahyla lisbella Pereira, Rocha, Folly, da Silva & Santana, 2018	MNRJ 58975	4 (0.8)	x	–	–	–	–	–
Phyllodytes luteolus (Wied-Neuwied, 1821)	MNRJ 93698	2 (0.4)	x	–	LC	LC	LC	Decreasing
Phyllomedusa burmeisteri Boulenger, 1882	MNRJ 93759	8 (1.6)	x	–	LC	LC	LC	Stable
Scinax gr. *ruber*	MNRJ 93763	1 (0.2)	–	–	LC	LC	LC	Stable
Scinax cf. *x-signatus* (Spix, 1824)	MNRJ 93707	1 (0.2)	x	–	–	–	–	Stable
Trachycephalus mesophaeus (Hensel, 1867)	MNRJ 93679	1 (0.2)	x	–	LC	LC	LC	Decreasing
Family Craugastoridae (Craugastorinae)								
Haddadus binotatus (Spix, 1824)	MNRJ 93770-1	117 (22.9)	x	–	LC	LC	LC	Stable
Euparkerella robusta Izecksohn, 1988	MNRJ 60996-4	2 (0.4)	x	x	VU	DD	CR	Decreasing
Family Cycloramphidae								
Crossodactylus gaudichaudii Duméril & Bibron, 1841	MNRJ 93688	23 (4.6)	x	–	LC	LC	LC	Decreasing
Thoropa cf. *lutzi* Cochran, 1938	MNRJ 93829-30	3 (0.6)	x	–	EN	DD	EN	Decreasing
Thoropa miliaris (Spix, 1824)	MNRJ 93788-9	67 (13.5)	x	–	LC	LC	LC	Stable
Zachaenus parvulus (Girard, 1853)	MNRJ 93764	2 (0.4)	x	–	LC	LC	DD	Decreasing

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Family Hylodidae								
Hylodes babax Heyer, 1982	MNRJ 92566	6 (1.2)	x	–	–	–	DD	–
Hylodes lateristrigatus (Baumann, 1912)	MNRJ 93112	35 (7.0)	x	–	LC	LC	LC	Decreasing
Family Odontophrynidae								
Proceratophrys boiei (Wied-Neuwied, 1824)	MNRJ 93819	1 (0.2)	x	–	LC	LC	LC	Stable
Family Microhylidae (Gastrophryninae)								
Chiasmocleis cf. *lacrimae* Peloso, Sturaro, Forlani, Gaucher, Motta & Wheeler, 2014	MNRJ 93717	2 (0.4)	–	–	–	–	–	–
Chiasmocleis schubarti Bokermann, 1952	MNRJ 93709	1 (0.2)	–	–	–	–	–	–
Myersiella microps (Duméril & Bibron, 1841)	MNRJ 93852	1 (0.2)	x		LC	LC	LC	Stable

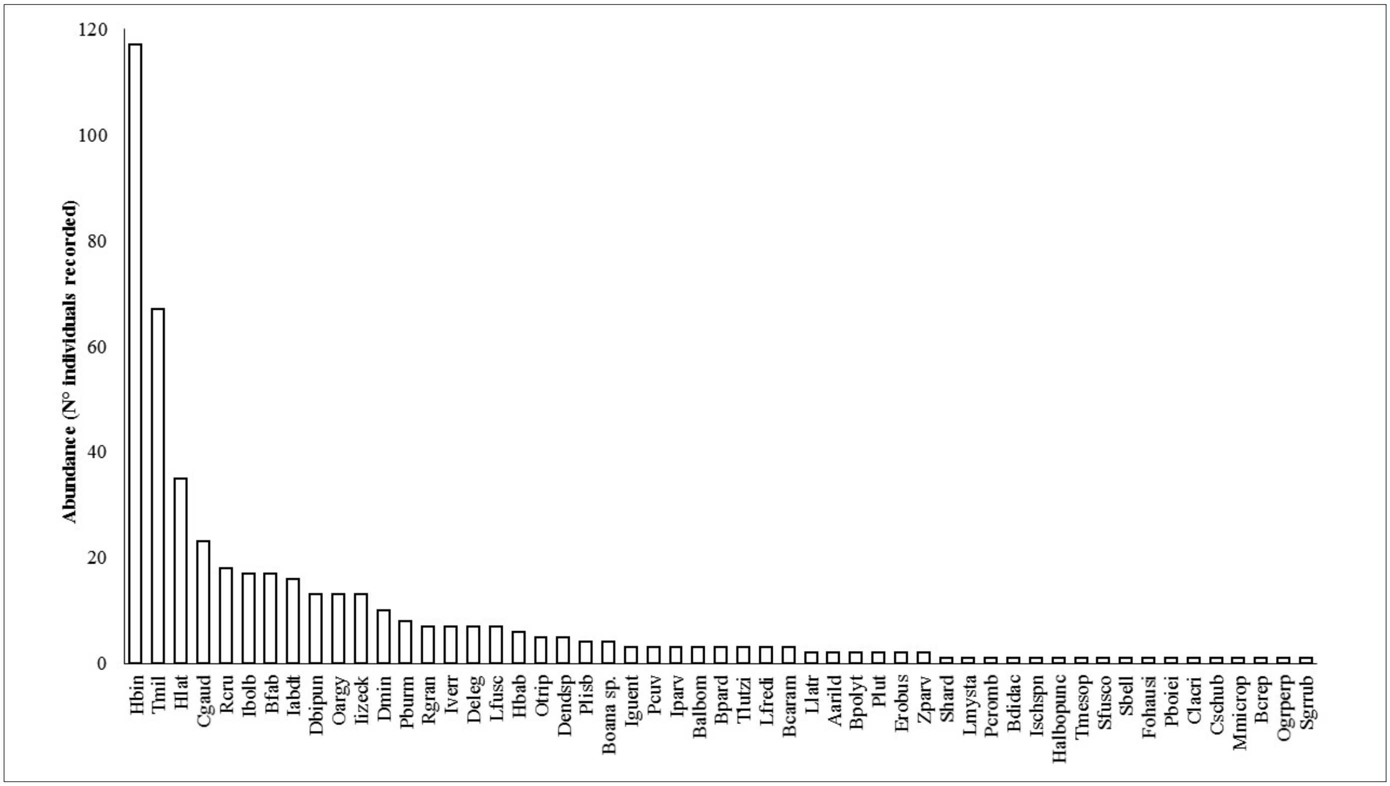


Figure 3. Species richness and abundance of amphibians recorded in the Serra das Torres Natural Monument (MONAST), Espírito Santo state, southeastern Brazil. Hbin = *Haddadus binotatus*; Tmil = *Thoropa miliaris*; Hlat = *Hylodes lateristrigatus*; Cgaud = *Crossodactylus gaudichaudii*; Rcru = *Rhinella crucifer*; Ibolb = *Ischnocnema bolbodactyla*; Bfab = *Boana faber*; Iabdt = *Ischnocnema abdita*; Dbipun = *Dendropsophus bipunctatus*; Oargy = *Ololygon argyreornata*; Iizeck = *Ischnocnema* cf. *izecksohni*; Dmin = *Dendropsophus minutus*; Pburm = *Phyllomedusa burmeisteri*; Rgran = *Rhinella granulosa*; Iverr = *Ischnocnema verrucosa*; Deleg = *Dendropsophus elegans*; Lfusc = *Leptodactylus fuscus;* Hbab = *Hylodes babax;* Otrip = *Ololygon* cf. *tripui*; Dendsp = *Dendropsophus* sp; Plisb = *Phasmahyla lisbella*; Boana sp. = *Boana* sp; Iguent = *IIschnocnema* cf. *guentheri*; Pcuv = *Physalaemus cuvieri*; Iparv = *Ischnocnema parva*; Balbom = *Boana albomarginata*; Bpard = *Boana pardalis;* Tlutzi = *Thoropa* cf. *lutzi*; Lfredi = *Luetkenotyphlus fredi*; Bcaram = *Bokermannohyla caramaschii*; Llatr = *Leptodactylus latrans;* Aarild = *Aplastodiscus arildae*; Bpolyt = *Boana* aff. *polytaenia*; Plut = *Phyllodytes luteolus*; Erobus = *Euparkerella robusta*; Zparv = *Zachaenus parvulus*; Shard = *Siphonops hardyi*; Lmysta = *Leptodactylus mystacinus*; Pcromb = *Physalaemus crombiei*; Bdidac = *Brachycephalus didactylus*; Ischspn = *Ischnocnema* sp.; Halbopunc = *Hypsiboas albopunctatus*; Tmesop = *Trachycephalus mesophaeus*; Sfusco = *Scinax* cf. *x-signatus*; Sbell = *Scinax* cf. *belloni* ; Fohausi = *Fritziana ohausi*; Pboiei = *Proceratophrys boiei*; Clacri = *Chiasmocleis* cf. *lacrimae*; Cschub = *Chiasmocleis schubarti*; Mmicrop = *Myersiella microps*; Bcrep = *Boana crepitans*; Ogrperp = *Ololygon* gr. *perpusilla*; Sgrrub = *Scinax* gr. *ruber*.

state red list (Ferreira et al. *in press*) and by the IUCN (2021). Nine anuran species are classified as Data Deficient, DD (IUCN 2021), and the populations of 12 species are considered to be declining (IUCN 2020, Table 1).

In the MONAST, the amphibians were found predominantly in five types of microhabitat: leaf litter, bromeliads, trees, ponds, and streams. The microhabitat occupied most frequently was the leaf litter of the forest floor, followed by ponds, streams, trees, and bromeliads (Figure 9). We recorded

Figure 4. Amphibian species recorded in the Serra das Torres Natural Monument (MONAST), Espírito Santo state, southeastern Brazil. (A) *Phasmahyla lisbella*; (B) *Euparkerella robusta*; (C) *Ololygon argyreornata*; (D) *Ololygon* cf. *belloni*; (E) *Chiasmocleis schubarti*; (F) *Ischnocnema abdita*; (G) *Zachaenus parvulus*; (H) *Ischnocnema verrucosa*. Photographs: Jane C. F. Oliveira.

Figure 5. Amphibian species recorded in the Serra das Torres Natural Monument (MONAST), Espírito Santo state, southeastern Brazil. (I) *Ololygon* cf. *tripui*; (J) *Luetkenotyphlus fredi*; (K) *Siphonops hardyi*; (L) *Hylodes lateristrigatus*; (M) *Phyllomedusa burmeisteri*; (N) *Aplastodiscus arildae*; (O) *Thoropa* cf. *lutzi*; (P) *Crossodactylus gaudichaudii*. Photographs: Jane C. F. Oliveira.

25 species perched in vegetation at heights up to three meters above the ground, while 22 species (43%) were observed exclusively in the leaf litter (Figure 10). The stream-dwelling species were recorded on the ground and in the vegetation at heights up to 1.2 m. The streams at which the amphibians were encountered had a mean width of 96.2 cm, mean depth 10.58 cm, and mean temperature of 20.5°C (Table 2).

Discussion

Species richness and abundance. The Atlantic Forest is one of the world's most threatened biodiversity hotspots (Myers et al. 2000, Mittermeier et al. 2005), and the remaining forests probably contain more than 600 amphibian species (Rossa-Feres et al. 2017). In the present study, we recorded an important sample of this diversity, which represents approximately 9% of the amphibian species found in the Atlantic Forest.

The Serra das Torres Natural Monument (MONAST) has relatively higher amphibian species richness and abundance in comparison with the nearest remnants of ombrophilous forest that have been surveyed in the

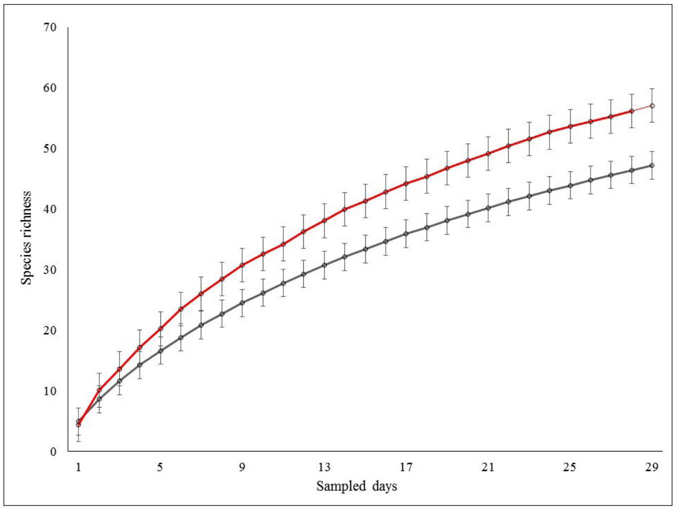


Figure 6. Accumulation curve (black line) and the species estimates (red line) based on Bootstrap estimator, both with 95% confidence intervals, for amphibians recorded at the Serra das Torres Natural Monument (MONAST) in Espírito Santo state, southeastern Brazil.

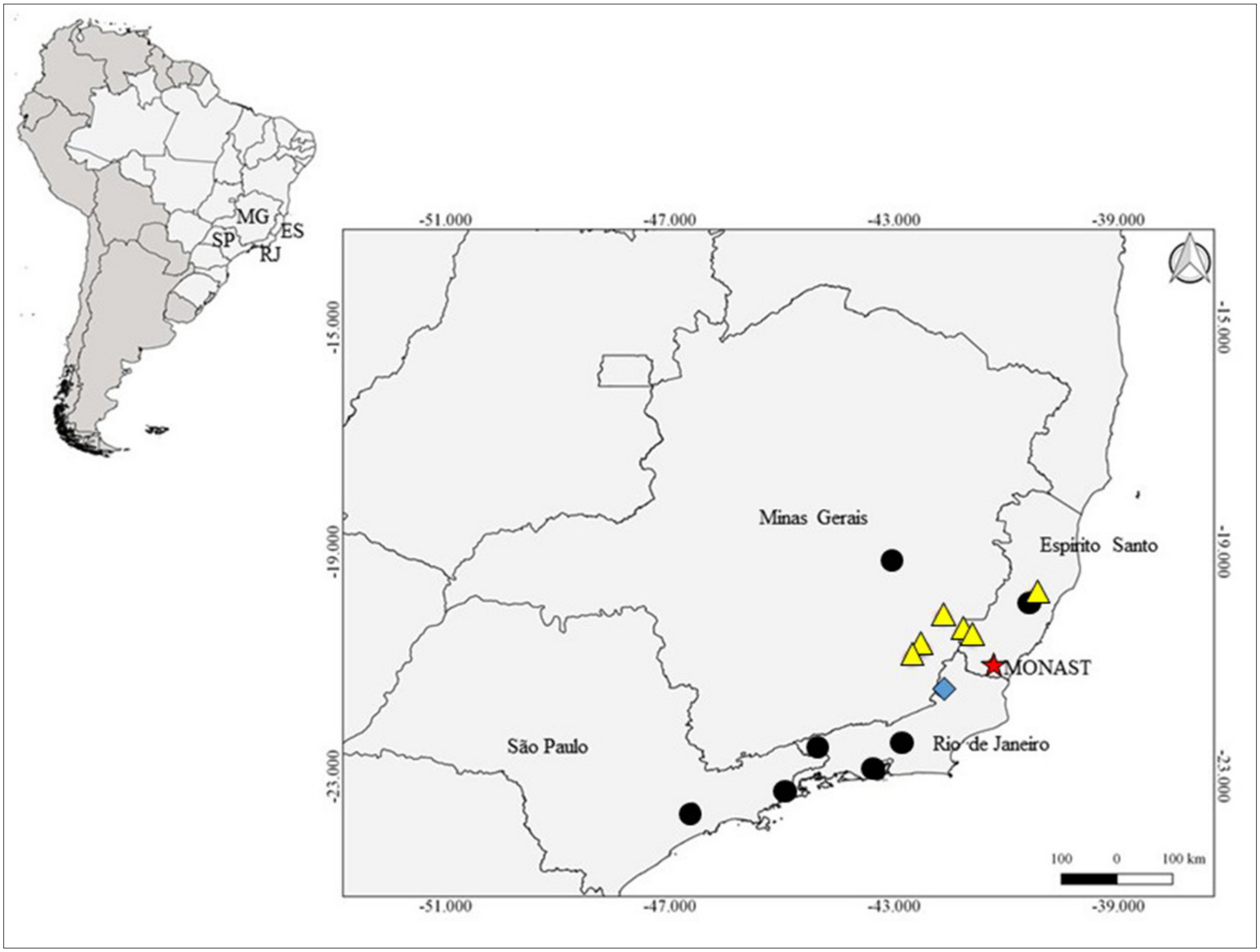


Figure 7. Geographic distribution of amphibian species recorded in the Serra das Torres Natural Monument (MONAST: red star), Espírito Santo state, southeastern Brazil: black dot, nearest previously known locality of *Siphonops hardyi*; yellow triangles, the nearest previously known locality of *Hylodes babax*; blue diamond, the nearest previously known locality of *Phasmahyla lisbella*.

Atlantic Forest, as Duas Bocas Biological Reserve, Forno Grande State Park, São Roque Canaã, Mata das Flores State Park, and Marechal Floriano, all in Espírito Santo state, and the Desengano State Park, in the Rio de Janeiro state (Figure 11). These differences are even more accentuated in many cases if the variation in sampling is taken into consideration, given that our study was based on only 30 days of survey. The 43 anuran species (and no gymnophionans) known to occur in the Forno Grande State Park were recorded over six years of sampling (Montesinos et al. 2012), while only 13 anuran species were recorded during a 10-day winter survey in the Desengano State Park, which is the nearest reserve to the MONAST, and has twice the area of forest (Siqueira et al. 2011). Only the Guapiaçu Ecological Reserve is known to have a higher species richness (n = 73 species) than the MONAST, although this total was recorded over a sampling period of more than 10 years (Almeida-Gomes et al. 2014). In addition, it is also important to note that the cumulative species curves for the MONAST did not reach the asymptote, with estimated (n = 60) exceeding observed species richness (n = 54) by more than 10%. The total number of amphibian species currently known to occur in the Brazilian state of Espírito Santo is 133 (Almeida et al. 2011), of which 39% are found in the MONAST, which reinforces the importance of this remnant for conservation and as a reservoir of genetic diversity. Our findings also reinforce the efficacy of the Rapid Assessment method for the evaluation of species richness from other forest remnants in the region, which have yet to be surveyed systematically.

The richest anuran family recorded in the MONAST was Hylidae, which is consistent with the composition of amphibian communities in other Atlantic Forest remnants in the region, such as the Mata das Flores State Park (Pereira-Ribeiro et al. 2019), the Pedra Azul-Forno Grande Corridor (Montesinos et al. 2012), and the Desengano State Park (Siqueira et al. 2011). The Hylidae is the second most speciose anuran family, worldwide (see Frost 2020), and is the richest family in the ombrophilous formations of the Atlantic Forest, in which about 470 hylid species are currently known to occur (Rossa-Feres et al. 2017). The second richest family at MONAST was the Brachycephalidae, direct-developing leaf litter frogs that inhabit the forest floor. These species were similarly abundant in previous surveys of the MONAST (Oliveira et al. 2013) and their abundance is usually associated with the leaf litter depth (Van Sluys 2007, Oliveira et al. 2013). A deeper leaf litter layer may also maintain a higher level of humidity on the forest floor, which may influence the occurrence of the litter-dwelling species in the MONAST (Oliveira et al. 2013). Within the forest, the presence

Table 2. Previous and present records of amphibian species whose geographical distribution were increased or filled in Serra das Torres Natural Monument (MONAST), Espírito Santo state, southeastern Brazil. Geographical coordinates are in decimal degrees, WGS84 datum. MPGE = Museu Paraense Emílio Goeldi, Pará, Brazil; MNRJ = Museu Nacional, Rio de Janeiro, Brazil. Source data: CRIA/speciesLink: http://www.splink.org.br/ (last access on 13/03/2021).

Taxon	Previous record: locality, municipality and/or Brazilian state, coordinates, source data	Record in the present study: municipality, coordinates
Hylodes babax (MNRJ 92566)	Caparaó State Park (type locality), Minas Gerais/Espírito Santo, -20.5414 -41.6672, CRIA/SpeciesLink	Atílio Vivacqua, -21.0097 -41.2249
	Uaimií State Forest, -20.4833 -43.9500, Ouro Preto, Minas Gerais, Pirani et al. (2010)	
	Santa Teresa, Espírito Santo, -19.9167 -40.6, Cria/SpeciesLink	
	Simonésia, Minas Gerais, -20.1239 - 42.0014, Cria/SpeciesLink	
	Araponga, Minas Gerais, -20.6667 -42.5208, Cria/SpeciesLink	
	Ervalia, Minas Gerais, -20.8400 -42.5208, Cria/Specieslink	
Phasmahyla lisbella (MNRJ 58975)	Ventania Environmental Protection Area, Rio de Janeiro (type locality), -21.3353 -42.2042, Pereira et al. (2018)	Atílio Vivacqua, -21.0097 -41.2249
Siphonops hardyi (MPEG41563)	Ipiranga, São Paulo, -23.590612 -46.605462, Maciel et al. (2009)	Mimoso do sul, -21.0107 -41.2476
	Cunha, São Paulo, -23.075969 -44.956067, Maciel et al. (2009)	
	Porto Real, Rio de Janeiro (type locality), -22.422361 -44.301557, Maciel et al. (2009)	
	Pedra Branca State Park, Rio de Janeiro, -22.932691 -43.472243, Maciel et al. (2009)	
	Tijuca National Park, Rio de Janeiro, -22.964565 -43.268453, Maciel et al. (2009)	
	Serra dos Órgãos, Rio de Janeiro, -22.401149, -42.828546, Maciel et al. (2009)	
	Augusto Ruschi Biological Reserve, Espírito Santo, -19.910980 -40.549299, Maciel et al. (2009)	
	Ferros, Minas Gerais, -19.248330 -42.999445, Maciel et al. (2009)	

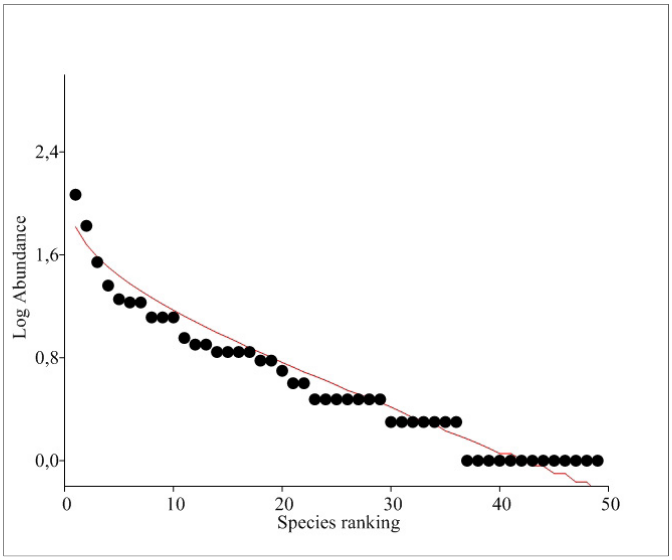


Figure 8. Whittaker abundance, plotted on a $\log_2$ scale, and the log-series adjusted abundance of the amphibian community of the Serra das Torres Natural Monument (MONAST), Espírito Santo state, southeastern Brazil.

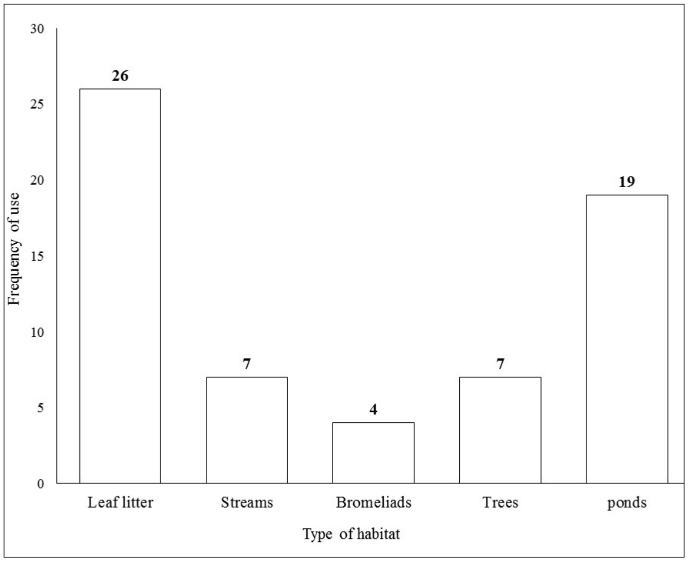


Figure 9. Frequency of the microhabitats used by the amphibian species recorded in the Serra das Torres Natural Monument (MONAST), Espírito Santo state, southeastern Brazil.

Table 3. Mean depth, width, and temperature of water from the streams sampled in the present study, and the distance between the sites at which specimens were recorded and the streams.

Stream depth (cm)			**Stream width (cm)**		
Mean	**Max.**	**Min**	**Mean**	**Max.**	**Min**
10.58	60.0	1.0	96.2	260.0	2.0

Water temperature (°C)			**Distance between specimen and stream (cm)**		
Mean	**Max.**	**Min**	**Mean**	**Max.**	**Min**
20.5	25.0	19.0	50.0	1000.0	0

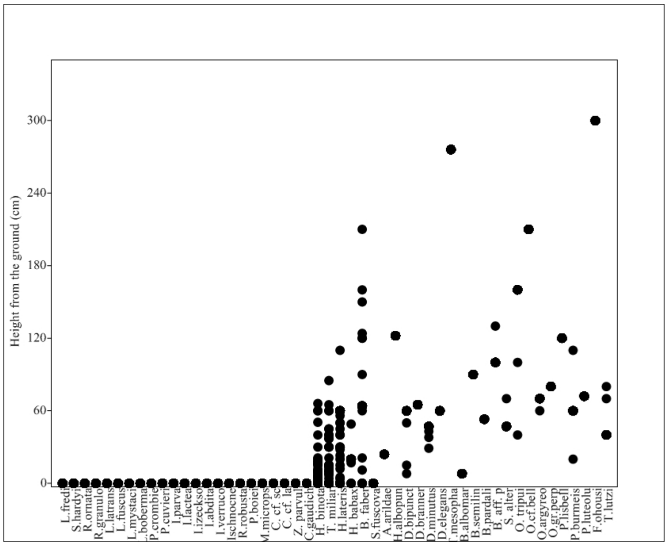


Figure 10. Vertical distribution, according to microhabitat use, of the amphibian species recorded in Serra das Torres Natural Monument (MONAST), Espírito Santo state, southeastern Brazil.

of deep leaf litter is generally the result of a greater local canopy cover, and the maintenance of the forest remnants in the MONAST clear of human impact will be essential for the conservation of their natural habitats and, in turn, the species they contain.

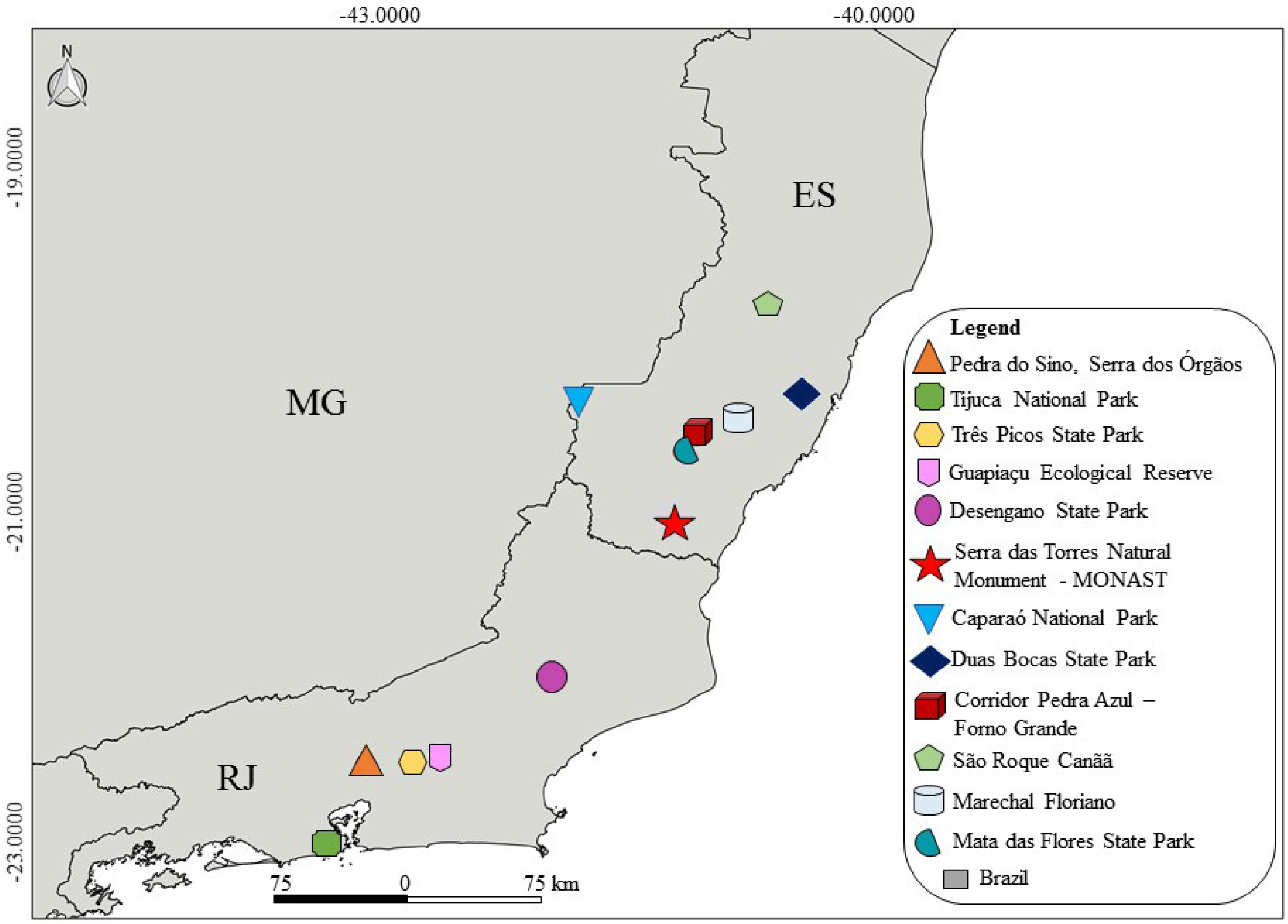
The abundance of anurans recorded in the present study followed a logarithmic model of distribution, which is typical of a community in which most species are rare and found within a limited area (Magurran 2004). Indeed, we recorded only three relatively high abundant species: the leaf litter inhabitant *Haddadus binotatus* (n = 117 individuals, 25.3% of the total abundance), and two stream-dwelling frogs, *Thoropa miliaris* (n = 67 or 14.5%) and *Hylodes lateristrigatus* (n = 35, 7.5%). *Haddadus binotatus* is a direct-developing leaf litter frog which makes this species independent of water bodies on the ground for its reproduction (Canedo & Rickli 2006, Nogueira-Costa & Carvalho-e-Silva 2010), but it is often associated with deep leaf litter and humid substrates (Oliveira et al. 2013). *Thoropa miliaris* inhabits rocky habitats in forest environments, presents semi-terrestrial tadpoles that live in thin, slow-flowing films of water on rocky surfaces bordering rivulets (Rocha et al. 2002), and it is not frequently abundant (e.g., 2.9% of anuran abundance in Ilha Grande State Park, Rio de Janeiro state, Rocha et al. 2011; 1.2% of anuran abundance in Duas Bocas Biological Reserve, Espírito Santo state, Linause et al. 2020). Although there is an extensive database on the stream-dwelling species of the Atlantic Forest, the variation in the abundance of these species, and the environmental factors that determine this variation, are still poorly understood. *Hylodes lateristrigatus* occurs in the states of Espírito Santo and Rio de Janeiro, and the presence of this species in the MONAST fills a major gap in its known distribution (Vrcibradic et al. 2014). Species of the genus *Hylodes* are associated with rheophilic habitats in the Atlantic Forest (e.g., Pombal et al. 2002, Canedo & Pombal 2007), and they may be considered indicators of habitat quality (e.g., Weygoldt 1989).

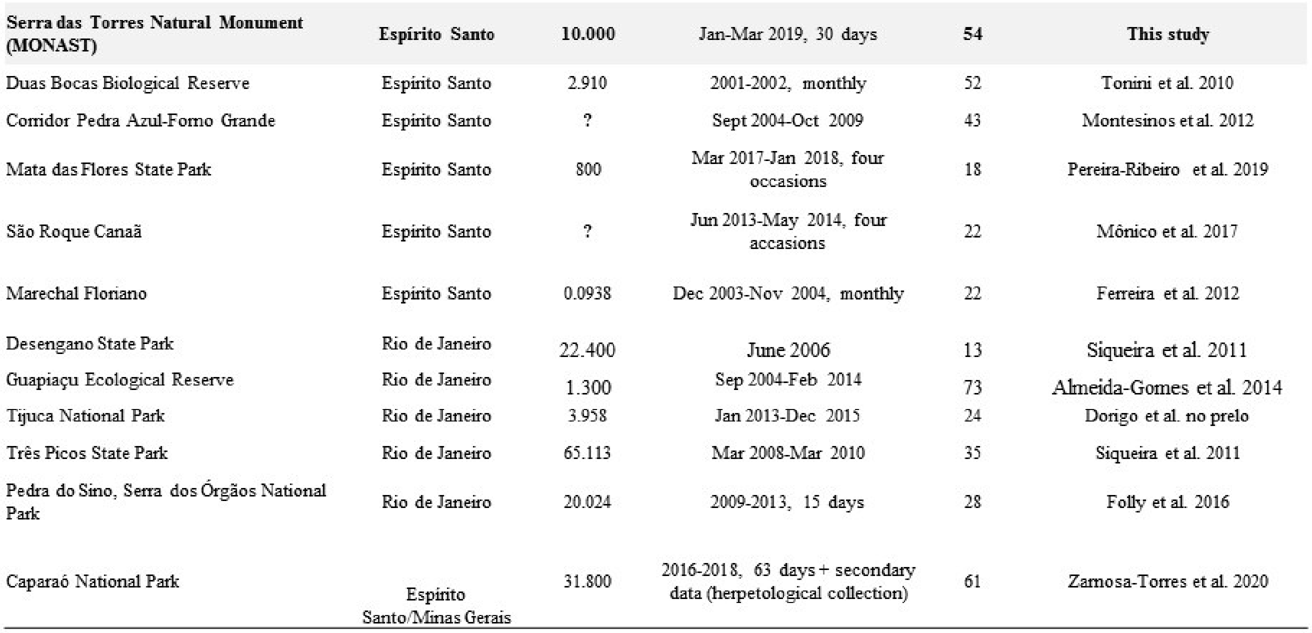
Most species in a community tend to be rare (Bracken & Low 2012) and have unique traits that contribute to the long-term stability of the ecosystem (Mouillot et al. 2013, Jain et al. 2014). Some characteristics of rare species, such as their reduced abundance, limited geographic ranges, and greater susceptibility to environmental impacts, makes them more vulnerable to the risk of local extinction (Wilsey & Polley 2004, Purvis et al. 2000). This is typical for most of the rare species in the MONAST. The two gymnophionan species (*Luetkenotyphlus fredi* and *Siphonops hardyi*), for example, have restricted ranges and their biology is poorly known (e.g., Maciel et al. 2009, 2019). *Luetkenotyphlus fredi* was recorded and described during the present study and is currently known only from the MONAST and one other small forest in southern Espírito Santo state, the Mata do Ouvidor, in the municipality of Itapemirim (Maciel et al. 2019). Only four individuals of this species have been captured up to now (one from Mata do Ouvidor and three from the MONAST) and all these individuals were recorded in preserved habitats.

In the present study, the least abundant anuran species were associated with the leaf litter, including *Brachycephalus didactylus*, *Chiasmocleis* cf. *schubarti*, and *Myersiella microps*. The flea-toad *Brachycephalus didactylus* is known to be abundant at the present study site (see Oliveira et al. 2013), although it is probably restricted to a small portion of the MONAST, and we recorded this species at just one of the 18 sample sites. This miniaturized leaf litter frog (SVL = 11.0 mm) is one of the world's smallest tetrapods (Estrada & Hedges 1996, Lehr & Catenazzi 2009). The MONAST is the only forest in Espírito Santo state known to have a population of *B. didactylus* (Oliveira et al. 2012), with all the other known localities of the species being found in Rio de Janeiro state (Almeida-Santos et al. 2011).

Geographic distribution and gaps. We extend the known geographic distribution of two anuran species in the present study. One of these species, *Phasmahyla lisbella*, was described in early 2018, and our record is its northernmost known locality, which represents a range extension of 110 km to the northeast of the nearest previous record, in the municipality of Miracema (21°20' S, 42°12' W, WGS84 datum), in the state of Rio de Janeiro (Pereira et al. 2018). In 2019, we published the first record of this species in the MONAST (Oliveira et al. 2009), although we identified the specimen as *P. guttata* because *P. lisbella* was not available at that time. Given this, we are hereby correcting this account and presenting the first record of *P. lisbella* for the Espírito Santo state.

The second species, *Hylodes babax,* was previously known from four localities: (i) type locality, Caparaó National Park, on the division between Minas Gerais and Espírito Santo states, (ii) Serra do Brigadeiro State Park, in the Mantiqueira mountain range; (iii) Uaimií State Forest, in the southern Espinhaço range (Pirani et al. 2010); and (iv) in the municipality of Santa Teresa (Ferreira et al. *in press*). *Hylodes babax* is





Serra das Torres Natural Monument (MONAST)	**Espírito Santo**	**10.000**	Jan-Mar 2019, 30 days	**54**	**This study**
Duas Bocas Biological Reserve	Espirito Santo	2.910	2001-2002, monthly	52	Tonini et al. 2010
Corridor Pedra Azul-Forno Grande	Espirito Santo	?	Sept 2004-Oct 2009	43	Montesinos et al. 2012
Mata das Flores State Park	Espirito Santo	800	Mar 2017-Jan 2018, four occasions	18	Pereira-Ribeiro et al. 2019
São Roque Canaã	Espirito Santo	?	Jun 2013-May 2014, four accasions	22	Mônico et al. 2017
Marechal Floriano	Espirito Santo	0.0938	Dec 2003-Nov 2004, monthly	22	Ferreira et al. 2012
Desengano State Park	Rio de Janeiro	22.400	June 2006	13	Siqueira et al. 2011
Guapiaçu Ecological Reserve	Rio de Janeiro	1.300	Sep 2004-Feb 2014	73	Almeida-Gomes et al. 2014
Tijuca National Park	Rio de Janeiro	3.958	Jan 2013-Dec 2015	24	Dorigo et al. no prelo
Três Picos State Park	Rio de Janeiro	65.113	Mar 2008-Mar 2010	35	Siqueira et al. 2011
Pedra do Sino, Serra dos Órgãos National Park	Rio de Janeiro	20.024	2009-2013, 15 days	28	Folly et al. 2016
Caparaó National Park	Espirito Santo/Minas Gerais	31.800	2016-2018, 63 days + secondary data (herpetological collection)	61	Zamosa-Torres et al. 2020

Figure 11. Comparison of amphibian species richness of the Serra das Torres Natural Monument (MONAST; red star) with nearby remnants of Atlantic Forest from the Espírito Santo and Rio de Janeiro states in southeastern Brazil. ES = Espírito Santo state; RJ = Rio de Janeiro state; MG = Minas Gerais state.

considered to be Data Deficient by the IUCN (2020) and in the Espírito Santo state (Ferreira et al., *in press*) mainly due to the limited data on its range (Rocha et al. 2004a). Here, we extend its known geographical range approximately 86 km from the nearest locality, in the Caparaó National Park, representing the southernmost known record of this species in Brazil. *Hylodes babax* occurs in the MONAST together with

H. lateristrigatus, in Atílio Vivacqua and Muqui municipalities, as well as in Santa Teresa municipality, all in the Espírito Santo state (Heyer & Cocroft 1986).

Siphonops hardyi has a highly disjunct distribution, with gaps in its known occurrence in southeastern Brazil, in several disconnected remnants (Maciel et al. 2009). This species has been recorded in Ipiranga municipality and Serra da Mantiqueira, both in São Paulo state, Porto Real municipality (type locality), Pedra Branca State Park, Tijuca National Park, and the Serra dos Órgãos (regional designation for Serra do Mar range), all in Rio de Janeiro state, and in the municipality of Ferros, in Minas Gerais state. In the Espírito Santo state *S. hardyi* is known only from Santa Teresa and Domingos Martins municipalities (Maciel et al. 2009, 2019), and therefore our record from the MONAST fills a major gap in the known geographical distribution of this caecilian species.

Endemism, threats, and our contributions. The amphibians recorded in the MONAST are important representatives of the biological diversity of the Atlantic Forest. Most species recorded by us (71%) are endemic to this forest remnant, and among them two species are endemic to the Espírito Santo state: *Euparkerella robusta* and *Luetkenotyphlus fredi.* The only gymnophionan species known to be endemic to the Espírito Santo state is *L. fredi* (Maciel et al. 2019), although there is no data on the ecology of this species. Species of the genus *Euparkerella* are small leaf litter terrestrial frogs with globular bodies (Izecksohn 1988). Up to now, *E. robusta* was known to be endemic to the municipality of Mimoso do Sul, where the first individuals were recorded and described (Izecksohn 1988), while we have now recorded for the Espírito Santo state a second population, which is protected within the MONAST in the municipality of Atílio Vivacqua (Oliveira et al. 2013; present study). As there are no records of *E. robusta* outside the MONAST, this conservation unit may be responsible for the protection of this species.

Several threatened species were recorded in the MONAST. *Euparkerella robusta* is listed as Critically Endangered (CR) in the Espírito Santo state (Ferreira et al. *in press*) and as Vulnerable (VU) by the IUCN (2020). *Thoropa* cf. *lutzi* is classified as Endangered (EN) in the IUCN red list and in the state red list. *Thoropa* cf. *lutzi* has been recorded previously in the states of Rio de Janeiro, Minas Gerais, and Espírito Santo, although no populations have been confirmed in Rio de Janeiro state for more than 30 years (ICMBio 2018), and the MONAST probably protects the last remaining population of this species in the Espírito Santo state. Nine are listed as Data Deficient (DD): *Brachycephalus didactylus*, *Euparkerella robusta*, *Hylodes babax*, *Ischnocnema* cf. *izecksohni*,, *Ischnocnema lactea*, *Ischnocnema verrucosa, Siphonops hardyi*, *Thoropa* cf. *lutzi*, and *Zachaenus parvulus* (IUCN 2020). Two of these species (*B. didactylus* and *Z. parvulus*) were recorded in the Espírito Santo state for the first time in the MONAST (Oliveira et al. 2012) and this is the only known locality for these species in the state. The large number of species evaluated as endemic, threatened, data deficient, and unknown conservation status (Table 1) reinforces the need for the conservation of this forest remnant.

Spatial distribution of species and associated habitats. The leaf litter was the habitat most used by the amphibians recorded in the MONAST, and five families (42% of the species) are found exclusively in this component of the forest, followed by pond environments. Leaf litter-dwelling amphibians are an important component of the forest anuran community and a wide variety of biotic and abiotic factors are associated with their species richness, density, and abundance, as altitude (Siqueira et al. 2014), structure and composition of the litter layer (Van Sluys et al. 2007), and humidity and depth of leaf litter (e.g., Giaretta et al. 1997, Oliveira et al. 2013). Our study reinforces previous findings in the MONAST (Oliveira et al. 2013), which indicate the importance of this forest remnant for the conservation of the region's leaf litter fauna. Data on the structure of leaf litter frog communities from the Espírito Santo state are available only from the MONAST (Oliveira et al. 2013) and Duas Bocas Biological Reserve (Vagmaker et al. 2020) and there is a considerable gap on the knowledge of these communities in the Atlantic Forest further north along the eastern coast of Brazil.

Six species recorded in the MONAST are streams inhabitants. *Hylodes lateristrigatus* and *H. babax* were recorded in the same streams, and the sharing of both spatial and acoustic niches by these species is an interesting phenomenon, which should be investigated further. The stream-dwelling species used the habitat vertically from zero to 1.25 m, which probably reflects their morphological characteristics. Although we surveyed all habitats extensively, most species were recorded in small rivulets, relatively small and shallow bodies of water. The presence of *H. babax* and *H. lateristrigatus* (the latter, in most sampled streams) indicates good water quality and well-preserved environments (e.g., Motta-Tavares et al. 2019). These species require clean water and are sensitive to anthropogenic impacts (Weygoldt 1989, Hatano et al. 2002, Motta-Tavares et al. 2019), and although additional studies are recommended for species of the genus *Hylodes*, it is known that amphibians that breed in ephemeral and often isolated bodies of water (e.g., headwater streams) are especially vulnerable to changes in temperature (Rome et al. 1992). Once again, we emphasize the need to isolate the MONAST forest from human disturbance because even minor alterations of these aquatic environments may impact the temperature of the water and its quality, leading to local extinction of these frogs (e.g., Weygoldt 1989, Blaustein et al. 2010).

Two other microhabitats used most frequently by amphibians are trees and tank bromeliads. The MONAST has a high diversity of bromeliads, with several rocky outcrops (inselbergs) covered by *Alcantarea extensa* (Magnago et al. 2008), which may store a large volume of water and that is usually inhabited by several anuran species in the Brazilian Atlantic Forest (e.g., Rocha et al. 2004b, Pontes et al. 2013). The low number of anuran species recorded by us in these microhabitats in the MONAST is possible due to their relative inaccessibility (high height of trees and steepness of inselbergs).

Recommendations for the conservation of amphibians in the MONAST. The MONAST is one of the largest Atlantic Forest conservation units in the Brazilian state of Espírito Santo, and one of the state's last remaining refuges of substantial ombrophilous forest cover. The combination of the large area of the MONAST with the quality of its forests contributes to its herpetological diversity, including its reptiles (Oliveira et al. 2020). We recommend the following measures to guarantee the conservation of these species in the MONAST: (1) the implementation of reforestation programs in areas of unused pasture to guarantee the connectivity of the forest fragments, a measure already recommended by Magnago et al. (2008); (2) the protection of rocky outcrops, including the limitation of rock climbing, due to the abundance of tank bromeliads that may contain many animal and plant species, including frogs; (3) the expansion of the programs that already involve the local residents in the vicinity of the MONAST, for the protection of local springs, including the "*Águas da Comunidade*" project, which is currently restricted to a small area of the MONAST; (4) the implementation of programs for the recovery of the riparian forests throughout the entire area of the MONAST; (5) the implementation of long-term education programs for the residents of the area surrounding the MONAST to limit the use of pesticides, and encourage the sustainable use of natural resources; and (6) the implementation of sustainable tourism practices, including the prohibition of new trails, the access of visitors to the forest interior, and the presence of motor vehicles within the areas of forest. In other words, tourism should be limited to the existing areas of access.

The Serra das Torres Natural Monument has a significant amphibian fauna and constitutes an important reservoir of the amphibian diversity of the Brazilian state of Espírito Santo and of the Atlantic Forest biome. This conservation unit includes several endangered amphibian species and one endemic anuran (*Euparkerella robusta*), and currently, it represents the only reserve in the Espírito Santo that has populations of *B. didactylus*, *E. robusta*, *P. lisbella*, and *Z. parvulus,* which reinforces the importance for its conservation in coming years.

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Author contributions

Jane C. F. Oliveira: Substantial contribution to the conception and design of the study; contribution to the acquisition of the data; contribution to the analysis and interpretation of the data; contribution to the writing of the manuscript; contribution to the critical review of the manuscript, appending intellectual content.

Rafael dos Santos, Mateus Leite Lopes-Silva, Bárbara Risse-Quaioto, Cátia Moura Militão, and Flávia A. L. Belmoch: contribution to data collection.

Lorena P. Vasconcelos Barros and Pedro Fatorelli: Contribution to data collection; contribution to the critical review of the manuscript.

José P. Pombal Jr: Contribution to the critical review of the manuscript; contribution to identification of the species.

Carlos Frederico Duarte Rocha: Substantial contribution to the conception and design of the study; contribution to the acquisition of the data; contribution to the analysis and interpretation of the data; contribution to the writing of the manuscript; contribution to the critical review of the manuscript, appending 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

Historical survey of research related to fire management and fauna conservation in the world and in Brazil

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Abstract: Fire is a key ecological factor affecting biodiversity structure and composition. Fires' effects on biodiversity can be beneficial or harmful depending on how, where, when, and why they occur. The impacts of fire on fauna vary according to species ecology and the fire regime. To understand the research effort relating fire, fauna, and mammals, we surveyed papers published in World and in Brazil. Only 5% of the publications between 1970 and 2019 with fire subject dealt with fauna and 0.5% with mammal. For Brazil, we obtained 7% of papers for fauna and 3% for mammal. The Brazilian Biome with more papers was Cerrado, followed by Atlantic Forest, Amazon, Pampas, Caatinga and Pantanal. The United States of America and Australia stand out as protagonists in their continents with the largest papers number. The volume of research is related to investment in Research and Development and to occurrence of fires. The slope of temporal trend shows the terms related to wildfire have more papers than prescribed burn and there is less interest in fauna and mammal research. It is necessary to form research groups with these themes as research lines and intensify research relating fire ecology and mammals. There is yet no unified understanding of how fire may influence animal diversity and how it influences the vegetative structure and subsequently the resources which wildlife rely on. We consider this information is essential to establish efficient conservation policies.

Keywords: *Scientometric Evaluation; Bushfire; Forest Fire; Controlled Burn; Mammal; Fire Ecology.*

Levantamento de artigos científicos relacionados à gestão do fogo e a conservação da fauna no mundo e no Brasil

Resumo: O fogo é um fator ecológico que pode determinar os padrões de diversidade, estrutura e composição da biodiversidade. Assim, o fogo pode ser favorável ou prejudicial, dependendo de como, onde, quando e porquê ocorre. Os impactos do fogo na fauna variam de acordo com a ecologia das espécies e o regime de fogo. Levantamos a quantidade de artigos publicados no mundo e no Brasil para entender o esforço de pesquisa que relaciona fogo, fauna e mamíferos. Apenas 5% das publicações entre 1970 e 2019 com o assunto fogo tratam de fauna e 0,5% de mamíferos. Para o Brasil, obtivemos 7% dos artigos para fauna e 3% para mamíferos. O bioma brasileiro com mais artigos foi o Cerrado, seguido por Mata Atlântica, Amazônia, Pampa, Caatinga e Pantanal. Os países que se destacam como protagonistas em seus continentes, com maior número de publicações, são Estados Unidos da América e Austrália. O volume de pesquisas está relacionado aos investimentos em pesquisa e desenvolvimento e à ocorrência de incêndios florestais. A regressão linear demonstra que os termos relacionados a incêndios florestais têm mais publicações do que os relacionados a queimas prescritas e há menos interesse em pesquisas relacionadas a fauna e a mamíferos. Diante disso, acreditamos ser necessário formar grupos de pesquisa nesses temas e intensificar os estudos relacionando ecologia do fogo e mamíferos. Ainda não existe um entendimento único sobre a influência do fogo na diversidade de animais e na estrutura da vegetação e, subsequentemente, nos recursos dos quais a vida selvagem depende. Consideramos que essas informações são essenciais para estabelecer políticas públicas de conservação mais eficientes.

Palavras-chave: *Cienciometria; Incêndio Florestal; Queimada; Mamíferos; Ecologia do Fogo.*

Introduction

Wildfire is a major driver of ecosystem structure and function (Bowman et al. 2009; He et al. 2019) and is a key determinant of diversity, structure and composition of biological communities (Whelan 1997). The effects of fire on vegetation are well known, but the same cannot be said about its effect on fauna (Briani & Vieira 2006; Frizzo et al. 2011, Kelly et al. 2012, Arruda et al. 2018). This lack of information hinders assessments for the use of fire as a tool for management of natural areas (Mistry 1998b).

Fire occurs on all continents, caused either by natural factors such as volcanism and lightning, or by anthropogenic causes. Hardesty et al. (2005) assigned the world's ecosystems into three categories according to their associations with fire: fire-dependent, fire-sensitive, and fire-independent. In Brazil, fire occurs in all its six biomes. Pivello (2011) classified the Cerrado (Brazilian Savanna), Pampa (Southern Brazilian Grassland) and Pantanal (Brazilian Wetland) as fire-dependent because they are fire-prone ecosystems; the Amazon and Atlantic Forests as fire-sensitive, and the Caatinga (Semi-Arid Scrub Forest) as fire-independent. However, even non-pyrophyte environments nowadays suffer from frequent and intense wildfires due to climate change (Jolly et al. 2015) and other factors such as deforestation and habitat degradation, which also modify the fire regime and enhance its negative impacts (Brando et al. 2020).

Fire effects may be beneficial or detrimental depending on the circumstances. Fires can lead to habitat and biodiversity loss in fire-sensitive ecosystems, nevertheless fire is necessary to maintain native species, habitats and landscape in fire-prone ecosystems (Myers 2006). Species responses to fires vary depending on the ecology of each species and the fire regime, especially frequency, intensity, season, and size of the burned area (He et al. 2019). Fire impacts can be positive or negative, and direct or indirect (Smith 2000, Yarnell et al. 2007, Frizzo et al. 2011) and are linked to specific microhabitat preferences. In addition, functional traits of fauna can be used to predict species-specific responses to fire (Santos et al. 2016) and can be used as bioindicators of ecological disturbance (Arruda et al. 2020).

Prescribed burn can be defined as any supervised fire conducted to meet specific management objectives (Santín & Doerr 2016), contrasting to wildfires, which are unplanned (Morgan et al. 2020), tend to affect large areas, and are usually detrimental to people, crops, infrastructure, and the environment. Land managers frequently use prescribed burn to reduce the extent of wildfires and to benefit biodiversity, but evidence supporting the positive effects of prescribed burn for biodiversity are mixed (Pastro et al. 2011, Harper et al. 2018).

In general, the dramatic character of wildfires has contributed to a societal feeling of fear toward fires, which has prevailed even among researchers, which tend to emphasize the negative effects of wildfires on biodiversity in detriment of alternative perspectives, such as the view of fire as a natural and beneficial component of ecosystem dynamics (Komarek 1969, Batista et al. 2018, Duringan et al. 2020). However, assessments of fire impacts must consider not only wildfires but also natural fires, prescribed burns, and fire regimes, since species are adapted not to fire, but to regimes (Smith 2000, Keely et al. 2011). A better understanding of the effects of different fire regimes on biodiversity and ecosystem function is fundamental to establish sound public policies for natural resource management (Durigan & Rattter 2016).

Biodiversity is essential to maintain Ecosystem Services (ES) (Cardinale et al. 2012), and mammals are particularly important providers of ES as they comprise a highly diversified group that play key and disproportionate roles in ecosystems (Davidson et al. 2012, Sarasola et al. 2016), from pollination (Ratto et al. 2018) and seed dispersal (Torres et al. 2020) to top-down population control by predators (Ripple et al. 2014) and soil engineering (Villarreal et al. 2008, Davidson et al. 2012, Villar et al. 2020).

In this study, we conducted a scientometric evaluation of papers relating wildfire and prescribed burn to fauna in general and mammals in particular. More specifically, we evaluate the spatial distribution and temporal trends of research relating fires to wildlife and assess the relative importance of a range of different terms in fire research. In addition, we spotlight fire research in Brazil. Finally, we use the assembled information to identify gaps and suggest priorities for future research and public policy.

Material and Methods

1. *Literature search*

For the selection of database were consulted Elsevier Scopus database (www.scopus.com) and Web of Science Core Collection database (www.isiknowledge.com) in 2020 March, but we used only Elsevier Scopus database. The search was restricted to articles and reviews, using the following expressions in title, abstract and keywords: wildfire or bushfire or "forest fire"; (wildfire or bushfire or "forest fire") and (animal* or fauna); (wildfire or bushfire or "forest fire") and mammal*; "prescribed burn*" or "prescribed fire"; "prescribed burn*" or "prescribed fire" and (animal* or fauna); "prescribed burn*" or "prescribed fire" and mammal*.

2. *Geographical distribution of studies*

The search for papers published between 1945 and 2019 used the "Analyze Search Results" and "Documents by Country or Territory" tools available in the Elsevier Scopus database to compare representativeness of different continents and countries in published literature.

We also relate the number of papers to the number of Moderate Resolution Imaging Spectroradiometer (MODIS) sensors hotspots (INPE 2020) by countries. MODIS Sensors is the most operational and systematic set of data available and produced for a global comparison. Medians and quartiles of number of hotspots by continent and country, and the boxplot graph, were obtained by means of the R Software.

The data available by UNESCO (2020) was used to relate resources spending in Research and Development (R&D) and number of papers published in each country.

3. *Temporal trends in publications*

We used Elsevier Scopus database to search publications from 1970 to 2019 to assess temporal trends in fire research. The Excel program was used to perform linear regressions to evaluate the scientific production over time.

4. *Fire research in Brazil*

The search for Brazil was restricted to articles and reviews, using the following expressions in the title, abstract and keywords: brazil* and (wildfire or bushfire or "forest fire"); brazil* and (wildfire or bushfire or "forest fire") and (animal* or fauna); brazil* and (wildfire or bushfire or "forest fire") and mammal*; brazil* and ("prescribed burn*" or "prescribed fire"), brazil* and "prescribed burn*" or "prescribed fire" and (animal* or fauna); brazil* and "prescribed burn*" or "prescribed fire" and mammal*.

In addition, we used the Scientific Electronic Library Online database (https://scielo.org/), a Brazilian database. The search was conducted in March 2020 and considered publications from 1909 to 2019. The search was restricted to articles using the following expressions in the topics using terms in Portuguese: incêndios florestais or incêndio florestal (wildfire); incêndio florestal or incêndios florestais and fauna (wildfire and fauna); incêndio florestal or incêndios florestais and mamífero* (wildfire and mammal); queimada or fogo (burn or fire); queimada or fogo and fauna (burn or fire and fauna); queimada or fogo and mamífero* (burn or fire and mammal); queima prescrita (prescribed burn); queima controlada or manejo do fogo (control burn or fire management); queima controlada or manejo do fogo and fauna (control burn or fire management and fauna); queima controlada or manejo do fogo and mamífero* (control burn or fire management and mammal). We agglutinate the search incêndio florestal, queimada or fogo (wildfire, burn or fire) in Fire, and queima prescrita, queima controlada or manejo do fogo (prescribed burn, control burn or fire management) in Prescribed Burn.

To analyze the number of papers by Brazilian biomes, the search carried out in Elsevier Scopus database between 1970 e 2019, was restricted to articles and reviews, using the following expressions in title, abstract and keywords: brazil* and (cerrado or savanna) fire*; brazil* and (cerrado or savanna) fire* and (animal* or fauna); brazil* and (cerrado or savanna) fire* and mammal*; "atlantic forest*" fire*, atlantic forest* fire* and (animal* or fauna); atlantic forest* fire* and mammal*; "amazon forest*" fire*; amazon forest* fire* and (animal* or fauna); amazon forest* fire* and mammal*; caatinga fire*; caatinga fire* and (animal or fauna); caatinga fire* and mammal*; ("campos sulinos" or pampas) fire*; ("campos sulinos" or pampas) fire* and (animal* or fauna); ("campos sulinos" or pampas) fire* and mammal*; (pantanal or "south america" wetland*) fire*; (pantanal or "south america" wetland*) fire* and (animal* or fauna); (pantanal or "south america" wetland*) fire* and mammal*. We agglutinated wildfire, bushfire and forest fire in Wildfire, prescribed burn and prescribed fire in Prescribed Burn, and animal and fauna in Fauna, as this research concepts were used for the same purpose.

We used the number of MODIS's hotspots (INPE 2020) by Brazilian biomes to related to number of papers.

Results

1. Literature search

Scopus returned approximately 20% more publications in most search terms than Web of Science Core Collection, so we restrict our analysis to this dataset. The search returned 35,133 papers published between 1945 and 2019 involving Wildfire and Prescribed Burn, of which 1,828 were related to Fauna and 544 to Mammal. Most papers were related to wildfires (84%), with fewer papers investigating Prescribed Burn (16%) (Figure 1A).

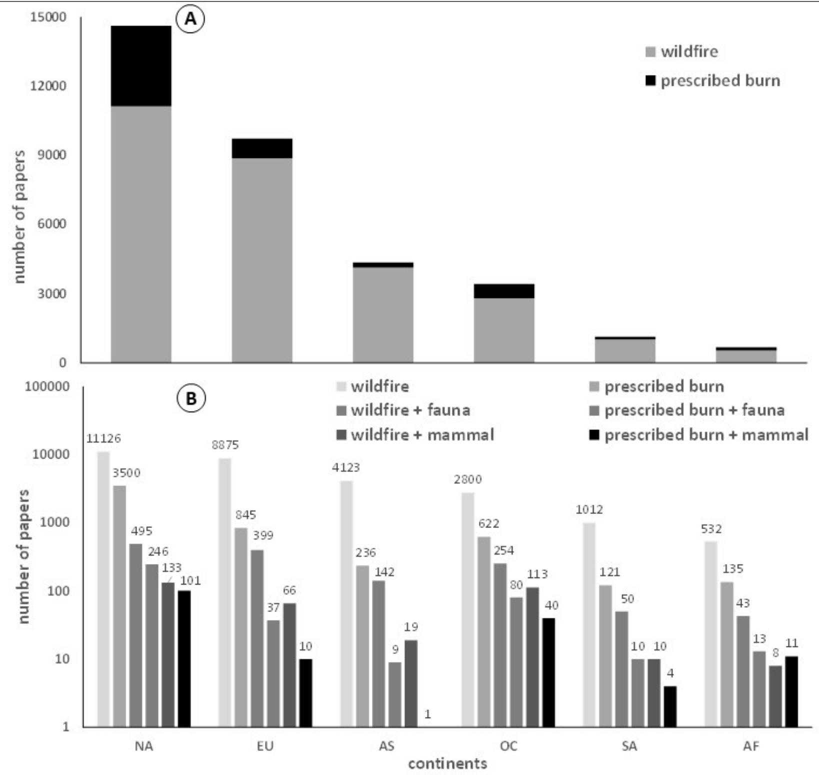

Figure 1. Number of papers on Wildfire plus Prescribed Burn (A) and number of papers for different search terms demonstrated on a Log scale (B) by continents (AF: Africa, AS: Asia, EU: Europe, NA: North America, OC: Oceania, SA: South America)

The oldest papers found in our search date from 1894 and were published in France and in the USA. Both papers deal with political issues and impacts on the economy and human lives, without ecological issues (Fisher 1894, Anonymous 1894). The first papers on Prescribed Burn only appeared 70 years later. Both papers were published in Australia: one discusses prescribed burn as a preventive action against wildfires, without discussing conservation (McArthur 1966), while the other discusses the positive and negative effects of prescribed burning and wildfire for vegetation recovery and recruitment (Henry & Florence 1966).

2. *Geographical distribution of studies*

Most studies were conducted in North America (42%), followed by Europe, Asia, Oceania, South America, and Africa (28%, 12%, 10% 3% and 2% respectively), three percent of papers lacked location data. The predominance of North America was observed for all search terms, but Europe was almost as important for search terms Wildfire, Wildfire + Fauna, and Prescribed Burn and Oceania for prescribed burn terms searched (Figure 1B).

In most continents there are countries predominating in search returns, with South Africa (ZAF), China (CHN), Spain (ESP), the United States of America (USA), Australia (AUS) and Brazil (BRA) leading fire research in their respective continents (Table 1). Nevertheless, there are huge differences between leading countries from different continents in the number of papers. For example, Brazil is the leading country in South America but lags far behind the USA, publishing the equivalent to 6% and 2% of USA publications on Wildfire and Prescribed Burn respectively.

The largest investors in Research and Development (R&D) are also top publishers (Figure 2). USA and CHN are the major R&D spenders in the world and dominate publications in their continents. AUS is the 13th largest global spender in R&D and responds for more than 94% of publications in Oceania. BRA is the only South American country listed among the 15 largest R&D investors and is the top publisher in the continent. Finally, ZFA is the top R&D investor in the African continent (UNESCO 2020).

The occurrence of fires may explain the distribution of fire research among countries at the global or continental level. Figure 3 compares continents and their leading publishing countries in relation to their historical average number of MODIS hotspots. Leading publishers either have the largest number of hotspots in their continents (CHN, USA, AUS and BRA) or are in the top quartile of their continents (ZAF and ESP).

3. *Temporal trends in publications*

There were more search returns related to Wildfire (82%) than to Prescribed Burn (18%) in the 26,748 papers found between 1970 and 2019 (Figure 4A). A minor proportion of these papers related Fauna to Wildfire or Prescribed Burn (Figure 4B). We found 1,078 papers relating Wildfire to Fauna and 286 relating it to Mammal (Figure 4B, 4C). We found 371 papers relating Prescribed Burn to Fauna and 166 relating it to Mammal (Figure 4B, 4C). The first paper on this subject was published in the USA in the 1980s. We also found that the proportion of publications relating fires to fauna in general or to mammals in particular are insignificant: only 5% of Wildfire and 7% of Prescribed Burn papers were related to Fauna, and 1% of Wildfire and 3% of Prescribed Burn papers were related to mammals.

Our results show the increasing publication rates over the past 20 years (Figure 5A, 5B). We observed a significant ($p < 0.05$) growth in publication rates for all terms except Prescribed Burn + Mammal with different growth rates among each search term.

4. *Fire research in Brazil*

We found 487 papers from Brazil, published between 1970 and 2019 and it matches 2% of all papers from the world. Eighty-eight percent of these belonged to the Wildfire category and only 12% to Prescribed Burn (Figure 4D), reflecting a pattern found at a global scale. We found few papers relating Fauna and Mammal with Wildfire or Prescribed Burn (Figure 4E, 4F).

The first Brazilian publications referring to Wildfire are from the 1980s and relate them to gas emissions (Leslie 1981; Kirchhoff & Marinho 1989), deforestation-pasture-fires (Uhl & Buschbacher 1985), and national legislation (Anonymous 1989). Apart from a brief mention to Prescribed Burn by Leslie (1981), the subject only started to appear regularly from the 1990s onward. Noteworthy papers include Pivello & Coutinho (1992) and Prins et al. (1998) on gas emissions and nutrients; Miranda et al. (1993) on soil and air temperature variation; Mistry (1998a) on lichens as bioindicators; Pivello & Norton (1996) on modeling software and Vieira (1999) on impacts of fire on small mammal in Cerrado.

We obtained 31 papers on Wildfire + Fauna in Brazil and nine on Wildfire + Mammal, while for Prescribed Burn + Fauna and Prescribed Burn + Mammal had four papers each, amounting to than 10% of total publications found from Brazil (Figure 4E, 4F).

The search in the Scielo database returned 124 papers about Wildfire, six on Wildfire + Fauna, three on Wildfire + Mammal and

Table 1. Countries accounting for most published fire research by continent (AF: Africa, AS: Asia, EU: Europe, NA: North America, OC: Oceania, SA: South America) for different search terms

	Wildfire		Wildfire + Fauna		Wildfire + Mammal		Prescribed Burn		Prescribed Burn + Fauna		Prescribed Burn + Mammal	
Continents	**Countries**	**%**	**Countries**	**%**	**Countries**	**%**	**Countries**	**%**	**Countries**	**%**	**Countries**	**%**
AF	ZAF	36	ZAF	30	ZAF	88	ZAF	57	ZAF	31	KEN	45
AS	CHN	30	CHN	18	JPN	16	CHN	41	CHN	56	IND	100
EU	ESP	20	GBR	17	ESP	21	ESP	21	SWE	22	*	*
NA	USA	78	USA	79	USA	83	USA	92	USA	91	USA	92
OC	AUS	94	AUS	96	AUS	97	AUS	96	AUS	99	AUS	100
SA	BRA	53	BRA	72	BRA	80	BRA	58	ARG	50	BRA	100

* no dominance, ARG: Argentina, AUS: Australia, BRA: Brazil, CHN: China, ESP: Spain, GBR: United Kingdom, IND: India, JPN: Japan, KEN: Kenya, SWE: Sweden, USA: United States of America, ZAF: South Africa

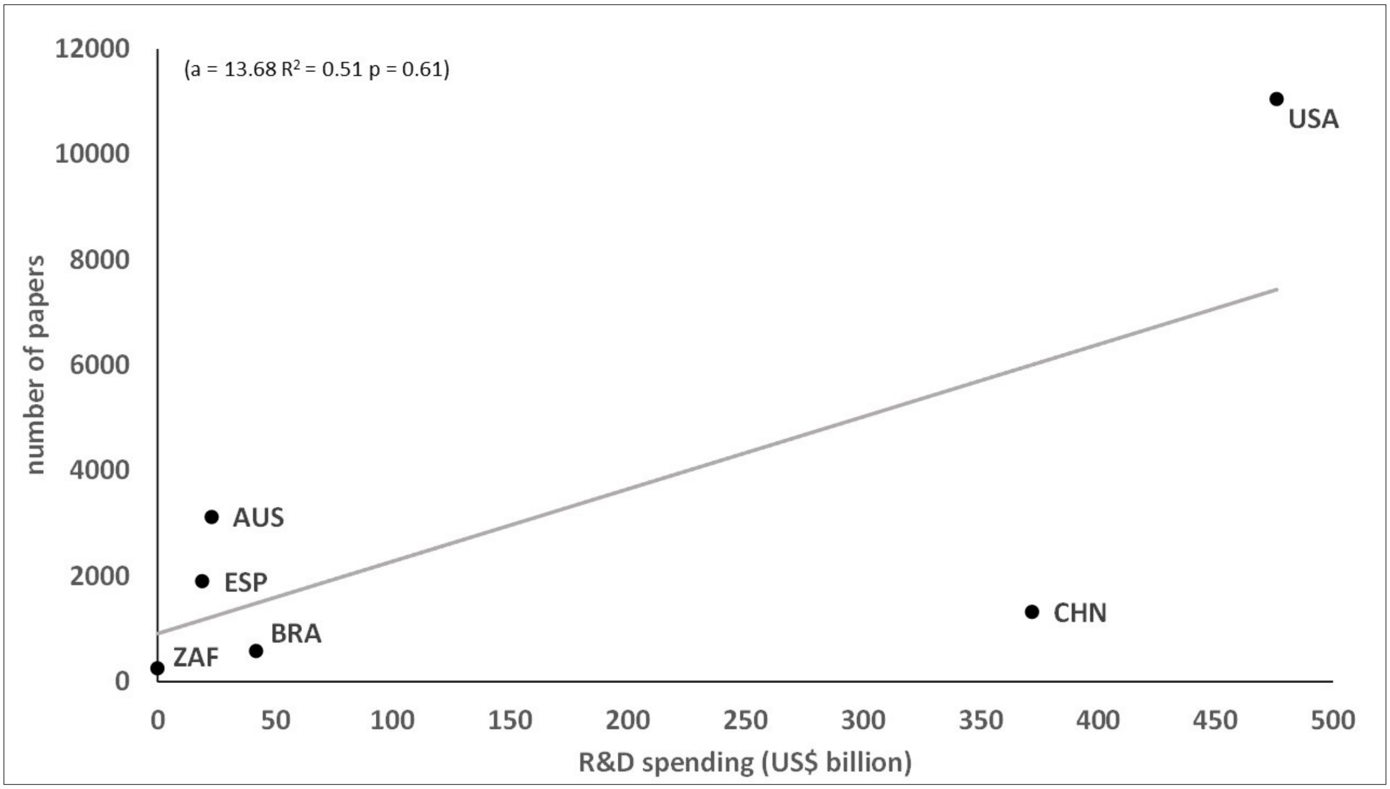

Figure 2. Number of papers published related to resources spending in Research and Development by countries (AUS: Australia, BRA: Brazil, CHN: China, ESP: Spain, USA: United States of America, ZAF: South Africa). (a: slope, R^2: coefficient of determination, p: significance probability). The degree of freedom is one for linear regression

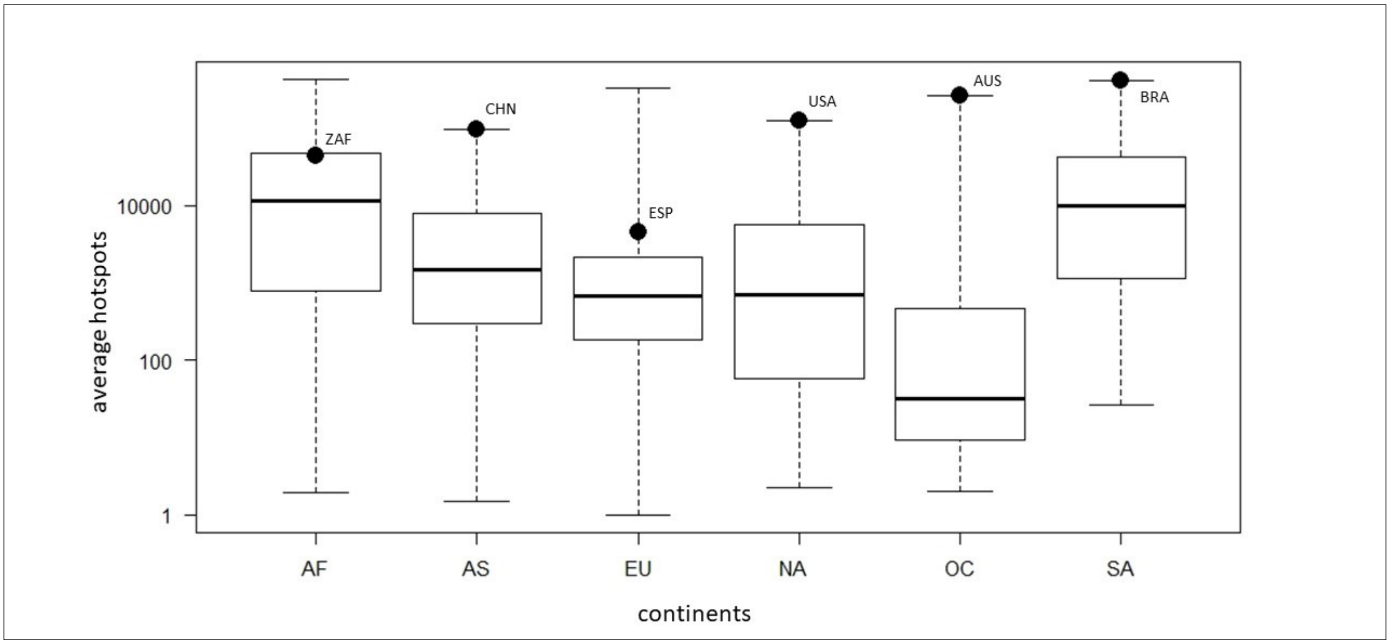

Figure 3. Boxplot of the average number of MODIS hotspots between 2002 and 2019 by continents demonstrated on a Log scale (AF: Africa, AS: Asia, EU: Europe, NA: North America, OC: Oceania, SA: South America), highlighting the countries in black points (AUS: Australia, BRA: Brazil, CHN: China, ESP: Spain, USA: United States of America, ZAF: South Africa). Middle line represents the median, the rectangle extends the first and third quartile range, and whiskers extend to the minimum and maximum value

six on Prescribed Burn. No papers about Prescribed Burn + Fauna and Prescribed Burn + Mammal were found. Even in Portuguese, in the last 100 years, the number of papers is very low.

We found a positive temporal relationship with the number of published papers for Wildfire Brazil (Figure 5C), Wildfire Brazil + Fauna and Wildfire Brazil + Mammal (Figure 5D), although the relationship was weak for the later. There was no significant temporal trend for any of the searched terms for Prescribed Burn Brazil (Figure 5D).

Considering the average number of hotspots per km² by Biome between the years 2002 and 2019, Pantanal had the highest average,

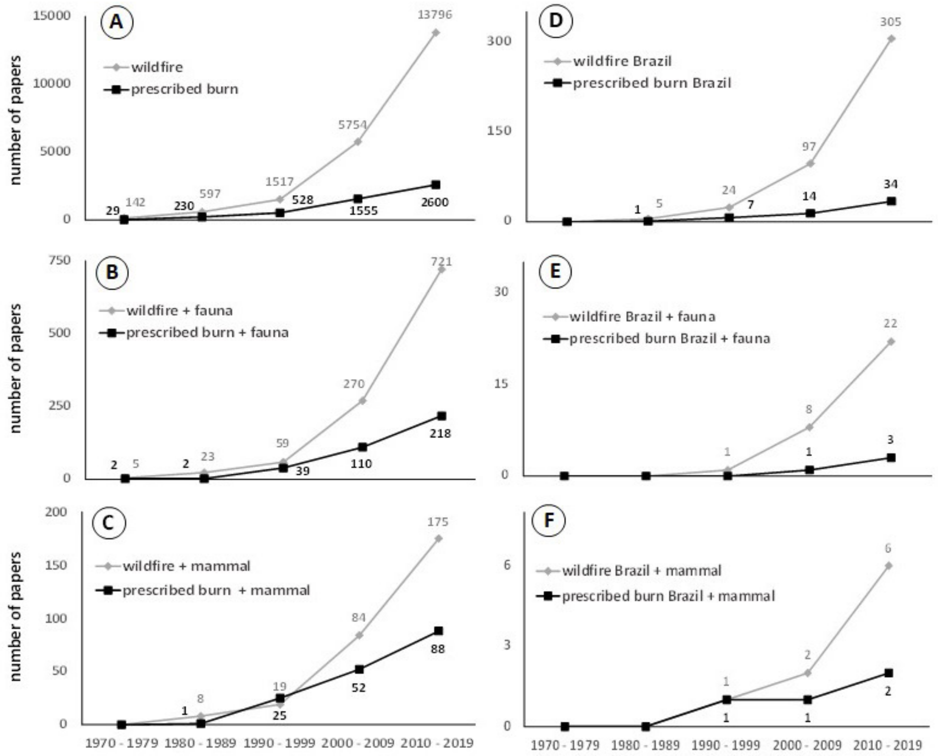

Figure 4. Historic number of papers since 1970 to 2019, divided by decades, comparing the published (A) Wildfire and Prescribed Burn, (B) Wildfire + Fauna and Prescribed Burn + Fauna, (C) Wildfire + Mammal and Prescribed Burn + Mammal, (D) Wildfire Brazil and Prescribed Burn Brazil, (E) Wildfire Brazil + Fauna and Prescribed Burn Brazil + Fauna and (F) Wildfire Brazil + Mammal and Prescribed Burn Brazil + Mammal

followed by Cerrado, Amazon Forest, Caatinga, Atlantic Forest and Pampa. The geographic distribution of 961 papers with fire research in Brazil seems to be unrelated to the average number of hotspots (Table 2).

The Scopus search returned only nine papers for the terms Wildfire Brazil + Mammal. Three papers were about small mammals and six dealt with mid-sized to large mammals. For the terms Prescribed Burn Brazil + Mammal we found only four papers, all dealing with small mammals.

Discussion

Fire research has been conducted on all continents. NA and EU dominate most (70%) of all global research related to fire management. USA and AUS stand out as protagonists in their continents and with the largest papers number in comparison to other countries. The dominance of these countries in total number of papers (USA: 34% and AUS: 9%) is related to the historical knowledge of original peoples and their relationship with fire. In these countries the knowledge of use of controlled fire by indigenous and aboriginal people was valued and absorbed by European colonists (Johnson & Hale 2002, Morgan et al. 2020).

The volume of research is related to investment in R&D (Figure 2) and to the occurrence of fires, measured as the number of hotspots in each country (Figure 3). The dominance of NA in the number of papers is probably related to high investment of the USA and Canada in R&D and their historical tradition in science and technology. Similarly, the EU, the next continent in the number of papers, has several countries that invest heavily in research, such as ESP and GBR. The third continent is AS with CHN as the main country and the second with the largest investments in R&D. However, the correlation between investment and number of papers was weak as not all countries invest proportionately in research related to wildfire. CHN is the country with the largest number of hotspots in Asia (Figure 3) but when considering the territory's size, fire becomes relatively less important than in other countries, suggesting that the subject is not so relevant for investments in R&D (Figure 2).

Another factor that may explain why some countries lead fire research at the global or continental level is the occurrence of fire. We found that the leading countries in fire research at each continent (CHI, USA, AUS and BRA) are also those with more hotspots (Figure 3). MODIS hotspots have been widely used to study the occurrence of fire on a global scale as they provide highly relevant information about fire events, their spatial and seasonal trends, allowing comparisons. However, they do not necessarily reflect wildfire sizes, as the relationships between active fires and burnt areas are not constant in space and time (Hantson et al. 2013). The proportion of publications relating fires to fauna in general or to mammals in particular are insignificant. This indicates a large gap in the knowledge of responses to fire by the fauna and mammal. This is even more evident when we consider papers from the last 50 years (Figure 4B, 4C).

As for temporal trends in publication rates (Figure 5A, 5B) we observed that the slope for Wildfire is 7.5 times higher than for Prescribed Burn and rates for Wildfire increased eighteen times more than the term Wildfire + Fauna. This reveals a low research interest in Prescribed Burn or in responses of fauna and mammals to fire. However, we note that the dominance of the term Wildfire in search returns may be due to the fact that the other terms are sub-topics in Wildfire subject.

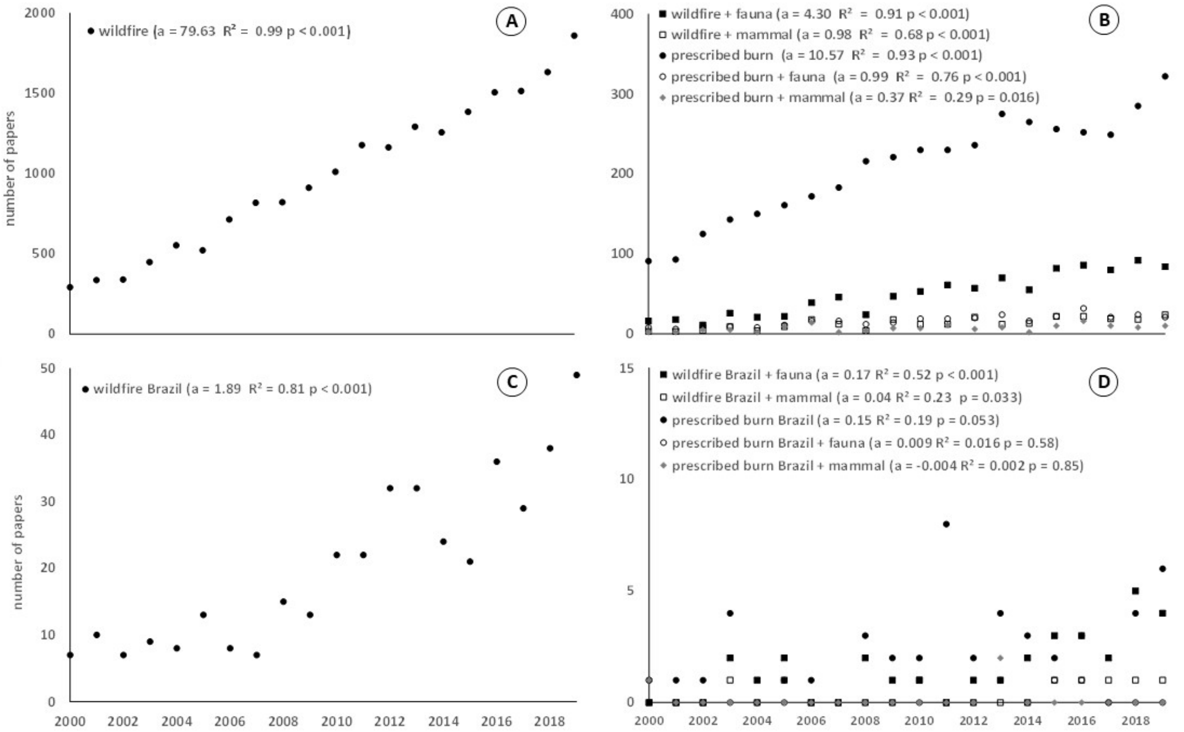

Figure 5. Scatter plot of number of papers between 2000 and 2019 in World: (A) Widfire; (B) Widfire + Fauna, Widfire + Mammal, Prescribed Burn, Prescribed Burn + Fauna, Prescribed Burn + Mammal; and in Brazil: (C) Widfire; (D) Widfire + Fauna, Widfire + Mammal, Prescribed Burn, Prescribed Burn + Fauna, Prescribed Burn + Mammal (a: slope, R^2: coefficient of determination, p: significance probability). The degree of freedom is one for linear regressions

Table 2. Distribution of average of hotspots and number of papers for different search terms by Brazilian Biomes. (Source: INPE and SCOPUS)

Brazilian Biomes	Hotspots / km2	Fire	Fire + Fauna	Fire + Mammal
Pantanal	0,041	35	6	1
Cerrado	0,037	529	57	22
Amazon Forest	0,029	115	43	4
Caatinga	0,023	64	8	1
Atlantic Forest	0,018	141	40	12
Pampa	0,006	77	12	5

The priority that was given to wildfires in detriment to prescribed burn probably derives from the severe social and economic impacts of the former, which includes loss of human lives, and damage to property and crops (Stephenson et al. 2013). This is understandable since a better understanding of behavior of uncontrolled and dangerous fire is a necessary first step for planning and executing preventive actions, especially with the use of fire. This also partially explains why research on prescribed burn only started to appear later. Studies on prescribed burn are still in their infancy. A better understanding of role of prescribed burns in fire control and wildlife management are urgently needed to guide actions to minimize the negative impacts of wildfires and favor fire as an ecological factor.

Wildfires are an important issue at global level, and their importance tends to increase as the global climate changes (Anderegg et al. 2020). Although research on wildfires in general has been increasing consistently, the same cannot be said about research on prescribed burns and faunal and mammal responses to fires. These research areas demonstrate a large gap in knowledge and need incentive.

The scenario is similar in Brazil, with proportionally fewer papers relating fire to fauna and mammals. This highlights the urgent need for further studies on mammal responses to fire, especially considering that the country is a megadiverse country and the second in diversity of the mammals with 678 terrestrial species, of which 102 are officially classified as threatened (ICMBio/MMA 2018a).

The Brazilian red list of endangered species aims to guide prevention, conservation, and management to minimize threats and risks for endangered wildlife. This list is also a tool to understand the conservation status of biodiversity and define priorities for public policies regarding conservation and use of natural resources (ICMBio/MMA 2018b). We believe that a sound knowledge of the sensitivity of wildlife species to fires is paramount to effective conservation action. The growth rate of publication in Wildfire in Brazil was 42 times lower than global rate, and Prescribed Burn publications remained stagnant. This demonstrates the large knowledge gap in Brazilian research on these issues and emphasizes the need for more investment in this field. The need for more research relating fire ecology and mammals can be illustrated by the diverging results reported by different studies on rodent responses to fire. A study on the effects of fire on *Necromys lasiurus* found negative effects (Vieira 1999), other reported no effects (Layme et al. 2004) and yet other found that the species benefited from fires (Briani et al. 2004). This indicates that the available data is still incipient and represents limited spatial and temporal scales (Frizzo et al. 2011). For example, some researchers, such as Briani et al. (2004), argue that in the Cerrado the ability of small mammals to cope with fires and the great dissimilarity among post-burning seral stages suggest that a mosaic of areas representing different post-fire seral stages could increase the regional diversity of this group. There is no unified understanding of how fire may influence vertebrate diversity and how fire influences vegetative structure and subsequently, food resources that wildlife rely on (Darracq 2016).

In Brazil, more than half of all research related to fire has been conducted in Cerrado, maybe because of predominance of pyrophyte savanna physiognomies in the Biome. Nevertheless, other Biomes also demand attention as they are also subject to wildfires, especially the Pantanal, a fire-dependent Biome too, with highest hotspot average but smallest number of papers. The Amazon comes next with a particularly high concentration of hotspots in its southern portion, known as the “Arc of deforestation” (Brando et al. 2020).

In the last 50 years, only 166 papers relating Fauna and Wildfire have been published for any Biome in Brazil. For mammals, the number is even lower with only 45 papers. The Caatinga and Pantanal Biomes score a single publication each. Borges et al. (2015) and Arruda et al (2018) found that only 8% of all papers about Cerrado fires referred to mammals. Frizzo et al. (2011) found that only 20 out of 1,512 fire papers (< 1%) were related to fauna. Arruda et al. (2018) did not found any temporal trend in the number of scientific publications relating mammals and fire in Cerrado.

The growing interest in the effects of fire in Cerrado may be due to the biome complexity: both high and low frequencies of fire can have negative effects on biodiversity (Maravalhas & Vasconcelos 2014; Anjos et al. 2016), and proper fire management programs based on scientific knowledge are still in development (Durigan & Ratter 2016). In Brazil, there is a pressing need for fire policies to conserve Cerrado (Durigan & Ratter 2016). A better knowledge about the effects of fire on different taxa and regions of the biome may help to create sound guidelines for fire management policies (Arruda et al. 2018). This analysis for Cerrado extends to other Biomes as well. We understand that fire management should cover a range of actions from fire exclusion in sensitive areas to prescribed burn in pyrophytic environments or to favor endangered species, going through the use of fire to protect sensitive environments and standardizing the use of fire for farming.

The Brazilian National Congress in currently discussing a federal bill aiming the Integrated Fire Management (Federal Bill 11276/2018 www.camara.leg.br/proposicoesWeb/prop_mostrarintegra?codteor=1703491&filename=Tramitacao-PL+11276/2018). The bill aims to propose instruments for analyzing the impacts of fires and integrated fire management on land use change, ecosystem conservation, public health, flora, fauna, and climate change. If approved, this Law will assist implementation of prevent and fight wildfire activities by integrating private sector with federal and state-level infrastructure and actions, improving the biodiversity and natural resources conservation. We believe that this law may encourage the financing and targeting of research projects related to fire ecology and biodiversity conservation. We still lack an unified understanding of how fires directly or indirectly influence fauna diversity and how this in turn affects their conservation and the ecosystem services they provide. This information is essential to establish sound conservation policies in a changing world.

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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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