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Inventory

Scavengers flesh flies (Diptera, Sarcophagidae) from two phytophysiognomies in the state of Maranhão, Northeastern of Brazil

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Abstract: Flesh flies (Sarcophagidae) have been found in a wide range of natural and anthropogenic environments, from forests to deserts. The state of Maranhão, located in Northeastern Brazil, has a diverse phytogeography, but few faunistic studies have been conducted in this area. Therefore, the objective of this study was to inventory species of Sarcophagidae and compare abundance patterns between the Cerrado (savanna-like vegetation) and riparian forests in the municipality of Codó, state of Maranhão. Twelve sampling events were carried out from the second half of 2015 to the first half of 2017. This resulted in 3,220 specimens, 27.15% of which were males, from nine genera and 27 species. A total of 491 specimens (16 species) were collected in the Cerrado, and 383 specimens (21 species) in the riparian forest. Peckia (Sarcodexia) lambens (Wiedemann) was the most abundant species (56,18% of the specimens sampled), followed by *Peckia (Peckia) pexata* (Wulp) (13%); *Peckia (Euboettcheria) collusor* (Curran & Walley) (13%), and *Peckia (Peckia) chrysostoma* Wiedemann (10%). Only P. (E.) collusor was found in greater abundance in the Cerrado. *Oxysarcodexia angrensis* (Lopes), *Peckia (Peckia) enderleini* (Engel), and *Retrocitomiya andina* Lopes are all new records to Maranhão and the entire Northeast Region of Brazil. *Titanogrypa (Cuculomyia) albuquerquei* (Lopes) is also a new to Maranhão.
Keywords: *Calyptratae, cerrado; insects; inventory; Oestroidea; riparian forest.*

Moscas necrófagas (Diptera, Sarcophagidae) de duas fitofisionomias no estado do Maranhão, Nordeste do Brasil

Resumo: As moscas Sarcophagidae podem ser encontradas em vários tipos de ambientes, naturais ou antropizados, desde florestas até desertos. O estado brasileiro do Maranhão, localizado na Região Nordeste, possui uma grande variedade de áreas fitogeográficas, mas poucos estudos faunísticos tem sido realizados nesta região. Portanto, o objetivo deste estudo foi inventariar as espécies de sarcofagídeos e comparar os seus padrões de abundância entre as áreas de cerrado (vegetação tipo savana) e de mata ciliar do município de Codó, estado do Maranhão. Foram realizadas 12 coletas, do segundo semestre de 2015 ao primeiro semestre de 2017. Foram coletados 3.220 espécimes, dos quais 27,15% são machos, representados por nove gêneros e 27 espécies. No cerrado foram coletados 491 espécimes (16 espécies), na mata ciliar foram coletados 383 espécimes (21 espécies). As espécies mais abundantes foram Peckia (Sarcodexia) lambens (Wiedemann) (56,18% dos indivíduos amostrados), *Peckia (Peckia) pexata* (Wulp) (13%), *Peckia (Euboettcheria) collusor* (Curran & Walley) (13%) e *Peckia (Peckia) chrysostoma* Wiedemann (10%). Apenas P. (E.) collusor foi significativamente mais abundante na área de cerrado. *Oxysarcodexia angrensis* (Lopes), *Peckia (Peckia) enderleini* (Engel) e *Retrocitomiya andina* Lopes são novos registros para a Região Nordeste do Brasil e *Titanogrypa (Cuculomyia) albuquerquei* (Lopes) é novo registro para o estado do Maranhão.
Palavras-chave: *Caliptradas; cerrado; insetos; inventario; Oestroidea; floresta ripária.*

Introduction

Sarcophagidae, or flesh flies, is one of the most diverse families of Calyptratae flies, with over 3,100 species divided into three subfamilies: Miltogramminae, Paramacronychiinae, and Sarcophaginae (Pape et al. 2011, Piwczynski et al. 2017). The Neotropical Region harbors one of the most diverse Sarcophagidae faunas, with over 800 species, many of which belong to the subfamily Sarcophaginae (Pape 1996, Pape & Dahlem 2010). There is only one species of Paramacronychiinae, which is found in the Galapagos Islands, and only a few species Miltogramminae are known to exist in this region (Pape 1996). In Brazil, which has one of the most diverse fauna of Sarcophagidae, the Sarcophaginae account for 94% of the species (Mello-Patiu 2020).

In the larval stage, flesh flies have the most diverse feeding habits among all Calyptratae fly families (Dahlem 1991, Pape & Dahlem 2010). Most larvae of Miltogramminae are kleptoparasites in solitary hymenopteran nests; however, there are also scavenger species (Piwczynski et al. 2017). The larvae of the Paramacronychiinae and Sarcophaginae can be saprophagous, coprophagous, kleptoparasites in hymenopteran nests, predators of other insects' eggs, parasitoids of other arthropods, and vertebrate parasites (Shewell 1987, Dahlem 1991, Pape & Dahlem 2010).

The larvae of several Sarcophaginae species are scavengers, meaning they feed on decomposing tissues of dead animals, including humans (Pape & Dahlem 2010). Adults can be found on or near carcasses, which serve as a food source, breeding site, and substrate for immature development. This is why flesh flies are considered to be one of the most important indicators in forensic studies (Guo et al. 2014, Sharma et al. 2015, Fakoorziba et al. 2017, Pavaraj et al. 2018, Jang et al. 2019, Oliveira et al. 2019, Vairo & Moura 2021). Furthermore, Sarcophaginae are an ideal taxonomic group for ecological studies because they can be easily collected in a variety of environments using traps containing decomposing organic matter (Sousa et al. 2016).

Flesh flies are found on all continents and in a wide range of terrestrial environments, from deserts to various types of forests (Shewell 1987). While some species can be found in several different habitats, others are restricted to a few specific locations (Carvalho-Filho et al. 2017, Camargo et al. 2018). Several Sarcophagidae species prefer open and sunny environments, such as pastures and forest clearings, and some of them have successfully colonized urban areas (Mulieri et al. 2011, Sousa et al. 2011, 2016, Vasconcelos et al. 2014).

Brazil is the largest country in South America; hence, it is home to a diverse range of habitats and plant communities, some of which are endemic, such as the Caatinga, an arid ecoregion in Northeastern Brazil (Silva et al. 2017, Tabarelli et al. 2018). The Cerrado, which is similar to African savannas and has direct contact with other biomes, is one of Brazil's most common vegetation types (Viera et al. 2019, Dutra & Silva 2020). The Cerrado has a diverse phytophysiognomy, ranging from more open vegetation types, such as "*campo limpo*", "*campo sujo*", and "*cerrado*" *sensu stricto*, to more dense vegetation types, such as riparian forests surrounding streams, rivers, and lakes (Werneck 2011, Araújo et al. 2016, Rios et al. 2016, Silva et al. 2017, Eloy et al. 2019, Zuin 2020). The vegetation is denser in the riparian forest, with small and large trees growing close together under compact canopies (Castro et al. 2012, Kuntschik et al. 2014). Because riparian forests are an intermediate environment between the open Cerrado and more highly forested areas, species from both habitats can be found there (Silva et al. 2017, Dufek et al. 2020a). As a result, these environments are critical for the preservation of biodiversity, as well as serving as ecological corridors between many types of habitats (Silva et al. 2017).

Many studies on the Sarcophagidae fauna of the Cerrado have been conducted in various regions of Brazil, particularly in the Central-West and Southeast areas (Rosa et al. 2011, Mello-Patiu et al. 2014, Paseto et al. 2019, Toma et al. 2020). Sousa et al. (2016) carried out a comprehensive research on the scavenger Sarcophagidae fauna in several types of phytophysiognomy, including the Cerrado in the northeastern Brazilian state of Maranhão. However, none of these studies addressed the fauna of the riparian forest. Therefore, the goal of this study is to inventory the scavenger Sarcophagidae species and compare their abundance patterns in "*cerrado*" *sensu stricto* and riparian forest areas in the eastern portion of the state of Maranhão, in a transition zone between the Cerrado and the Caatinga biomes.

Material and Methods

1. Study area

This study was carried out in the municipality of Codó (04°28'57,54805" S; 43°55'03,84603" W), located in the eastern portion of the state of Maranhão, Northeastern Brazil, in an area of "*cerrado*" *sensu stricto*, on the villages of Roncador and Mirindiba, at the margins of the BR316 road, in areas of riparian forests surrounding the rivers Saco and Codozinho, both tributaries of the Itapecuru river (IBGE, 2019a) (Figure 1). The municipality has a land area of 4,361 km² (IBGE, 2019), with the Cerrado as its main phytogeographic domain, with different phytophysiognomies depending on the region's ground topography "*campo cerrado*", "*cerrado*" *sensu stricto* and "*cerradão*" (Feitosa & Almeida 2002, Correia-Filho 2011, Lopes Sobrinho et al. 2014). Furthermore, the region also harbors riparian forests, gallery forests, and babassu forest, which are overshadowed by the babassu palm tree (*Attalea speciosa* Mart. ex Spreng) (Correia-Filho 2011). The climate of the region is subhumid and semiarid, with total annual precipitation ranging between 1200 and 2000 mm. The wet season lasts from December to May, and the dry season from June to November. The annual average temperature varies between 26º C and 27º C, and the average relative humidity fluctuates between 65% and 85% (Correia-Filho 2011).

2. Data collection

We carried out 12 sampling events, two in the second half of 2015, three in 2016, and seven in the first half of 2017. The Sarcophagidae were captured using fly traps similar to those described by Almeida et al. (2003) and baited with 50 g of bovine lungs. To kill all captured insects, we placed pyrethroid (k-othrine) insecticide-impregnated tape inside the collector bag. Traps were attached to tree branches 1.2 meters above ground. The minimum distance between traps was one kilometer, and each trap was left in the field for 48 hours. We set up 60 traps in total, 30 in Cerrado areas and 30 in riparian forest areas. In each sampling event, we set up five traps per area.

The Sarcophagidae were separated, labeled, identified, and counted at the Federal University of Maranhão (UFMA), Codó Campus, state of Maranhão, Brazil. Because the main characteristics used to identify the species are based on the male terminalia, only males were identified at species level. The following studies were used for identification: Lopes (1956, 1976), Guimarães (2004), Carvalho & Mello-Patiu (2008), Vairo et al. (2011, 2015), Buenaventura & Pape (2013), Mulieri *et al*. (2016), Mello-Patiu & Salazar-

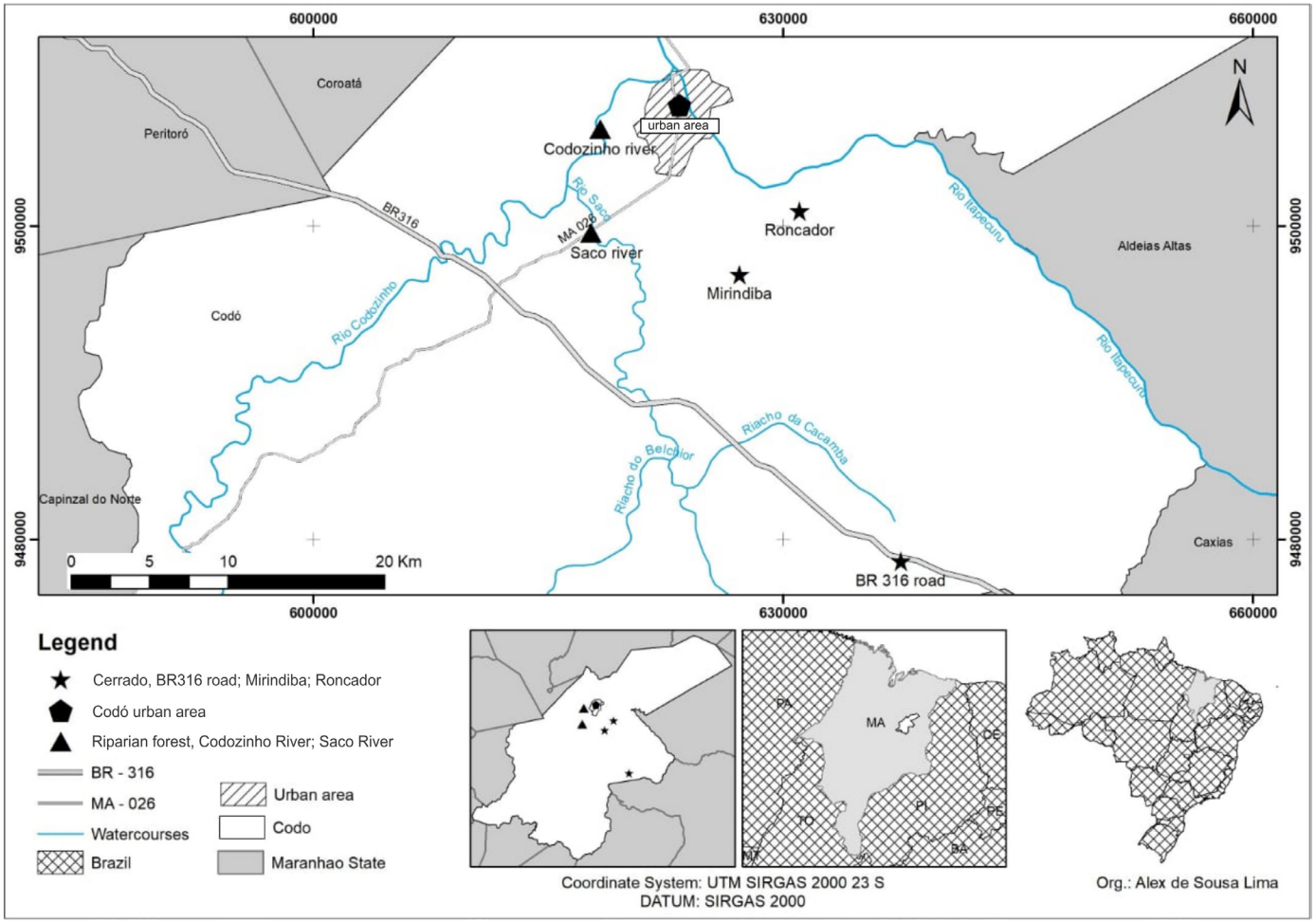


Figure 1. Location of the study area in the municipality of Codó, state of Maranhão, Brazil. Source: IBGE, 2019b (Modified by A.S. Lima).

Souza (2016), and Souza et al. (2020). We also compared our samples to specimens identified in the entomological collection of the Museu Paraense Emlio Goeldi (MPEG) in Belém, state of Pará, Brazil. All specimens were either deposited in the Coleção Zoológica do Maranhão (CZMA) of the State University of Maranhão (UEMA), at the Caxias Campus, or in the MPEG.

3. Data analysis

The abundance of each species was used as a continuous dependent variable, and the different habitat types as categorical independent variables (two levels: Cerrado and riparian forest). Each trap in each sampled area served as our sample unit. Before comparing the abundance values for the most representative species (more than 40 sampled specimens) of both habitat types, we tested the premises of variance homogeneity (Levene test) and normality (Shapiro test). Because the premises were not met, we log-transformed the response variables and tested for the same premises; if they were met, we performed ANOVA for one factor. In this case, however, the chart was created using data from the non log-transformed response variable in order to avoid the loss of biological effects of species abundance. When the premises were not satisfied even after transformation, we used data from the non-log-transformed response variable to perform the non-parametric Kruskal-Wallis test (Zar 2008). Using the R software, we performed statistical analysis and created charts (R Core Team 2020). When p-values were ≤ 0.05, we considered the results significant.

Results and Discussion

We collected a total of 3,220 sarcophagid specimens, of which 2,346 (72.85%) were female and 874 (27.15%) were male (Table 1). Females were more abundant in carcasses and traps containing decomposing animal tissue because they use these substrates as larviposition sites and as a protein source for egg development (Ferraz 1992, Archer & Elgar 2003, Bänziger & Pape 2004). Thus, including females in the analyses can improve the reliability of the results regarding ecological and forensic issues. However, because there are few taxonomic tools that would allow us to identify female individuals, such as taxonomic keys and taxonomic descriptions, the majority of ecological and forensic studies on flesh flies only identify males to the genus or species level.

The males sampled belong to nine genera and 27 species, three of which (*Oxysarcodexia angrensis* (Lopes, 1933), *Peckia* (*Peckia*) *enderleini* (Engel, 1931), and *Retrocitomyia andina* (Lopes, 1985))

Table 1. Abundance of Sarcophagidae by genus in the study areas (cerrado and riparian forest), in the municipality of Codó, MA, Brazil.

	COLLECTION AREA		**TOTAL**
	Cerrado	**Riparian forest**	
Females	1.593	753	2.346
Males	491	383	874
TOTAL	**2.084**	**1.136**	**3.220**

are new records for the Northeast Region, and one (*Titanogrypa* (*Cuculomyia*) *albuquerquei* (Lopes, 1976)) is a new record for the state of Maranhão (Table 2). *Peckia* (*P.*) *enderleini* has been found primarily in the southern South America (Argentina, Paraguay, Bolivia, and Brazil (states of Mato Grosso, Mato Grosso do Sul, Rio Grande do Sul, and São Paulo)) (Buenaventura & Pape 2013, Toma et al. 2020). Therefore, this is the most northern-located record for this species in the continent. This species was also one of the most abundant among the scavenger sarcophagids sampled with traps containing bovine liver in a Cerrado area of the state of Mato Grosso do Sul (Toma et al. 2020), indicating a preference for this habitat type. However, we only found one specimen in the current study, which could be attributed to the type of bait used or to environmental conditions, as the Cerrado areas of Maranhão are drier than those in the state of Mato Grosso do Sul.

Retrocitomyia andina has been recorded in Bolivia and Peru (Mello-Patiu & Salazar-Souza 2016), but it was recently found in Amazonian grasslands in Brazil (Souza 2018). These grasslands are dry habitats, similar to Cerrado areas, implying that this species may be associated with these types of habitats, as has been observed for other *Retrocitomyia* species (*e.g., Retrocitomyia mizuguchiana* Tibana & Xerez, 1985).

Oxysarcodexia angrensis is found in a wide distribution, ranging from Central America (Costa Rica and Panama) to Southeast Brazil (São Paulo), but it had yet to be recorded in the Brazilian Northeast Region. *Titanogrypa* (*C.*) *albuquerquei* had previously been recorded in the Bahamas, Cuba, and Brazil, but only in the Brazilian state of Piauí (Pape 1996). As a result, Maranhão is the second Brazilian state where this species has been recorded. The presence of new records indicates that the Sarcophagidae fauna in Brazil's Northeast Region is diverse but still understudied, as previously highlighted by other authors (Barbosa et al. 2015, Sousa et al. 2015).

Peckia (eight species) and *Oxysarcodexia* (eight species) were the genera with highest species richness. These were also the most abundant genera, with 801 (91.64%) *Peckia* and 46 (5.26%) *Oxysarcodexia* specimens

Table 2. Composition and abundance of Sarcophagidae species collected in the cerrado and riparian forest in the municipality of Codó, MA, Brazil. * First record for Northern Region. ** First record for state of Maranhão.

SPECIES	COLLECTION AREA		TOTAL
	Cerrado	Riparian forest	
Blaesoxipha (*Gigantotheca*) *stallengi* (Lahille, 1907)	1	0	1
Helicobia morionella (Aldrich, 1930)	1	0	1
Lipoptilocnema misella (Lopes, 1938)	0	1	1
Oxysarcodexia amorosa (Schiner,1868)	0	1	1
Oxysarcodexia angrensis (Lopes, 1933)*	1	0	1
Oxysarcodexia avuncula (Lopes, 1933)	0	1	1
Oxysarcodexia fringidea (Curran & Walley, 1934)	0	2	2
Oxysarcodexia modesta Lopes, 1946	1	4	5
Oxysarcodexia thornax (Walker, 1849)	1	29	30
Oxysarcodexia timida Aldrich, 1916	2	4	6
Peckia (*Euboettcheria*) *anguilla* (Curran & Walley, 1934)	3	0	3
Peckia (*Euboettcheria*) *collusor* (Curran & Walley, 1934)	91	22	113
Peckia (*Peckia*) *chrysostoma* (Wiedemann, 1830)	9	77	86
Peckia (*Peckia*) *enderleini* (Engel, 1931)*	0	1	1
Peckia (*Peckia*) *pexata* (Wulp, 1895)	72	42	114
Peckia (*Peckia*) *uncinata* (Hall, 1933)	0	2	2
Peckia (*Sarcodexia*) *lambens* (Wiedemann, 1830)	300	181	481
Peckia (*Squamatodes*) *ingens* (Walker, 1849)	0	1	1
Peckiamyia abnormalis (Hall, 1937)	1	0	1
Ravinia belforti (Prado & Fonseca, 1932)	1	0	1
Ravinia effrenata (Walker, 1861)	1	1	2
Retrocitomyia andina Lopes, 1985*	0	4	4
Retrocitomyia mizuguchiana Tibana & Xerez, 1985	5	4	9
Retrocitomyia retrocita (Hall, 1933)	0	1	1
Titanogrypa (*Airypel*) *cryptopyga* Lopes, 1956	0	1	1
Titanogrypa (*Cuculomyia*) *albuquerquei* (Lopes, 1976)**	1	1	2
Titanogrypa (*Cuculomyia*) *luculenta* (Lopes, 1938)	0	3	3
TOTAL	491	383	874

(Table 2). Likewise, they were the most diverse genera in studies conducted in other Cerrado areas in the state of Maranhão (Sousa et al., 2015, 2016), the Central-West (Mello-Patiu et al. 2017, Toma et al. 2020), and Southeast regions of Brazil (Rosa et al. 2011, Mello-Patiu et al. 2014), as well as for other biomes, such as the Amazon Rainforest (Sousa et al. 2011) and the Atlantic Forest (Leandro & D'Almeida 2005, Barbosa et al. 2014, Lopes et al. 2018). *Peckia* and *Oxysarcodexia* are two of South America's most species-rich genera (Buenaventura & Pape 2013, Souza et al. 2020), and many of its species have scavenger larvae (Pape & Dahlem 2010). They are among the most important genera in terms of forensic and ecological studies in the Neotropical Region due to their abundance, diversity, and scavenger habit.

The low abundance of *Oxysarcodexia* may be related to habitat type, as some species in this genus prefer forested environments (Valverde-Castro et al. 2017). Certain species sampled in this study were also found to be in low abundance in previous studies conducted in Cerrado areas using decomposing animal organic matter (Rosa et al. 2011, Toma et al. 2020). Furthermore, because some *Oxysarcodexia* species are coprophagous (Pape & Dahlem 2010), the type of bait used may have influenced our results.

Peckia (*Sarcodexia*) *lambens* (Wiedemann, 1830) was the most abundant species found (56,18% specimens sampled), followed by *Peckia* (*Peckia*) *pexata* (Wulp, 1895) (13%), *Peckia* (*Euboettcheria*) *collusor* (Curran & Walley, 1934) (13%), and *Peckia* (*Peckia*) *chrysostoma* (Wiedemann, 1830) (10%). The remaining species account for 9% of all sampled specimens (Table 2). *Peckia* (*S.*) *lambens* is native to the southern United States of America (USA), several Caribbean islands, nearly all of South America, and has been introduced to the Cook Islands and French Polynesia. This widespread distribution is most likely due to the species' high ecological plasticity, which allowed it to colonize a wide range of environments, including heavily populated ones (Camargo et al. 2018, Sousa et al. 2020); furthermore, its larvae consume a variety of food sources. They can be insect parasitoids, predators of dying scorpions and insects, cause myiasis in birds and mammals, and scavengers of dead vertebrates and invertebrates. As a result, this is one of the most abundant species used in ecological and forensic studies (Alves et al. 2014a, b, Vasconcelos et al. 2015, Sousa et al. 2016, Souza & Zuben 2016, Dufek et al. 2020a). There was no difference in abundance between open habitats and riparian forests in Cerrado areas, as expected for a species with high ecological plasticity (X^2 = 0.0611, df = 1, p = 0.434, Kruskal-Wallis nonparametric test) (Figure 2).

Even though *P.* (*P.*) *pexata* has a wide distribution, ranging from Texas to Argentina, and can be found in both forested and open habitats (Ferreira 1979, Linhares 1981, Couri et al. 2000, Sousa et al. 2011, 2016, Valverde-Castro et al. 2017, Dufek et al. 2020b), it is not commonly seen in primary forests (Camargo et al. 2018). Hence, it may be associated with open and dry environments, such as the Cerrado and grasslands (Barros et al. 2008, Carvalho-Filho et al. 2018, Toma et al. 2020). Nevertheless, it was abundant in both open habitats and riparian forests in the studied area, with no significant differences between them (One-way ANOVA: $F_{(1, 58)}$ = 2.370, p = 0.129) (Figure 3).

Peckia (*E.*) *collusor* is a generalist species that can be found in a variety of habitats, including urban forests (Linhares 1981, D'Almeida 1984, Dias et al. 1984, Yepes-Gaurisas et al. 2013), open vegetation, and urban areas (Sousa et al. 2011, 2016, Mello-Patiu et al. 2014). Nevertheless, the difference in abundance between open areas and the riparian forest was significant in our study (X^2 = 4.769, df = 1, p = 0.029, Kruskal-Wallis nonparametric test) (Figure 4). Sousa et al. (2016) and Valverde-Castro et al. (2017) also sampled fewer specimens of this species in forested habitats than in open habitats.

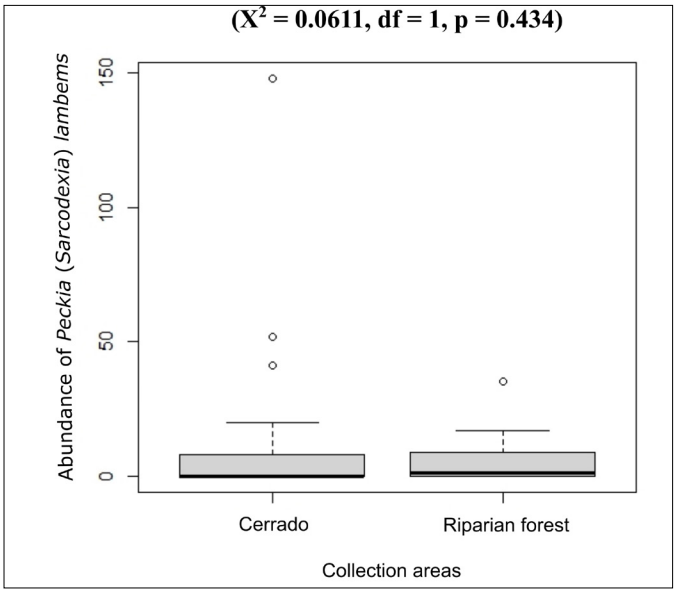


Figure 2. Relationship between the abundance of *Peckia* (Sarcodexia) *lambens* and the collection areas habitats (Cerrado and Riparian forest), in Codó municipality, Maranhão. Medians of the abundances between the two habitat types were not significantly different (p>0.05; the Kruskal-Wallis two-tailed test). Data: — = median; ▭ 25%-75% ⊥ Min-Max ; ° = Outlier.

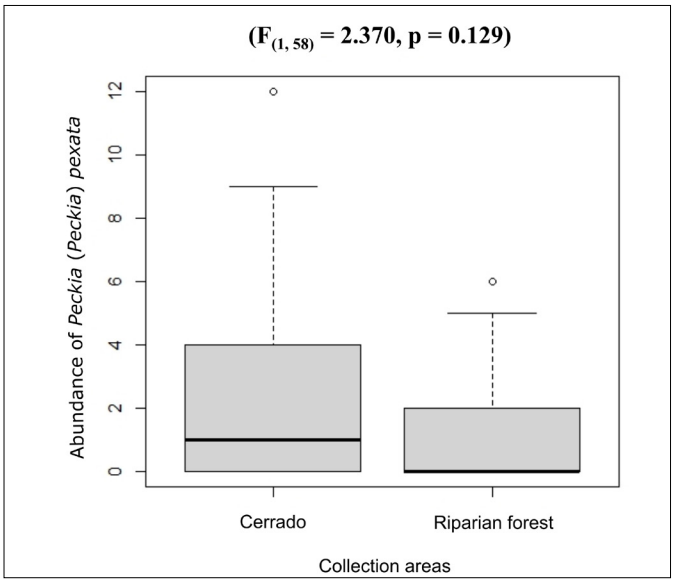


Figure 3. Relationship between the abundance of *Peckia* (Peckia) *pexata* and the collection areas habitats (Cerrado and Riparian forest), in Codó municipality, Maranhão. Means of the abundances between the two habitat types were not significantly different (p>0.05; ANOVA one-way test). Data: — = means; ▭ 25%-75% ⊥ Min-Max ; ° = Outlier.

Peckia (*P.*) *chrysostoma* is a widely distributed species (found from Southern United States to Southern Brazil) and an important representative of the scavenger fauna in Brazil, where it can be found in a variety of habitats, including cities (Yepes-Gaurisas et al. 2013, Carmo & Vasconcelos 2016, Barbosa et al. 2017). Therefore, it is consistently one of the most abundant species in ecological and forensic studies in South America (Alves et al. 2014a, b, Sousa et al. 2016, Valverde-Castro et al. 2017). This species was abundant in both open and riparian habitats, with no significant differences between them (X^2 = 0.073, df = 1, p = 0.788, Kruskal-Wallis nonparametric test) (Figure 5).

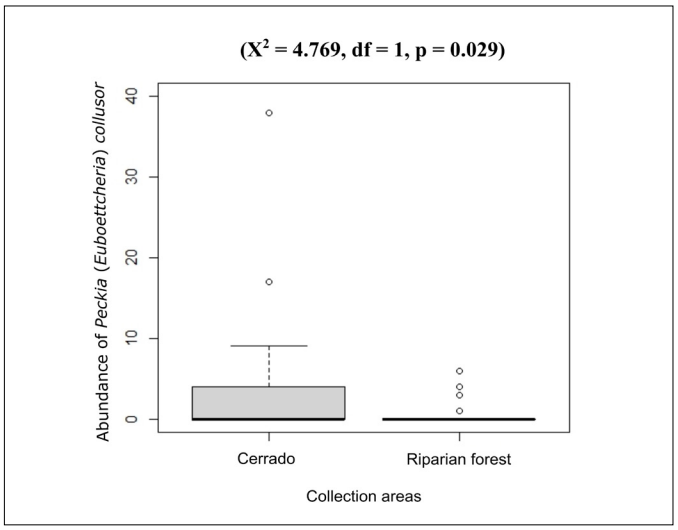


Figure 4. Relationship between the abundance of *Peckia* (Euboettcheria) *collusor* and the collection areas habitats (Cerrado and riparian Forest), in Codó municipality, Maranhão. Medians of the abundances between the two habitat types were significantly different ($p<0.05$; Kruskal-Wallis two-tailed test). Dados: — = median; ▭ 25%-75% ⊥ Min-Max ; º = Outlier.

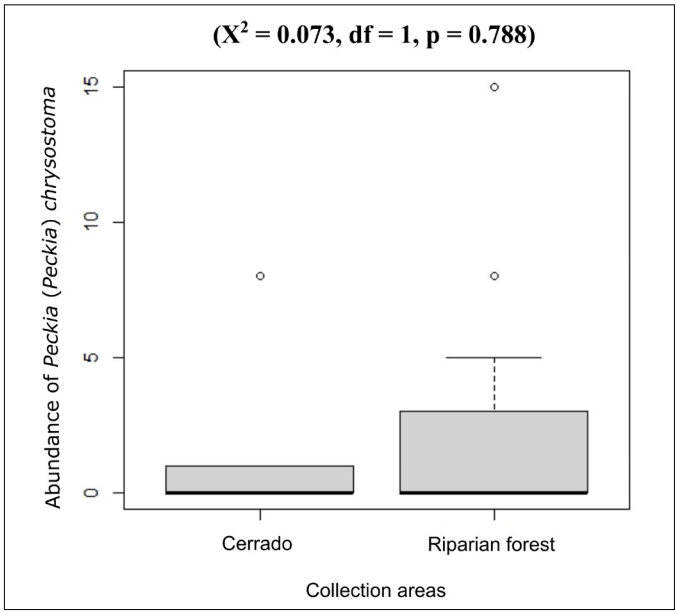


Figure 5. Relationship between the abundance of *Peckia* (Peckia) *chrysostoma* and the collection areas habitats (Cerrado and Riparian forest), in Codó municipality, Maranhão. Medians of the abundances between the two habitat types were not significantly different ($p>0.05$; Kruskal-Wallis two-tailed test). Dados: — = median; ▭ 25%-75% ⊥ Min-Max ; º = Outlier.

Of the total number of specimens sampled, 2,084 were found in Cerrado areas and 1,136 in riparian forests. Flesh flies, both males and females, were more abundant in open areas of Cerrado. These findings are consistent with previous research, which found that species belonging to this family were more abundant in open environments (pastures, clearings, and savannas) than in adjacent forests (Sousa et al., 2011, 2016, Yepes-Gaurisas et al. 2013). The majority of the species of Sarcophagidae found in this study have a wide geographical distribution in both Brazil and South America, being present in various phytogeographic domains such as the Amazon Rainforest, Atlantic Forest, Cerrado, and Caatinga (Alves et al. 2014a, b, Mello-Patiu et al. 2014, 2017, Sousa et al. 2016, Barbosa et al. 2017).

However, some of the species sampled, such as *Lipoptilocnema misella* (Lopes, 1938), *R. mizuguchiana*, and *Blaesoxipha* (*Gigantotheca*) *stallengi* (Lahille, 1907), are most likely associated with open and/or dry habitats. In a study conducted in different biomes of the state of Maranhão, *R. mizuguchiana* and *B.* (*G.*) *stallengi* were only sampled in savannas and swamps, which are open environments (Sousa et al. 2016). *Lipoptilocnema misella* was only identified in the Brazilian states of Goiás, Maranhão, Mato Grosso, and Minas Gerais (Mulieri et al. 2016, Sousa et al. 2016). Because this species, like many others in the same genus, is associated with Cerrado areas (Mulieri et al. 2016), it is absent in forensic studies and lists of scavenger flesh flies in the Amazon (Vairo et al. 2014, Ramos-Pastrana et al. 2018).

In Brazil, only two species of the subgenus *Squamatodes* are found: *Peckia* (*Squamatodes*) *ingens* (Walker, 1849) and *Peckia* (*Squamatodes*) *trivittata* (Curran, 1927), the former being more common in forested habitats and the latter in more open ones such as the Cerrado (Barros et al. 2008, Valverde-Castro et al. 2017, Camargo et al. 2018). This is most likely why the abundance of *P.* (*S.*) *ingens* was low in the studied area. Sousa et al. (2016), on the other hand, sampled 39 specimens in Cerrado areas and none in the Amazon rainforest in the state of Maranhão.

The species *L. misella*, *Oxysarcodexia amorosa* (Schiner, 1868), *Oxysarcodexia avuncula* (Lopes, 1933), *Oxysarcodexia fringidea* (Curran & Walley, 1934), *P.* (*P.*) *enderleini*, *Peckia* (*Peckia*) *uncinata* (Hall, 1933), *P.* (*S.*) *ingens*, *R. andina*, *Retrocitomyia retrocita* (Hall, 1933), *Titanogrypa* (*Cuculomyia*) *luculenta* (Lopes, 1938) and *Titanogrypa* (*Airypel*) *cryptopyga* (Lopes, 1956), were found only in the riparian forest, although in low abundance (less than 5 specimens) (Table 2). According to Macedo (1993), Castro et al. (2012), and Kuntschik et al. (2014), riparian forests have great ecological importance because of their faunistic, floristic, and microbiotic composition, thus playing an important role in forming corridors that promote gene flow. The presence of species of Sarcophagidae in riparian forests that were absent in open areas, as well as new species records, suggest that this vegetation type is also important for the conservation of the family's biodiversity in the Cerrado. Nonetheless, anthropogenic activities, particularly logging, cattle raising, and agriculture, are drastically altering riparian forests in the municipality of Codó, because these areas typically have fertile soils (Castro 2012, Kuntschik et al. 2014, Kutzmy et al. 2019).

Conclusions

We identified 27 species of scavenger Sarcophagidae in the studied areas, three of them were new records for the Northeast Region (*Oxysarcodexia angrensis*, *Peckia* (*Peckia*) *enderleini* and *Retrocitomiya andina*), and one for the state of Maranhão (*Titanogrypa* (*Cuculomyia*) *albuquerquei*). This highlights the importance and necessity of conducting more surveys in the region, especially in areas such as riparian forests, where the sarcophagid fauna has not yet been adequately sampled. The habitat type only significantly affected the abundance of *Peckia* (*Euboettcheria*) *collusor*, which was more abundant in open areas. *Peckia* (*Peckia*) *chrysostoma*, *P.* (*P.*) *pexata*, and *P.* (*S.*) *lambens* were generalists in the studied areas. This study contributes to the understanding of the spatial distribution of different Sarcophagidae species in "*cerrado*" *sensu stricto* and riparian forest areas, reducing the knowledge gap for this group in the Northeast Region of Brazil.

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Author Contributions

Raimundo Francisco Oliveira Nascimento: 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.

José Orlando de Almeida Silva: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Fernando da Silva Carvalho-Filho: Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Conflicts of Interest

There is no conflict of interest.

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Article

Correlations between morphological fruit types, fruit and seed colors, and functional groups

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Abstract: The associations between morphological fruit types, fruit and seed colors, and functional plant traits: life forms, epiphytism, physiology, nutritional relationships, fruit phenology, and successional stage, were determined for 1,139 plant species from contrasting plant communities. Texture and dehiscence were closely related. Dehiscence is largely associated with dry tissues; indehiscence, however, is an attribute of both dry and fleshy fruits. The number of morphological fruit types was 28 or 55 for Gray's and Spjut's classifications, respectively. Fruits were predominantly dark in color (brown, purple-black, black or green), whilst seeds had both dark and light colors (brown, beige, or black). The most representative associations were mainly found between the more abundant fruit types and the colors most common. Asymmetries in the level of specialization, whereby less common fruit and seed colors tended to be associated with the most common fruit types, were also found. Fleshy fruits showed more variation as regards their coloration, and only drupes and berries showed a tendency towards a specific color: purple-black. The relationships among fruit type and color, seed color, and functional plant traits revealed the following trends: trees produced both fleshy and dry fruits; shrubs produced fleshy fruits; and herbaceous species, dry fruits. Woody species tended to have dark or bright colors, depending on their seed dispersal mechanisms and phylogenetic relations. Epiphytes were associated with dry-dehiscent fruits and brown seeds, and parasitic-hemiparasitic species had predominantly fleshy-indehiscent fruits. Pioneer species were more likely to have dry fruits, whereas fleshy fruits tended to be more frequent in late successional stage species. The C4 species, mostly herbs, had mainly one-seeded dry fruits, but multi-seeded fruits in succulent-CAM species showed morphologically diverse fruit types. Unripe and ripe fruits showed seasonal changes, especially during the rainy-dry transition period for the most abundant morphological fruit types, dry fruits during the dry period and fleshy fruited species was positively associated with the rainy season. All these trends are discussed with regard to their environmental significance and the relationships between fruit morphology, colors and functional groups. .

Keywords: *Morphological fruit type; fruit color; fruit phenology; functional group; plant life form; successional stage.*

Correlaciones entre tipos morfológicos de frutos, colores de frutos y semillas y grupos funcionales

Resumen: Las asociaciones entre tipos morfológicos de frutos, colores de frutos y semillas y los grupos funcionales de las plantas: formas de vida, epifitismo, fisiología, relaciones nutricionales, fenología de frutos y estado sucesional fueron determinados para 1139 especies de plantas de comunidades contrastantes. La textura y dehiscencia estaban muy relacionadas. Dehiscencia está estrechamente asociada con tejidos secos, pero indehiscencia es un atributo de frutos secos y carnosos. El número de tipos morfológicos de frutos fue 28 y 55 para la clasificación de Gray y Spjut respectivamente. Los frutos fueron predominantemente de colores oscuros (marrón, negro-purpura, negro o verdes), mientras que las semillas tenían colores claros y oscuros (marrón, beige o negro). Las asociaciones más representativas fueron principalmente encontradas entre los tipos de frutos más abundantes y los colores más comunes. También se encontraron asimetrías en los niveles de especialización, donde los colores menos comunes de frutos y semillas estuvieron asociados con los tipos de frutos más comunes. Los frutos carnosos mostraron más variación en su coloración, y solo las drupas y bayas tendieron a colores específicos como negro-purpura. Las relaciones entre tipo de fruto y color, color semilla y rasgos funcionales de las plantas revelaron las siguientes tendencias: arboles producen frutos secos y carnosos; arbustos frutos carnosos y hierbas producen frutos secos. Las especies leñosas tendieron a tener colores oscuros y brillantes, relacionados con su mecanismo de dispersión y filogenia. Epifitas estuvieron asociadas con frutos secos dehiscentes y semillas marrones, y las especies

parásitas-hemiparásitas tenían predominantemente frutos carnosos indehiscentes. Las especies pioneras tenían comúnmente frutos secos, mientras que los frutos carnosos tendieron a ser más frecuentes en especies de estados sucesionales tardíos. Las especies C4, principalmente hierbas, tenían frutos secos con una semilla, mientras que frutos polispermos en especies CAM mostraron diversos tipos de frutos. La fenología de frutos maduros e inmaduros mostro cambios estacionales para los más abundantes tipos morfológicos, especialmente durante el periodo de transición lluvia-sequia, frutos secos en el periodo seco y frutos carnosos durante el periodo lluvioso. Todas estas tendencias son discutidas con relación a las características ambientales y de acuerdo con las relaciones entre tipos morfológicos de frutos, colores y grupos funcionales.

Palabras claves: *Tipo morfológico fruto; color fruto; estado sucesional; fenología fruto; forma de vida; grupo funcional.*

Introduction

Fruits represent a crucial phase of angiosperm life cycle. By definition, a fruit is the mature ovary which, in the majority of cases, contains the seeds (Font Quer 2001, Simpson 2019), although other definitions include accessory flower structures that accompany the developed ovary (Spjut 2004). Fruits and flowers have evolved together whereby the ovules were covered and enclosed by the carpelar leaves, and subsequently the carpels transformed into the pericarps of the fruit at maturity (Taylor and Kirchner 1996, Spjut 2004, Vialette-Guiraud and Scutt 2009). A fruit, then, may be initially considered as a structure that protects an ensemble of seeds in which the carpels and pericarps shield the ovules and seeds against extreme climatic conditions, herbivory and predispersal seed predation, during flowering, pollination, unripe fruit development and ripe fruit phases (Chambers and MacMahon 1994). Accordingly, fruits are plant organs with multiple associations.

Fruit morphology is described according to two basic traits: pericarp texture and dehiscence. Many floral characteristics such as gynoecium structure and the number of flowers determine morphological fruit type, including in many cases accessory flower structures and inflorescences that accompany fruits. The multiplicity of possible combinations of fruit parts has led to the identification of a large and complicated variety of fruit types, which have been classified in different way according to the criteria used. Two main systems of fruit classification are currently considered in comparative studies: 1) the traditional fruit classification set out by Gray (1877), based mainly on the texture of the pericarp (fleshy or dry), and the pattern of dehiscence or indehiscence together with gynoecium structure, and 2) the systematic fruit type treatment given by Spjut (1994) based on pericarp and antocarp (ripened ovary with attached floral parts, persistent or accrescent) types, in addition to gynoecium structure. Both classification systems provide valuable evidence for evolutionary and ecological trends in fruit morphology. However, they may offer different interpretations of the possible ecological relationships among morphological fruit types, fruit and seed colors, and the associations of these with functional groups.

Variations in the characteristics of fruits are frequently related to specific flower morphology and may be phylogenetically influenced. About 28% of 281 angiosperm families produce fleshy fruits, 20% contain species with either fleshy or dry fruits "mixed families" and 53% produce only dry fruits (Fleming 1991). However, morphological fruit types of certain clades are, in many cases, modified by ecological factors and by the potential relationships between fruit morphology and functional groups, such as life form, carbon metabolism pathway, and epiphytism. Regarding life form, herbaceous species tend to bear dry fruits, and woody species (shrubs and trees) fleshy fruits (Herrera 1984, Willson et al. 1989, French 1991, Possete et al. 2015, Wotton & McAlpine 2015); vines may exhibit variation according to forest type (Willson et al. 1989, Possete et al. 2015). Fruit types, and fruit and seed colors are also representative of successional stages, with dry fruits being more abundant in open vegetation communities (e.g. Arbeláez & Parrado-Rosselli 2005) and fleshy fruits in forests (Carpenter et al. 2003, Chen et al. 2004, Buitrón-Jurado & Ramírez 2014, Hilje et al. 2015). In addition, the frequencies of fruit types may differ between vegetation strata (Yamamoto et al. 2007) and reproductive phenology: dry fruits are often produced during the dry season and fleshy fruits during the rainy season (Wheelwright & Janson 1985, Jordano 1993, Bulhão & Figueiredo 2002, Bentos et al. 2008). In this context, many plant species synchronize fruiting and dispersal with the onset of the rainy season to maximize seedling development and establishment (Oliveira 1998).

The color of fruits and seeds is an attribute frequently associated with advertising (Ridley 1930, Stiles 1982, Knight & Siegfried 1983, Wheelwright & Janson 1985, Cazetta et al. 2009). Colorful fruits have different functions: to attract dispersal agents; reveal fruit localization; and give a visual indication of fruit ripeness (Ridley 1930). Fruit color may have two other functions: to be conspicuous and attractive (Wheelwright & Janson 1985). The function most often ascribed to the colors of bird-dispersed fruit is the former: their enhanced visibility increases their chances of being seen by potential seed dispersers. Bright colors are thus the "flag" (Ridley 1930, Stiles 1982) that catches the birds' attention. If conspicuousness were the sole reason for color displays in bird-dispersed fruits, however, we would expect comparable fruit displays under similar visibility conditions. In addition to signaling location, the color of a fruit may convey information about its quality that would influence a bird's choosing of that fruit (Wheelwright & Janson 1985, Schaefer & Schmidt 2004). However, fruit and seed colors may have functions other than that of advertising. For example, dark colors (blue, black, and brown) may absorb more radiation in the visible spectrum than pale colors (white, yellow, orange and red) (Wheelwright & Janson 1985). Fruit colors may also affect the thermal regime of developing fruits and their enclosed seeds; be a side-effect of secondary chemical production that protects the fruit from predispersal damage; or have other physiological functions (Willson et al. 1989). Green and developing fruits may also contribute a major proportion of their own photosynthate (Bazzaz et al. 1979). Light-colored seeds have also been significantly associated with rapid germination times (Stringam et al. 1974, Daun & DeClercq 1988, Thompson 1993, Debeaujon et al. 2000). Dark colors, such as black, brown and blue, could absorb greater amounts of solar radiation, which might increase their temperature and thus accelerate metabolism and ripening speed (Janzen 1983, Wheelwright & Janson 1985), as well as providing a protective function due to their high anthocyanin content (Schaefer

2011). Furthermore, fruit color can be related to morphological fruit types: drupes and berries are often colorful, whereas loculicidal capsules tend to be brown (Knight & Siegfried 1983, López & Ramírez 1989, Ibarra-Manríquez & Cornejo-Tenorio 2010). Therefore, fruit and seed color functions are indicative of both biotic and abiotic interactions, for example, attracting or avoiding animals.

Morphology and color are significant attributes of fruits and seeds and can be associated with diverse functions of the plant species life cycle. Fruit morphology and fruit and seed colors may either complement, or be independent from, each other. Morphological fruit type, consumer type and fruit size are all dependent on each other, whereas fruit color is related to both fruit size and consumer type, which themselves act independently from each other (Knight & Siegfried 1983). The great diversity of morphological fruit types, and fruit and seed colors, and their multiple combinations, are not necessarily independent of morphological, physiological and ecological plant attributes. Such relationships, although still poorly understood, must be line with those factors that maximize plant fitness, and will thus vary according to life history characteristics. Hence, morphological fruit types, and fruit and seed colors must be traits that can be related to plant functional groups. Phenotypic integration among traits has the potential to influence ecological communities through direct and indirect linkages within networks of interacting species. Associations among traits could thus potentially impact how the combined effects of direct and indirect selection on interactions shape the trajectories of coevolution under different environmental conditions (Assis et al. 2020).

We suggest that morphological fruit types and the colors associated with them should be analyzed ecologically, irrespective of dispersal syndromes and natural reproductive efficiency. This kind of analysis has not yet been attempted, and could enable us to establish whether morphological fruit types, and fruit and seed colors, represent ecological attributes that can be associated with particular functional groups, such as life form, epiphytism, carbon metabolism pathway, nutritional relationships, seasonality of fruit phenology, and the successional stage of the plant species. Morphological fruit types deserve their own ecological analysis in order to determine trends and relationships between fruit morphology, fruit and seed colors, and plant functional groups. In this context, we posed the following questions: 1- What kinds of associations occur among morphological fruit types, fruit colors and seed colors? 2- Are morphological, ecological and physiological functional groups of plant species related to the morphological fruit types of Gray (1877) and Spjut (1994), and fruit and seed colors? 3- What are the functional groups that best explain fruit morphology and fruit and seed colors?

Material and Methods

1. Study areas

The plant communities we surveyed were extremely varied in their vegetation structure and complexity, and the selection we made also took account of climatic factors (temperature and precipitation) and altitude. Mean annual temperatures and mean annual precipitations ranged from 2.8 to 28.7°C and from 330.5 to 2428.4 mm of rain, respectively, across the plant communities studied, and included communities at sea level to close to 4,000 m (Table 1)**.** Plant species were surveyed from 27 sites in Venezuela in ten geographic areas, and included plant communities belonging to five vegetation types: 1) dry forests, 2) meadows, 3) shrublands, 4) wet forests, and 5) wetlands. Each vegetation type included a large variety of plant communities. Dry forests were comprised of secondary dry forest, the forest–savanna ecotone, gallery forest, and a riparian dry forest, with a temporary river during the rainy season. Wet forests included cloud forest, dwarf cloud forest, and riparian wet forest. Meadow vegetation was predominantly herbaceous and included savanna, littoral meadow, psammophilous meadow, and disturbed grassland. Shrublands were represented by mesothermic, xerophytic, and high mountain shrublands, a littoral shrubland containing a mix of shrubs and herbs (Atoll) and bushland. Wetlands are permanently flooded plant communities, and were comprised of broad–leaved meadow, palm swamp, and mangrove communities. Three disturbed communities with different levels and times of disturbance were also surveyed: 1) a bushland several years after disturbance (bushland is a term for land which supports remnant vegetation or land which is disturbed but still retains a predominance of the original flora and structure [Draper & Richards 2009]), 2) a fallow, secondary savanna represented by an abandoned area of cultivated, uncultivated, and disturbed grassland, and 3) an area of savanna annually disturbed by fire, grazing and machinery (mainly agricultural).

2. Plant species selection and taxonomic aspects.

Plant species were selected in such a way as to maximize the number of plant families, genera and species studied. As noted above, plant species from 27 plant communities were surveyed. In addition, 30 plant species from other sites in Venezuela were considered in the analyses, including some plant species from previous studies (see Table 1). A previous analysis of the association between taxonomy and plant species composition (N. Ramírez and H. Briceño, in preparation) showed that three orders (Fabales, Malphigiales and Poales) and one family, Fabaceae, were dominant in the species examined. Specifically, the frequency of dry fruits was higher than that of fleshy fruits and significantly correlated with the Fabales and Poales orders, and the Fabaceae family. In addition, indehiscent fruits were significantly more abundant than dehiscent fruits in the sample examined, and correlated with Poales species. The frequencies of simple (indehiscent) fruits, originating from one flower, and rhexocarpic (dehiscent) fruits were also significantly high in the sample studied. However, only rhexocarpic fruits were significantly correlated with Fabales species.

3. Morphological fruit types

Fruits were initially classified with regards to their texture (fleshy and dry fruit types) and dehiscence (dehiscent and indehiscent fruit types). After this first classification they were grouped according to two systems: 1- The traditional classification set out by Gray (1877), and 2- The systematic treatment given by Spjut (1994). Gray's (1877) system is based on the texture of the pericarp (fleshy or dry); the pattern of dehiscence or indehiscence; the shape and size of the fruit; carpel and ovule number; fruit that develop from one flower; fruit that develop from a single carpel or fused carpels (single fruit); those that develop from several separate carpels of a single gynoecium (aggregate fruit); and those that develop from more than one flower (multiple fruit or infrutescence). Spjut's (1994) classification system is based on the presence of a pericarp (ripened ovary without any attached floral

parts) or antocarp (ripened ovary with attached floral parts, either persistent or accrescent); gynoecial structure (apocarpous, syncarpous or schizocarpous); and the distinction between fruits that develop from one flower, and those that develop from more than one flower. In addition, compound (aggregate) gynoecia are recognized when they become united to form compound fruit (from more than one flower). This classification system includes 95 different fruit types, primarily grouped into two large categories: spermatocarpia (naked seeds), and eucarpia (covered seeds). The second of these contains five sub-categories: simple fruits (fruit not dispersed from a pericarpium, developing from one flower); rhexocarpic fruits (fruit dispersed by the opening of the pericarp); schizocarpic fruits (fruitlets derived from a compound pistil separating into its carpellary constituents); multiple fruits (a single flower producing multiple fruitlets, apocarps); and compound fruits (fruits derived from more than one flower).

4. Fruit and seed colors

Fruits and seeds were characterized according to their color at maturity. Fruit and seed color generally refers to the external surface, although the color of the internal surface of some dehiscent fruit was also considered when it differed from that of the external surface. We grouped the different tonalities of the fruit and seed colors we observed into broader color categories. Thus, dark-brown, light-brown, and reddish-brown tonalities were all included in the category "brown" ; light yellow was described as "yellow" ; and dark-green, brownish-green, and jade-green tonalities were all considered as "green". The category "purple-black" unified fruits and seeds with dark and very dark purple tonalities, and those close to black that were difficult to fit into other color categories. The categories were then sorted into three large groups: 1- dark colors (black, brown, green, blue, purple-black), 2- bright colors (orange, pink, red, yellow), and 3- light colors (beige, white). Fruits and seeds were also classified as single-colored or bi-colored according to the number of different colors on a single fruit and/or seed at maturity. In the case of dehiscent fruits, bi-colored fruits refer to the different colors on the internal and external surfaces of the pericarp.

5. Functional groups

5.1 Life forms and succulence

Plant life forms were determined using criteria previously described (Ramírez & Herrera 2017). Plant life forms were established according to their structure, height, woodiness, ramification type, and life span, into five categories: tree, shrub, liana, perennial herb, and annual herb. As a first grouping, plant species were separated into perennial and short-lived (or annual) species. Short-lived species were herbaceous plants in which more than 80% of the individuals surveyed died over the two year observation period in the permanent plots surveyed (minimum of ten individuals per species per plot). Perennial species were those species with an extended life cycle and multiple reproductive events. This latter condition included monocarpic perennial species as they are long-lived. We did not consider plant distribution across the vertical profile of the communities, thus epiphytic species were included as herbaceous species (short-lived or perennial) depending on their life span. Some parasitic epiphytes (e.g. *Phthirusa* spp.) were included as climbing species because their branches creep along the host plant. Species were also classified as succulents (having specialized fleshy tissue in a plant organ for the conservation of water) and non-succulents.

5.2 Nutritional relationships

Plant species were classified as regards how they obtain their nourishment, into three categories: 1- Autotrophy, plants that synthesize their own food, 2- hemiparasite and parasite, plants that partially or wholly obtain their nourishment from other living plants, and 3- insectivores, plants that partially obtain their nourishment from insects. The conditions of parasitism, hemiparasitism, and insectivory were mostly inferred by the habit of the plant, and / or whether it had modified, leaves, or roots, and then confirmed with systematic studies (Judd et al. 1999, Smith at al. 2004). In some cases, information about nutritional relationships was taken from previous studies (Ramírez et al. 2012).

5.3 Carbon metabolism pathway

Plant species were classified according to which of the three main carbon assimilation pathways, C_3, C_4 or CAM (Crassulacean acid metabolism) they employ. Information about the carbon metabolism pathways of plant species was taken from previous studies (Ramírez & Briceño 2015, Ramírez & Herrera 2017).

5.4 Epiphytism

Plant species were classified according to their substrate type as: epiphytes, when one plant grows on another host plant; or non-epiphytes (terrestrial), when the plant species grows directly in the soil.

5.5 Successional condition

Plant species were also grouped with regard to their successional stage in a community as: 1- late seral or climax species, and 2- pioneer species. Late seral species were found growing in natural or undisturbed areas, whereas pioneers were found growing in disturbed areas, impacted mainly from fires and / or agricultural machinery.

5.6 Fruit phenology

Lastly, the plant species were classified according to their unripe (fruit development times), and ripe fruit phenology using data from previous studies (Castillo 1977, Sobrevila 1978, Colonnello 1980, López 1981, Tuges 1982, Sobrevila et al. 1983, Gómez 1984, Berry 1984, Ramírez & Brito 1987, Ramírez et al. 1988, Hokche & Ramírez 1990, Seres & Ramírez 1993, Ruiz-Zapata 1994, Guzmán 1995, LLamoza-Solórzano 1998, Xena et al. 1999, Castro-Laportte & Ruíz-Zapata 2000, Lemus-Jiménez & Ramírez 2002, Nassar & Ramírez 2004, Herrera & Nassar 2009, Ramírez 2009, Ramírez & Briceño 2011, López & Ramírez 2013). For statistical purposes, discrete climatic periods when fruit phenology was observed were established for each plant species as follows: rainy season, dry season, and rainy-dry transition period. Plant species fruiting during the transition period included plant species that also fruited in the rainy and/or dry seasons as well as those that fruited exclusively during the transition period.

6. Data Analysis

Independence test was used to determine whether fruit structural types: fruit texture (dry or fleshy), and fruit dehiscence (dehiscent or indehiscent), differed from each other according to the functional groups identified (life-form, successional stage, nutritional relationship,

carbon metabolism pathway, plant succulence, epiphytism, unripe fruit phenology, and ripe fruit phenology). The level of dependence and interactions between these two categories were determined using a log-linear analysis of frequency: a method of interpreting the data in cross-tabulation tables (Statsoft 2007). When the log-linear analysis of frequency was significant, the residual frequencies, i.e. the observed minus the expected frequencies, were estimated for each cell of the two factor comparison table, and then standardized and tested for significance. This analysis enabled us to establish which pairs of variables deviated significantly from expected values (Legendre & Legendre 1993) and thus contributed more to the association. Significant and positive residuals indicated a strong association between the categories, and significant and negative residuals, an unusual occurrence. The level of dependence and interactions using log-linear analysis of frequency was also employed for analyzing the relationships between fruit texture and dehiscence.

The associations between pairs of fruit attributes: morphological fruit types *vs*. fruit and seed color, were analyzed using bipartite graphs (Dormann et al. 2008, R core Team 2015), which graphically represent a two mode network consisting of two sets of nodes with interactions (associations) between (but not within) them (Bascompte & Jordano 2007). We determined the following descriptors when analyzing fruit morphology, fruit color and seed color associations: 1- the number of morphological fruit types according to Gray's classification, 2- the number of morphological fruit types according to Spjut's classification, 3- the number of fruit color classes, 4- the number of seed color classes, 5- the total number of potential associations, 6- the total number of recorded associations, and 7- the frequency of the number of associations (i.e. 1, 2, 3, ……n) for each pair of comparisons, namely, fruit color-Gray's classification; fruit color-Spjut's classification; seed color-Gray's classification; seed color-Spjut's classification; and fruit-seed color. We also calculated the mean number of associations per fruit type according to Gray and Spjut, fruit color class, and seed color class. Connectance, defined here as the percentage of associations with respect to the total possible, in analogy with the measure used in interaction webs (Jordano 1987), was also determined for each pair of items analyzed.

Results

1. Morphological fruit types

1.1 The texture and dehiscence of fruit types

We characterized the fruits of 1,139 plant species according to structural type (Table 1). The categories of fruit texture and dehiscence were found to be statistically dependent on each other (df = 1, χ^2 = 268.01; P= 0.0) and all residuals were significant at P<0.05. Overall, there were twice the number of species with dry fruits (N=790; 69.4%) than fleshy fruits (N= 349; 30.6%) in the sample. In contrast, the number of species with indehiscent fruits (N= 640; 56.2%) was only slightly higher than that of those with dehiscent fruits (N= 499; 43.8%). Similarly, the number of species with dry-dehiscent fruits, (N= 472; 59.7%) was only slightly higher than that of those with dry-indehiscent fruits (N= 321, 40.3%). In contrast, fleshy fruits were mostly indehiscent (N= 322, 92.3%), and only a few (N= 27, 7.7%) species with dehiscent fruits were recorded.

1.2 Frequencies of morphological fruit types

The number and frequency of each morphological fruit type according to Gray and Spjut are given in Appendix S1. The sample examined contains a large diversity of fruit types (Figure 1). We recorded 28 morphological fruit types according to Gray's classification (type I fruits) and 55 following Spjut (type II fruits). The most abundant morphological fruit types (N≥10 and ≥10%) were type I fruits: loculicidal capsule (N=165, 14.5%), berry (N=165, 14.5%), drupe (N= 131, 11.5%), and achene (N= 125, 11.0%), and type II fruits: loculicidal capsule (N= 161, 14.1%) and bacca (N= 122, 10.7%). Comparisons between the fruit classification systems (I and II) revealed many coincidences as regards nomenclature and the general morphology of many fruit types (i.e. berry, loculicidal capsule, drupe, septicidal capsule, legume, and silique). Nevertheless, type I fruits departed from type II fruits in some cases (Figure S1). For example, achenes and schizocarps in Gray's classification correspond to a variety of fruit types following Spjut.

2. Fruit and seed colors

Eleven single-colored and seven bi-colored categories were observed for the fruits and seeds studied. The single-colored categories identified were: beige, black, blue, brown, green, orange, pink, red, white, yellow, and purple-black. Black was the most common color of the bi-colored fruits and seeds, and brown, white, yellow and red occurred in the following combinations: white+black, black+yellow, and green+red in fruits, and black+red, black+yellow, brown+white, brown+yellow, and white+black in seeds. Many fleshy indehiscent and dehiscent fruits were bi-colored. For example, the white+black drupes of *Tournefourtia volubilis*, and the fleshy, dehiscent fruits of *Capparis flexuosa*, with their external green and internal red surfaces contrasting with the black and white seed colors. Bi-colored patterns were mainly found on the seed coats, for example the red+black seed coat and aril of *Erythrina mitis,* and the black seed coat and yellow aril of *Connarus venezuelensis*.

The number and frequencies of the fruit and seed colors identified are given in Table 2. Fruits (N≥10 and ≥10%) were mostly brown (N= 644, 56.5%) followed by purple-black (N= 125, 11.0%) and black (N= 95, 8.3%). Seeds tended to be brown (N=666, 58.5%), beige (N= 185, 16.4%) or black (N= 136, 11.9%). The lowest frequencies of single-colored fruits / seeds were bright (orange and pink), light (white and beige) and dark (blue) fruits (0.7-1.5%), and dark (green and blue) and bright (orange and red) seeds (0.2-1.8%). All categories of bi-colored fruits / seeds occurred at the same or lower frequencies than categories of single-colored fruits / seeds. The number of bi-colored categories of fruits and seeds also differed with fruits showing three different bi-colored combinations, and seeds five different combinations.

3. Associations between fruit and seed colors

The fruit and seed color comparison analysis revealed large variations in the colors of the fruits and seeds (Figure 2), as well as within-species differences between fruit and seed color, except that plants with brown fruits tended to produce brown seeds (N= 470, 72.9%). Nevertheless, species with brown fruits were also associated with nine other seed colors, the most abundant and frequent (N≥10 and ≥10%) being black and beige (Appendix S2). Brown was also the most common seed color for purple-black, yellow, red, and green fruits. In



Figure 1. Fruits of some studied species ordered by family. **Acanthaceae**: (A) *Ruellia tuberosa* L. **Apocynaceae:** (B) *Calotropis gigantea* (L.) Dryand. in W.T. Aiton. **Aquifoliaceae:** (C) *Ilex subrotundifolia* Steyermark. **Bignoniaceae:** (D) *Tecoma stans* (L.) Juss. ex Kunth. **Bixaceae:** (E) *Cochlospermum vitifolium* (Willd.) Sprengel. **Boraginaceae:** (F) *Cordia dentata* Poir. **Brassicaceae:** (G) *Draba chionophila* S.F. Blake. **Bromeliaceae:** (H) *Tillandsia recurvata* (L.) L. **Cactaceae:** (I) *Cereus hexagonus* (L.) Mill.; (J) *Pilosocereus lanuginosus* (L.) Byles & G.D. Rowley. **Campanulaceae:** (K) *Siphocampylus reticulatus* (Willd. ex Schult.) Klotzsch & H. Karst. ex Vatke. **Capparaceae:** (L) *Capparis hastata* Jacq. **Clusiaceae**: (M) *Clusia pusilla* Steyerm. ssp. *pusilla*. **Combretaceae:** (N) *Laguncularia racemosa* (L.) C.F. Gaertn. **Convolvulaceae:** (O) *Ipomoea pes-caprae* (L.) R. Br.; (P) *Operculina alata* Urb. **Crassulaceae**: (Q) *Kalanchoe pinnata* (Lam.) Pers. **Cucurbitaceae**: (R) *Cucumis dipsaceus* Ehrenb. ex Spach. **Euphorbiaceae**: (S) *Chamaesyce dioeca* (Kunth) Millsp.; (T) *Cnidoscolus urens* (L.) Arthur; (U) *Hura crepitans* L. **Fabaceae:** (V) *Abrus precatorius* L.; (W) *Lupinus meridanus* Moritz ex C. P. Smith; (X) *Macroptilium atropurpureum* (Moc. & Sessé ex DC.) Urb; (Y) Pithecellobium unguis-cati (L.) Benth.; (Z) *Pterocarpus acapulcensis* Rose. **Heliconiaceae:** (AA) *Heliconia bihai* (L.) L. **Lecythidaceae:** (AB) *Couroupita guianensis* Aubl. **Loranthaceae:** (AC) Phthirusa stelis (L.) Kuijt. **Malvaceae:** (AD) *Ceiba pentandra* (L.) Gaertn.; (AE) *Thespesia populnea* (L.) Sol. ex Corrêa. **Onagraceae:** (AF) *Ludwigia octovalvis* (Jacq.) Hara. **Orquidaceae:** (AG) *Epidendrum secundum* Jacq. **Passifloraceae:** (AH) *Passiflora foetida* var. *hispida* (DC. ex Triana & Planch.) Killip. **Pentaphylacaceae:** (AI) *Ternstroemia crassifolia* Benth. **Phyllanthaceae:** (AJ) *Margaritaria nobilis* L. f. **Phytolaccaceae:** (AK) *Phytolacca icosandra* L.; (AL) *Rivina humilis* L. **Polygonaceae:** (AM) *Coccoloba uvifera* (L.) L. **Portulacaceae:** (AN) *Portulaca oleracea* L. **Salicaceae:** (AO) *Hecatostemon completus* (Jacq.) Sleumer. **Sapindaceae:** (AP) *Urvillea ulmacea* Kunth. **Zygophillaceae:** (AQ) *Guaiacum officinale* L.; (AR) *Tribulus cistoides* L. **Photographers and photographies**: J. Delgado (A, B, D, E, H), J. Grande (C, F, I, K, M, O, P, Q, U, W, X, Y, Z, AA, AB, AC, AD, AG, AH, AI, AL, AQ, AR), G. Colonnello (AJ), H. Briceño (G, AK), C. Aranguren (J), Y. Barrios (L, S, AE, AF, AM, AN, AO, AP), A. Villareal (N), K. Garcia (R) y B. Gil (T, V).

addition, beige seeds were most commonly found with black, brown, green, purple-black, red, white or yellow fruits (Appendix S2); black seeds were associated with brown or green fruits; and white seeds were most frequently found with black fruits. The fruit and seed color arrangements of some dehiscent fruits produced some bi-colored fruit-seed structures, such that some fruits contained bright seeds and/or a bright internal surface. These types of combinations were mainly found in dry-dehiscent fruits (e.g. *Abarema ferruginea*) and fleshy-dehiscent fruits (e.g. *Capparis flexuosa, Clusia pusilla*).

The bipartite network analysis showed 71 different associations (links) between fruit and seed colors, representing 39% of the total possible number of links (Table 3). The fruit color/seed color class ratio and the seed color/fruit color class ratio were both close to one. In contrast, the mean number of associations per fruit color and the mean number of associations per seed color were both slightly higher than 5.0.

4. Morphological fruit types and fruit and seed colors

4.1 The texture and dehiscence of fruits vs. fruit and seed colors

Fruit colors could be associated with structural fruit types such that most of the dry fruits were brown or black, whereas most of the fleshy fruits were purple-blacks, yellows or reds (Table 2). Comparisons between dry and fleshy fruits according to color categories showed that brown, black, and beige fruits were more often dry than fleshy. In contrast, the number of fleshy fruits that were purple-black, yellow, red, white, and blue was higher than the number of dry fruits with those colors. The most abundant fruit color was brown for both dehiscent and indehiscent fruits. Purple-black, black, yellow, and red were also common colors for indehiscent fruits. The statistical comparisons with

Table 2. Relationship between structural fruit types and fruit and seed colors. Asterisk indicates the significant frequency (P<0.05) between dry and fleshy and between dehiscent and indehiscent fruits or seeds of the same color.

Fruit and seed colors	Structural fruit types				Total
	Texture		Dehiscence		
	Dry	Fleshy	Dehiscent	Indehiscent	
	N(%)	N(%)	N(%)	N(%)	N(%)
Fruit Color					
Beige	14(100.0)*	0(0.0)	5(35.7)	9(64.3)	14(1.2)
Black	95(100.0)*	0(0.0)	3(3.2)	92(96.8)*	95(8.3)
Black+Yellow	0(0.0)	1(100.0)	0(0.0)	1(100.0)	1(0.001)
Blue	0(0.0)	10(100.0)*	0(0.0)	10(100.0)*	10(0.87)
Brown	617(95.8)*	27(4.2)	427(66.3)*	217(33.7)	644(56.54)
Green	35(48.0)	38(52.0)	28(38.4)	45(61.6)	73(6.41)
Green+Red	6(46.2)	7(53.8)	10(76.9)*	3(23.1)	13(1.14)
Orange	4(40.0)	6(60.0)	4(40.0)	6(60.0)	10(0.87)
Pink	0(0.0)	8(100.0)	2(25.0)	6(75.0)	8(0.70)
Purple-Black	5(4.0)	120(96.0)*	2(1.6)	123(98.4)*	125(10.97)
Red	5(8.0)	52(91.2)*	9(15.8)	48(84.2)*	57(5.00)
White	4(23.5)	13(76.5)*	2(11.8)	15(88.2)*	17(1.49)
White+Black	0(0.0)	1(100.0)	0(0.0)	1(100.0)	1(0.001)
Yellow	5(7.0)	66(93.0)*	7(9.9)	64(90.1)*	71(6.23)
Seed Color					
Beige	118(63.8)	67(36.2)	21(11.3)	164(88.7)*	185(16.24)
Black	93(68.4)	43(31.6)	81(59.6)	55(40.4)	136(11.94)
Black+Red	8(100.0)	0(0.0)	8(100.0)	0(0.0)	8(0.70)
Black+Yellow	1(25.0)	3(75.0)	1(25.0)	3(75.0)	4(0.35)
Blue	3(100.0)	0(0.0)	3(100.0)	0(0.0)	3(0.26)
Brown	480(72.1)*	186(27.9)	346(51.9)	320(48.1)	666(58.47)
Brown+White	1(50.0)	1(50.0)	2(100.0)	0(0.0)	2(0.17)
Brown+Yellow	1(33.3)	2(66.7)	2(66.7)	1(33.3)	3(0.26)
Green	2(10.0)	18(90.0)*	1(5.0)	19(95.0)*	20(1.76)
Orange	2(13.3)	13(86.7)*	14(93.3)*	1(6.7)	15(1.32)
Red	2(33.3)	4(66.7)	4(66.7)	2(33.3)	6(0.53)
White	68(89.5)*	8(10.5)	1(1.3)	75(96.7)*	76(6.67)
White+Black	11(73.3)*	4(26.7)	15(100.0)*	0(0.0)	15(1.32)
Total ssp.	790(69.4)*	349(30.6)	499(43.8)	640(56.2)	1139

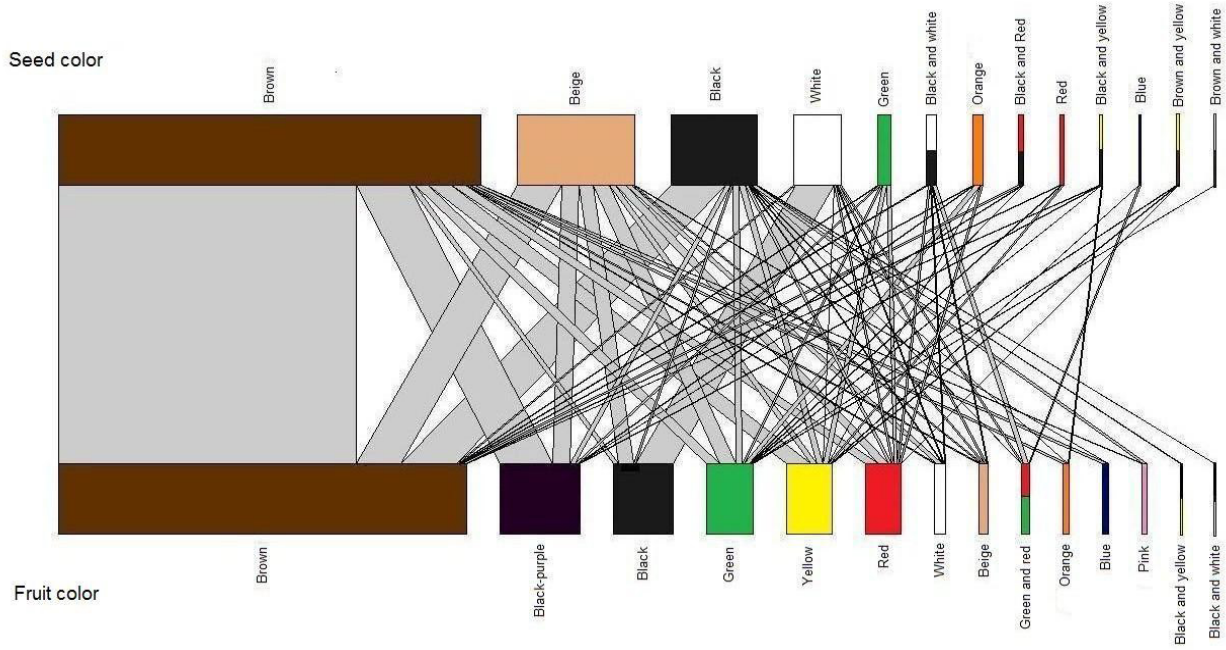


Figure 2. Bipartite graph showing the links between fruit and seed colors.

Table 3. Morphological fruit types, fruit colors, and seed colors web parameters determined in the sample examined.

Fruit type vs. fruit color	Number of fruit types	Number of fruit color classes	All possible associations	Number of associations recorded (connectance)	Number of fruit types / number of fruit color classes ratio	Number of fruit color classes/ number of fruit types ratio	Mean number of associations recorded per fruit color	Mean number of associations recorded per fruit type
Grey fruits	28	14	392	97 (24.7)	2.00	0.50	6.93	3.46
Spjut fruits	55	14	770	144(18.7)	3.93	0.25	10.29	2.62
Fruit type vs. seed color	Number of fruit types	Number of seed color classes	All possible associations	Number of associations recorded (connectance)	Number of fruit types / number of seed color classes ratio	Number of seed color classes/ number of fruit types ratio	Mean number of associations recorded per seed color	Mean number of associations recorded per fruit type
Gray fruits	28	13	364	91(25.0)	2.15	0.46	7.00	3.25
Spjut fruits	55	13	715	140(19.6)	4.23	0.24	10.77	2.55
Fruit color classes vs. seed color classes	Number of fruit color classes	Number of seed color classes	All possible associations	Number of associations recorded (connectance)	Number of fruit color classes/ number of seed color classes ratio	Number of seed color classes/ number of fruit color classes ratio	Mean number of associations recorded per seed color classes	Mean number of associations recorded per fruit color classes
	14	13	182	71(39.0)	1.08	0.93	5.46	5.07

regard to the colors of dehiscent and indehiscent fruits showed that dehiscent fruits were most frequently brown and green+red, whereas indehiscent fruits were more likely to be purple-black, black, yellow, red, white, or blue (Table 2).

The most common seed colors were brown, beige, black, or white for dry fruits, and brown, beige, or black for fleshy fruits (Table 2). The statistical comparisons done between the seed colors of dry and fleshy fruits showed that a significantly higher proportion of dry fruits have brown, white or white+black seeds compared to fleshy fruits, and more fleshy fruits contain green or orange seeds than dry fruits. The analysis of the seed colors of dehiscent and indehiscent fruits revealed that dehiscent fruits were significantly more likely to contain orange or white+black seeds than indehiscent fruits, and indehiscent fruits were more likely to contain beige, white, or green seeds compared to dehiscent fruits.

4.2 Gray and Spjut fruit types and fruit colors

We found several major associations between morphological fruit types (I and II) and fruit colors (Appendix S1). The most common fruit color was brown for a large number of the morphological fruit types classified according to Gray's (1877) system (Figure 3). Fourteen of these morphological fruit types were represented by more than ten plant species (e.g. loculicidal capsule, followed by schizocarp, legume, and septicidal capsule) and some fruit types were exclusively brown (e.g. craspedium, loment, and samara). Achenes were well represented and predominantly black. As regards fleshy fruits, drupes and berries, more than twenty species of each of these fruit types were either purple-black, red or yellow. Brown was also the most common fruit color for morphological fruit types following Spjut (1994). Eleven brown colored fruit types were represented by more than ten plant species (e.g. loculicidal capsule, legume, and septicidal capsule, coccarium and ceratium) and some fruit types were exclusively brown (e.g. craspedium, loment, samara, and samarium). Cypselas were very abundant and predominantly black (Figure 4). As for the Gray (1877) classification system, fleshy fruits, drupes and baccas following Spjut (1994) were predominantly purple-black, red or yellow.

The bi-partite network analysis of the morphological fruit types according to Gray *vs* fruit colors revealed 97 different links, representing 24.7% of the total possible number (Table 3). The ratio between morphological fruit types and fruit color classes was four times higher than the ratio between fruit color classes and morphological type I fruits. The mean number of associations per fruit color was approximately twice the mean number of associations per morphological type I fruit. The relationship between the morphological fruit types according to Spjut and fruit colors showed comparable patterns (Table 3). However, there were 144 bi-partite network links between the Spjut morphological fruit types and fruit colors, representing 18.7% of the total possible number. The ratio between the morphological type II fruits and fruit color classes were much higher than the ratio between the fruit color classes and the morphological type II fruits. The mean number of associations per fruit color was approximately four times the mean number of associations per morphological fruit type.

The majority of fruit types (I and II) were associated with only one color (Figure 5). Nevertheless, a large proportion of the Spjut morphological fruit types were also associated with two fruit colors, and a few fruit types (both I and II) were associated with more than seven fruit colors (Figure 5).

The most common fruit types were associated with the same color categories, independent of the classification system used (I or II) (e.g. capsules and brown, schizocarps and brown, legumes and brown, and achenes and black). In other cases, asymmetrical associations as regards the level of specialization were recorded, whereby less common morphological fruit types (less than 1.0% of the total) tended to be associated with the most frequent fruit color classes. (See Figures 3 and 4). Asymmetry at the level of specialization was also observed between the least common fruit colors and the most common morphological fruit types (I and II). Thus, the lowest fruit color frequencies (white, beige, blue, orange, pink and bi-colored) were associated with the well-represented fruit types: capsule, berry and drupe (Figures 3 and 4).

4.3 Gray and Spjut fruit types and seed colors

According to Gray's classification system, twelve well-represented fruit types (N≥10; ≥10%) had brown seeds (Appendix S3). Most plant species with brown seeds showed the following fruit types: berry,

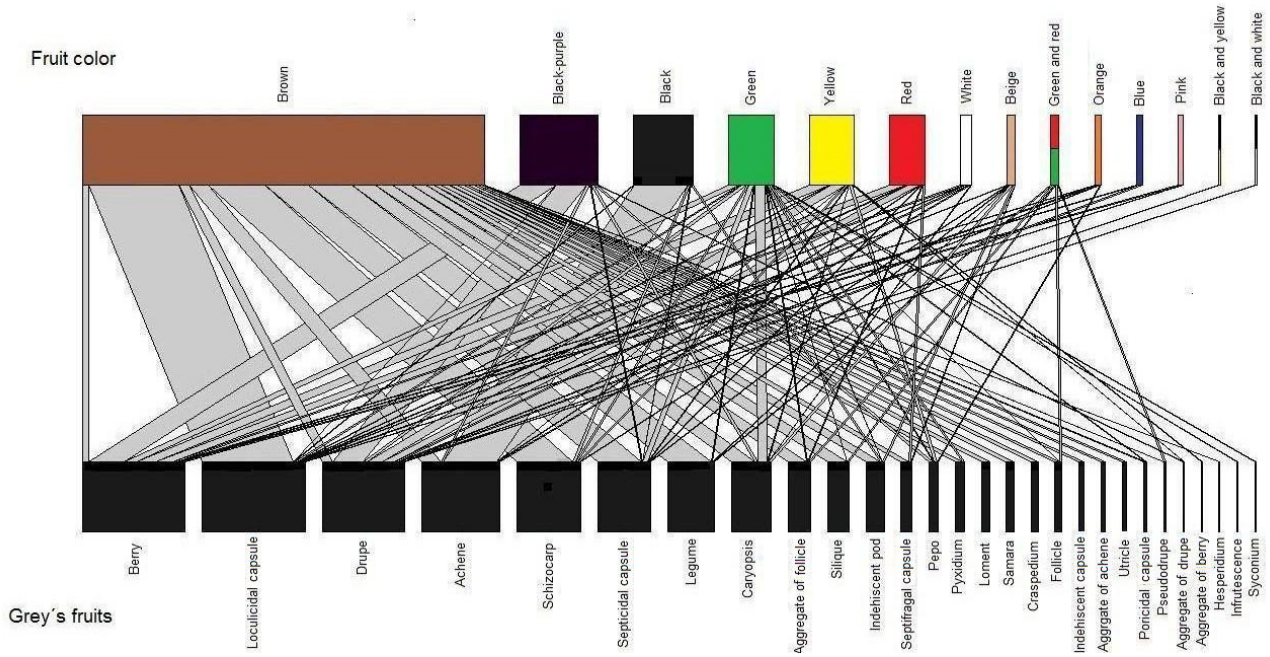


Figure 3. Bipartite graph showing the links between morphological fruit types according to Gray and fruit colors.

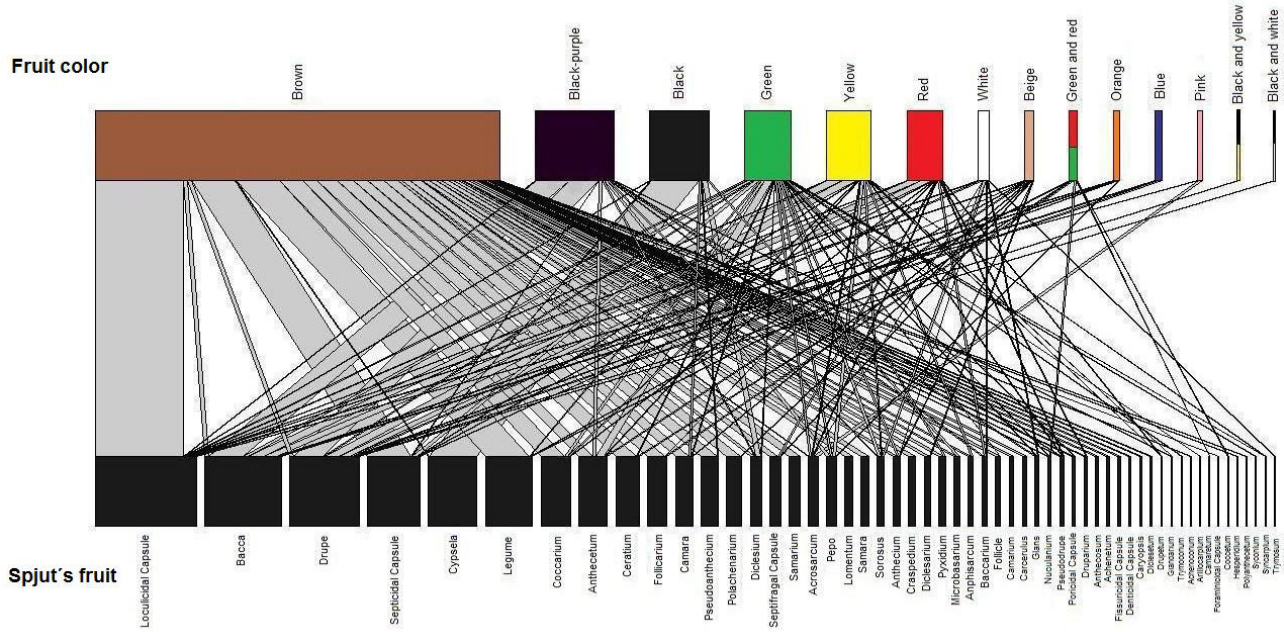


Figure 4. Bipartite graph showing the links between morphological fruit types according to Spjut and fruit colors.

schizocarp, loculicidal capsule, drupe, septicidal capsule and legume (Figure 6), and some fruit types always contained brown seeds (samara, craspedium and loment). A high number of plant species with caryopsis, drupe and berry morphological fruit types had beige seeds and a high number of achenes contained beige or white seeds. In contrast, a large number of loculicidal capsules and berries contained black seeds. The most frequent seed color associated with the morphological fruit types according to Spjut was brown followed by beige. Brown seeds were more numerous and frequent in loculicidal capsule, bacca, drupe, and legume, followed by coccarium and ceratium fruit types (Figure 7). Many plant species encompassing six morphological fruit types contained beige seeds; the highest numbers and percentages of these was found in anthecetum and pseudoanthecium fruit types, and some (samara, craspedium and loment) fruit types had exclusively brown seeds

The bi-partite network analysis used to determine the associations (or links) between morphological type I fruits (Gray's classification) and seed colors revealed 91 different links, representing 25.0% of the total possible number (Table 3). The ratio between the morphological fruit types and seed color classes was more than four times higher than the ratio between seed color classes and morphological type I fruits. The mean number of associations per seed color was more than twice the mean number of associations per morphological type I fruit. The same

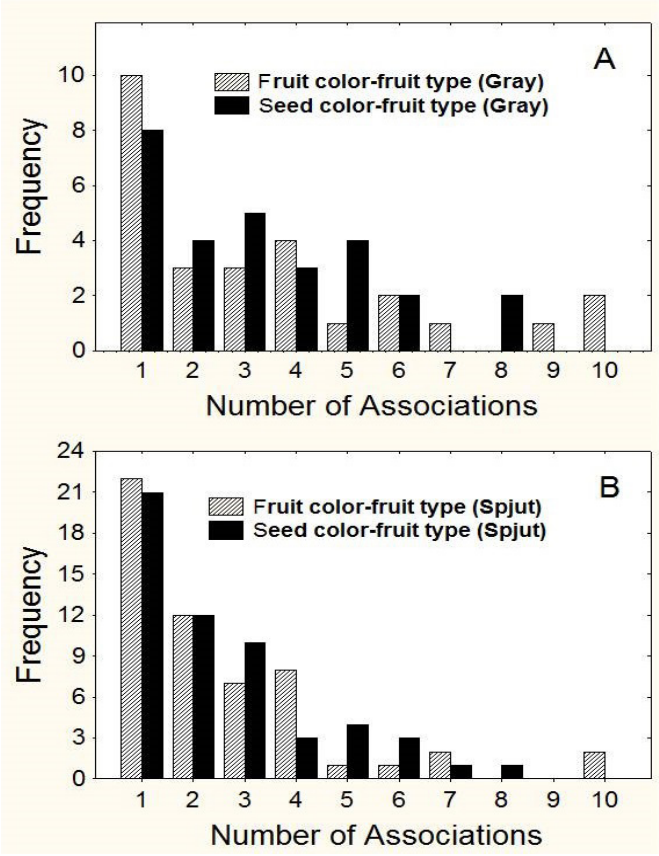


Figure 5. Frequency distributions of the number of associations of fruit types with fruit and seed colors for both Gray's (A) and Spjut's (B) classification systems.

analysis done for the morphological fruit types following Spjut and seed colors gave 140 different links, representing 19.6% of the total possible number. The ratio between morphological type II fruits and seed color classes was much higher than the ratio between seed color classes and morphological type II fruits. The mean number of associations per seed color class was more than four times the mean number of associations per morphological type II fruit.

Most fruit types (I and II) were associated with one seed color (Figure 5), however, twelve type II fruits were associated with two seed colors and a few fruit types (I and II) were associated with eight seed colors (Figure 5). Many links were also asymmetrical as regards the level of specialization, whereby the less common morphological type I and II fruits (less than 1.0%) tended to be associated with the most common seed color classes (See Figures 6 and 7). Asymmetry at the level of specialization was also observed between the less common seed colors and the most common morphological fruit types (I and II) as follows: green, orange, red, blue and bi-colored seeds were associated with the best-represented fruit types (e.g. capsule, berry, drupe, and legume) (Figures 6 and 7).

5. *Morphological fruit types and functional groups*

5.1 *The texture and dehiscence of fruits and functional groups*

Fruit texture was significantly associated with life form, successional stage, nutritional relationship, carbon metabolism pathway, and fruit phenology (Table 4). Residual analyses indicated strong correlations between fleshy fruits and shrubs, and between dry fruits and annual herbs; and unusual occurrences between dry fruits and shrubs, and between fleshy fruits and herbaceous species. Similarly, fleshy fruits were strongly associated with late seral species, and there was an unusual occurrence between fleshy fruits and pioneer species. Fleshy fruits were also tightly linked to parasitic and hemiparasitic species; C_4 species positively correlated with dry fruits and negatively with fleshy fruits; and fruit dehiscence was significantly associated with life form, nutritional relationship, carbon metabolism pathway, succulence, epiphytism and ripe fruit phenology (Table 4). Dehiscent and indehiscent fruits were similarly represented in herbaceous species, but indehiscent fruits were more common in trees, shrubs, and lianas. The fruits of parasitic and hemiparasitic species were also mostly indehiscent and matched the frequency of fleshy fruited species. All insectivorous species had dehiscent fruits which corresponded with dry-fruited species. Dehiscent fruits were more abundant than indehiscent fruits for CAM species. In contrast, C_4 species had predominantly indehiscent fruits, and significantly unusual dehiscent fruits. Dehiscent fruits were found more often than indehiscent fruits in succulent species, and the opposite was true for non-succulents. Epiphytism was found to be independent of fruit texture, although epiphytes had predominantly dry fruits. Dehiscent fruits were found significantly more often than indehiscent fruits in epiphytic species, and indehiscent fruits were not generally associated with epiphytism. Both ripe and unripe fruit phenology was significantly associated with fruit texture, whereby fleshy-fruited species were positively associated with the rainy season and an uncommon occurrence of unripe and ripe fleshy-fruited species was observed during the dry season. Ripe and unripe fruit phenologies of dry-fruited species were positively associated with the dry season and unusual during the rainy season. Only ripe fruit phenology was significant for fruit dehiscence: plant species with indehiscent fruits tended to produce mature fruits during the rainy season (Table 4).

5.2 *Gray and Spjut fruit types and functional groups*

The frequency of fruit types (I and II) for each functional group can be seen in Appendix S4. The analysis of the relationships between morphological type I fruits and life forms showed that the most frequent fruit types in trees were berry, drupe, legume and indehiscent pod; for shrubs: berry and drupe; lianas: pepo; perennial herbs: achene, berry, loculicidal capsule, septicidal capsule, caryopsis, and schizocarp; and annual herbs: achene, loculicidal capsule, caryopsis, and schizocarp. Similarly, the analysis of the relationships between morphological type II fruits and life forms showed that the most frequent fruit types for trees were bacca, camara, and drupe; for shrubs: bacca and drupe; lianas: pepo, samarium and septifragal capsule; perennial herbs: anthecetum, cypsela, loculicidal capsule, pseudoanthecium, and septicidal capsule; and annual herbs: cypsela and loculicidal capsule (Appendix S4). The most frequent fruit types were berry, loculicidal capsule, septicidal capsule, and drupe in late seral species; and achene, caryopsis, schizocarp, and legume in pioneer species. The most numerous and frequent type II fruits were bacca, camara, ceratium, drupe, loculicidal capsule, and septicidal capsule for late seral species; and anthecetum, cypsela, legume, polachenarium, and septifragal capsule for pioneer species (Appendix S4). Both fruit types (I and II) were predominantly associated with autotrophic plants. C_3 species were associated with almost all fruit types when type I fruits and carbon metabolism pathways

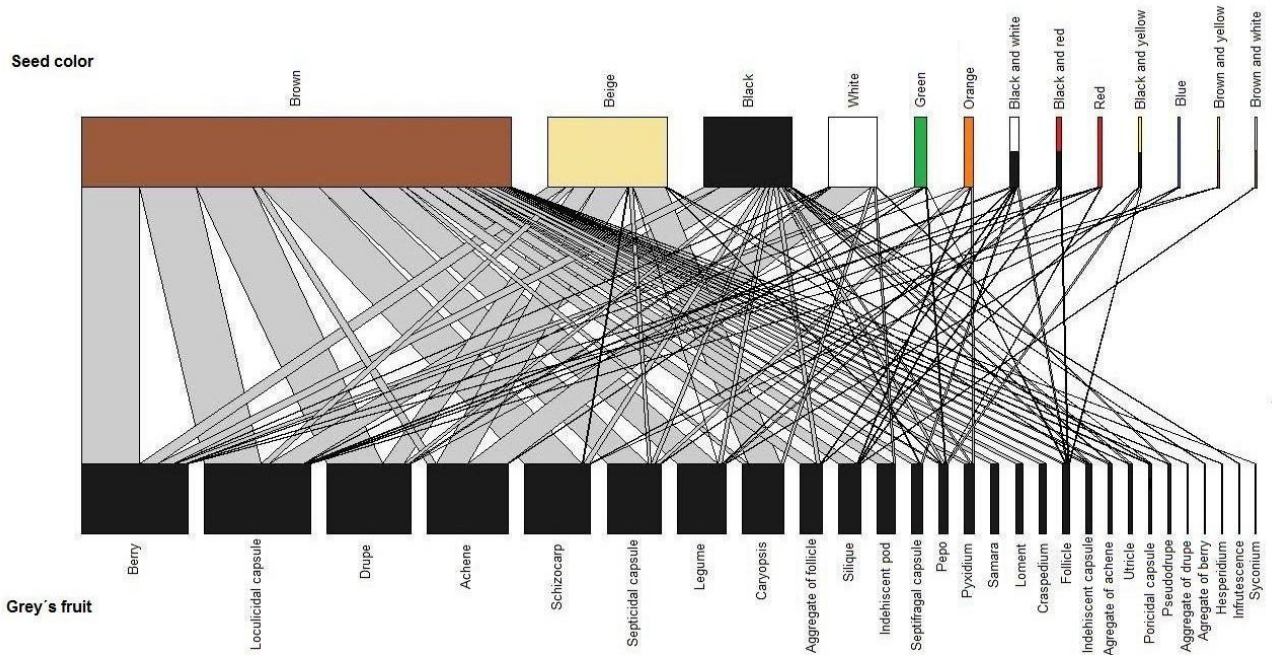


Figure 6. Bipartite graph showing the links between morphological fruit types according to Gray and seed colors.

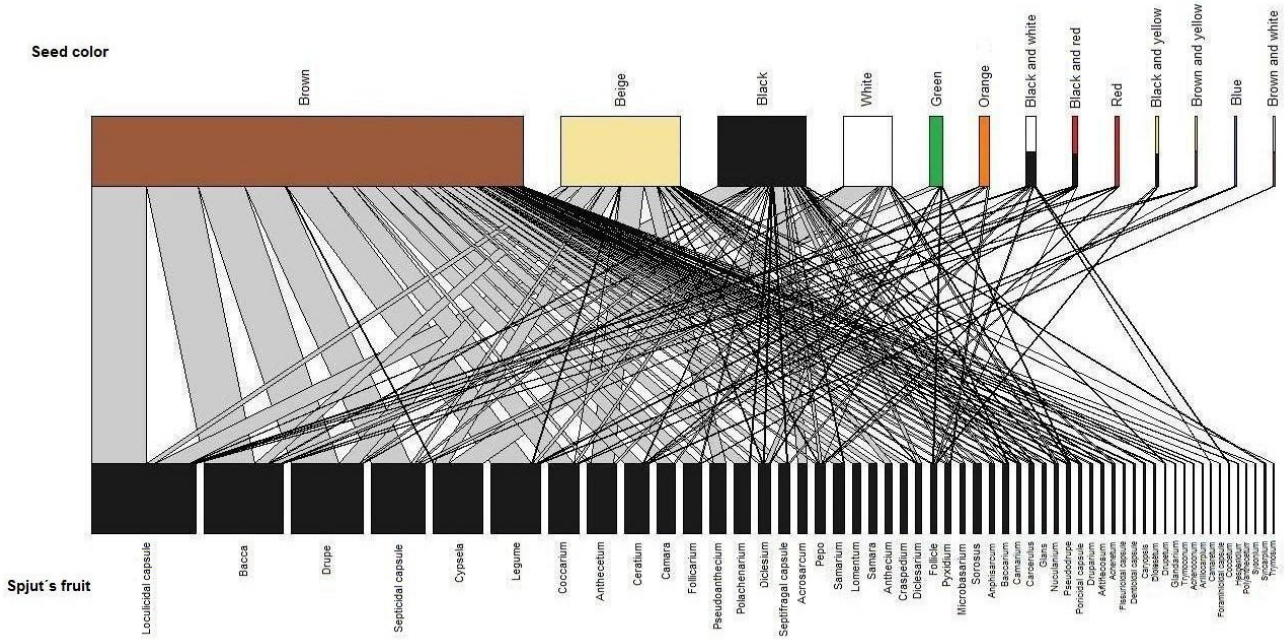


Figure 7. Bipartite graph showing the links between morphological fruit types according to Spjut and seed colors.

were compared. However, caryopsis and utricle fruit types from Gray's system, and anthecetum and pseudoanthecium fruit types from Spjut's system were mostly C_4 species. In addition, many succulents and CAM species produced acrosarcum fruit types. Nonetheless, in general, the most abundant and frequent fruit types I and II were associated with non-succulent species. Septicidal capsule was the main morphological fruit type found in epiphytes (Appendix S4).

Seasonality in unripe and ripe fruit phenology during the transition period between the rainy and dry seasons was recorded for the most abundant morphological type I (e.g. achene, berry, drupe, loculicidal capsule, and schizocarp) and type II (e.g. bacca, drupe, loculicidal capsule, and septicidal capsule) fruits. A few plant species tended to produce more unripe fruits during the rainy season: caryopsis and silique following Gray's classification and anthecetum, ceratium and coccarium, according to Spjut's classification (Appendix S4). Other species tended to produce ripe fruits during the rainy season: drupes and siliques (Gray's classification), and drupes (Spjut's classification). In contrast, samara and samarium fruit types mainly ripened during the dry season.

6. *Fruit and seed colors and functional groups*

The number and percentage of the fruit and seed colors studied, and their frequencies according to the functional groups identified are shown

Table 4. Relationship between structural fruit types and functional groups

Functional group	Fruit Structural Types				
	Texture		Dehiscence		
	Dry	Fleshy	Dehiscent	Indehiscent	Total
	N(%)	N(%)	N(%)	N(%)	N
Life form					
Tree	109(57.98)	79(42.02)	74(39.36)	114(60.64)	188
Shrub	77(36.49)[d]	134(63.21)[a]	71(33.65)	140(66.35)	211
Liana	49(37.12)	83(62.88)	56(42.42)	76(57.58)	132
Perennial herb	346(81.60)	78(18.402)[d]	206(48.58)	218(51.42)	424
Annual herb	175(95.11)[b]	9(4.89)[d]	92(50.00)	92(50.00)	184
χ2 (P=)	209.5 (0.0000)		17.7 (0.0014)		
Successional condition					
Late seral	334(59.75)	225(40.25)[b]	258(46.15)	301(53.85)	559
Pioneer	456(78.62)	124(21.38)[d]	241(41.55)	339(58.45)	580
χ2 (P=)	48.3 (0.0000)		2.01(N.S.)		
Nutritional relation					
Autotrophe	779 (70.05)	333(29.94)	488(43.88)	624(56.11)	1112
Parasite-Hemiparasite	3(15.79)	16(84.21)[b]	3(15.79)	16(84.21)	19
Insectivore	8(100.00)	0(0.0)	8(100.00)	0(0.0)	8
χ2 (P=)	29.73 (0.0000)		16.3(0.0003)		
Carbon metabolism					
C3	668(67.34)	324(32.66)	447(45.06)	545(54.94)	992
C4	85(97.70)[b]	2(2.30)[d]	12(13.79)[b]	75(86.21)[a]	87
CAM	36(61.02)	23(38.98)	39(66,10)	20(33.90)	59
χ2 (P=)	36.7 (0.0000)		45.9 (0.0000)		
Succulence					
Succulent	773(63.48)	42(36.52)	61(53.04)	54(46.96)	115
Non-succulent	717(70.02)	307(29.98)	438(42.77)	586(57.23)	1024
χ2 (P=)	0.4 (N.S.)		6.7 (0.0094)		
Epiphytism					
Epiphyte	21(84.00)	4(16.00)	22(88.00)[b]	3(12.00)[c]	25
Non-Epiphyte	769(69.03)	345(30.97)	477(42.82)	637(57.18)	1114
χ2 (P=)	2.6 (N.S)		20.3(0.0000)		
Unripe fruit phenology					
Rainy	117(58.5)	83(41.5)[a]	87(43.5)	113(56.5)	200
Dry	57(89.1)	7(10.9)[c]	38(59.4)	26(40.6)	64
Rainy-dry	372(70.9)	153(29.1)	239(45.5)	286(54.5)	525
χ2 (P=)	23.3 (0.000009)		5.2 (N.S.)		
Ripe fruit phenology					
Rainy	101(48.6)[d]	107(51.4)[b]	83(39.9)	125(60.1)	208
Dry	134(88.7)[a]	17(11.3)[d]	82(54.3)	69(45.7)	151
Rainy-dry	306(72.0)	119(28.0)	196(46.1)	229(53.9)	425
χ2 (P=)	69.9 (0.000000)		7.3 (0.025930)		

Superscript indicates significance residual analysis: a = positive residual at P<0.05 b = Positive residual at P<0.01; c = negative residual at P<0.05; d = Negative residual at P<0.01

in Appendix S4. The most common colors (N>10; ≥10%) were brown and purple-black for fruits, and brown, beige, and black for seeds. The relationships between fruit colors and life forms showed that the most frequent colors were brown, green or yellow for trees; purple-black or red for shrubs; and black or brown for perennial and annual herbs. The main fruit colors that could be associated with the successional stage were brown or purple-black for both pioneer and late seral stage species. In addition, black fruits were significantly correlated with pioneer species, and green or yellow fruits with late seral species. Most autotrophs, C_3 and non-succulent species had single-colored fruits; pink fruits were common for CAM and succulent species; and brown was the most frequent color for the fruits and seeds of epiphytes.

Brown was the most common seed color for species in all the life forms studied. Nevertheless, the most frequent seed colors were orange and white+black for trees; orange and beige for shrubs; beige, black, green, and white for perennial herbs; and white for annual herbs. Brown, beige and black were the most abundant and frequent seed colors for both pioneer and late seral species. However, white seeds were also significantly associated with pioneer species, and green and orange seeds with late seral species. Autotrophs, C_3 and non-succulent species generally had single-colored seeds, and green seeds were common in parasitic and hemiparasitic (mistletoe) species (Appendix S4). Fruit and seed colors exhibited some trends according to fruit phenology (Appendix S4). Unripe and ripe fruits produced during the rainy-dry transition period were often black, brown, green, or purple-black. Unripe red or yellow fruits were also produced during this period. However, ripe red or yellow fruits were most common during the rainy season. Beige, black, brown, green, orange, and white were the most abundant seed colors during the rainy-dry transition period.

Discussion

1. Morphological fruit types

A first analysis of fruit structures indicates that texture and dehiscence are closely related. Dehiscence is an attribute largely associated with dry tissues adapted to fruit opening by the desiccation of the fibers. Nonetheless, dehiscence was also found in a few fleshy fruits (e.g. *Clusia* spp.). The pericarp of dehiscent fruits protects seeds until dehiscence and may also be involved in dispersion during fruit opening, after which seed protection and dispersal is determined exclusively by seed attributes. In contrast, indehiscence is an attribute associated with both dry and fleshy fruits, and principally involves fruit adaptations related to enclosure of the seeds, although it is also associated with a variety of reproductive and ecological functions (Cippollini & Stiles 1992, Mack 2000). Dry-indehiscent fruits may be primarily adapted for seed defense from animals and parasites by means of the hard fibrous cover which acts as a shield (Bodmer 1991, Doster & Michailides 1999). Nevertheless, the high diversity of modifications of the pericarp and anthocarp in indehiscent fruits also reflects adaptations to seed dispersal (e.g. Mamut et al. 2014). The ratio of species with dry fruits to those with fleshy fruits has been found to be similar in tree species from Southern Africa (Knight & Siegfried 1983). Many other studies, however, have shown that species with dry fruits outnumber those with fleshy fruits in varying proportions (Gordon 1998, Silva & Rodal 2009, Silva et al. 2013, Possete et al. 2015) including in our survey where the number of species with dry fruits was more than twice the number with fleshy fruits. A phylogenetic study revealed that the majority of plant families produce dry fruits (Fleming 1991). Thus, the high frequency of species with dry fruits observed seems to agree with expected ratio for fruit texture types.

The most abundant fruit types found in the samples studied were loculicidal capsules, berries (baccas), drupes and achenes. This agrees with previous studies which also note that capsules tend to be the main fruit type in the forest-shrub ecosystem (Arbeláez & Parrado-Rosselli 2005), although berries and drupes may be dominant in some rain forests (Carpenter et al. 2003, Chen et al. 2004, Ibarra-Manríquez & Cornejo-Tenorio 2010, Buitrón-Jurado & Ramírez 2014). Thus, the relative frequencies of morphological fruit types seem to vary according to ecological attributes. Nevertheless, the influence of the phylogenetic component is also significant as the majority of plant families produce dry fruits (Fleming 1991, Heywood et al. 2007, Fleming and Kress 2011), and in some cases the relationships between fruit types, seed dispersal strategies and vegetation life forms have been best explained by angiosperm phylogeny (Kuhlmann & Ribeiro 2016). The frequencies of fruit type we observed could thus also be influenced by the taxonomic composition of the samples, in which species from the Fabales, Malphigiales and Poales orders, and the Fabaceae family were overrepresented (N. Ramírez & H. Briceño, in preparation), and contributed significantly to the abundance of dry-dehiscent and dry-indehiscent fruits. Nonetheless, the most dominant orders and families in the sample we examined formed a different group to that of "most frequent fruit types". Hence we did not consider the phylogeny of the plant species as a major factor in our analysis.

The classification systems of Gray (1877) and Spjut (1994) coincided in many areas as regards nomenclature and the general morphology of the fruit types studied (i.e. berries, loculicidal capsules, drupes, septicidal capsules, legumes, and siliques). Most of the similarities between the two systems are for simple fruits (fruit not dispersed from the pericarpium; developing from one flower) and rhexocarpic fruits (fruit dispersed by the opening of the pericarp). This is because the differences in the fruit types according to each system mostly refer to anthocarp structure (see Spjut 1994), which may thus be considered as the main source of adaptations related to functional groups.

2. Fruit and seed colors

Eleven single-colored and seven bi-colored categories were found in the samples studied; fruits were predominantly dark in color (brown, purple-black or black) whereas seeds could be either dark or light (brown, beige, black or white). The similarity in both the number and classes of fruit and seed colors may reflect well-adjusted color arrangements between fruits and seeds. Fruit/seed color and seed/fruit color ratios were both close to one, suggesting that the relative frequencies of fruit and seed colors are finely balanced. Likewise, the high diversity of links between fruit and seed colors, and between seed and fruit colors showed many similarities and multiple combinations. Fruit and seed color associations revealed a large proportion of linkages (39%), whereby the most common colors were preferentially associated with each other, and the less frequent colors were usually associated with those that were well represented. Specifically, the four seed color categories with the highest frequencies (brown, beige, black, and white) were generally associated with the most common fruit colors (brown,

purple-black, and black). Preliminary findings from the complex networks analysis suggest that the associations between fruit and seed colors form three modules: 1- black fruits and white seeds; 2- brown fruits, and brown or black seeds; and 3- purple-black fruits and beige seeds (Y. Barrios unpubl. results). However, brown fruits with brown seeds were the only really significant combination (72.9%), and were mainly associated with dry-dehiscent fruits. In addition, brown fruits and beige seeds stood out as module hubs within the network (Y. Barrios unpubl. results), and thus represent highly connected nodes linked to many other nodes within their own module (Olesen et al. 2007). Additional analyses showed that this network was symmetrical according to the levels of specialization of the fruit and seed color categories, and was characterized by specificity indexes with low averages for both fruit and seed colors (Y. Barrios unpubl. results).

The least common color categories for single-colored fruits were white, beige, blue, orange, and pink, and for single-colored seeds, green, orange, red and blue. Thus, blue and orange coincided in that they showed some of the lowest frequencies for both fruits and seeds. Further relationships recorded between the relative frequencies of fruit and seed colors were: 1- white and beige colors were comparatively more common in seeds than in fruits, 2- green and red colors occurred at lower frequencies in seeds compared to fruits, and 3- pink was only found in fruits. In spite of this, orange fruits appear as the main fruit color for animal dispersed seeds (Willson & Thompson 1982, Wheelwright & Janson 1985, Mikich & Silva 2001, Selwyn & Parthasarathy 2006) but are infrequent for plants with other dispersal strategies (Liu et al. 2014). White fruits occur at low frequencies in several different plant communities (Willson & Thompson 1982), and could represent specific associations between fruit color and particular seed disperser species (Guaraldo et al. 2013), or may be unapparent to many undesirable frugivorous animals. Likewise, less common colors such as blue, orange and pink in fruits and seeds might also represent specific color-based adaptations for attracting a particular seed disperser. For example, lizards are an unusual seed disperser, and have been found to prefer white-blue fruits from open habitats (Wotton et al. 2016). Some fruit and seed colors occurring at low frequencies may be associated with certain types of plant communities and habitats. For instance, most of the bright-blue fruits and seeds were from cloudy-rainy plant communities. Green seeds were uncommon and mostly associated with photosynthesis in mangroves and mistletoes, and red seeds were mainly arillated seeds dispersed by birds. All categories of bi-colored fruits and seeds were also found at low frequencies, which contrast with previously recorded results: two- and three-color combinations have been found to be quite common in fruit dispersed by vertebrates (Wheelwright & Janson 1985, Willson et al. 1989, Mikich & Silva 2001, Galetti et al. 2011). Thus, a high frequency of bi-colored fruits can be related to frugivorous animal-driven dispersal, and a low frequency of bi-colored fruits is expected for surveys of overall fruit color categories. However, multicolor fruit-seed structures, resulting from the combination of fruit and seed colors, may increase the frequency of multicolor attractive units.

Fruit and seed colors also differed as regards the number of bi-colored categories. More color combinations for seeds compared to fruits can be primarily associated with contrasting color combinations between the seed coat and accessory structures such as arils. Bi-colored seed combinations may be also related to the large number of plant species with bird-dispersed seeds (Galetti et al. 2011). Bi-colored seeds are, in some cases, also associated with cryptic seeds providing no nutritious pulp (Ridley 1930, van der Pijl 1972). The high number of bi-colored seed combinations found in our study can thus be correlated with different functions and alternative dispersal mechanisms. The most common colors of bi-colored fruits and seeds included black combined with one of three other colors, and combinations of brown, white, yellow, and red. Accordingly, the presence of the color black in bi-colored fruits and seeds seems to have the function of providing a sharp contrast to a bright color. Two- and three-color combinations usually involve black with other colors, usually red and/or yellow (Willson & Melampy 1983, Wheelwright & Janson 1985, Willson et al. 1989). Our results suggest that the black+red seed combination is common in tropical zones. Other combinations of colors and patterns may, however, be found depending on the plant species examined.

Fruits may be bi-colored due to the combination of fruit and seed colors, and this may also result in fruits with more than two colors. The exocarp or aril is usually the colorful structure, although other fruit parts including elaisomes and fruit/seed contrasts may also act as visual attractants (van der Pijl 1982). Thus, the combinations of fruit and seed colors may represent significant adaptations enabling bi-colored fruit-seed structures to have different functions, where texture and dehiscence may also be involved. Most of these multicolored structures are found in dehiscent bi-colored fruits where attractiveness may increase if a brightly colored seed is visible as part of the fruit-seed structure. Seed attraction may also be enhanced when fruit color contrasts with seed color, or when seed coat and aril colors differ. Asymmetries in the level of specialization between the fruit or seed colors with the lowest frequencies and the well-represented morphological fruit types suggest that uncommon colors could represent a specialized trait for animal dispersal, or as protection *via* crypsis against herbivory (Cazetta et al. 2009). Asymmetrical associations between the least common morphological fruit types and the most common fruit or seed color classes were found for many rare fruit types which had fruits or seeds with a variety of functions.

3. *Fruit types and fruit and seed colors*

Morphological fruit types according to Gray showed association values (connectance) of close to 24% for the fruits and seeds studied, and were higher than the values calculated using Spjut's classification. These differences can be mainly explained by the higher number of fruit categories in Spjut's *vs.* Gray's classification. The lower connectance between fruit and seed colors following Spjut's classification indicates that the associations were relatively specific, i.e. each fruit type was linked to a comparatively low number of seed or fruit colors, respectively. Accordingly, the ratios between the number of fruit types and the number of fruit color classes, and between the number of fruit types and the number of seed color classes were higher for Spjut's than for Gray's classification. The mean number of links recorded per fruit color was close to the mean number of links recorded per seed color for both fruit types (I and II). However, the values for type II fruits were higher than those for type I fruits, which again can be related to the higher number of fruit categories considered by Spjut (including modifications of the anthocarp) which results in a greater diversity of associations, leading to multiple combinations. The mean number of links per fruit type (I and II) was lower than the mean number of links per fruit and seed color: more than twice as low for type I fruits, and

more than four times as low for type II fruits. Such trends indicate that the mean number of associations for each fruit and seed color increases with an increase in the number of fruit types, and that the mean number of associations for each fruit type slightly decreases with an increase in the number of fruit types.

Adaptations to a specific set of mutualists may occur more frequently than currently acknowledged in color signaling, even in megadiversified networks of mutualistic interactions (Renoult et al. 2014). The frequency distribution of the number of color-based interactions per fruit type indicates that despite the large number of associations, the majority of fruit types (I and II) were single-colored, although bi-colored fruits and seeds were also common for type II fruits. On the other hand, only a few fruit types were associated with more than eight fruit and seed colors, and therefore with a well-defined (leptokurtic) connectivity distribution (Jordano et al. 2003). In this context, the distribution of the associations between these attributes agrees with complex networks theory: large numbers of nodes have only one or two links, and only a few nodes have a large number of links. These frequency distributions of the number of color-based interactions among fruit types also suggests that there are asymmetries in the level of specialization (Bascompte & Jordano 2007), whereby less common fruit and seed colors tend to be associated with the most common fruit types (both I and II).

The most significant associations were mainly found in dry fruits with the most common being brown with loculicidal capsules, and black with achenes. Septicidal capsules, legumes, and schizocarps also tended to be brown. In fact, several studies have shown that most dry fruits are brown (López & Ramírez 1989, Knight and Siegfried 1983, Parisca & Ramírez 1989, Carpenter et al. 2003, Ibarra-Manríquez & Cornejo-Tenorio 2010, Possete et al. 2015). The pods and capsules surveyed in different tropical forests were also mostly brown (Selwyn & Parthasarathy 2006, Ibarra-Manríquez & Cornejo-Tenorio 2010). The predominance of dark fruits can be related to their higher capacity to absorb solar radiation which might accelerate metabolism and ripening times (Janzen 1983, Wheelwright & Janson 1985), and could also provide a protective function due to the high concentrations of anthocyanins (Schaefer 2011) and tannins. In addition, the color black may act as a protective barrier against insolation for seeds in dry-indehiscent fruits. Dark colors absorb more radiation in the visible spectrum than pale colors (Wheelwright & Janson 1985) thus shielding seeds from it. Brown is the main plant tissue color at the end of the developmental processes of any plant organ, as well as the color of dry tissues; fibrous plant tissues are also often brown (Esau 1953). The brown fruits and seeds of species with dehiscent fruits may constitute a protective trait in several ways: the aposematic coloration of brown fruits may advertise the unattractiveness of the fruit to animal predators (Knight & Siegfried 1983). Brown indehiscent fruits, and brown seeds from dehiscent fruits could also avoid predation through crypsis (matching soil color) as proposed by Liu et al. (2014). The fibrous nature of mostly dry-brown fruits and seeds from dehiscent fruits is a characteristic significantly related to fruit protection, and is favored under strong selection pressure from herbivores (Bodmer 1989, 1991). In fact, dehiscence in fruits has been associated with both fiber content and seed protection (Gautier-Hion et al. 1985). To summarize, the brown coloration of dry fruits at maturity could be associated with several adaptive functions: 1- brown could be considered as the least expensive color (compared to bright colors); 2- brown fruits may be cryptic, thus making them unapparent to herbivores; 3- abiotic dispersal is independent of any specific color, such as that employed by indehiscent-brown fruits; 4- explosive dehiscent fruits require a fibrous fruit-wall for dispersal; 5- dehiscence and brown fruits may also converge in cases where seeds may act as both dispersal unit and self-protective structure.

Bright fruits, together with purple-black (dark) fruits are more likely to interact with the environment than seeds (which are frequently enclosed in indehiscent fruits, or dark seeds are produced by dark fruits), which could explain the greater diversity in the coloration of the former. Most fleshy-fruited species are conspicuously displayed by having fruits that are brightly colored when ripe (French 1991). Fleshy fruits were somewhat less specific as regards their color, and only drupes and berries (baccas) tended to be a particular color, purple-black, which agrees with the commonly found association between these types of fruit and the dispersal of seeds by animals at the community level (Willson & Thompson 1982, Knight & Siegfried 1983, Wheelwright & Janson 1985, López & Ramírez 1989, Willson et al. 1989, Bosque et al. 1995, Selwyn & Parthasarathy 2006, Ibarra-Manríquez & Cornejo-Tenorio 2010, Buitrón-Jurado & Ramírez 2014). The dominance of purple-black drupes and berries may also be related to the number of species belonging to the following plant families: Melastomataceae, Lauraceae, Rubiaceae, Aquifoliaceae, and Symplocaceae (Wheelwright & Janson 1985, Buitrón-Jurado & Ramírez 2014). However, no effects of phylogenetic constraints, either at the family or the genus level, have been found when explaining community-wide variations and patterns in fruit color (Janson 1983, Willson et al. 1989). Purple-black fruits have been associated with the visual perception of birds, which are considered the main seed dispersers in both temperate and tropical sites (Willson et al. 1989). Moreover, purple-black fleshy fruits may absorb more radiation in the visible spectrum (Wheelwright & Janson 1985) thereby raising fruit temperatures and leading to an increase in metabolic and developmental rates (Janzen 1983). The predominance of purple-black over red in fleshy fruits relying on bird seed dispersal seems to be a characteristic feature of most plant communities (Knight & Siegfried 1983, Wheelwright & Janson 1985, Nakanishi 1996, Galetti et al. 2011) except savannas (Donatti et al. 2007). Bright (red and yellow) colors show lower specificity according to fruit types, although fleshy fruits, drupes and berries are often these colors. Bright colors are a key characteristic of fruits because they raise the probability that the fruits will be noticed or selected, and consequently that their seeds will be dispersed (Wheelwright & Janson 1985). In addition to signaling location, fleshy fruit colors may convey information about fruit quality that would influence a bird's choice of meal (Wheelwright & Janson 1985). Different colored fruits seem to be dispersed by different dispersal agents, although this is a tendency rather than a rule. In fact, plant-seed dispersal networks show low levels of specificity **(**Blüthgen et al. 2007**),** although drupes and berries favored by birds for seed dispersal are more likely to be brightly colored, whereas those eaten principally by mammals tend to be yellow or green (Knight & Siegfried 1983, Willson et al. 1989, Voigt et al. 2004, Galetti et al 2011). Yellow- fleshy fruits are generally found in relatively low frequencies at the community level (Willson & Thompson 1982, Chen et al. 2004, Possete et al. 2015). In this study we recorded comparatively low numbers of yellow-fruited species, despite the inclusion of a few yellow-dry fruits in the plant species examined.

Morphological fruit types and seed colors exhibited similar associations as compared to fruit type and color. The seeds of fleshy and dry fruits may form clusters around the same color. For example, brown seeds are associated with berries, schizocarps, loculicidal capsules, drupes, septicidal capsules and legumes; indicating that brown is the most common seed color irrespective of fruit texture and dehiscence. In fact, the seed coat is brown in diverse fruit types (Parisca & Ramírez 1989, López & Ramírez 1989, Gordon 1998). The frequency distributions of the number of seed color links per fruit type also suggests the existence of very cohesive associations, with clusters of the most common fruit types and color categories converging among themselves. Specifically, a high number of dry-indehiscent and fleshy-indehiscent fruits had beige seeds (achene, caryopsis, drupes and berries), and beige, white, and green seeds were more abundant in indehiscent than dehiscent fruits. The predominance of light-colored seeds in indehiscent fruits is probably related to a thin seed coat, low fiber content, and no protective function given by the fruit. Beige seeds were the second most common seed color and form several clusters with achene and caryopsis (anthecetum and pseudoanthecium) fruit types; and white seeds form a large cluster with achenes. The high frequencies of beige and white seeds in the sample examined agrees with previous studies of diverse fruit types (López & Ramírez 1989, Gordon 1998) and seems to be related to the high proportion of these seeds in dry-indehiscent fruits. These trends show that light colored seeds are associated with dark indehiscent fruits, and that black seeds may occur in both dehiscent and indehiscent fleshy fruits. For example, achenes (cypselas) were predominantly black with a high number of species with white or beige seeds. Light-colored seed coats seem not to interact directly with either biotic or abiotic factors, and thus in species with these seed colors, fruit color could be more important. Dark fruit colors, for example, could protect the seeds from biotic and abiotic factors and could thus be associated with a great variety of functions (Cazetta et al. 2009). In some cases, however, light-colored seeds are significantly associated with rapid germination (Thompson 1993, Gordon 1998, Debeaujon et al. 2000). Hence, light colors in seeds could be linked to basic processes to do with the establishment and development of seedlings (Debeaujon et al. 2000), and in some cases with abiotic seed dispersal.

Brown seeds seem to be mainly associated with dehiscent fruits which are mostly brown and sometimes black, and are the most common colors found in plant species. Dark colors (black and brown) may give protection against physical factors as they absorb more radiation in the visible spectrum than pale colors (Wheelwright & Janson 1985). This also raises fruit temperature, thus increasing metabolic rate and speeding up the ripening process (Janzen 1983). Hence, dark colors could contribute to providing energy for germination and may also protect embryos from radiation. In addition, brown and black seeds are related to high fiber tissues (Stringam et al. 1974, Daun & DeClercq 1988) and may provide protection against post-dispersal seed predation (Bodmer 1989, 1991). Moreover, brown and black colors may enable seeds to avoid advertising their presence to post-dispersal seed predators through crypsis with the soil, and might also serve as protective mimetic colors in species that employ abiotic seed dispersal mechanisms (Nystrand & Granström 1997). Brown and black seeds, in combination with their structure, are also associated with plant species dispersed by granivorous animals (e.g. Pirk & Casenave 2006). In some animal dispersed species, black seeds may be combined with a contrasting color of one or more parts of a fruit, such as the pulp of some fleshy fruits (e.g. some Cactaceae). Two-color combinations of seeds are usually black plus another color, and are found in some animal dispersed fruits (Willson et al. 1989, Wheelwright & Janson 1985). A higher proportion of brown, white or bi-colored (black+white) seeds were found in dry fruits compared to fleshy fruits, and green or orange seeds were more likely to be found in fleshy fruits than dry fruits. The most common color found in both fruits and seeds, however, was brown. Brown fruits coincided with brown seeds in numerous fruit types: loculicidal capsule, schizocarp, legume, and septicidal capsule, and included fruit types and seeds that were exclusively brown (samara, craspedium and loment). Brown seeds were also found in the most abundant fleshy indehiscent fruits: purple-black, red or yellow berries and drupes, and can be related to seed protection. For example, berries are ingested by animals and the seeds need some protection for their survival which might be given by a fibrous-brown seed-coat (Bodmer 1989, 1991, Parisca & Ramírez 1989).

4. Fruit types, fruit and seed colors, and functional groups

Morphological fruit types show attributes that are closely related to their different colors and diverse functional traits. Hence, color, dehiscence, texture and their corresponding morphological fruit types following either Gray (1877) or Spjut (1994) were predominantly associated with plant life form, epiphytism, physiology, nutritional relationships, fruit phenology, and the successional stage they inhabit

Fruit texture and dehiscence were associated with particular life forms: fleshy and dry fruits with trees, fleshy fruits with shrubs, and dry-dehiscent and dry-indehiscent fruits with herbs. This agrees with Fleming (1991) who found that dry fruits were dominant in herbaceous plant families whilst woody families had a more even mix of fruit types with fleshy fruits predominating. Other studies indicate that fleshy fruits are strongly linked to shrubs whilst dry fruits are associated with annual herbs, suggesting that fruit texture may be influenced by plant size, woodiness, and life span (Burrows 1994, Herrera 2002a, b, Patterson & Givnish 2002, Bolmgren & Eriksson 2005). Selection pressures on shrubs may favor the production of fleshy fruits as the perennial woody condition is structurally adapted for the production of high quality fruits that require large amounts of water. In fact, fleshy fruit production is positively selected for at sites with high moisture and soil fertility because the large metabolic costs associated with the production of edible pulp are more likely to be met under these conditions (Willson et al. 1989, Almeida-Neto, et al. 2008, Buitrón-Jurado & Ramírez 2014). In forests, species with fleshy fruits tend to be understory species, particularly shrubs and small trees (Herrera 1984, French 1991). The higher frequency of shrubs with fleshy fruits compared to tree species might be also related to the relatively small size of shrubs compared to trees: tall trees commonly have dry-wind seed dispersal mechanisms. Low frequencies of fleshy fruits among tree and vine species, and higher frequencies among shrubs have also been associated with dry forests compared to wetter ones (Willson et al. 1989). The high frequencies of dry fruits and the minimal occurrence of fleshy fruits among annual herbs have been found repeatedly (Willson et al. 1989, Possete et al. 2015), and seem to be influenced by the low energetic cost and shorter development period of dry fruits, which are also undemanding of water and energy to complete growth. The strong associations found between

dry fruits (dehiscent and indehiscent) and herbs may be related to the relatively small plant size, short lived life cycle, and inexpensive fruits.

The most frequent fruit and seed colors were associated with the different life forms and successional stages. Thus, trees and shrubs, mostly from late successional stages, had brown, green, yellow and purple-black fruits (shrubs also produced red fruits). The relationships between life form and fruit color are mainly determined by the links between texture, color and the seed dispersal mechanism. Brown, green and yellow fruits in woody species are associated with dry and fleshy fruits in trees, and mostly fleshy fruits in shrubs. Dry fruits in trees are frequently brown but some species produce green fruits (Knight & Siegfried 1983, Noir et al. 2002, Selwyn & Parthasarathy 2006, Yamamoto et al. 2007, Ibarra-Manríquez & Cornejo-Tenorio 2010). On the other hand, the fleshy fruits found in some tree species are green or yellow and usually dispersed by mammals (Janson 1983, Knight & Siegfried 1983, Voigt et al. 2004, Galetti et al 2011). Previous studies indicate that purple-black and red are the main fruit colors for tree species (Willson & Thompson 1982, Janson 1983, Knight & Siegfried 1983, Wheelwright & Janson 1985, Burrows 1994, Voigt et al. 2004, Ibarra-Manríquez & Cornejo-Tenorio 2010), most likely because birds are the most common dispersal agents in the canopies of tropical forests (Wheelwright & Janson 1985). In contrast, herbaceous species, frequently from pioneer successional stages, generally produce dark (black and brown) fruits, although some pioneers have purple-black fruits. Dark fruits in herbaceous species can be explained by the associations between dry, dehiscent and indehiscent fruits, and their dispersion mechanisms which may be abiotic, or biotic through non-frugivorous animals: granivochory or epizoochory. Epizoochory is a well-known dispersal syndrome for herbaceous colonizing species (Graae 2002, Devlaeminck et al. 2005), and seed dispersal by granivores and wind is frequently found for herbs growing in disturbed areas (Ramírez 2005, Hilje et al. 2015).

The absence of a clear relationship between seed color, life form and successional stage is probably due to the fact that seed color in many indehiscent fruits is little linked to environmental and biotic factors, unlike seed color in dehiscent fruits which are therefore under stronger selection pressures. Brown was the most common color for seeds in plant species of all life forms and the two successional stages considered. Other associations observed among the most common seed colors, life forms and successional stages were: beige and black for perennial herbs, and white for annual herbs (generally pioneer species). In contrast, orange and white+black seeds found in woody and late successional stage species may be related to specialized frugivorous dispersal mechanisms (Cazetta et al. 2009).

Epiphytes are perennial herbs that grow on a host plant and tend to have dry-dehiscent fruits and brown seeds. Dry-dehiscent fruits such as capsules are frequently associated with wind dispersal mechanisms (Burrows 1994) and are often found in epiphytes (Miller 2005). It is also likely that there is some taxonomic effects as wind dispersed species are common in epiphytic Bromeliaceae and Orchidaceae (Benzing 1990; Hughes et al. 1994; Mori & Brown 1994, Miller 2005). The abundance of capsules in epiphytic species may be related to: 1- wind dispersal, because they enable the release of light seeds during the dispersal period (Madison 1977, Hughes et al. 1994), 2- the fact that wind-dispersal of capsule-derived light (in weight) seeds is an appropriate dispersal mechanism for epiphytes due to their position in the vegetation strata (Madison 1977, Hughes et al. 1994), 3- the distribution of epiphytes in the highest vegetation strata as regards the vertical organization of the plant communities where they are found, which represents an adaptation for wind dispersal (Madison 1977, Kelly 1985) and 4- the fact that epiphytic species may be physiologically limited because of the restricted availability of water (Zotz & Hietz 2001) and capsules could be an adequate inexpensive fruit type under these conditions.

In contrast, parasitic-hemiparasitic species had predominantly fleshy fruits. Most of the parasitic-hemiparasitic species with indehiscent-fleshy fruits belong to the Santalaceae (Miller 2005, Viscaceae (Kuijt 2005) and Loranthaceae (Kuijt 2001)), which are phylogenetically related (APG IV 2016) and produce green seeds. Fleshy fruits in parasitic-hemiparasitic species are also associated with: 1- nutritional dependency on the host plant, which seems to enable the production of expensive fleshy fruits that are similar to the types of fleshy fruits found in woody species (Willson et al. 1989, Carpenter et al. 2003, Bolmgren & Erikksson 2010, Buitrón-Jurado & Ramírez 2014). Fleshy fruit production is positively selected for under high moisture conditions as the high metabolic costs associated with the production of edible pulp can be met (Willson et al. 1989, Almeida-Neto, et al. 2008, Buitrón-Jurado & Ramírez 2014). 2- The vertebrate dispersal syndrome which is a common dispersal syndrome in parasitic-hemiparasitic species (Hughes et al. 1994). Parasitic mistletoes tend to show host specificity (Nadkami et al. 2001), and show directionality in the dispersal process towards the exposed branches of suitable host plants. Green seeds are common in the parasitic-hemiparasitic families, Santalaceae and Loranthaceae (Miller 2005). Green seeds in parasitic-hemiparasitic species also seem to be related to the photosynthetic capacity of the seeds and the recruitment process on bare woody surfaces. In order to survive parasitic plants must be dispersed to the limbs of suitable host plants, and once there they produce a haustorium which penetrates the host during establishment. This process may be enhanced by green seeds and their photosynthetic capacity. Developing green fruits may contribute a major proportion of their own photosynthate (Bazzaz et al. 1979) suggesting that mature green seeds may also contribute photosynthetically to their maintenance and consequently may be viable for longer. Mature green fruits may also avoid frugivory by crypsis, or be involved in more specific plant-animal interactions.

Morphological fruit types are noticeably correlated with successional stages. Dry fruits occur more frequently in pioneer species and fleshy fruits tend to be abundant in late successional stage species. Many late successional stage woody species produce berries or drupes. In contrast, herbs from disturbed areas are associated with achene and caryopsis (anthecetum) fruit types. These trends are in line with the associations found between herbs with dry fruits growing in open habitats (Arbeláez & Parrado-Rosselli 2005, Lorts et al. 2008, Bolmgren & Erikksson 2010), and between fleshy fruits produced by trees and shrubs growing in closed habitats and at the climax end of a successional sequence (the latter being less frequent in disturbed habitats) (Herrera 1984, Willson et al. 1989, Carpenter et al. 2003, Lorts et al. 2008, Bolmgren & Erikksson 2010, Buitrón-Jurado & Ramírez 2014). In addition, indehiscent fruits in natural habitats could be related to a more stable environment, where fleshy-indehiscent fruits predominate (Opler et al. 1980). In contrast, dehiscent fruits were more common than indehiscent fruits in disturbed habitats, which correlates with the morphological adaptions (multi-seeded dry fruit) of some colonizing species (Arbeláez

& Parrado-Rosselli 2005). In summary, fleshy-indehiscent fruits occur predominantly in undisturbed areas, while dehiscent and indehiscent dry fruits are more abundant for pioneer species growing in disturbed areas.

The relationships between life form and morphological fruit type also include the carbon metabolism pathway employed by plant species. Thus C_4 species are herbaceous **(**Medina 1995, Ramírez & Briceño 2015**)** and are mainly associated with caryopsis (anthecetum and pseudoanthecium) fruit types. Most of these plant species grow in savannas and disturbed areas (Medina 2002, Ramírez & Briceño 2015). The most abundant fruit types in C_4 and CAM species are taxonomically influenced. As previously mentioned, C_4 species are herbs and produce principally dry-indehiscent one-seeded fruits. For example, caryopsis is a classic morphological fruit type of Poaceae (Silberbauer-Gottsberger 1984, Amaral et al. 2013). In contrast, multi-seeded dry-dehiscent, capsule, fleshy-indehiscent, and acrosarcum fruit types are typical of CAM and succulent species, mostly from the Cactaceae (Spjut 1994). Moreover, most C_4-herbaceous species grow in disturbed habitats (Ramírez & Briceño 2015) and their caryopses are mainly dispersed by epizoochory and anemochory (Silberbauer-Gottsberger 1984, Amaral et al. 2013). All these attributes seem to point towards a general colonizing strategy of some herbaceous species. In contrast, the multi-seeded fruits of succulent-CAM species exhibit diverse morphological fruit types, and consequently varied fruit strategies. For example, pink fruits common in succulent-CAM species are dispersed by animals and well represented in the Cactaceae.

5. Fruit types and fruit phenology

The most abundant morphological fruit types, both according to Gray (1877) (e.g. achenes, berries, drupes, loculicidal capsules, and schizocarps), and Spjut (1994) (e.g. baccas, drupes, loculicidal capsules, and septicidal capsules) exhibited seasonal changes in their unripe and ripe fruit phenologies, especially during the rainy-dry transition period. This agrees with previous studies undertaken in different plant communities (Oliveira & Moreira 1992, Jordano 1993, Batalha & Martins 2004, Freitas et al. 2013). Fruit phenology during the rainy season and rainy-dry transition period may signify that this is the optimal time for dispersal and/or ripening. The variety of morphological fruit types found during these periods also suggests that the ripening and dispersal of dry and fleshy fruits is associated in some way with the rainy season. Ripe, fleshy fruits are dispersed by animals and are frequently associated with the rainy season (Oliveira & Moreira 1992, Batalha & Martins 2004). On the other hand, the relationship of dry fruits (capsules, achenes, and schizocarps) to the dry season and rainy-dry transition period could be due to the diverse adaptations they have for dispersion by granivorous animals, and ballistic, and wind dispersal. Other factors that may influence the seasonality of diverse fruit types during the rainy season and rainy-dry transition period are irradiance, which could affect fruit development times (Zimmerman et al. 2007), and the synchronization of fruiting and dispersal with the onset of the rainy season to maximize the chances of seed germination and seedling establishment (Oliveira 1998).

Dry fruits were common in ecosystems with low annual precipitation such as the seasonal Caatingas (Sobral & Machado 2001, Silva & Rodal 2009, Silva et al. 2013). Ripe and unripe dry fruit phenologies associated with the dry season may represent a strategy related to the relatively low cost of dry fruits. Dry fruit production during the dry season may be also related to abiotic seed dispersal. Thus, many wind-dispersed winged fruit types such as samara and samarium are produced during the dry season (Wikander 1984, Devineau 1999, Cortés-Flores et al. 2019). The synchronization of dry fruits with the dry season may also be phylogenetically constrained (Bulhão & Figueiredo 2002). The ripe and unripe fruit phenologies of dry fruit species unusually associated with the rainy season suggest that the production of these types of fruits is in some way independent of the season, and that the contribution of the rains to the ripening process and ripe fruit phenologies is only significant in a few cases. The presence of unripe caryopsis and silique (Gray 1877), and anthecetum, ceratium and coccarium (Spjut 1994) fruit types during the rainy season suggest that the ripening process of these predominantly dry fruits is, nevertheless, affected by the rains, or alternatively, it is flowering that is mainly associated with the rainy season, which is itself closely related to unripe fruit phenology during this period. Dry fruits associated with an herbaceous life form can also be related to fruit phenology: herbs, which produce predominantly dry fruits, tend to fruit during the rainy season (Ramírez 2009, Ramírez & Briceño 2011, López & Ramírez 2013). In addition, unripe dry-fruit phenology shows that developmental processes are related to the presence of rain and thus probably depend on an adequate water supply to complete the ripening phase (Lombardini & Rossi 2019). Most of these dry fruits ripen during the rainy-dry transition period or the dry season, which could represent adaptations to wind and granivorous seed dispersal (Cortés-Flores et al. 2019).

The ripe and unripe fruit phenologies of fleshy-fruited species are positively associated with the rainy season, although uncommon occurrences of fleshy fruit during the dry season have been previously recorded (Oliveira & Moreira 1992, Jordano 1993, Batalha & Martins 2004). The abundance of fleshy fruits during the rainy season seems to agree with the elevated costs associated with their production, and the fact that the quality of fleshy fruits is related to their water content. In addition, most fleshy fruits are ripe indehiscent fruits, and are produced during the rainy season due to positive selection for a high moisture environment (Willson et al. 1989, Mclaren & Mcdonald 2005, Almeida-Neto et al. 2008, Buitrón-Jurado & Ramírez 2014). Thus, unripe fleshy fruit phenology during the rainy season seems to be related to the ripening process of expensive fleshy fruits. Furthermore, the presence of unripe fleshy fruit during the rainy season could be associated with woody life forms because the structural patterns of these plant species mean that they are comparatively less limited by low water and nutrient availability (Rathcke & Lacey 1985).

6. Fruit phenology and fruit and seed colors

Unripe and ripe dark (black, brown, green, or purple-black), fruits were common during the rainy-dry transition period. Unripe red or yellow fruits were also abundant during this time. Brightly colored fruits, however, are more frequent on average during the rainy season (Wheelwright & Janson 1985). This seems to correspond to the ripening of red and yellow fruits before the rainy season, and agrees with the high frequencies of fruits with these colors during the rainy season. The ripening of bright fleshy fruits during the rainy season can be mostly explained by the association between bright colors, fleshy fruits, and animal dispersal. As regards seed colors, no specific associations were observed, although beige, black, brown, green, orange, and white were the most abundant seed colors during the rainy-dry transition period.

Large-scale comparisons suggest that fruit color, rather than other morphological and chemical fruit traits, reflects the selection pressures exerted by different frugivore assemblages (Voigt et al. 2004). Probably, seed color diversity derived from contrasting textures, dehiscence and combinations of these attributes could result from factors independent of reproductive phenology. Seeds from dehiscent and indehiscent fruits differed according to the mechanisms of protection, dispersal, physiology and recruitment. Multi-species analysis of fruit types and seed color combinations showed a highly diverse assemblage, and suggests that seed color is independent of fruit phenology

Conclusion

The taxonomic structure may provide similar insights as the phylogenetic approach (e.g. Corbelli et al. 2015, Fan et al. 2017). In this context, the influence of large taxonomic groups as families and orders may, in some cases, influence the main conclusions derived from the results obtained. The four most common seed color categories were generally associated with the most common fruit colors. Particular associations between fruit morphology and fruit and seed colors could be taxonomically influenced. For instance, most of the rhexocarpic fruits are brown, dehiscent, and their seeds are frequently brown; a large number of these plant species belong to one of the most frequent order found in the sample examined (22.4% of Fabales; N. Ramírez & H. Briceño, in preparation). However, the more representative associations were mainly found for dry fruits: brown color with a loculicidal capsule fruit type, which may be widely represented in a variety of lineages. The largest groups represented in the sample examine [Lamids (17.4%), Malvids (21.10%), and Fabids (27.26%), N. Ramírez & H. Briceño, in preparation] contain many mixed families producing dry and fleshy fruits. Therefore, dry-dehiscent fruits and their associations with brown seeds are not necessarily influenced taxonomically in all cases. Fleshy fruits were somewhat less specific as regards color, and the only significant associations found were that drupes and berries (baccas) were usually purple-black, with brown or beige seeds. Such associations come from different lineages and taxonomic groups (Rubiaceae, Solanaceae, Myrtaceae, Melastomataceae, Humiriaceae, Passifloraceae) and suggest no evident taxonomic constraints. Similar conclusion has been previously proposed for fleshy fruits (Janson 1983; Willson et al. 1989). Asymmetries in the level of specialization, where less frequent fruit and seed colors tended to be related to the most common fruit types, and seem variations without taxonomic or phylogenetic consequences.

Morphological fruit types have attributes that are closely related to different colors and diverse functional plant traits. Thus, trees were associated with fleshy and dry fruits, shrubs with fleshy fruits, and herbs with dry-dehiscent and dry-indehiscent fruits. Dry fruits occurred more frequently in pioneer species and late successional stage plants, mostly woody species, tended to have fleshy fruits. Such relations seem to be largely independent of taxonomic effects; however, some specific correlations are influenced taxonomically. The abundance of plant families containing a large variety of attributes, called mixed families, which are well-represented in the three largest groups found in the sample examine (see above, N. Ramírez & H. Briceño, in preparation) could be provide independence taxonomic. Our results agree with previous study where mixed families, species producing non-fleshy fruits tend to be herbs or vines growing in open and/or frequently disturbed habitats. In these families, fleshy fruits are usually produced by woody plants (trees and shrubs) in closed, less frequently disturbed habitats (Bolmgren & Erikksson 2010). Additionally, the distribution of plant families producing fleshy fruits does not differ significantly among the five lineages recognized in the APG (basal angiosperms, monocots, basal eudicots, asterids, and rosids) (Fleming & Kress 2011). On the other hand, the C_4 species are herbs and produce mainly dry-indehiscent, one-seeded fruits, which are influenced taxonomically. Most of these plant species are Poaceae and grow in disturbed areas and their fruits and seeds are influenced taxonomically since Poales represent 27.6% of perennial herbs in the sample examined (N. Ramírez & H. Briceño, in preparation). Epiphytes usually had dry-dehiscent fruits and brown seeds (Orchidaceae and Bromeliaceae) and predominantly fleshy fruits in parasitic-hemiparasitic species (Santalaceae and Loranthaceae) were taxonomically influenced. However, dry-dehiscent fruits and brown seed in epiphytes belong to two different orders and clades (see APG 2016). The relationships among phenology, morphology and color of fruits, where dry fruit were associated with the dry season, and fleshy fruit species were positively associated with the rainy season may be not taxonomically influenced because seasonality is mainly related with life forms and fruit texture (see above). Thus, the presence of ripe bright-fleshy fruits during the rainy season was mostly explained by the association between bright color, fleshy fruits, woody life form, water availability, and animal dispersal. Moreover, herbaceous species, with dry fruits are also associated with the rainy period. By the contrary, the occurrence of dry fruits during the dry period is mainly explained by the association between dry fruit, woody life form and abiotic dispersal.

Supplementary Material

The following online material is available for this article: Appendix S1 - Distribution of Gray (1877) and Spujt (1994) fruit types according to fruit color. Appendix S2 - Relationship between fruit and seed colors. Percentages are relative values to each raw, except total fruit colors. Appendix S3 - Distribution of Gray (1877) and Spujt (1994) fruit types according to seed color.Appendix S4 - Number and percentage of Gray (1877) and Spjut (1994) fruit types, fruit color, and seed color according to functional groups. Figure S1 - Bipartite graph showing the links between morphological fruit types

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Table 1. Plant species, family, study locality, functional goups, fruit types and fruit and seed colors of 1,139 plant species studied.

FAMILY SPECIES	Locality[1]	Carbon metabolism	Succulence[2]	Life form[3]	Epiphytism[4]	Nutritional relationship[5]	Successional stage[6]	Fruit texture[7]	Fruit dehiscence[8]	Fruit type Gray	Fruit type Spjut	Fruit color	Seed color
ACANTHACEAE													
Bravaisia integerrima (Spreng.) Standl.	1, 2	C3	Ns	Tr	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Justicia guianensis (N.E. Br.) Wassh.	18,19	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Justicia secunda Vahl	2, 7, 21	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Justicia stipitata Wassh. & Arroyo	7	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Mendoncia tovarensis (Klotzsch & H. Karst. ex Nees) Leonard	6, 7	C3	Ns	L	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Ruellia geminiflora Kunth	24, 25	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Ruellia humboldtiana (Nees) Lindau	40	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Ruellia macrophylla Vahl	7	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Ruellia paniculata L.	41	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Ruellia tuberosa L.	1, 5	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
ADOXACEAE													
Viburnum tinoides L. f.	6	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
AIZOACEAE													
Sesuvium edmonstonei Hook. f.	13	CAM	S	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Sesuvium portulacastrum (L.) L.	12, 13	C3	S	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Trianthema portulacastrum L.	5	C4	S	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
ALISMATACEAE													
Echinodorus grandiflorus (Cham. & Schltdl.) Micheli	27	C3	Ns	Ah	T	A	D	D	I	Agregate of achene	Achenetum	Brown	Black
Limnocharis laforestii Griseb.	27	C3	Ns	Ph	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Sagittaria guayanensis Kunth	26	CAM	Ns	Ah	T	A	M	D	I	Agregate of achene	Achenetum	Brown	Black
AMARANTHACEAE													
Achyranthes aspera L.	5, 27	C3	Ns	Ph	T	A	D	D	I	Utricle	Diclesarium	Brown	Brown
Alternanthera halimifolia (Lam.) Standl. ex Pittier	9, 12	C4	Ns	Ph	T	A	D	D	I	Utricle	Diclesarium	Brown	Black
Alternanthera pungens Kunth	5	C4	Ns	Ph	T	A	D	D	I	Utricle	Diclesarium	Brown	Black

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Amaranthus crassipes Schltdl.	5	C4	Ns	Ah	T	A	D	D	D	Pyxidium	Pyxidium	Brown	Black
Amaranthus dubius Mart. ex Thell.	1, 5	C4	Ns	Ah	T	A	D	D	D	Utricle	Diclesarium	Brown	Black
Gomphrena alba Farmar	9	C4	Ns	Ph	T	A	D	D	I	Utricle	Diclesarium	Brown	Black
Iresine angustifolia Euphrasén	2, 27	C3	Ns	Ph	T	A	D	D	I	Utricle	Diclesarium	Brown	Black
ANACARDIACEAE													
Spondias mombin L.	22, 27	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Yellow	Brown
Toxicodendron striatum (Ruiz & Pav.) Kuntze	6	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Red	White
ANNONACEAE													
Anaxagorea acuminata (Dunal) A. DC.	3	C3	Ns	Tr	T	A	M	D	D	Agregate of follicle	Follicarium	Brown	Black
Annona jahnii Saff.	22, 24, 27	C3	Ns	Sh	T	A	M	F	I	Aggregate of berry	Syncarpium	Yellow	Black
Xylopia aromatica (Lam.) Mart.	22, 24, 27	C3	Ns	Tr	T	A	M	F	D	Agregate of follicle	Follicarium	Green+Red	Black
APIACEAE													
Apium leptophyllum (Pers.) F. Muell. ex Benth.	1	C3	Ns	Ah	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Asorella jualianii Math & Constance	4	C3	Ns	Ph	T	A	M	D	D	Schizocarp	Coccarium	Brown	Black
APOCYNACEAE													
Aspidosperma fendleri Woodson	6, 7	C3	Ns	Tr	T	A	M	D	D	Agregate of follicle	Follicarium	Brown	Brown
Blepharodon mucronatum (Schldl.) Decne.	22, 24, 25	C3	Ns	L	T	A	M	D	D	Agregate of follicle	Follicarium	Brown	Brown
Blepharodon pictum (Vahl) W.D. Stevans	18	C3	Ns	L	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Blepharodon ulei Schltr.	18	CAM	Ns	L	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Calotropis gigantea (L.) Dryand. In W.T. Aiton	11	C3	S	Sh	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Calotropis procera (Aiton) W.T. Aiton	5, 9	C3	S	Sh	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Ditassa bolivarensis (R.W. Holm) Morillo	18	C3	Ns	Ph	T	A	M	D	D	Agregate of follicle	Follicarium	Brown	Brown
Ditassa tatei Gleason & Moldenke	15, 16, 17	C3	Ns	Ph	T	A	M	D	D	Agregate of follicle	Follicarium	Brown	Brown
Galactophora schomburgkiana Woodson	15, 16	C3	Ns	Sh	T	A	M	D	D	Agregate of follicle	Follicarium	Brown	Brown
Macroscepis urceolatum (Kart.) Williams	24, 25	C3	Ns	L	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Mandevilla benthamii (A. DC.) K. Schum.	14-17	C3	Ns	Ph	T	A	M	D	D	Agregate of follicle	Follicarium	Brown	Brown

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Mandevilla gracilis (Kunth) J.F. Morales	18	C3	Ns	L	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Mandevilla subsagittata (Ruiz & Pav.) Woodson	1	C3	Ns	L	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Marsdenia condensiflora S.F. Blake	5	C3	Ns	L	T	A	M	D	D	Agregate of follicle	Follicarium	Brown	Brown
Marsdenia xerophylica Dugand	22, 24, 27	C3	Ns	L	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Matelea maritima (Jacq.) Woodson	24, 27	C3	Ns	L	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Metastelma hirtella (Oliver) Liede	17, 18, 19	C3	Ns	L	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Metastelma parviflorum (Sw.) R. Br. ex Schult.	1	C3	Ns	L	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Plumeria inodora Jacq.	5	C3	Ns	Tr	T	A	M	D	D	Agregate of follicle	Follicarium	Brown	Brown
Sarcostema clausum (Jacq.) R & Schum	5	CAM	Ns	L	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Stapelia gigantea N.E. Br.	31	CAM	S	Ph	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Tabernaemontana amygdalifolia Jacq.	2	C3	Ns	Sh	T	A	M	F	D	Agregate of follicle	Follicarium	Red	Brown+ yellow
Thevetia ahouai (L.) A. DC.	2	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Red	Brown
AQUIFOLIACEAE													
Ilex danielis Killip & Cuatrec.	17, 18	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Ilex polita Steyerm.	16	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Ilex retusa Klotzsch in R. M. Schomb.	15, 16, 17	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Ilex sideroxyloides (Sw.) Griseb.	21	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Ilex subrotundifolia Steyermark	15	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
ARACEAE													
Anthurium ellipticum K. Koch & Bouché	5	C3	Ns	Ph	T	A	M	F	I	Berry	Baccarium	Red	Black
Anthurium hookeri Kunth	21	C3	Ns	Ph	T	A	M	F	I	Berry	Baccarium	White	White
Anthurium nymphaeifolium K. Koch & C.D. Bouché	6	C3	Ns	Ph	T	A	M	F	I	Berry	Baccarium	Red	Brown
Caladium bicolor Vent.	22, 24	C3	Ns	Ph	T	A	D	F	I	Berry	Baccarium	Red	Beige
Dieffenbachia seguine (Jacq.) Schott	3, 7	C3	Ns	Ph	T	A	M	F	I	Berry	Sorosus	Yellow	Brown
Montrichardia arborescens (L.) Schott	26	C3	Ns	Sh	T	A	M	F	I	Berry	Sorosus	Yellow	Brown
Philodendron hederaceum (Jacq.) Schott	22, 27	C3	Ns	L	T	A	M	F	I	Berry	Sorosus	White	Beige

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Philodendron macroglossum Schott	7	C3	Ns	L	T	A	M	F	I	Berry	Sorosus	White	Beige
Philodendron ptarianun Steyerm. var. rugosum	15, 17	C3	Ns	Ph	T	A	M	F	I	Berry	Sorosus	White	Beige
Xanthosoma undipes (K. Koch & C.D. Bouché) K. Koch	7	C3	Ns	Ph	T	A	M	F	I	Berry	Sorosus	White	Brown
ARALIACEAE													
Schefflera glabrata (Kunth) Frodin	6	C3	Ns	Tr	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
ARECACEAE													
Bactris guineensis (L.) M. E. Moore	22, 27	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Bactris setulosa H. Karst.	7	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Yellow	Brown
Chamaedorea pinnatifrons (Jaqc.) Oersted	6, 7	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Copernicia tectorum (H.B.K.) Martius	27	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Euterpe precatoria Mart.	21	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Brown	Brown
Geonoma simplicifrons Willd.	7	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Geonoma spinescens H. Wendl. ex Burret	7	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Geonoma tenuis Burret	7	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Mauritia flexuosa L.f.	3, 26	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Brown	Brown
Socratea karstenii F.W. Staufer & Balslev	7	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Yellow	Brown
ARISTOLOCHIACEAE													
Aristolochia pannosoides Hoehne	22, 24	C3	Ns	L	T	A	M	D	D	Septicidal capsule	Ceratium	Brown	Brown
ASPARAGACEAE													
Agave cocui Trel.	1, 5	CAM	S	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Black	Black
ASTERACEAE													
Achyrocline satureioides (Lam.) DC.	8, 18, 20	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Ageratum conyzoides subsp. latifolium (Cav.) M.F. Johnson	18	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Aldama dentata La Llave	1	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Alloispermun caracasanum (Kunth) H. Rob.	1	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Austroeupatorium inulifolium (Kunth) R.M. King & H. Rob.	18, 20	C3	Ns	Sh	T	A	D	D	I	Achene	Cypsela	Black	White

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Ayapana amygdalina (Lam.) R.M. King & H. Rob.	18-20	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Baccharis leptocephala DC.	18-20	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Baccharis trinervis Pers	1, 5-7, 21	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Bidens pilosa L.	1, 21, 23-25, 27	C3	Ns	Ah	T	A	D	D	I	Achene	Diclesium	Black	White
Calea alchioides S.F. Blake	20	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Calea cardonae Maguire & Wurdack	16	C3	Ns	Ph	T	A	M	D	I	Achene	Cypsela	Black	White
Calea divaricata Benth.	17	C3	Ns	Ph	T	A	M	D	I	Achene	Cypsela	Black	White
Calea lucidivenia Gleason & S.F. Blake	14-16	C3	Ns	Ph	T	A	M	D	I	Achene	Cypsela	Black	White
Calea nana Maguire	19	C3	Ns	Ph	T	A	M	D	I	Achene	Cypsela	Black	White
Calea oliveri B.L. Rob. & Greenm.	19	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Calea solidaginea Kunth	21	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Carramboa badilloi (Cuatrec.) Cuatrec.	28	C3	Ns	Sh	T	A	M	D	I	Achene	Diclesium	Black	White
Centratherum punctatum Cass. var. Punctatum	20	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	Beige
Chromolaena ivifolia (L.) R.M. King & H. Rob.	24, 25	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Chromolaena laevigata (Lam.) R.M. King & H. Rob.	15, 17, 18	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Chromolaena odorata (L.) R.M. King & H. Rob.	1, 24, 25	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Chromolaena thurnii (B.L. Rob.) R.M. King & H. Rob.	19, 20	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Coespeletia alba (A.C. Smith.) Cuatrec. (feme)	4	C3	S	Ph	T	A	M	D	I	Achene	Cypsela	Black	Beige
Coespeletia moritziana (Schultz Bip ex Wedd.) Cuatrec.	4	C3	S	Sh	T	A	M	D	I	Achene	Cypsela	Black	Beige
Coespeletia spicata (Sch. Bip. ex Wedd.) Cuatrec.	4	C3	S	Sh	T	A	M	D	I	Achene	Cypsela	Black	Beige
Coespeletia timotensis (Cuatrec.) Cuatrec.	4	C3	S	Sh	T	A	M	D	I	Achene	Cypsela	Black	Beige
Condylidium iresinoides (Kunth) R.M. King & H. Rob.	1, 5	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Conocliniopsis prasiifolia (DC.) R.M. King & H. Rob.	21	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Conyza bonariensis (L.) Cronquist	3, 5, 21	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	Beige
Delilia biflora (L) kuntze	1	C3	Ns	Ah	T	A	D	D	I	Achene	Diclesium	Black	White

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Eclipta alba (L.) Hassk.	5, 21	C3	Ns	Ah	T	A	D	D	I	Achene	Diclesium	Black	White
Egletes prostrata (Sw.) Kuntze	9, 11	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Elephantopus mollis Kunth	18, 24, 25	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	Brown
Emilia fosbergii Nicolson	1, 21	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	Beige
Erechtites hieraciifolius (L.) Raf. ex DC.	19, 20	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	Beige
Espeletia angustifolia Cuatrecasas	4	C3	S	Ph	T	A	M	D	I	Achene	Cypsela	Black	Beige
Espeletia batata Cuatrec.	4	C3	S	Ph	T	A	M	D	I	Achene	Cypsela	Black	Beige
Espeletia schultzii Wedd.	4	C3	S	Ph	T	A	M	D	I	Achene	Cypsela	Black	Beige
Espeletia semiglobulata Cuatrec.	4	C3	S	Ph	T	A	M	D	I	Achene	Cypsela	Black	Beige
Espeletia sp.	4	C3	S	Ph	T	A	M	D	I	Achene	Cypsela	Black	Beige
Espeletia sp.	4	C3	S	Ph	T	A	M	D	I	Achene	Cypsela	Black	Beige
Espeletia sp.	4	C3	S	Ph	T	A	M	D	I	Achene	Cypsela	Black	Beige
Galinsoga parviflora Cav.	1	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Gnaphalium antennarioides DC. (Fem)	28	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	Beige
Gongylolepis benthamiana R. H. Schomb.	15-17	C3	Ns	Sh	T	A	M	D	I	Achene	Cypsela	Black	White
Hypochaeris sessiliflora Kunth	4	C3	Ns	Ph	T	A	M	D	I	Achene	Cypsela	Black	White
Ichthyothere terminalis (Spreng) S.F. Blake	20	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Lagascea mollis Cav.	1	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Lasiocephalus longipenicillatus (Schultz-Bip. ex Sandw.) Cuatrec.	4	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Launaea intybacea (Jacq.) Beauverd	5	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Lepidaploa bolivarensis (V.M. Badillo) H. Rob.	15, 17	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Lepidaploa ehretiifolia (Benth.) H. Rob.	19	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Lepidaploa gracilis (Kunth) H. Rob.	19, 20	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Lepidaploa salzmannii (DC.) H. Rob.	18-20	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Libanothamnus neriifolius (Bonpl. Ex Kunth) A. Ernst.	8, 28	C3	S	Sh	T	A	M	D	I	Achene	Cypsela	Black	Beige
Mikania johnstonii B.L. Rob.	7, 21	C3	Ns	L	T	A	D	D	I	Achene	Cypsela	Black	White
Mikania micrantha Kunth	18, 27	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Mikania psilostachya DC.	15, 18	C3	Ns	L	T	A	D	D	I	Achene	Cypsela	Black	White

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Monticalia imbricatifolia (Sch. Bip. ex Wedd.) C. Jeffrey	4	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Neurolaena lobata (L.) Cass.	21	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Oyedaea verbesinoides DC.	1, 6	C3	Ns	Tr	T	A	D	D	I	Achene	Diclesium	Black	White
Parthenium hysterophorus L.	1	C4	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Pluchea symphytifolia (Mill.) Gillis	1, 5	C3	Ns	Sh	T	A	D	D	I	Achene	Cypsela	Black	White
Porophyllum leiocarpum (Urb.) Rydb.	1	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Porophyllum ruderale (Jacq.) Cass.	5	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Praxelis pauciflora (Kunth) R.M. King & H. Rob.	3, 25	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Ruilopezia atropurpurea (A.C. smith) Cuatrec.	28	C3	S	Ph	T	A	M	D	I	Achene	Cypsela	Black	Beige
Ruilopezia flocossa (Standley) Cuatrec. (feme)	28	C3	S	Ph	T	A	M	D	I	Achene	Cypsela	Black	Beige
Ruilopezia lindenii (Schultz-Bip. Ex Wedd.) Cuatrec.	28	C3	S	Ph	T	A	M	D	I	Achene	Cypsela	Black	Beige
Ruilopezia marcescens (S.F. Blake) Cuatrec.	4	C3	S	Ph	T	A	M	D	I	Achene	Cypsela	Black	Beige
Senecio formosus Kunth	4	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	Beige
Stomatochaeta condensata (Baker) Maguire & Wurdack	14-17	C3	S	Sh	T	A	M	D	I	Achene	Cypsela	Black	White
Tessaria integrifolia Ruiz & Pav.	5	C3	Ns	Sh	T	A	D	D	I	Achene	Cypsela	Black	White
Tridax procumbens L.	1, 5	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Trixis divaricata (Kunth) Spreng.	1	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Trixis inula Crantz	1	C3	Ns	Tr	T	A	D	D	I	Achene	Cypsela	Black	White
Verbesina caracasana B.L. Rob. & Greenm.	1, 24, 27	C3	Ns	Ah	T	A	D	D	I	Achene	Diclesium	Black	White
Vernonia brasiliana (L.) Druce	25, 27	C3	Ns	Ph	T	A	D	D	I	Achene	Cypsela	Black	White
Vernonia cinerea (L.) Less.	21	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Vernonia gracilis Kunth	1	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Vernonia miersiana	18	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Vernonia remotiflora Rich.	23, 25	C3	Ns	Ah	T	A	D	D	I	Achene	Cypsela	Black	White
Wedelia calycina Rich.	1, 5, 21	C3	Ns	Ph	T	A	D	D	I	Achene	Diclesium	Black	White
Wulffia stenoglossa (Cass.) DC.	21, 24	C3	Ns	L	T	A	D	F	I	Achene	Pseudodrupe	Yellow	White
AVICENNIACEAE													

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Avicennia germinans (L.) L.	10, 13	C3	Ns	Tr	T	A	M	D	D	Follicle	Follicle	Green	Green
BATACEAE													
Batis maritima L.	10, 13	C3	S	Ph	T	A	D	F	I	Infrutescence	Syncarpium	Green	Black
BEGONIACEAE													
Begonia humilis Dryand.	7	C3	Ns	Ah	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
BIGNONIACEAE													
Arrabidaea corallina (Jacq.) Sandwith	1, 5, 27	C3	Ns	L	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Arrabidaea mollissima (Kunth) Bureau & K. Schum.	22, 24	C3	Ns	L	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Arrabidaea oxycarpa Urb.	24	C3	Ns	L	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Arrabidaea pubescens (L.) A.H. Gentry	22, 24, 27	C3	Ns	L	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Digomphia laurifolia Benth.	14, 15, 17	C3	Ns	Sh	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Godmania macrocarpa (Benth.) Hemsl.	24, 25	C3	Ns	Tr	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Jacaranda mimosifolia D. Don	1	C3	Ns	Tr	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Jacaranda obtusifolia Bonpl. ssp. obtusifolia	24, 25, 27	C3	Ns	Tr	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Pithecoctenium crucigerum (L.) A.H. Gentry	27	C3	Ns	L	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Pleonotoma clematis (Kunth) Miers	3, 24	C3	Ns	L	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Tabebuia chrysantha (Jacq.) G. Nicholson	1	C3	Ns	Tr	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Tanaecium jaroba Sw.	27	C3	Ns	L	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Tecoma stans (L.) Juss. ex Kunth	1	C3	Ns	Tr	T	A	D	D	D	Silique	Ceratium	Brown	Brown
BIXACEAE													
Cochlospermum vitifolium (Willd.) Sprengel	24, 25	C3	Ns	Tr	T	A	M	D	D	Loculicidal capsule	Ceratium	Brown	Black
BONNETIACEAE													
Bonnetia sessilis Benth.	14-17	C3	Ns	Sh	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
BORAGINACEAE													
Bourreria cumanensis (Loefl.) O.E. Schulz	2, 5	C3	Ns	Tr	T	A	M	D	I	Schizocarp	Samarium	Brown	Brown
Bourreria exsucca Jacq.	12	C3	Ns	Tr	T	A	M	D	I	Schizocarp	Samarium	Brown	Brown
Cordia aristeguietae G. Agostini	6	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Red	Brown
Cordia curassavica (Jacq.) Roem. & Schult.	1, 5, 21, 24, 25	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Red	Beige
Cordia dentata Poir.	5, 27	C3	Ns	Tr	T	A	D	F	I	Drupe	Drupe	White	Beige

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Cordia globosa (Jacq.) Kunth & Andrews ex A. DC.	1, 5, 12	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Red	Beige
Cordia polycephala (Lam.) I.M. Johnst.	1, 21, 22, 25	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Red	Beige
Cordia toqueve Aublet	22, 24	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	White	Beige
Heliotropium angiospermum Murray	1, 5	C3	Ns	Ah	T	A	D	F	I	Drupe	Druparium	Brown	Brown
Heliotropium curassavicum L.	9, 11, 12	C3	S	Ph	T	A	D	F	I	Drupe	Drupe	White	Brown
Heliotropium gnaphalodes L.	9, 11, 13	C3	S	Ph	T	A	M	F	I	Drupe	Druparium	Brown	Brown
Heliotropium indicum L.	1, 9, 11, 12	C3	Ns	Ah	T	A	D	F	I	Drupe	Druparium	Brown	Brown
Heliotropium ternatum Vahl.	5	C4	Ns	Ph	T	A	D	F	I	Drupe	Drupe	Brown	Brown
Rochefortia spinosa (Jacq.) Urb.	5, 27	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Tournefortia maculata Jacq.	24	C3	Ns	L	T	A	M	F	I	Drupe	Drupe	Black+ Yellow	Black
Tournefortia volubilis L.	1, 5, 21	C3	Ns	L	T	A	M	F	I	Drupe	Drupe	White+Black	Black
BRASSICACEAE													
Draba chionophila S.F. Blake	4	C3	S	Ph	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Draba funckeana Linden & Planch.	4	C3	Ns	Ph	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Lepidium bipinnatifidium Desv.	4	C3	Ns	Ph	T	A	D	D	D	Silique	Ceratium	Brown	Orange
Lepidium virginicum L.	1	C3	Ns	Ph	T	A	D	D	D	Silique	Ceratium	Brown	Orange
BROMELIACEAE													
Aechmea fendleri André	7, 21	CAM	S	Ph	E	A	M	F	I	Berry	Bacca	Blue	Brown
Aechmea lasseri L.B. Sm.	7	CAM	S	Ph	E	A	M	F	I	Berry	Bacca	Blue	Brown
Brocchinia acuminata L.B. Sm.	15	C3	S	Ph	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Brocchinia reducta Baker	15-17	C3	Ns	Ph	T	I	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Brocchinia steyermarkii L.B. Sm.	14	C3	S	Ph	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Bromelia chrysantha Jacq.	22, 27	CAM	S	Ph	T	A	M	F	I	Berry	Bacca	Yellow	Black
Catopsis berteroniana (Schult. & Schult. f.) Mez	16, 17	C3	Ns	Ph	E	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Catopsis nutans (Sw.) Griseb	7	C3	Ns	Ph	E	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Glomeropitcairnia erectiflora Mez	21	C3	S	Ph	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Guzmania nubigena L.B. Sm.	7	C3	S	Ph	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown

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Lindmania geniculata L.B. Sm. var. geniculata	17	C3	S	Ph	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Lindmania guianensis (Beer) Mez	14-17	C3	S	Ph	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Pitcairnia altensteinii (Lk.,Kl. & Otto) Lem.	7	C3	Ns	Ph	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Tillandsia balbisiana Schult. f.	1, 2	CAM	S	Ph	E	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Tillandsia circinnata Schltdl.	5	CAM	S	Ph	E	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Tillandsia complanata Benth.	6, 7	CAM	Ns	Ph	E	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Tillandsia elongata Kunth var. subimbricata (Baker) L.B. Sm.	2	CAM	Ns	Ph	E	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Tillandsia flexuosa Sw.	1, 5, 16, 27	CAM	S	Ph	E	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Tillandsia funckiana Baker	31	C3	Ns	Ph	E	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Tillandsia recurvata (L.) L.	1,5	CAM	S	Ph	E	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Tillandsia schiedeana Steud	29	CAM	S	Ph	E	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Tillandsia utriculata L.	1	CAM	S	Ph	E	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Tillandsia variabilis Schltdl.	1	CAM	Ns	Ph	E	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Vriesea platynema Gaudich.	7	C3	Ns	Ph	E	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Vriesea splendens (Brongn.) Lem.	7	C3	Ns	Ph	E	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Vriesea tequendamae (Andrè) L.B. Sm.	30	C3	Ns	Ph	E	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
BURMANNIACEAE													
Burmannia bicolor Mart.	14	C3	Ns	Ah	T	A	M	D	D	Poricidal capsule	Poricidal capsule	Brown	Brown
BURSERACEAE													
Bursera simaruba (L.) Sarg.	1, 2	C3	Ns	Tr	T	A	M	F	I	Pseudodrupe	Nuculanium	Green+Red	White
Protium heptaphyllum (Aubl.) Marchand	3, 22	C3	Ns	Tr	T	A	M	F	I	Pseudodrupe	Nuculanium	Green+Red	White
Protium unifoliolatum Engl.	3	C3	Ns	Tr	T	A	M	F	I	Pseudodrupe	Nuculanium	Green+Red	White
CACTACEAE													
Cereus hexagonus (L.) Mill.	1, 22	CAM	S	Tr	T	A	M	F	I	Berry	Acrosarcum	Brown	Black
Cereus horrispinus (Backeb.) Backeb.	12	CAM	S	L	T	A	M	F	I	Berry	Acrosarcum	Pink	Black
Epiphyllum phyllanthus (L.) Haw.	3, 7	CAM	S	Ph	E	A	M	F	D	Berry	Acrosarcum	Pink	Black

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Mammillaria mammillaris (L.) H. Karst.	5	CAM	S	Ph	T	A	M	F	I	Berry	Acrosarcum	Red	Black
Melocactus andinus R. Gruber ex N. P. Taylor	32	CAM	S	Ph	T	A	M	F	I	Berry	Acrosarcum	Pink	Black
Melocactus curvispinus Pfeiff. (herma)	5, 9, 12	CAM	S	Ph	T	A	M	F	I	Berry	Acrosarcum	Pink	Black
Melocactus schatzlii W. Till & R. Gruber	31	CAM	S	Ph	T	A	M	F	I	Berry	Acrosarcum	Pink	Black
Opuntia caracasana Salm-Dyck	5, 9, 12	CAM	S	Ph	T	A	D	F	I	Berry	Acrosarcum	Yellow	Black
Opuntia elatior Mill.	5	CAM	S	Sh	T	A	M	F	I	Berry	Acrosarcum	Yellow	Black
Pereskia guamacho F.A.C. Weber	5, 12	CAM	S	Tr	T	A	M	F	I	Berry	Acrosarcum	Green	Black
Pilosocereus lanuginosus (L.) Byles & G.D. Rowley	12	CAM	S	Tr	T	A	M	F	I	Berry	Acrosarcum	Green	Black
Pilosocereus moritzianus (Otto) Byles & G.D. Rowley	5	CAM	S	Tr	T	A	M	F	I	Berry	Acrosarcum	Pink	Black
Rhipsalis floccosa Salm-Dyck ex Pfeiff. ssp. pittieri (Britton & Rose) Barthlott & N.P. Taylor	6, 7	CAM	S	Ph	E	A	M	F	I	Berry	Acrosarcum	White	Black
Stenocereus griseus (Haw.) Buxb.	5	CAM	S	Tr	T	A	M	F	I	Berry	Acrosarcum	Pink	Black
Subpilocereus repandus (L.) Backeb.	12, 22	CAM	S	Tr	T	A	M	F	I	Berry	Acrosarcum	Green	Black
CALOPHYLLACEAE													
Caraipa llanorum Cuatrec.	3	C3	Ns	Tr	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Mahurea exstipitata Benth.	3, 18	C3	Ns	Tr	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
CAMPANULACEAE													
Centropogon cornutus (L) Druce	7, 18, 21	C3	Ns	Ah	T	A	D	F	I	Berry	Bacca	Red	Beige
Hippobroma longiflora (L) G.Don	21	C3	Ns	Ph	T	A	D	D	D	Poricidal capsule	Poricidal capsule	Green	Beige
Syphocampylus reticulatus (Willd. Ex Roem. & Schult.)	6, 7	C3	Ns	Ph	T	A	M	D	D	Poricidal capsule	Poricidal capsule	Green	Black
CANNABACEAE													
Celtis iguanaea (Jaqc.) Sarg.	1, 2	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Yellow	Brown
Trema micrantha (L.) Blume	3, 6	C3	Ns	Tr	T	A	D	F	I	Drupe	Drupe	Red	Black
CAPPARACEAE													
Capparis flexuosa (L.) L.	1, 2, 5	C3	Ns	Sh	T	A	M	F	D	Silique	Ceratium	Green+Red	White+ Black
Capparis hastata Jacq.	5, 27	C3	Ns	Sh	T	A	M	F	D	Silique	Ceratium	Green+Red	White+ Black

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Capparis odoratissima Jacq.	5	C3	Ns	Sh	T	A	M	D	D	Silique	Ceratium	Brown	Black+Red
Capparis tenuisiliqua Jacq.	2, 5	C3	Ns	Sh	T	A	M	D	D	Silique	Ceratium	Green	Brown+ White
Capparis verrucosa Jacq.	1, 5	C3	Ns	Sh	T	A	M	F	D	Silique	Ceratium	Green+Red	Brown+ White
CAPRIFOLIACEAE													
Valeriana phylicoides (Turcz.) Briq. (H)	4	C3	Ns	Sh	T	A	M	D	I	Achene	Cypsela	Brown	Brown
CARYOCARACEAE													
Caryocar microcarpum Ducke	3	C3	Ns	Tr	T	A	M	F	I	Drupe	Druparium	Brown	Brown
CARYOPHYLLACEAE													
Arenaria jahnii S.F. Blake	4	C3	Ns	Ph	T	A	M	D	D	Poricidal capsule	Poricidal capsule	Brown	Brown
Cerastium cephalanthum S.F. Blake	4	C3	Ns	Ah	T	A	M	D	D	Loculicidal capsule	Denticidal Capsule	Brown	Brown
CELASTRACEAE													
Cheiloclinium belizense (Standl.) A.C. Sm.	3	C3	Ns	L	T	A	M	F	I	Drupe	Drupe	Yellow	Brown
Maytenus karstenii Reissek	21	C3	Ns	Sh	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Orange	Black
Peritassa laevigata (Hoffmanns. ex Link) A.C. Sm.	3	C3	Ns	L	T	A	M	F	I	Drupe	Drupe	Yellow	Brown
CHRYSOBALANACEAE													
Couepia paraensis (Mart. & Zucc.) Benth. ex Hook. f.	3	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Yellow	Brown
Hirtella scabra Benth	16	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Licania heteromorpha Benth.	3	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Yellow	Brown
Licania membranacea Sagot ex Laness.	21	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Brown	Brown
Licania pyrifolia Griseb.	22, 27	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Brown	Brown
CLEOMACEAE													
Cleome aculeata L.	42	C3	Ns	Ah	T	A	D	D	D	Silique	Ceratium	Brown	Brown
Cleome anomala Kunth	43	C3	Ns	Sh	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Cleome arborea Schrad.	49	C3	Ns	Sh	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Cleome gynandra L.	48	C3	Ns	Ah	T	A	D	D	D	Silique	Ceratium	Brown	Brown
Cleome moritziana Klotzsch ex Eichler	6	C3	Ns	Ph	T	A	D	D	D	Silique	Ceratium	Brown	Brown
Cleome pilosa Benth.	7	C3	Ns	Ah	T	A	D	D	D	Silique	Ceratium	Brown	Brown
Cleome rutidosperma DC.	47	C3	Ns	Ah	T	A	D	D	D	Silique	Ceratium	Brown	Brown
Cleome speciosa Raf.	44	C3	Ns	Ah	T	A	D	D	D	Silique	Ceratium	Brown	Brown
Cleome spinosa Jacq.	1, 2, 27	C3	Ns	Ah	T	A	D	D	D	Silique	Ceratium	Brown	Brown
Cleome stenophylla Klotzsch ex Urb.	45	C3	Ns	Ah	T	A	D	D	D	Silique	Ceratium	Brown	Brown

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Cleome torticarpa Iltis & T. Ruiz Zapata	46	C3	Ns	Ph	T	A	D	D	D	Silique	Ceratium	Brown	Brown
Cleome viridiflora Schreb.	50	C3	Ns	Tr	T	A	M	D	D	Silique	Ceratium	Brown	Brown
Cleome viscosa L.	27	C3	Ns	Ah	T	A	D	D	D	Silique	Ceratium	Brown	Brown
CLUSIACEAE													
Clusia aff. brachystyla Maguire	17	C3	S	Sh	T	A	M	F	D	Septicidal capsule	Septicidal capsule	Red	Orange
Clusia alata Planch. & Triana	21	CAM	S	Sh	T	A	M	F	D	Septicidal capsule	Septicidal capsule	Red	Orange
Clusia columnaris Engl.	3, 18	C3	Ns	Tr	T	A	M	F	D	Septicidal capsule	Septicidal capsule	Green	Orange
Clusia fockeana Miq.	16, 17	C3	Ns	Tr	T	A	M	F	D	Septicidal capsule	Septicidal capsule	Green	Orange
Clusia grandiflora Splitg.	15, 18	C3	Ns	Tr	T	A	D	F	D	Septicidal capsule	Septicidal capsule	Green	Orange
Clusia minor L.	1, 21	CAM	S	Tr	T	A	D	F	D	Septicidal capsule	Septicidal capsule	Green	Orange
Clusia multiflora Kunth	6	C3	S	Tr	T	A	M	F	D	Septicidal capsule	Septicidal capsule	Purple-black	Orange
Clusia pusilla Steyerm. ssp. Pusilla	15, 17	C3	S	Sh	T	A	M	F	D	Septicidal capsule	Septicidal capsule	Green	Orange
Clusia schomburgkiana (Planch. & Triana) Benth. ex Engl.	17, 18	CAM	Ns	Tr	T	A	M	F	D	Septicidal capsule	Septicidal capsule	Green	Orange
Tovomita speciosa Ducke	3	C3	Ns	Tr	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
COMBRETACEAE													
Buchenavia reticulata Eichler	3	C3	Ns	Tr	T	A	M	F	I	Pseudodrupe	Pseudodrupe	Brown	Brown
Combretum decandrum Jacq.	27	C3	Ns	L	T	A	D	D	I	Samara	Diclesium	Brown	Brown
Combretum fruticosum (Loefl.) Stuntz	3, 24, 27	C3	Ns	L	T	A	D	D	I	Samara	Diclesium	Brown	Brown
Conocarpus erectus L.	11, 12, 13	C3	Ns	Tr	T	A	M	D	I	Achene	Achenoconum	Brown	Brown
Laguncularia racemosa (L.) C.F. Gaertn	10, 13	C3	Ns	Tr	T	A	M	D	I	Drupe	Diclesium	Green	Green
COMMELINACEAE													
Commelina erecta L.	1, 5	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Setcreasea purpurea Boom	1	C3	S	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Tradescantia zanonia (L.) Sw.	7	C3	Ns	Ph	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
CONNARACEAE													
Connarus venezuelanus Baill.	3, 24, 27	C3	Ns	Tr	T	A	M	D	D	Follicle	Follicle	Brown	Black+ Yellow
CONVOLVULACEAE													

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Convolvulus nodiflorus Desr.	1, 5	C3	Ns	L	T	A	D	D	D	Septifragal capsule	Septifragal capsule	Brown	Brown
Evolvulus tenuis Mart. ex Choisy ssp. longifolius (Choisy) Ooststr.	1	C3	Ns	Ph	T	A	D	D	D	Septifragal capsule	Septifragal capsule	Brown	Brown
Evolvulus tenuis Mart. ex Choisy ssp. sericatus (House) Ooststr.	5	C3	Ns	Ph	T	A	D	D	D	Septifragal capsule	Septifragal capsule	Brown	Brown
Ipomoea avicola D.F. Austin	5	C3	Ns	L	T	A	D	D	D	Septifragal capsule	Septifragal capsule	Brown	Brown
Ipomoea carnea Jacq.	2, 9, 11, 27	C3	Ns	Sh	T	A	D	D	D	Septifragal capsule	Septifragal capsule	Brown	Brown
Ipomoea pes-caprae (L.) R. Br.	9, 11	C3	Ns	L	T	A	M	D	D	Septifragal capsule	Septifragal capsule	Brown	Brown
Ipomoea sericophylla Meisn.	24, 25	C3	Ns	L	T	A	M	D	D	Septifragal capsule	Septifragal capsule	Brown	Brown
Ipomoea trifida (Kunth) G. Don	23, 24, 27	C3	Ns	L	T	A	D	D	D	Septifragal capsule	Septifragal capsule	Brown	Brown
Jacquemontia cumanensis Kuntze	5	C3	Ns	L	T	A	D	D	D	Septifragal capsule	Septifragal capsule	Brown	Brown
Jacquemontia pentantha (Jacq.) G. Don	24	C3	Ns	L	T	A	D	D	D	Septifragal capsule	Septifragal capsule	Brown	Brown
Jacquemontia tamnifolia (L.) Griseb.	23	C3	Ns	L	T	A	D	D	D	Septifragal capsule	Septifragal capsule	Brown	Brown
Merremia macrocalyx (Ruiz & Pavon) O`Donnell	6	C3	Ns	L	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Merremia umbellata (L.) Hall	5	C3	Ns	L	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Operculina alata Urb.	25	C3	Ns	L	T	A	D	D	I	Pyxidium	Foramicidal capsule	Brown	Brown
COSTACEAE													
Costus comosus (Jacq.) Roscoe	2, 27	C3	Ns	Ph	T	A	M	F	D	Loculicidal capsule	Loculicidal capsule	White	White+ Black
Costus spiralis (Jacq.) Roscoe	3, 7	C3	Ns	Ph	T	A	M	F	D	Loculicidal capsule	Loculicidal capsule	White	White+ Black
CRASSULACEAE													
Echeveria columbiana Poelln.	4, 8	CAM	S	Ah	T	A	M	D	D	Agregate of follicle	Follicarium	Brown	Brown
Kalanchoe daigremontiana Raym.-Hamet & H. Perrier	1	CAM	S	Ah	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
Kalanchoe pinnata (Lam.) Pers.	1	CAM	S	Ah	T	A	D	D	D	Agregate of follicle	Follicarium	Brown	Brown
CUCURBITACEAE													
Cayaponia racemosa (Mill.) Cogn.	24	C3	Ns	L	T	A	D	F	I	Pepo	Pepo	Yellow	Brown
Ceratosanthes palmata(L) Urb.	1, 2	C3	Ns	L	T	A	D	F	I	Pepo	Pepo	Purple-black	Green
Cucumis dipsaceus Ehrenb.	5	C3	Ns	L	T	A	D	F	I	Pepo	Pepo	Yellow	Brown

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Melothria trilobata Cogn.	27	C3	Ns	L	T	A	D	F	I	Pepo	Pepo	Purple-black	Black
Momordica charantia L.	2, 23	C3	Ns	L	T	A	D	F	D	Pepo	Pepo	Yellow	Red
Psiguria umbrosa (Kunth) C. Jeffrey	2	C3	Ns	L	T	A	D	F	I	Pepo	Pepo	Purple-black	Beige
CYCLANTHACEAE													
Asplundia caput-medusae (Hook. f.) Harling	7	C3	Ns	Ph	T	A	M	F	I	Berry	Sorosus	Green	Beige
Asplundia fendleri Harling	7	C3	Ns	Ph	T	A	M	F	I	Berry	Sorosus	Green	Beige
Asplundia moritziana (Klotzsch) Harling	7	C3	Ns	L	T	A	M	F	I	Berry	Sorosus	Green	Beige
Asplundia sp.	7	C3	Ns	L	T	A	M	F	I	Berry	Sorosus	Green	Beige
Cyclanthus bipartitus Poit. ex A. Rich.	3, 7	C3	Ns	Ph	T	A	M	F	D	Berry	Trymoconum	Green	Brown
Evodianthus funifer (Poit.) Lindm.	7	C3	Ns	L	T	A	M	F	I	Berry	Trymoconum	Green	Brown
CYPERACEAE													
Bulbostylis conifera (Kunth) C.B.Clarke	19, 25	C4	Ns	Ph	T	A	M	D	I	Achene	Pseudoanthecium	Brown	Beige
Bulbostylis junciformis (Kunth) C.B. Clarke	15, 23	C4	Ns	Ph	T	A	D	D	I	Achene	Pseudoanthecium	Brown	Brown
Bulbostylis lanata (Kunth) Lindm.	17, 19, 20	C4	Ns	Ph	T	A	D	D	I	Achene	Pseudoanthecium	Brown	Beige
Bulbostylis paradoxa (Spreng.) Lindm.	19	C4	Ns	Ph	T	A	M	D	I	Achene	Pseudoanthecium	Brown	Beige
Cephalocarpus rigidus Gilly	15	C3	Ns	Ph	T	A	M	D	I	Achene	Pseudoanthecium	Brown	Beige
Cyperus aggregatus (Willd) Endl	18	C4	Ns	Ph	T	A	D	D	I	Achene	Pseudoanthecium	Brown	Brown
Cyperus surinamensis Rottb.	3, 21, 27	C4	Ns	Ah	T	A	D	D	I	Achene	Pseudoanthecium	Brown	Beige
Eleocharis geniculata (L.) Roem. & Schult.	21	C3	Ns	Ah	T	A	M	D	I	Achene	Pseudoanthecium	Black	Beige
Fimbristylis annua (All.) Roem. & Schult.	23	C4	Ns	Ah	T	A	D	D	I	Achene	Pseudoanthecium	Brown	Beige
Fimbristylis cymosa R. Br.	13	C4	Ns	Ph	T	A	M	D	I	Achene	Pseudoanthecium	Brown	Brown
Hypolytrum pulchrum (Rudge) H. Pfeiff.	14, 19	C3	Ns	Ph	T	A	M	D	I	Achene	Pseudoanthecium	Brown	Beige
Lagenocarpus rigidus Kunth (Ness)	14-17, 19	C4	Ns	Ph	T	A	M	D	I	Achene	Pseudoanthecium	Brown	Brown
Rhynchospora barbata (Vahl.) Kunth	14, 15, 18, 19, 26	C4	Ns	Ph	T	A	D	D	I	Achene	Pseudoanthecium	Brown	Beige
Rhynchospora caracasana (Kunth) Boeckeler	19	C3	Ns	Ph	T	A	M	D	I	Achene	Pseudoanthecium	Brown	Beige
Rhynchospora curvula Griseb.	19	C4	Ns	Ah	T	A	M	D	I	Achene	Pseudoanthecium	Brown	Beige
Rhynchospora exaltata Kunth	15	C4	Ns	Ph	T	A	D	D	I	Achene	Pseudoanthecium	Brown	Beige

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Rhynchospora filiformis Vahl.	14	C3	Ns	Ah	T	A	M	D	I	Achene	Pseudoanthecium	Brown	Beige
Rhynchospora globosa (Kunth) Roem. & Schult.	14, 19, 26	C4	Ns	Ph	T	A	M	D	I	Achene	Pseudoanthecium	Brown	Beige
Rhynchospora marisculus Lindl. ex Nees	14, 21	C4	Ns	Ah	T	A	D	D	I	Achene	Pseudoanthecium	Brown	Brown
Rhynchospora mexicana (Liebm.) Steud.	19	C4	Ns	Ph	T	A	M	D	I	Achene	Pseudoanthecium	Brown	Brown
Rhynchospora nervosa (Vahl) Boeckeler	24	C4	Ns	Ph	T	A	M	D	I	Achene	Pseudoanthecium	Brown	Beige
Rhynchospora pilosa (kunth) Boeckeler	14, 16, 17, 19	C3	Ns	Ph	T	A	D	D	I	Achene	Pseudoanthecium	Brown	Beige
Rhynchospora rugosa (Vahl) Gale	19, 20, 21	C3	Ns	Ph	T	A	D	D	I	Achene	Pseudoanthecium	Brown	Beige
Rhynchospora tenuis Willd. ex Link	17	C3	Ns	Ph	T	A	D	D	I	Achene	Pseudoanthecium	Brown	Beige
Rhynchospora velutina (Kunth) Boeckeler	19, 26	C4	Ns	Ph	T	A	D	D	I	Achene	Pseudoanthecium	Brown	Beige
Scleria bracteata Cav.	21	C3	Ns	Ph	T	A	M	D	I	Achene	Glans	Purple-black	Beige
Scleria cyperina Willd. ex Kunth	3, 14, 15, 17, 19, 20	C3	Ns	Ph	T	A	M	D	I	Achene	Glans	White	Beige
Scleria distans Poir.	19	C3	Ns	Ph	T	A	D	D	I	Achene	Pseudoanthecium	Brown	Beige
Scleria latifolia Sw.	7	C3	Ns	Ph	T	A	D	D	I	Achene	Glans	Purple-black	Beige
Scleria melaleuca Rchb. ex Schltdl. & Cham.	24, 27	C3	Ns	Ph	T	A	D	D	I	Achene	Glans	White	Beige
CYRILLACEAE													
Cyrilla racemiflora L.	14, 15, 16, 17	C3	Ns	Ph	T	A	M	F	I	Drupe	Drupe	White	Beige
DILLENIACEAE													
Curatella americana L.	24, 25	C3	Ns	Tr	T	A	M	D	D	Agregate of follicle	Camaretum	Green+Red	White+ Black
Tetracera volubilis L.	27	C3	Ns	L	T	A	M	D	D	Agregate of follicle	Coccetum	Green+Red	White+ Black
DIOSCOREACEAE													
Dioscorea pilosiuscula Bertero ex Spreng.	24, 25	C3	Ns	L	T	A	D	D	D	Loculicidal capsule	Denticidal Capsule	Brown	Brown
Dioscorea trifoliata Kunth	1	C3	Ns	L	T	A	D	D	D	Loculicidal capsule	Denticidal Capsule	Brown	Brown
DROSERACEAE													
Drosera felix Steyerm. & L.B. Sm.	14, 15, 19	C3	Ns	Ph	T	I	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Drosera roraimae (Klotzsch ex Diels) Maguire & J.R. Laundon	14, 15, 19	C3	Ns	Ph	T	I	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
ERICACEAE													
Befaria sprucei Meisn.	6, 15-18	C3	Ns	Sh	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown

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Notopora schomburgkii Hook. f.	15-17	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Brown	Brown
Vaccinium euryanthum A.C. Sm.	15-17	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Beige
Vaccinium latifolium (Griseb.) Benth. & Hook. f.	21	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Beige
Vaccinium puberulum var. subcrenulatum (Klotzsch ex Meissner) Maguire, Steyerm. & Luteyn	15	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Beige
Vaccinium puberulum Klotzsch ex Meisn.	16, 17	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Beige
ERIOCAULACEAE													
Leiothrix flavescens (Bong.) Ruhland	14	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Beige
Paepalanthus dichotomus Klotzsch ex Körn.	14, 16, 17	C3	Ns	Ph	T	A	M	D	I	Indehiscent capsule	Carcerulus	Brown	Beige
Syngonanthus caulescens (Poir.) Ruhland	26	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Beige
Syngonanthus pakaraimensis Mold. var. Pakaraimensis	14-16	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Beige
Syngonanthus xeranthemoides (Bong.) Ruhland	14-17, 26	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Beige
ERYTHROXYLACEAE													
Erythroxylum amazonicum Peyr.	6	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Red	Brown
Erythroxylum citrifolium A. St.-Hil.	18	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Red	Beige
Erythroxylum cumanense Kunth	1	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Red	Beige
Erythroxylum densum Rusby	1	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Red	Beige
Erythroxylum havanense Jacq.	1, 2, 27	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Red	Beige
Erythroxylum orinocense Kunth	1, 22, 24, 27	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Red	Beige
Erythroxylum undulatum Plowman	1	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Red	Beige
EUPHORBIACEAE													
Acalypha cuspidata Jacq.	5	C3	Ns	Ph	T	A	M	D	D	Schizocarp	Coccarium	Brown	Brown
Acalypha macrostachya Jacq.	2	C3	Ns	Ph	T	A	M	D	D	Schizocarp	Coccarium	Brown	Brown
Caperonia palustris (L.) A. St.-Hil.	26, 27	C3	Ns	Ph	T	A	D	D	D	Schizocarp	Coccarium	Green	Brown

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Chaetocarpus schomburgkianus (Kuntze) Pax & K. Hoffm.	17, 18	C3	Ns	Tr	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Black+Red
Chamaesyce dioeca (Kunth) Millsp.	21	C4	Ns	Ah	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Chamaesyce hyssopifolia (L.) Small	1, 5, 23, 25	C4	Ns	Ah	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Chamaesyce lasiocarpa (Klotzsch) Arthur	21	C4	Ns	Ah	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Chamaesyce mesembryanthemifolia (Jacq.) Dugand	5, 9, 11, 13	C4	Ns	Ph	T	A	M	D	D	Schizocarp	Coccarium	Brown	Brown
Chamaesyce sp	13	C4	Ns	Ph	T	A	M	D	D	Schizocarp	Coccarium	Brown	Brown
Chamaesyce thymifolia (L.) Millsp.	21	C4	Ns	Ah	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Cnidoscolus urens (L.) Arthur	5, 9, 11, 12	C3	Ns	Ph	T	A	M	D	D	Schizocarp	Coccarium	Brown	Brown
Croton bredemeyeri Müll. Arg.	1	C3	Ns	Sh	T	A	M	D	D	Schizocarp	Coccarium	Brown	Brown
Croton conduplicatus Kunth	1	C3	Ns	Sh	T	A	M	D	D	Schizocarp	Coccarium	Brown	Brown
Croton flavens L .	9, 11, 12	C3	Ns	Ph	T	A	M	D	D	Schizocarp	Coccarium	Brown	Brown
Croton fragilis Kunth	1	C3	Ns	Sh	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Croton gossypiifolius Vahl	6	C3	Ns	Tr	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Croton hircinus Vent.	21	C3	Ns	Ph	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Croton hirtus L'Hér.	24, 26	C3	Ns	Ah	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Croton lobatus L.	5, 9, 11, 23	C3	Ns	Ah	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Croton ovalifolius Vahl	5	C3	Ns	Ph	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Croton punctatus Jacq.	9, 11, 12	C3	Ns	Ph	T	A	M	D	D	Schizocarp	Coccarium	Brown	Brown
Croton pungens Jacq.	1	C3	Ns	Sh	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Croton scaber Willd.	1	C3	Ns	Sh	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Croton trinitatis Millsp.	23	C3	Ns	Ah	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Dalechampia scandens L.	1, 24, 25, 27	C3	Ns	L	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Euphorbia cyathophora Murray	1	CAM	S	Ah	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Euphorbia gollmeriana Klotzsch ex Boiss.	5	CAM	S	Ph	T	A	D	D	D	Schizocarp	Coccarium	Yellow	Brown
Euphorbia graminea Jacq.	5	C3	Ns	Ah	T	A	D	D	D	Schizocarp	Coccarium	Yellow	Brown
Euphorbia heterophylla L.	1, 5	C3	S	Ah	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Hura crepitans L.	1, 2	C3	Ns	Tr	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Jatropha gossypifolia L.	5, 9, 11, 12	C3	Ns	Sh	T	A	M	D	D	Schizocarp	Coccarium	Brown	Brown
Pedilanthus tithymaloides (L.) Poit.	5	CAM	S	Ph	T	A	M	D	D	Schizocarp	Coccarium	Brown	Brown
Ricinus communis L.	1, 5	C3	Ns	Sh	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Tetrorchidium rubrivenium Poepp.	6, 7	C3	Ns	Tr	T	A	M	D	D	Schizocarp	Coccarium	Green	Red

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EUPHRONIACEAE												
Euphronia guianensis (R. H. Schomb.) Hallier f.	15-17	C3	Ns	Tr	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Green	Brown
FABACEAE												
Abarema ferruginea (Benth.) Pittier	17	C3	Ns	Tr	T	A	M	D	D	Legume	Legume	Green+Red	Blue
Abarema jupunba (Willd.) Britton & Killip	18	C3	Ns	Tr	T	A	D	D	D	Legume	Legume	Green+Red	Blue
Abrus precatorius L.	22, 24	C3	Ns	L	T	A	D	D	D	Legume	Legume	Brown	Black+Red
Acacia cf. farnesiana (L.) Willd.	27	C3	Ns	Tr	T	A	D	D	I	Indehiscent pod	Camara	Black	Brown
Acacia glomerosa Benth.	1, 2, 22	C3	Ns	Tr	T	A	M	D	I	Indehiscent pod	Camara	Brown	Brown
Acacia macracantha H. & B. ex Willd.	1, 27	C3	Ns	Tr	T	A	D	D	I	Indehiscent pod	Camara	Black	Brown
Acacia paniculata Willd.	1	C3	Ns	Tr	T	A	D	D	I	Indehiscent pod	Camara	Brown	Brown
Acacia tortuosa (L.) Willd.	5, 9, 11, 12	C3	Ns	Tr	T	A	D	D	I	Indehiscent pod	Camara	Black	Brown
Aeschinomene sp.	27	C3	Ns	Ah	T	A	D	D	I	Loment	Loment	Brown	Brown
Aeschynomene pratensis var. Caribaea Rudd	26	C3	Ns	Ah	T	A	D	D	I	Loment	Loment	Brown	Brown
Aeschynomene rudis Benth.	23	C3	Ns	Ah	T	A	D	D	I	Loment	Loment	Brown	Brown
Albizia lebbeck (L.) Benth.	27	C3	Ns	Tr	T	A	D	D	I	Indehiscent pod	Camara	Beige	Brown
Albizia pistaciifolia (Willd.) Barneby & J.W. Grimes	27	C3	Ns	Tr	T	A	D	D	I	Indehiscent pod	Camara	Beige	Brown
Bauhinia aculeata L.	1	C3	Ns	Tr	T	A	D	D	D	Legume	Legume	Brown	Brown
Bauhinia glabra Jacq.	1	C3	Ns	L	T	A	M	D	D	Legume	Legume	Brown	Brown
Bauhinia guianensis Aubl.	38	C3	Ns	L	T	A	M	D	D	Legume	Legume	Brown	Brown
Bauhinia multinervia (Kunth) DC.	37	C3	Ns	Tr	T	A	M	D	D	Legume	Legume	Brown	Brown
Bauhinia outimouta Aubl.	39	C3	Ns	L	T	A	M	D	D	Legume	Legume	Brown	Brown
Bauhinia pauletia Pers.	2	C3	Ns	Tr	T	A	D	D	D	Legume	Legume	Brown	Brown
Bauhinia purpurea L.	1	C3	Ns	Tr	T	A	D	D	D	Legume	Legume	Brown	Brown
Bauhinia rutilans Spruce ex Benth.	7	C3	Ns	L	T	A	M	D	D	Legume	Legume	Brown	Brown
Bauhinia siqueiraei Ducke	39	C3	Ns	Tr	T	A	M	D	D	Legume	Legume	Brown	Brown
Bauhinia ungulata L.	3, 22,24, 27	C3	Ns	Tr	T	A	M	D	D	Legume	Legume	Brown	Brown
Bowdichia virgilioides Kunth	22,24	C3	Ns	Tr	T	A	M	D	I	Indehiscent pod	Camara	Brown	Brown
Brownea birschellii Hook. f.	2	C3	Ns	Tr	T	A	M	D	D	Legume	Legume	Brown	Brown
Caesalpinia coriaria (Jacq.) willd.	2, 27	C3	Ns	Tr	T	A	D	D	I	Indehiscent pod	Camara	Brown	Brown

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Calliandra glomerulata H. Karst.	1	C3	Ns	Tr	T	A	D	D	D	Legume	Legume	Brown	Brown
Calliandra pakaraimensis R.S. Cowan	16	C3	Ns	L	T	A	M	D	D	Legume	Legume	Brown	Brown
Calliandra rigida Benth. (herma)	35	C3	Ns	Sh	T	A	D	D	D	Legume	Legume	Brown	Brown
Calliandra riparia Pittier	1	C3	Ns	Tr	T	A	D	D	D	Legume	Legume	Brown	Brown
Calopogonium mucunoides Desv.	24, 25, 27	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Brown
Campsiandra laurifolia Benth.	3	C3	Ns	Tr	T	A	M	D	D	Legume	Legume	Brown	Brown
Canavalia ensiformis (L.) DC.	27	C3	Ns	L	T	A	D	D	D	Legume	Legume	Beige	Brown
Cassia moschata Kunth	3, 22, 24, 27	C3	Ns	Tr	T	A	M	D	I	Indehiscent pod	Camara	Brown	Brown
Centrolobium paraense Tul.	22	C3	Ns	Tr	T	A	M	D	I	Samara	Samara	Brown	Brown
Centrosema brasilianum (L.) Benth.	5	C3	Ns	L	T	A	D	D	D	Legume	Legume	Brown	Brown
Centrosema plumieri (Turpin ex Pers.) Benth.	27	C3	Ns	L	T	A	D	D	D	Legume	Legume	Brown	Brown
Centrosema pubescens Benth.	24, 25	C3	Ns	L	T	A	D	D	D	Legume	Legume	Brown	Brown
Centrosema virginiana Benth.	1	C3	Ns	L	T	A	D	D	D	Legume	Legume	Brown	Brown
Cercidium praecox (Ruiz & Pav. ex Hook.) Harms	9, 11, 12	C3	Ns	Tr	T	A	M	D	I	Indehiscent pod	Camara	Brown	Brown
Chaetocalyx scandens (L.) Urb.	1, 5	C3	Ns	L	T	A	D	D	I	Loment	Loment	Brown	Brown
Chamaecrista cultrifolia Britton & Rose ex Britton & Killip	24, 25	C3	Ns	Ph	T	A	D	D	D	Legume	Legume	Brown	Brown
Chamaecrista desvauxii (Benth.) H.S. Irwin & Barneby	16, 17, 19	C3	Ns	Ph	T	A	M	D	D	Legume	Legume	Brown	Brown
Chamaecrista diphylla (L.) Greene	24	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Brown
Chamaecrista flexuosa (L.) Greene	25	C3	Ns	Ph	T	A	D	D	D	Legume	Legume	Brown	Brown
Chamaecrista nictitans var. pilosa (Benth.) H.S. Irwin & Barneby	1, 6	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Brown
Chamaecrista nictitans ??? var. patellaria (DC. ex Collad.) Kartesz & Gandhi	23, 24	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Brown
Chamaecrista ramosa (Vogel) H.S. Irwin & Barneby	16	C3	Ns	Ph	T	A	M	D	D	Legume	Legume	Brown	Brown
Chamaecrista serpens (L.) Greene	23	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Brown

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Chamaecrista sp.	21	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Brown
Chloroleucon mangense (Jacq.) Britton & Rose	1	C3	Ns	Tr	T	A	M	D	D	Legume	Legume	Brown	Brown
Clitoria guianensis (Aubl.) Benth.	25	C3	Ns	Ph	T	A	D	D	D	Legume	Legume	Brown	Brown
Copaifera pubiflora Benth.	22, 27	C3	Ns	Tr	T	A	M	D	D	Legume	Legume	Brown	White+
Black													
Coursetia caribaea (Jack.) Lavin	1, 5	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Brown
Coursetia ferruginea (Kunth) Lavin	1	C3	Ns	Tr	T	A	M	D	D	Legume	Legume	Brown	Brown
Crotalaria incana L.	1, 5, 9	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Black
Crotalaria micans Link	6	C3	Ns	Ph	T	A	D	D	D	Legume	Legume	Brown	Black
Crotalaria pumila Ortega	1	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Black
Crotalaria sp.	9	C3	Ns	Ph	T	A	D	D	D	Legume	Legume	Brown	Black
Dalbergia hygrophila (Mart. ex Benth.) Hoehne	3	C3	Ns	Sh	T	A	M	D	I	Indehiscent pod	Camara	Brown	Brown
Dalbergia monetaria L. f.	18	C3	Ns	Tr	T	A	M	D	I	Indehiscent pod	Camara	Brown	Brown
Dalea carthagenensis var. Barbata (Oerst.) Barneby	1	C3	Ns	Ah	T	A	D	D	I	Indehiscent pod	Camara	Brown	Brown
Delonix regia (Bojer ex Hook.) Raf.	31	C3	Ns	Tr	T	A	D	D	D	Legume	Legume	Brown	Brown
Desmanthus virgatus (L.) Willd.	1, 5	C3	Ns	Ph	T	A	D	D	D	Legume	Legume	Brown	Brown
Desmodium affine Schltdl.	1, 24	C3	Ns	Ah	T	A	D	D	I	Loment	Loment	Brown	Brown
Desmodium barbatum (L.) Benth. & Oersted	25, 26	C3	Ns	Ph	T	A	D	D	I	Loment	Loment	Brown	Brown
Desmodium canum Schinz & Thell.	1, 24, 25	C3	Ns	Ph	T	A	D	D	I	Loment	Loment	Brown	Brown
Desmodium incanum (Sw.) DC.	1, 21	C3	Ns	Ph	T	A	D	D	I	Loment	Loment	Brown	Brown
Dimorphandra macrostachya Benth. ssp. macrostachya	18	C3	Ns	Tr	T	A	M	D	D	Legume	Legume	Brown	Brown
Dioclea guianensis Benth.	3, 6	C3	Ns	L	T	A	M	D	D	Legume	Legume	Brown	Brown
Dolichos lablab L.	1	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Brown
Dycimbe fraterna Cowan	16	C3	Ns	Sh	T	A	M	D	D	Legume	Legume	Brown	Brown
Entada polystachya (L.) DC.	27	C3	Ns	L	T	A	M	D	I	Craspedium	Craspedium	Brown	Brown
Enterolobium cyclocarpum (Jacq.) Griseb.	2, 27	C3	Ns	Tr	T	A	M	D	I	Indehiscent pod	Camara	Brown	Brown
Eriosema rufum (Kunth) G. Don	25	C3	Ns	Ph	T	A	M	D	D	Legume	Legume	Brown	Black
Eriosema simplicifolium (DC.) G. Don	23	C3	Ns	Ph	T	A	D	D	D	Legume	Legume	Brown	Black

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Erythrina mitis Jacq.	1	C3	Ns	Tr	T	A	M	D	D	Follicle	Follicle	Brown	Black+Red
Galactia jussiaeana Kunth	3, 24, 25	C3	Ns	Ph	T	A	D	D	D	Legume	Legume	Brown	Brown
Galactia striata (Jaqc.) Urb.	1, 5, 23, 27	C3	Ns	L	T	A	D	D	D	Legume	Legume	Brown	Brown
Hymenaea courbaril L.	22, 27	C3	Ns	Tr	T	A	M	D	I	Indehiscent pod	Camara	Green	Brown
Indigofera hirsuta L.	23	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Brown
Indigofera microcarpa Desv.	27	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Brown
Indigofera pascuorum Benth.	23	C3	Ns	Ph	T	A	D	D	D	Legume	Legume	Brown	Brown
Indigofera suffruticosa Mill.	5, 27	C3	Ns	Ph	T	A	D	D	D	Legume	Legume	Brown	Brown
Inga ingoides (Rich.) Willd.	7	C3	Ns	Tr	T	A	D	D	I	Indehiscent pod	Camara	Brown	White
Inga macrantha J.R. Johnst.	21	C3	Ns	Tr	T	A	M	D	I	Indehiscent pod	Camara	Brown	White
Inga pilosula (Rich.) J.F. Macbr.	3	C3	Ns	Tr	T	A	M	D	I	Indehiscent pod	Camara	Brown	White
Leucaena leucocephala (Lam.) De Wit.	1, 5	C3	Ns	Sh	T	A	D	D	D	Legume	Legume	Brown	Brown
Lonchocarpus flendleri Benth.	1	C3	Ns	Tr	T	A	M	D	I	Indehiscent pod	Camara	Brown	Brown
Lonchocarpus hedyosmus Miq.	22, 27	C3	Ns	Tr	T	A	M	D	I	Indehiscent pod	Camara	Brown	Brown
Lupinus jahnii Rose ex Pittier	4	C3	Ns	Ph	T	A	D	D	D	Legume	Legume	Green	Brown
Lupinus meridanus Moritz ex C. P. Smith	4, 8	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Green	Brown
Machaerium dubium (Kunth) Rudd	27	C3	Ns	Tr	T	A	M	D	I	Indehiscent pod	Camara	Brown	Brown
Machaerium grandifolium Pittier	27	C3	Ns	Tr	T	A	M	D	I	Samara	Samara	Brown	Brown
Machaerium moritzianum Benth.	2, 22, 24	C3	Ns	L	T	A	M	D	I	Samara	Samara	Brown	Brown
Machaerium robiniifolium (DC.) Vogel	1, 2	C3	Ns	Tr	T	A	D	D	I	Samara	Samara	Brown	Brown
Macrolobium multijugum (DC.) Benth.	3	C3	Ns	Tr	T	A	M	D	I	Indehiscent pod	Camara	Brown	Brown
Macroptilium atropurpureum (Moc. & Sessé ex DC.) Urb	1	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Brown
Macroptilium longepedunculatum (Mart. ex Benth.) Urb.	23-25	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Brown
Macrosamanea amplissima (Ducke) Barneby & J.W. Grimes	3	C3	Ns	Tr	T	A	D	D	D	Follicle	Follicle	Brown	White+
Black													

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Mimosa albida Humb. & Bonpl. ex Willd.	1	C3	Ns	L	T	A	D	D	I	Craspedium	Craspedium	Brown	Brown
Mimosa arenosa (Willd.) Poir	5, 27	C3	Ns	Ph	T	A	M	D	I	Indehiscent pod	Camara	Brown	Brown
Mimosa camporum Benth.	23, 26	C3	Ns	Ah	T	A	D	D	D	Craspedium	Craspedium	Brown	Brown
Mimosa debilis Humb. & Bonpl. ex Willd.	23, 25	C3	Ns	Ah	T	A	D	D	D	Craspedium	Craspedium	Brown	Brown
Mimosa dormiens Humb. & Bonpl. ex Willd.	27	C3	Ns	Ph	T	A	D	D	I	Craspedium	Craspedium	Brown	Brown
Mimosa hirsutissima Mart.	24, 25	C3	Ns	Ph	T	A	D	D	I	Craspedium	Craspedium	Brown	Brown
Mimosa pigra L.	27	C3	Ns	Ph	T	A	D	D	I	Craspedium	Craspedium	Brown	Brown
Mimosa pudica L.	1, 23, 27	C3	Ns	Ah	T	A	D	D	I	Craspedium	Craspedium	Brown	Brown
Mimosa pudica L. var. tetrandra	16, 21	C3	Ns	Ah	T	A	D	D	I	Craspedium	Craspedium	Brown	Brown
Mimosa sensitiva L.	24	C3	Ns	L	T	A	D	D	I	Craspedium	Craspedium	Brown	Brown
Mimosa tenuiflora (Willd.) Poir.	25	C3	Ns	Tr	T	A	D	D	I	Indehiscent pod	Camara	Brown	Brown
Mimosa xanthocentra Mart.	24	C3	Ns	Ah	T	A	D	D	I	Craspedium	Craspedium	Brown	Brown
Neptunia plena (L.) Benth.	27	C3	Ns	Ah	T	A	D	D	D	Follicle	Follicle	Brown	Brown
Nissolia fruticosa Jaqc.	1	C3	Ns	L	T	A	D	D	I	Samara	Samara	Brown	Brown
Pachecoa prismatica (Sessé & Moc.) Standl. & B.G. Schub.	27	C3	Ns	Ph	T	A	D	D	I	Loment	Loment	Brown	Brown
Parkinsonia aculeata L.	5	C3	Ns	Tr	T	A	D	D	I	Indehiscent pod	Camara	Brown	Brown
Piscidia carthagenensis Jacq.	1, 2	C3	Ns	Tr	T	A	D	D	I	Loment	Loment	Brown	Brown
Pithecellobium dulce (Roxb.) Benth.	2, 12, 27	C3	Ns	Tr	T	A	D	D	D	Follicle	Follicle	Green+Red	White+ Black
Pithecellobium unguis-cati (L.) Benth.	5	C3	Ns	Sh	T	A	M	D	D	Follicle	Follicle	Green+Red	White+ Black
Platymiscium diadelphum S.F. Blake	1	C3	Ns	Tr	T	A	M	D	I	Samara	Samara	Brown	Brown
Platymiscium pinnatum (Jacq.) Dugand	24, 27	C3	Ns	Tr	T	A	M	D	I	Samara	Samara	Brown	Brown
Prosopis juliflora (Sw.) DC.	9, 11, 12	C3	Ns	Tr	T	A	M	D	I	Indehiscent pod	Camara	Brown	Brown
Pseudosamanea guachapele (Kunth) Harms	27	C3	Ns	Tr	T	A	M	D	D	Follicle	Follicle	Brown	Brown
Pterocarpus acapulcensis Rose	22, 27	C3	Ns	Tr	T	A	M	D	I	Samara	Samara	Brown	Brown
Rhynchosia melanocarpa Grear	24	C3	Ns	L	T	A	D	D	D	Legume	Legume	Brown	Black+Red
Rhynchosia minima (L)	5, 9, 21	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Black+Red
Senna obtusifolia (L.) H.S. Irwin & Barneby	2	C3	Ns	Sh	T	A	D	D	D	Legume	Legume	Brown	Brown

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Senna occidentalis (L.) Link	5, 9, 12	C3	Ns	Sh	T	A	M	D	D	Legume	Legume	Brown	Brown
Senna oxyphylla (Kunth) Irwin & Barneby	1, 21	C3	Ns	Sh	T	A	M	D	D	Legume	Legume	Brown	Brown
Senna pallida ?? var. Bahamensis H.S. Irwin & Barneby	1	C3	Ns	Sh	T	A	D	D	D	Legume	Legume	Brown	Brown
Senna pendula (Humb. & Bonpl. ex Willd.) H.S. Irwin & Barneby	24	C3	Ns	Sh	T	A	D	D	D	Legume	Legume	Brown	Brown
Senna robiniifolia (Benth.) H.S. Irwin & Barneby	1	C3	Ns	Tr	T	A	D	D	D	Legume	Legume	Brown	Brown
Sesbania exasperata Kunth	3, 27	C3	Ns	Ah	T	A	D	D	D	Legume	Legume	Brown	Brown
Stylosanthes viscosa (L.) Sw.	21	C3	Ns	Ph	T	A	D	D	I	Loment	Loment	Brown	Brown
Swartzia leptopetala Benth.	3	C3	Ns	Tr	T	A	M	D	D	Legume	Legume	Brown	Beige
Tachigali davidsei Zarucchi & Herend.	27	C3	Ns	Tr	T	A	M	D	I	Samara	Samara	Brown	Brown
Taralea cordata Ducke	17	C3	Ns	Sh	T	A	D	D	D	Legume	Legume	Brown	Brown
Tephrosia cinerea (L.) Pers.	5, 9, 12	C3	Ns	Ph	T	A	D	D	D	Legume	Legume	Brown	Brown
Trifolium repens L.	4, 8	C3	Ns	Ph	T	A	D	D	I	Indehiscent pod	Camara	Brown	Brown
Zapoteca caracasana (Jacq.) H.M. Hern.	1	C3	Ns	L	T	A	D	D	D	Legume	Legume	Brown	Brown
Zornia diphylla (L.) Pers.	21, 23, 25	C3	Ns	Ah	T	A	D	D	I	Loment	Loment	Brown	Brown
GENTIANACEAE													
Chelonanthus angustifolius (Kunth) Gilg.	3, 14, 17, 19	C3	Ns	Ah	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Chelonanthus purpurascens (Aubl.) Struwe & V.A. Albert	18	C3	Ns	Ph	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Coutoubea reflexa Benth	14, 17, 19	C3	Ns	Ph	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Beige
Coutoubea spicata Aubl.	3, 21	C3	Ns	Ph	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Beige
Curtia tenuifolia (Aubl.) Knobl. Subsp. tenuifolia	14, 16, 19	C3	Ns	Ah	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Enicostema verticillatum (L.) Engl. ex Gilg.	21	C3	Ns	Ph	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Beige
Gentiana sedifolia Kunth	4	C3	Ns	Ah	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Gentiana viridis Griseb.	4	C3	Ns	Ah	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Gentianella nevadensis (Gilg) see Weaver, Richard E. & Rüdenberg	4	C3	Ns	Ah	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Irlbachia nemorosa (Willd. ex Roem. & Schult.) Merr.	3, 14, 15, 17	C3	Ns	Ah	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown

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Lisianthius calygonus Ruiz & Pav.	6, 7	C3	Ns	Sh	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Schultesia brachyptera Cham.	26	C3	Ns	Ph	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Tetrapollinia caerulescens (Aubl.) Maguire & B.M. Boom	16	C3	Ns	Ah	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
GERANIACEAE													
Geranium meridense Pittier	4	C3	Ns	Ph	T	A	M	D	I	Schizocarp	Polachenarium	Brown	Brown
GESNERIACEAE													
Rechsteineria ignea (Mart) Fritsch.	26	C3	Ns	Ph	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
GNETACEAE													
Gnetum camporum (Markgr.) D.W. Stev. & Zanoni	17	C3	Ns	L	T	A	D	F	I	Drupe	Arillocarpium	Green	Brown
GOODENIACEAE													
Scaevola plumieri (L.) Vahl	11	C3	S	Sh	T	A	D	F	I	Drupe	Drupe	Purple-black	Brown
HELICONIACEAE													
Heliconia acuminata Rich.	3, 7	C3	Ns	Ph	T	A	M	F	I	Drupe	Drupe	Blue	Brown
Heliconia aurea G. Rodr.	7	C3	Ns	Ph	T	A	M	F	I	Drupe	Drupe	Blue	Brown
Heliconia bihai (L.) L.	7	C3	Ns	Ph	T	A	M	F	I	Drupe	Drupe	Blue	Brown
Heliconia psittacorum L. f.	3, 26	C3	Ns	Ph	T	A	D	F	I	Drupe	Drupe	Blue	Brown
Heliconia revoluta (Griggs) Standl.	7	C3	Ns	Ph	T	A	M	F	I	Drupe	Drupe	Blue	Brown
HUMIRIACEAE													
Humiria balsamifera Aubl.	15-17	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Beige
Vantanea minor Benth.	16	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Green	Beige
HYDROCHARITACEAE													
Thalassia testudinum Banks & Sol. ex K.D. Koenig	10, 13	C3	Ns	Ph	T	A	M	D	I	Indehiscent capsule	Anphisarcum	Brown	Brown
HYPERICACEAE													
Hypericum laricifolium Juss.	4	C3	Ns	Sh	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Vismia baccifera (L.) Triana & Planch.	3, 6, 7	C3	Ns	Tr	T	A	D	F	I	Berry	Bacca	Brown	Beige
Vismia falcata Rusby	26	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Brown	Beige
Vismia guianensis (Aubl.) Pers.	15, 18	C3	Ns	Tr	T	A	D	F	I	Berry	Bacca	Brown	Beige
HYPOXIDACEAE													
Hypoxis decumbens L.	1	C3	Ns	Ph	T	A	D	D	D	Septifragal capsule	Septifragal capsule	Brown	Black
IRIDACEAE													
Cipura paludosa Aubl.	3, 25, 27	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown

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Cypella linearis (Kunth) Baker	25	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Orthrosanthus chimboracensis (Kunth) Baker	4, 8	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Sisyrinchium tinctorium Kunth	4	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Sisyrinchium vaginatum Spreng.	18	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Trimezia fosteriana Steyerman	14	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Trimezia martinicensis (Jacq.) Herb.	6	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
IXONANTHACEAE													
Ochthocosmus attenuatus Steyerm. & Luteyn	17	C3	Ns	Tr	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Ochthocosmus longipedicellatus Steyerm. & Luteyn	17	C3	Ns	Sh	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Ochthocosmus roraimae Benth.	16	C3	Ns	Sh	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
JUGLANDACEAE													
Juglans venezuelensis W.E. Manning (♀)	36	C3	Ns	Tr	T	A	M	F	I	Drupe	Pseudodrupe	Yellow	Brown
JUNCACEAE													
Luzula racemosa Desv.	4	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Beige
LAMIACEAE													
Aegiphila integrifolia var. guianensis (Moldenke) López-Pal.	3, 18, 22, 24	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Yellow	Brown
Aegiphila mollis Kunth	22, 24, 26, 27	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Yellow	Brown
Aegiphila parviflora Moldenke	24	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Yellow	Brown
Amasonia campestris (Aubl.) Moldenke	3, 24, 25	C3	Ns	Ph	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Hyptis conferta var. angustata (Briq.) A. Pool & Harley	26	C3	Ns	Ph	T	A	D	D	I	Schizocarp	Diclesarium	Brown	Black
Hyptis dilatata Benth.	26	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Diclesarium	Brown	Brown
Hyptis mutabilis (Rich.) Briq.	24	C3	Ns	Ah	T	A	D	D	D	Schizocarp	Camarium	Brown	Black
Hyptis suaveolens (L.) Poit.	3, 20, 22-24, 27	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Diclesarium	Brown	negra
Marsypianthes chamaedrys (Vahl) Kuntze	23	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Camarium	Brown	Black

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Salvia coccinea Buc'hoz ex Etl.	1	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Camarium	Brown	Brown
Vitex capitata Vahl	24, 27	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
LAURACEAE													
Cassytha filiformis L.	14, 16, 17, 26	C3	Ns	L	T	P	M	F	I	Berry	Bacca	Red	Brown
Endlicheria anomala (Nees) Mez	3	C3	Ns	Tr	T	A	M	F	I	Berry	Bacca	Red	Brown
Nectandra pichurin Mez ex T. Durand & B.D. Jacks.	26, 27	C3	Ns	Tr	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Ocotea duidensis Moldenke	15	C3	Ns	Sh	T	A	M	F	I	Berry	Glans	Green	Brown
Ocotea leucoxylon (Sw.) Laness.	21	C3	Ns	Tr	T	A	M	F	I	Berry	Glans	Purple-black	Brown
Persea caerulea (Ruiz & Pav.) Mez	21	C3	Ns	Tr	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Persea sp.	21	C3	Ns	Tr	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
LECYTHIDACEAE													
Couroupita guianensis Aubl.	2	C3	Ns	Tr	T	A	M	F	I	Indehiscent capsule	Anphisarcum	Brown	Black
Lecythis ollaria L.	27	C3	Ns	Tr	T	A	M	D	D	Pyxidium	Pyxidium	Brown	Brown
LENTIBULARIACEAE													
Utricularia amethystina St. Hil.	19	C3	Ns	Ah	T	I	D	D	D	Pyxidium	Fissuricidal capsule	Brown	Brown
Utricularia juncea Vahl	14, 16, 17	C3	Ns	Ah	T	I	M	D	D	Pyxidium	Fissuricidal capsule	Brown	Brown
Utricularia longeciliata DC. in A. DC.	14, 16, 17	C3	Ns	Ah	T	I	M	D	D	Pyxidium	Fissuricidal capsule	Brown	Brown
Utricularia subulata L.	2, 16, 17	C3	Ns	Ah	T	I	M	D	D	Pyxidium	Fissuricidal capsule	Brown	Brown
LOASACEAE													
Gronovia scandens L.	1	C3	Ns	Ah	T	A	D	D	I	Achene	Diclesium	Black	Brown
LOGANIACEAE													
Bonyunia minor N.E. Br.	17	C3	Ns	Sh	T	A	M	D	D	Poricidal capsule	Poricidal capsule	Brown	Brown
Spigelia anthelmia L.	1, 23, 25	C3	Ns	Ah	T	A	D	D	D	Pyxidium	Pyxidium	Brown	Brown
Strychnos guianensis (Aubl.) Mart.	3	C3	Ns	L	T	A	M	F	I	Berry	Bacca	Yellow	Brown
Strychnos sp.	3	C3	Ns	L	T	A	M	F	I	Berry	Bacca	Yellow	Brown
LORANTHACEAE													
Oryctanthus alveolatus (Kunth) Kuijt	3, 24, 25	C3	S	Ph	T	P	M	F	I	Berry	Bacca	Yellow	Green
Phthirusa delicatula Rizzini	1	C3	Ns	L	T	P	M	F	I	Berry	Bacca	Red	Green
Phthirusa stelis (L.) Kuijt	1, 3, 13, 15-18, 22, 24, 25, 27	C3	Ns	L	T	P	M	F	I	Berry	Bacca	Red	Green

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Psittacanthus calyculatus (DC.) G.	27	C3	S	Ph	T	P	M	F	I	Berry	Bacca	Purple-black	Green
Psittacanthus collum-cygni Eichl.	24, 25	C3	S	Ph	T	P	M	F	I	Berry	Bacca	Purple-black	Green
Struthanthus gracilis (Gleason) Steyerm. & Maguire	17, 18	C3	Ns	L	T	P	M	F	I	Berry	Bacca	Red	Green
Struthanthus sp.	16	C3	Ns	L	T	P	M	F	I	Berry	Bacca	Red	Green
Struthanthus syringifolius (Mart.) Mart.	17, 18	C3	S	Ph	T	P	M	F	I	Berry	Bacca	Red	Green
Tripodanthus acutifolius (Ruiz & Pav.) Tiegh.	16	C3	Ns	Ph	T	P	M	F	I	Berry	Bacca	Purple-black	Green
LYTHRACEAE													
Cuphea denticulata Kunth	21	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Cuphea micrantha Kunth	23	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Cuphea odonellii Lourteig	26	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Pehria compacta (Rusby) Sprague	1	C3	Ns	Tr	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
MALPIGHIACEAE													
Banisteriopsis acapulcensis var. Llanensis B. Gates	24	C3	Ns	L	T	A	D	D	I	Schizocarp	Samarium	Brown	Brown
Banisteriopsis muricata (Cav.) Cuatrec.	1, 24, 27	C3	Ns	L	T	A	D	D	I	Schizocarp	Samarium	Brown	Brown
Banisteriopsis pulcherrima (Sandwith) B. Gates	18	C3	Ns	L	T	A	D	D	I	Schizocarp	Samarium	Brown	Brown
Bunchosia mollis Benth.	25	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Red	Beige
Byrsonima concinna Benth	17, 18	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Green	Beige
Byrsonima crassifolia (L.) Kunth	15, 17-19, 22, 24, 25	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Yellow	Beige
Byrsonima karstenii W.R. Anderson	6	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Yellow	Beige
Byrsonima verbascifolia (L.) DC.	19	C3	Ns	Ph	T	A	M	F	I	Drupe	Drupe	Yellow	Beige
Gaudichaudia albida Schltdl. & Cham.	1	C3	Ns	L	T	A	M	D	I	Schizocarp	Samarium	Brown	Brown
Heteropteris laurifolia (L.) A. Juss.	21	C3	Ns	L	T	A	M	D	I	Schizocarp	Samarium	Brown	Brown
Heteropterys prunifolia (Kunth) W.R. Anderson	1, 5	C3	Ns	L	T	A	D	D	I	Schizocarp	Samarium	Brown	Brown
Malpighia emarginata DC.	5	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Red	Brown
Malpighia glabra L.	1, 2	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Red	Beige
Malpigia sp.	2	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Red	Beige
Tetrapteris styloptera A. Juss.	3, 18	C3	Ns	L	T	A	D	D	I	Schizocarp	Samarium	Brown	Brown

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Tetrapterys pusilla Steyerm.	14	C3	Ns	L	T	A	M	D	I	Schizocarp	Samarium	Brown	Brown
MALVACEAE													
Abutilon giganteum (Jacq.) Sweet	1	C3	Ns	Sh	T	A	D	D	D	Schizocarp	Polachenarium	Brown	Brown
Abutilon stenopetalum Garcke	5	C3	Ns	Sh	T	A	D	D	D	Schizocarp	Polachenarium	Brown	Brown
Abutilon umbellatum (L.) Sweet Hort.	1	C3	Ns	Ph	T	A	D	D	D	Schizocarp	Polachenarium	Brown	Brown
Acaulimalva purdiaei (A. Gray) Krapov.	4	C3	Ns	Ph	T	A	D	D	D	Schizocarp	Polachenarium	Brown	Brown
Bastardia viscosa (L.) Kunth	5, 12, 13	C3	Ns	Ph	T	A	D	D	D	Schizocarp	Polachenarium	Brown	Brown
Byttneria scabra Loefl.	26	C3	Ns	Sh	T	A	M	D	I	Schizocarp	Camarium	Brown	Brown
Ceiba pentandra (L.) Gaertn.	1, 2, 27	C3	Ns	Tr	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Corchorus hirsutus L.	9	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Gaya gaudichaudiana A. St.-Hil.	1	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Samarium	Brown	Brown
Guazuma ulmifolia Lam.	1, 2, 27	C3	Ns	Tr	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Black	Black
Helicteres guazumifolia Kunth	24, 27	C3	Ns	Sh	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Black	Black
Heliocarpus americanus L.	1, 6	C3	Ns	Tr	T	A	D	D	I	Indehiscent capsule	Carcerulus	Brown	Brown
Herissantia crispa (L.) Brizicky	1	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Polachenarium	Beige	Black
Hibiscus phoeniceus Jacq.	5	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Luehea candida (DC.) Mart.	22, 27	C3	Ns	Tr	T	A	M	D	D	Capsula Loculicida	Capsula Loculicida	Brown	Brown
Luehea speciosa Willd.	1	C3	Ns	Tr	T	A	M	D	D	Capsula Loculicida	Capsula Loculicida	Brown	Brown
Malvastrum americanum (L.) Torr.	5, 9, 11, 12	C3	Ns	Ph	T	A	D	D	I	Schizocarp	Polachenarium	Brown	Brown
Malvastrum coromandelianum (L.)	1	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Polachenarium	Brown	Brown
Melochia caracasana Jaqc.	1	C3	Ns	Sh	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Melochia crenata Vahl.	13	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Melochia nodiflora Sw.	1, 27	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Melochia parvifolia Kunth	23, 24, 27	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Melochia pyramidata var. pyramidata	5	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black

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Melochia tomentosa L.	5, 21	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Melochia villosa var. villosa	26	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Pachira aquatica Aubl.	3, 18	C3	Ns	Tr	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Pachira quinata (Jacq.) W.S. Alverson	33	C3	Ns	Tr	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Pavonia cancellata (L.) Cav.	23-25, 27	C3	Ns	Ph	T	A	D	D	I	Schizocarp	Polachenarium	Brown	Brown
Peltaea trinervis (C. Presl) Krapov. & Cristóbal	23, 25	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Polachenarium	Brown	Brown
Pseudabutilon spicatum (Kunth) R.E. Fr.	25, 27	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Polachenarium	Brown	Brown
Sida acuta Burm. f.	21	C3	Ns	Ph	T	A	D	D	I	Schizocarp	Polachenarium	Brown	Brown
Sida aggregata C. Presl	24, 25, 27	C3	Ns	Ph	T	A	D	D	I	Schizocarp	Polachenarium	Brown	Brown
Sida ciliaris L.	1, 5, 23	C3	Ns	Ph	T	A	D	D	I	Schizocarp	Polachenarium	Brown	Brown
Sida glomerata Cav.	23	C3	Ns	Ph	T	A	D	D	I	Schizocarp	Polachenarium	Brown	Brown
Sida glutinosa Comm. ex Cav.	1	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Polachenarium	Brown	Brown
Sida linifolia Cav.	20, 23	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Polachenarium	Brown	Brown
Sida rhombifolia L.	21, 27	C3	Ns	Ph	T	A	D	D	I	Schizocarp	Polachenarium	Brown	Brown
Sida spinosa L.	1, 5	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Polachenarium	Brown	Brown
Sida tuberculata R.E. Fr.	23	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Polachenarium	Brown	Brown
Thespesia populnea (L.) Sol. ex Corrêa	13	C3	Ns	Tr	T	A	M	D	I	Schizocarp	Polachenarium	Brown	Black
Triumfetta semitriloba Jacq.	24	C3	Ns	Sh	T	A	D	D	I	Indehiscent capsule	Carcerulus	Brown	Brown
Triumfetta sp.	27	C3	Ns	Sh	T	A	D	D	I	Indehiscent capsule	Carcerulus	Brown	Brown
Waltheria americana L.	13	C3	Ns	Ph	T	A	D	D	I	Indehiscent capsule	Carcerulus	Brown	Black
Waltheria indica L.	13, 20, 23	C3	Ns	Ah	T	A	D	D	I	Indehiscent capsule	Carcerulus	Brown	Black
Wissadula contracta (Link) R.E. Fr.	1	C3	Ns	Ph	T	A	D	D	D	Schizocarp	Polachenarium	Brown	Brown
Wissadula periplocifolia (L.) C. Presl ex Thwaites	24, 27	C3	Ns	Ph	T	A	D	D	D	Schizocarp	Polachenarium	Brown	Brown
MARANTACEAE													
Calathea allouia (aubl.) Lindl.	7	C3	Ns	Ph	T	A	M	F	D	Loculicidal capsule	Loculicidal capsule	Pink	Brown
Calathea sp.	7	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Maranta arundinacea L.	24, 27	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Yellow	Brown
Maranta casupito Jacq.	7	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Orange	Brown

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Stromanthe jacquinii (Roem. & Schult.) H. Kenn. & Nicolson	7	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Orange	Brown
Stromanthe tonckat (Aubl.) Eichler	6, 7	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Orange	Brown
Thalia geniculata L.	26, 27	C3	Ns	Ph	T	A	M	D	I	Indehiscent capsule	Carcerulus	Brown	Brown
MARCGRAVIACEAE													
Ruyschia tremadena (Ernst) Lundell	6, 21	C3	Ns	L	T	A	M	F	I	Berry	Bacca	Green	Red
Souroubea guianensis Aubl.	3, 7	C3	Ns	L	T	A	M	F	I	Berry	Bacca	Yellow	Beige
MARTYNIACEAE													
Craniolaria annua L.	24	C3	S	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
MAYACACEAE													
Mayaca sellowiana Kunth	26	C3	Ns	Ah	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Beige	Black
MELASTOMATACEAE													
Aciotis acuminifolia (Mart. Ex DC.) Triana	18	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Green	Brown
Blakea monticola J.R. Johnst.	21	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Red	Brown
Chaetolepis lindeniana (Naudin) Triana	4	C3	Ns	Sh	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Clidemia capitata Benth.	15	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Clidemia capitellata (Bonpl.) D. Don	18, 20	C3	S	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Beige
Clidemia capitellata var. dependens (Pav. ex D. Don) J.F. Macbr.	26	C3	S	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Beige
Clidemia fendleri Cogn.	6, 7	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Clidemia octona (Bonpl.) L. O. Williams Subsp. Guayanensis Wurdack.	7, 18	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Clidemia pustulata DC.	18	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Clidemia sericea D. Don.	7, 18-20	C3	Ns	Ph	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Clidemia urceolata DC.	21	C3	Ns	Ph	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Comolia microphylla Benth.	14, 16, 17	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Desmoscelis villosa (Aubl.) Naudin	19, 26	C3	Ns	Ah	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Graffenrieda latifolia (Naudin) Triana	6, 7	C3	Ns	Tr	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Beige	Beige
Henriettea granulata O. Berg & Triana	18	C3	Ns	Tr	T	A	D	F	I	Berry	Bacca	Brown	Brown
Macairea lasiophylla (Benth) Wurdack	14, 19	C3	Ns	Ah	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Beige

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Macairea pachyphylla Benth.	15	C3	Ns	Sh	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Beige
Macairea parvifolia Benth.	15, 16	C3	Ns	Sh	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Beige
Marcetia taxifolia (A. St.-Hil.) DC.	15-19	C3	Ns	Sh	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Beige
Meriania sclerophylla Triana	14, 15, 17	C3	Ns	Sh	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Meriania urceolata Triana	17	C3	Ns	Sh	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Miconia alata (Aubl) D.C.	2, 18	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Miconia albicans (Sw.) Steud.	7, 18, 20	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Green	Brown
Miconia aplostachia (Bonpl.) DC.	3, 18	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Miconia araguensis Wurdack	6, 7	C3	Ns	Ph	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Miconia ciliata (Rich.) DC.	6, 7, 15, 17, 18	C3	Ns	Ph	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Miconia dodecandra Cogn.	6, 7	C3	Ns	Tr	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Miconia ibaguensis (Bonp.) Triana	6, 18	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Miconia laevigata (L.) D. Don	1, 6	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Miconia minutiflora (Bonpl.) DC.	7, 21	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Beige
Miconia phaeophylla Triana	7, 15, 17, 18	C3	Ns	Tr	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Miconia rubiginosa (Bonpl.) DC.	7, 18	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Miconia rufescens (Aubl.) DC.	3, 7, 18, 19	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Red	Brown
Miconia stephananthera Ule	26	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Beige
Miconia sylvatica (Schltdl.) Naudin	6, 7	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Miconia tuberculata (Naud) Triana	6, 7	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Microlicia benthamiana Triana ex Cogn	14, 16	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Pterolepis glomerata (Rottb.) Miq.	26	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Rhynchanthera serrulata (Rich.) DC.	26	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Siphanthera cordifolia (Benth.) Gleason	14-17, 19	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Tibouchina fraterna N.E. Brow.	14, 15, 17	C3	Ns	Sh	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Beige

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Tibouchina geitneriana (Schltdl.) Cogn.	6, 7	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Beige
Tococa guianensis Aublet	3, 15, 18	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Tococa nitens (Benth.) Triana	14, 15, 17	C3	Ns	Ph	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
MELIACEAE													
Trichilia hirta L.	1, 6	C3	Ns	Tr	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Red
MENISPERMACEAE													
Cissampelos ovalifolia DC.	23	C3	Ns	Ph	T	A	D	F	I	Drupe	Drupetum	Red	White
Cissampelos pareira L.	22, 27	C3	Ns	L	T	A	D	F	I	Drupe	Drupetum	Red	White
Orthomene schomburgkii (Miers) Barneby & Krukoff	3	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupetum	Yellow	Beige
MONTIACEAE													
Calandrinia acaulis Kunth	4	C3	S	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Mona meridensis (Friedrich) Ö. Nilsson	4	C3	S	Ah	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
MORACEAE													
Dorstenia sabanensis Cuatrec.	22, 24	C3	Ns	Ph	T	A	M	D	I	Achene	Trymosum	White	Beige
Ficus obtusifolia Kunth	1	C3	Ns	Tr	T	A	M	F	I	Syconium	Syconium	Green	Brown
Sorocea sprucei (Baill.) J.F. Macbr.	1, 27	C3	Ns	Tr	T	A	M	D	I	Achene	Sorosus	Purple-black	Beige
MUNTINGIACEAE													
Muntingia calabura L.	1, 2, 5	C3	Ns	Tr	T	A	D	F	I	Berry	Bacca	Yellow	Beige
MYRTACEAE													
Blepharocalyx eggersii (Kiaersk.) Landrum	21	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Calycolpus goetheanus (DC.) O. Berg	18	C3	Ns	Tr	T	A	D	F	I	Berry	Bacca	Green	Beige
Eugenia biflora (L.) DC.	22, 24, 27	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Eugenia casearioides (Kunth) DC.	1	C3	Ns	Tr	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Eugenia mcvaughii Steyerm. & Lasser	1	C3	Ns	Tr	T	A	D	F	I	Berry	Bacca	Yellow	Brown
Eugenia protenta McVaugh	18	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Eugenia punicifolia (Kunth) DC.	3, 18	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Red	Brown
Myrcia albidotomentosa (Amshoff) McVaugh	15-17	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Myrcia fallax (Rich.) DC.	3, 6	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Myrcia magnoliifolia DC.	18	C3	Ns	Tr	T	A	D	F	I	Berry	Bacca	Red	Brown
Myrcia sp.	21	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Red	Brown

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Myrcia splendens (Rich.) DC.	6, 7	C3	Ns	Tr	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Plinia pinnata L.	3	C3	Ns	Tr	T	A	M	F	I	Berry	Bacca	Orange	Brown
Psidium guineense Sw.	1, 3, 18, 20, 24, 27	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Yellow	Beige
Psidium laruotteanum Cambess.	19	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Red	Beige
Psidium salutare (Kunth) O. Berg	24, 27	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Brown	Brown
Psidium sartorianum (O. Berg) Nied.	1	C3	Ns	Tr	T	A	M	F	I	Berry	Bacca	Yellow	Beige
Siphoneugena dussii (Krug & Urb.) Proença	6	C3	Ns	Tr	T	A	M	F	I	Berry	Bacca	Purple-black	Beige
NARTHECIACEAE													
Nietneria paniculata Steyerman	14	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
NYCTAGINACEAE													
Boerhavia diffusa L.	5	C3	Ns	Ah	T	A	D	D	I	Achene	Diclesium	Brown	Brown
Boerhavia erecta L.	5	C3	Ns	Ah	T	A	D	D	I	Achene	Diclesium	Brown	Beige
Guapira opposita (Vell.) Reitz	6	C3	Ns	Tr	T	A	M	F	I	Drupe	Diclesium	Purple-black	Black
Guapira pacurero (Kunth) Lundell	5, 21, 22, 24	C3	Ns	Sh	T	A	M	F	I	Drupe	Diclesium	Purple-black	Black
Mirabilis violacea (L.) Heimerl	1	C3	Ns	Ah	T	A	D	F	I	Drupe	Diclesium	Brown	Brown
NYMPHAEACEAE													
Nymphaea pulchella DC.	34	C3	Ns	Ph	T	A	M	F	D	Hesperidium	Hesperidium	Brown	Brown
OCHNACEAE													
Ouratea gillejana (Dwyer) Sandwith & Maguire	15-17	C3	Ns	Sh	T	A	M	F	I	Aggregate of drupe	Glandarium	Purple-black	Brown
Ouratea guildingii (Planch.) Urb.	21	C3	Ns	Tr	T	A	M	F	I	Aggregate of drupe	Glandarium	Yellow	Brown
Poecilandra pumila Steyerm.	14, 16, 19	C3	Ns	Sh	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Poecilandra retusa Tul.	15-17	C3	Ns	Sh	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Sauvagesia amoena Ule	19	C3	Ns	Ph	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Sauvagesia angustifolia Ule	15, 17	C3	Ns	Ph	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Sauvagesia erecta L.	18, 20, 21	C3	Ns	Ph	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Sauvagesia fruticosa Mart. & Zucc.	17	C3	Ns	Ph	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Black
Sauvagesia guianensis (Eichler) Sastre	14	C3	Ns	Ph	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown

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Sauvagesia rubiginosa A. St.-Hil.	16, 26	C3	Ns	Ph	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Beige	Brown
ONAGRACEAE													
Ludwigia decurrens Walter	26	C3	Ns	Ah	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Ludwigia erecta (L) Hara	18	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Ludwigia nervosa (Poir.) H. Hara	26	C3	Ns	Sh	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Ludwigia octovalis (Jacq.) Hara	18, 21	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Oenothera epilobiifolia Kunth	4	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
ORCHIDACEAE													
Beadlea lindleyana (Link, Klotzsch & Otto) Garay & Dunst.	1	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Catasetum discolor (Lindl.) Lindl.	15, 16	C3	S	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Cleistes rosea Lindl.	19	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Cleistes stricta (C. Schweinf.) Garay & Dunst.	15	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Cyrtopodium parviflorum Lindl.	19	CAM	S	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Cyrtopodium punctatum (L.) Lindl.	1	CAM	S	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Epidendrum dendrobioides Thunb.	14	C3	S	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Epidendrum elongatum Jacq.	15, 21	CAM	S	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Epidendrum ibaguense Kunth	15, 16-19	CAM	S	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Epidendrum johnstonii Ames	21	CAM	S	Ph	E	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Epidendrum nocturnum Jacq.	7, 21	CAM	S	Ph	E	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Epidendrum orchidiflorum Salzm. ex Lindl.	16	CAM	S	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Epidendrum secundum Jacq.	15-19	CAM	S	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Epidendrum tumuc-humaciense (Veyret) Carnevali & G.A. Romero-Gonzalez	15-17	C3	S	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Epistephium duckei Huber	15, 17	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown

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Eriopsis biloba Lindl.	15-17	C3	S	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Govenia fasciata Lindl.	7	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Govenia utriculata (Sw.) Lindl.	7	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Habenaria repens Nutt.	24	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Habenaria schomburgkii Lindl. ex Benth.	17, 19	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Habenaria speciosa Poepp. & Endl.	21	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Koellensteinia tricolor (Lindl.) Rehb. F.	14	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Lophiaris carthagenensis (Jacq.) Braem	1	CAM	S	Ph	E	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Lophiaris lopezii	1	CAM	S	Ph	E	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Myrosmodes cochleare Garay	4		S	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Oeceoeclades maculata (Lindl.) Lindl.	1, 22, 24	CAM	S	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Oncidium cebolleta (Jacq.) Sw.	22, 24, 27	CAM	S	Ph	E	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Oncidium nudum Bateman ex Lindl.	1	CAM	S	Ph	E	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Ponthieva racemosa (Walter) C. Mohr	1	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Sobralia elisabethae R.H. Schomb.	3, 15-17	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Spiranthes laxa (Poepp. & Endl.) C. Schweinf.	21	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
OROBANCHACEAE													
Bartsia laniflora Benth.	4	C3	Ns	Ph	T	P	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Buchnera palustris (Aubl.) Spreng.	14, 17-19, 26	C3	Ns	Ah	T	P	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Black
Castilleja fissifolia L. f.	4, 8	C3	Ns	Ph	T	P	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
OXALIDACEAE													
Oxalis barrelieri L.	1	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Oxalis frutescens L.	21	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Green	Brown
PASSIFLORACEAE													
Passiflora auriculata Kunth	3, 18	C3	Ns	L	T	A	D	F	I	Pepo	Pepo	Purple-black	Black+ Yellow

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Passiflora cyanea Mast.	21	C3	Ns	L	T	A	M	F	I	Pepo	Pepo	Yellow	Black
Passiflora edulis Sims	1, 6	C3	Ns	L	T	A	D	F	I	Pepo	Pepo	Orange	Black+ Yellow
Passiflora foetida var. hispida (DC. ex Triana & Planch.) Killip	5, 12, 13	C3	Ns	L	T	A	D	F	I	Pepo	Pepo	Green	Black+ Yellow
Passiflora pulchella Kunth	22, 24	C3	Ns	L	T	A	D	F	I	Pepo	Pepo	Purple-black	Black
Passiflora sclerophylla Harms	15, 17	C3	Ns	L	T	A	M	F	I	Pepo	Pepo	Green	Brown
Passiflora serrulata Jaqc.	22, 24, 27	C3	Ns	L	T	A	M	F	I	Pepo	Pepo	Green	Black
Passiflora suberosa L.	1, 21	C3	Ns	L	T	A	D	F	I	Pepo	Pepo	Purple-black	Black
Passiflora vitifolia Kunth	3	C3	Ns	L	T	A	M	F	I	Pepo	Pepo	Yellow	Brown
Turnera curassavica Urb.	9	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Turnera scabra Millsp.	1	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Turnera ulmifolia var. intermedia Urb.	23, 27	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
PENTAPHYLACACEAE													
Ternstroemia crassifolia Benth.	15-17	C3	Ns	Sh	T	A	M	F	D	Pyxidium	Pyxidium	Green	Orange
Ternstroemia pungens Gleason	15-17	C3	Ns	Sh	T	A	M	F	D	Pyxidium	Pyxidium	Green	Orange
Ternstroemia retusifolia Kobuski	16, 17	C3	Ns	Sh	T	A	M	F	D	Pyxidium	Pyxidium	Green	Orange
PHYLLANTHACEAE													
Hyeronima moritziana (Muell.-Arg.) Pax & Hoffm.	6, 7	C3	Ns	Tr	T	A	M	F	I	Berry	Bacca	Yellow	Brown
Margaritaria nobilis L. f.	7, 21	C3	Ns	Tr	T	A	M	D	D	Schizocarp	Coccarium	Yellow	Blue
Phyllanthus majus Steyerm.	14, 15	C3	Ns	Sh	T	A	M	D	D	Schizocarp	Coccarium	Green	Brown
Phyllanthus niruri L.	1, 5	C3	Ns	Ah	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Phyllanthus stipulatus (Raf.) G.L. Webster	18, 20	C3	Ns	Ah	T	A	D	D	D	Schizocarp	Coccarium	Green	Beige
Richeria grandis Vahl	6	C3	Ns	Tr	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Beige
PHYTOLACCACEAE													
Phytolacca icosandra L.	8	C3	Ns	Ph	T	A	D	F	I	Berry	Baccarium	Purple-black	Brown
Phytolacca rivinoides Kunth & C.D. Bouché	1, 3, 6-8	C3	Ns	Ah	T	A	D	F	I	Berry	Baccarium	Purple-black	Black
Rivina humilis L.	1, 2	C3	Ns	Ph	T	A	D	F	I	Berry	Baccarium	Red	Black
Trichostigma octandrum (L.) H. Walter	1	C3	Ns	L	T	A	D	F	I	Berry	Baccarium	Purple-black	Black
PICRAMNIACEAE													
Picramnia caracasana Engl.	1	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Red	Brown
PLANTAGINACEAE													

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Scoparia dulcis L.	18, 24, 25	C3	Ns	Ah	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
POACEAE													
Agrostis breviculmis Hithc.	4	C3	Ns	Ph	T	A	M	D	I	Caryopsis	Anthecium	Brown	Beige
Andropogon bicornis L.	3, 18, 20	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Beige	White
Andropogon fastigiatus Sw.	23	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Beige	White
Andropogon leucostachyus Kunth	3, 21	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Beige	White
Andropogon selloanus (Hack.) Hack.	3, 25, 26	C4	Ns	Ph	T	A	M	D	I	Caryopsis	Anthecetum	Beige	White
Aristida adscensionis L.	5	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Beige
Aristida moritzii Henrard	23	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Beige
Aristida recurvata Kunth	14, 19	C4	Ns	Ph	T	A	M	D	I	Caryopsis	Anthecetum	Brown	Beige
Aristida torta (Nees) Kunth	18, 19	C4	Ns	Ph	T	A	M	D	I	Caryopsis	Anthecetum	Brown	Beige
Axonopus anceps (Mez.) Hitch.	14, 18, 19, 20	C4	Ns	Ph	T	A	M	D	I	Caryopsis	Anthecetum	Green	Beige
Axonopus canescens (Nees ex Trin.) Pilg.	18, 19, 24, 25	C4	Ns	Ph	T	A	M	D	I	Caryopsis	Anthecetum	Green	Beige
Axonopus fissifolius (Raddi) Kuhlm	19, 23	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Green	Beige
Axonopus flabelliformis Swallen	14, 16, 17, 19	C4	Ns	Ph	T	A	M	D	I	Caryopsis	Anthecetum	Green	Beige
Bothriochloa pertusa (L.) A.Camus	5	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Brown
Calamagrosty fribrovaginata Lægaard	4	C3	Ns	Ph	T	A	M	D	I	Caryopsis	Anthecium	Brown	Beige
Cenchrus brownii Roem. & Schult.	5	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Antecosum	Brown	Brown
Cenchrus ciliaris L.	5	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Antecosum	Brown	Brown
Cenchrus echinatus L.	5	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Antecosum	Brown	Brown
Chloris barbata Sw.	1	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecium	Brown	Beige
Chloris inflata Link	5	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecium	Brown	Beige
Chloris virgata Sw.	1	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Anthecium	Brown	Beige
Dactyloctenium aegyptium	5	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Anthecium	Brown	Brown
Echinolaena inflexa (Poir) Chase	14-20	C3	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Beige
Festuca fragilis (Luces) B. Briceño	4	C3	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecium	Brown	Beige
Hyparrhenia rufa (Nees) Stapf	24, 25	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Brown
Ichnanthus nemorosus (Sw.) Döll	1, 21	C3	Ns	Ph	T	A	M	F	I	Caryopsis	Anthecetum	Purple-black	Beige
Lasiacis anomala Hitchc.	24, 27	C3	Ns	Ph	T	A	M	F	I	Caryopsis	Anthecetum	Purple-black	Beige
Lasiacis divaricata (L.) Hitchc.	21	C3	Ns	Ph	T	A	M	F	I	Caryopsis	Anthecetum	Purple-black	Beige

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Lasiacis sorghoidea Hitchc.	1, 2	C3	Ns	Ph	T	A	M	F	I	Caryopsis	Anthecetum	Purple-black	Beige
Leersia ligularis Trin.	1	C3	Ns	Ph	T	A	M	D	I	Caryopsis	Anthecium	Green	Beige
Mesosetum chaseae Luces	23	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Beige
Mesosetum pittieri Hitchc.	23	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Beige
Mesosetum rottboellioides (Kunth) Hitchc.	14,19	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Beige
Olyra latifolia L.	7, 21	C3	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecium	White	Beige
Panicum cyanescens Nees ex Trin.	3, 14, 16-20, 26	C3	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Green	Beige
Panicum hispidifolium Swallen	23	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Anthecetum	Green	Beige
Panicum micranthum Kunth	18, 19	C3	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Green	Beige
Panicum nervosum Lam.	15	C3	Ns	Ph	T	A	M	D	I	Caryopsis	Anthecetum	Green	Beige
Panicum rudgei Roem. & Schult	18, 19	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Green	Beige
Panicum stenodes Griseb	19, 26	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Anthecetum	Green	Beige
Panicum venezuelae Hack.	1	C3	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Green	Beige
Pariana stenolemma Tutin	7	C4	Ns	Ph	T	A	M	D	I	Caryopsis	Anthecium	Beige	Beige
Paspalum conjugatum P.J. Bergius	21	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Brown
Paspalum convexum Humb. & Bonpl. ex Flüggé	23	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Anthecetum	Purple-black	Beige
Paspalum fimbriatum Kunth	1	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Brown
Paspalum lanciflorum Trin.	14, 18-20	C3	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Beige
Paspalum multicaule Poir.	23, 26	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Brown
Paspalum stellatum Humb. & Bonpl. ex Flüggé	15	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Brown
Pennisetum setosum (Sw.) Rich.(	23	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Polyanthecetum	Brown	Beige
Raddiella esenbeckii (Steud.) C.E. Calderón & Soderstr.	19	C4	Ns	Ph	T	A	M	D	I	Caryopsis	Anthecetum	Green	Beige
Schizachirium sanguineum (Retz.) Alston	14, 20	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Beige
Schizachyrium microstachyum (Desv. ex Ham.) Roseng., B.R. Arrill. & Izag.	24	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Beige
Schizachyrium tenerum Ness	19	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Beige
Setaria setosa (sw.) Beauvois var. leiphylla (Nees) Kunth	1	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Beige
Setaria vulpiseta (Lam.) R.en & Schult	1, 5	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Beige

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Sorghum bicolor (L.) Moench	1, 5	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Anthecetum	Brown	Beige
Sporobolus indicus (L.) R. Br.	1	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Caryopsis	Brown	Beige
Sporobolus pyramidatus (Lam.) Hitchc.	5, 21	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Caryopsis	Brown	Beige
Sporobolus virginicus (L.) Kunth	11, 13	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Caryopsis	Brown	Beige
Thrasya trinitensis Mez	19	C4	Ns	Ph	T	A	M	D	I	Caryopsis	Anthecium	Green	Beige
Trachypogon spicatus (L. f.) Kuntze	3, 14-20, 25	C4	Ns	Ph	T	A	M	D	I	Caryopsis	Anthecetum	Brown	Beige
Tragus berteronianus schult.	5	C4	Ns	Ah	T	A	D	D	I	Caryopsis	Antecosum	Brown	Beige
Urochloa decumbens (Stapf) R.D. Webster	18, 20	C4	Ns	Ph	T	A	D	D	I	Caryopsis	Anthecetum	Green	Beige
Urochloa fusca (Sw.) B.F. Hansen & Wunderlin	1, 5	C4	Ns	Ph	T	A	D	F	I	Caryopsis	Anthecetum	Yellow	Beige
POLYGALACEAE													
Bredemeyera floribunda Willd.	1	C3	Ns	L	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	White
Monnima phytolaccifolia Kunth	8	C3	Ns	Ph	T	A	D	F	I	Drupe	Drupe	Purple-black	Brown
Monnina pubescens (Bonpl.) Kunth	6, 7	C3	Ns	Ph	T	A	D	F	I	Drupe	Drupe	Purple-black	Beige
Moutabea guianensis Aubl.	3	C3	Ns	L	T	A	M	F	I	Drupe	Drupe	Yellow	Brown
Polygala adenophora DC.	19	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Polygala appressa Benth.	16, 17, 19	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Polygala caracasana Kunth	1	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Polygala glochidiata Kunth	19	C3	Ns	Ah	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Polygala hygrophila Kunth	19	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Polygala longicaulis Kunth	3, 14, 18, 19	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Polygala paniculata L.	19- 21	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Polygala timoutou Aubl.	18, 19, 26	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Polygala variabilis Kunth	23	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Securidaca coriacea Bonpl.	24	C3	Ns	L	T	A	M	D	I	Samara	Samara	Brown	Brown
Securidaca paniculata Rich	18	C3	Ns	L	T	A	D	D	I	Samara	Samara	Brown	Brown
Securidaca scandens Jacq.	1	C3	Ns	L	T	A	D	D	I	Samara	Samara	Brown	Brown
POLYGONACEAE													
Coccoloba schomburgkii Meisn.	14-17	C3	Ns	Sh	T	A	M	F	I	Achene	Pseudodrupe	Brown	Green

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Coccoloba uvifera (L.) L.	5, 13	C3	Ns	Tr	T	A	D	F	I	Achene	Pseudodrupe	Purple-black	Brown
Rumex acetosella L.	4	C3	Ns	Ph	T	A	D	F	I	Achene	Pseudodrupe	Red	Beige
Rumex crispus L.	4	C3	Ns	Ph	T	A	D	D	I	Achene	Diclesium	Brown	Brown
PORTULACACEAE													
Portulaca elatior Mart. ex Rohrb.	5	C4	S	Ph	T	A	D	D	D	Pyxidium	Pyxidium	Brown	Black
Portulaca oleracea L.	5	C4	S	Ah	T	A	D	D	D	Pyxidium	Pyxidium	Brown	Black
PRIMULACEAE													
Cybianthus duidae (Gleason & Moldenke) G. Agostini	16, 17	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Cybianthus quelchii (N.E. Br.) G. Agostini	15	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Jacquinia aristata Jaqc.	5, 12	C3	Ns	Tr	T	A	M	F	I	Berry	Bacca	Green	Brown
Myrsine coriaceae (Sw.) R. Br. ex Roemer et Schult.	15, 18	C3	Ns	Tr	T	A	D	F	I	Drupe	Drupe	Purple-black	Beige
Myrsine guianensis (Aubl.) Kuntze	7, 21	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Green	Black
Rapanea ferruginea (Ruiz & Pav.) Mez	6, 7	C3	Ns	Tr	T	A	D	F	I	Drupe	Drupe	Yellow	Brown
PROTEACEAE													
Roupala minima Steyermark	19	C3	Ns	Ph	T	A	D	D	D	Follicle	Follicle	Brown	Brown
Roupala montana Aubl.	1, 17, 21	C3	Ns	Tr	T	A	M	D	D	Follicle	Follicle	Brown	Brown
RANUNCULACEAE													
Clematis dioica L.	6, 7	C3	Ns	L	T	A	D	D	I	Agregate of achene	Achenetum	Brown	Brown
RAPATEACEAE													
Stegolepis angustata Gleason	14-17	C3	Ns	Ph	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Stegolepis ptaritepuiensis Steyerm.	14, 15	C3	Ns	Ph	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
RHAMNACEAE													
Gouania polygama (Jaqc.) Urban	1, 22, 24, 27	C3	Ns	L	T	A	D	D	I	Schizocarp	Samarium	Brown	Black
RHIZOPHORACEAE													
Rhyzophora mangle L.	10, 13	C3	Ns	Tr	T	A	M	F	I	Berry	Bacca	Green	Green
ROSACEAE													
Acaena cylindristachya Ruiz & Pavon	4, 8	C3	Ns	Ph	T	A	D	D	I	Agregate of achene	Diclesetum	Brown	Brown
Acaena elongata L.	4	C3	Ns	Ph	T	A	D	D	I	Agregate of achene	Diclesetum	Brown	Brown
Lachemilla aphanoides (Mutis ex L.f.) Rothm.	4	C3	Ns	Ph	T	A	D	D	I	Agregate of achene	Diclesetum	Brown	Brown
Polylepis sericea Wedd.	4	C3	Ns	Tr	T	A	M	D	I	Achene	Diclesium	Brown	Brown
RUBIACEAE													

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Arcytophyllum nitidum (Kunth) Schltdl.	4, 8	C3	Ns	Sh	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Borreria acimoides (Burm.) DC.	21	C3	Ns	Ph	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Borreria assurgens (Ruiz & Pav.) Griseb.	1	C3	Ns	Ah	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Borreria capitata (Ruiz & Pav.) DC.	6, 15, 18, 19, 23	C3	Ns	Ph	T	A	D	D	D	Schizocarp	Microbasarium	Brown	Brown
Borreria verticillata (L.) G. Mey.	20, 27	C3	Ns	Ph	T	A	D	D	D	Schizocarp	Coccarium	Brown	Brown
Chalepophyllum guianense Hook f.	14, 16, 17	C3	Ns	Sh	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Chiococca alba (L.) Hitchc.	1	C3	Ns	L	T	A	M	F	I	Drupe	Drupe	White	Brown
Coccocypselum hirsutum Bartl. ex DC.	20	C3	Ns	Ph	T	A	D	F	I	Berry	Bacca	Blue	Brown
Coccocypselum lanceolatum (Ruiz & Pav.) Pers.	6, 7	C3	Ns	Ph	T	A	D	F	I	Berry	Bacca	Blue	Brown
Coutarea hexandra (Jaqc.) Schum.	1, 22	C3	Ns	Sh	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Declieuxia fruticosa (Willd. ex Roem. & Schult.) Kuntze	15-20	C3	Ns	Ph	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Diodia apiculata (Willd. ex R. & S.) Schum.	21, 23	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Microbasarium	Brown	Brown
Diodia multiflora DC.	26	C3	Ns	Ph	T	A	D	D	I	Schizocarp	Microbasarium	Brown	Black
Duroia genipoides Hook. f. ex K. Schum.	3	C3	Ns	Tr	T	A	M	F	I	Berry	Anphisarcum	Brown	Brown
Erithalis fruticosa ssp fruticosa	13	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Genipa americana var. caruto (Kunth) K. Schum.	1, 22	C3	Ns	Tr	T	A	M	F	I	Berry	Anphisarcum	Brown	Brown
Guettarda divaricata (Humb. & Bonpl. ex Schult.) Standl.	24, 27	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Purple-black	Brown
Guettarda roupalifolia Rusby	1	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Hillia parasitica Jacq.	7, 21	C3	S	L	T	P	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Beige
Machaonia ottonis (K. Schum.) Urb.	5	C3	Ns	Sh	T	A	D	D	I	Schizocarp	Diclesarium	Beige	Beige
Mitracarpus hirtus (L.) DC.	21	C3	Ns	Ah	T	A	D	D	D	Pyxidium	Pyxidium	Brown	Brown
Pagamea capitata Benth.	16, 17	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Pagameopsis garryoides (Standley) Steyerm.	15	C3	Ns	Ph	T	A	M	F	I	Drupe	Sorosus	Purple-black	Brown
Palicourea angustifolia Kunth	6	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Purple-black	Brown

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Palicourea crocea (Sw.) Schult.	7, 18	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Purple-black	Brown
Palicourea fendleri Standl.	6, 7	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Purple-black	Brown
Palicourea petiolaris Kunth	6, 7	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Purple-black	Brown
Perama galioides (Kunth) Poir.	14, 16-20	C3	Ns	Ph	T	A	D	D	D	Pyxidium	Pyxidium	Brown	Brown
Platycarpum orinocense Bonpl.	3	C3	Ns	Tr	T	A	M	F	D	Drupe	Drupe	Brown	Brown
Psychotria anceps Kunth	3, 26, 27	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Orange	Brown
Psychotria costularia (Baill.) Standl. & Steyerm.	6	C3	Ns	Ph	T	A	D	F	I	Drupe	Drupe	Purple-black	Brown
Psychotria hoffmannseggiana (Willd. ex Schult.) Borhidi	3, 20	C3	Ns	Sh	T	A	D	F	I	Drupe	Drupe	Purple-black	Brown
Psychotria microdon (DC.) Urb.	2	C3	Ns	Tr	T	A	D	F	I	Drupe	Drupe	Purple-black	Brown
Psychotria polycephala Benth	17, 18	C3	Ns	Ph	T	A	D	F	I	Drupe	Drupe	Blue	Beige
Randia dioica H. Karst.	1	C3	Ns	Tr	T	A	M	F	I	Berry	Anphisarcum	Yellow	Black
Randia hebecarpa Benth.	22, 24, 27	C3	Ns	Sh	T	A	M	F	I	Berry	Anphisarcum	Yellow	Black
Randia venezuelensis Steyerm.	3	C3	Ns	Sh	T	A	M	F	I	Berry	Anphisarcum	Yellow	Brown
Remijia densiflora ssp. stenopetala (Standl. & Steyerm.) Steyerm.	15	C3	Ns	Sh	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Beige
Rondeletia mollis S.F. Blake ex Steyerm.	1	C3	Ns	Sh	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Rosenbergiodendron formosum (Jacq.) Fagerl. var. densiflora Bartl. ex Schum.	24, 27	C3	Ns	Sh	T	A	M	F	I	Berry	Anphisarcum	Yellow	Black
Rudgea karstenii Standl.	6, 7	C3	Ns	Tr	T	A	D	F	I	Drupe	Drupe	Purple-black	Brown
Sabicea velutina Benth.	18	C3	Ns	L	T	A	D	F	I	Berry	Bacca	Red	Brown
Simira rubescens (Benth.) Bremek. ex Steyerm.	3	C3	Ns	Tr	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Sipanea galioides Wernham	14, 15, 18, 19	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
RUTACEAE													
Fagara culantrillo (Kunth) Schult. & Schult. f.	27	C3	Ns	Sh	T	A	M	D	D	Agregate of follicle	Coccarium	Brown	Black
Zanthoxylum aff. caribaeum Lam.	22, 24	C3	Ns	Tr	T	A	M	D	D	Agregate of follicle	Coccarium	Brown	Black
Zanthoxylum ciliatum Engl.	1	C3	Ns	Tr	T	A	M	D	D	Agregate of follicle	Coccarium	Green	Brown
Zanthoxylum fagara (L.) Sarg.	1	C3	Ns	Sh	T	A	M	D	D	Agregate of follicle	Coccarium	Green	Black

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Zanthoxylum rhoifolium Lam.	7	C3	Ns	Sh	T	A	M	F	D	Agregate of follicle	Coccarium	Red	Black
SALICACEAE													
Casearia guianensis (Aubl.) Urb.	21	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Yellow	Orange
Casearia hirsuta Sw.	22	C3	Ns	Sh	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Green	Brown+ Yellow
Casearia mollis Kunth	22, 24	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Yellow	Red
Casearia spinescens (Sw.) Griseb.	2	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Yellow	Brown+ Yellow
Casearia sylvestris Sw.	25	C3	Ns	Sh	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Green	Black+Red
Hecatostemon completus (Jacq.) Sleumer	27	C3	Ns	Sh	T	A	D	F	D	Loculicidal capsule	Loculicidal capsule	Yellow	Red
Prockia flava H. Karst.	1	C3	Ns	Tr	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
SANTALACEAE													
Phoradendron mucronatum (DC.) Krug & Urb.	1, 5	C3	S	Ph	T	P	M	F	I	Berry	Bacca	Yellow	Green
Phoradendron ottonis Eichler	1	C3	S	Ph	T	P	M	F	I	Berry	Bacca	Yellow	Green
Phoradendron rubrum (L.) Gris.quadrangulare (Kunth) Griseb.	1	C3	S	Ph	T	P	M	F	I	Berry	Bacca	Yellow	Green
Phoradendron semivenosum Rizzini	17	C3	S	Ph	T	P	M	F	I	Berry	Bacca	Yellow	Green
Phoradendron tubulosum Urb.	1	C3	S	Ph	T	P	M	F	I	Berry	Bacca	Yellow	Green
Thesium tepuiense Steyerm.	14	C3	Ns	Ph	T	P	M	F	I	Berry	Bacca	Yellow	Green
SAPINDACEAE													
Allophylus racemosus Sw.	22, 24, 27	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Yellow	Beige
Cardiospermum corindum L.	5	C3	Ns	L	T	A	D	D	D	Septifragal capsule	Septifragal capsule	Beige	White+ Black
Matayba opaca Radlk.	15	C3	Ns	Tr	T	A	M	F	D	Loculicidal capsule	Loculicidal capsule	Red	White+ Black
Matayba tovarensis Radlk.	6, 7	C3	Ns	Tr	T	A	M	F	D	Loculicidal capsule	Loculicidal capsule	Red	White+ Black
Melicoccus bijugatus Jacq.	1	C3	Ns	Tr	T	A	D	F	I	Drupe	Drupe	Green	Beige
Paullinia cururu L.	27	C3	Ns	L	T	A	D	F	D	Septifragal capsule	Septifragal capsule	Red	White+ Black
Paullinia fuscescens Kunth	1	C3	Ns	L	T	A	D	F	D	Septifragal capsule	Septifragal capsule	Red	White+ Black
Paullinia leiocarpa Griseb.	3	C3	Ns	L	T	A	D	F	D	Septifragal capsule	Septifragal capsule	Red	Brown
Serjania atrolineata C. Wright	2, 22, 24, 25	C3	Ns	L	T	A	D	D	I	Schizocarp	Samarium	Brown	Brown
Serjania paniculata Kunth	1	C3	Ns	L	T	A	D	D	I	Schizocarp	Samarium	Brown	Brown

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Serjania rhombea Radlk.	1	C3	Ns	L	T	A	D	D	I	Schizocarp	Samarium	Brown	Brown
Talisia hexaphylla Vahl	2	C3	Ns	Tr	T	A	D	F	I	Drupe	Drupe	Yellow	Black
Urvillea ulmacea Kunth	1, 5	C3	Ns	L	T	A	D	D	I	Schizocarp	Samarium	Brown	Brown
SAPOTACEAE													
Bumelia obtusifolia subesp. auxifolia (Roem. & Schult.) Cronquist	5	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Elaeoluma schomburgkiana (Miq.) Baill.	17	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Brown	Black
SARRACENIACEAE													
Heliamphora heterodoxa Steyerm.	15	C3	Ns	Ph	T	I	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
SCROPHULARIACEAE													
Capraria biflora L.	1, 5, 9, 11	C3	Ns	Ah	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Black
Veronica serpyllifolia L. var. humifusa (Dicks.) Vahl	4	C3	Ns	Ph	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
SIMAROUBACEAE													
Castela erecta Turpin	9, 11, 12	C3	Ns	Sh	T	A	M	F	I	Drupe	Druparium	Red	Brown
SMILACACEAE													
Smilax poeppigii Kunth	6	C3	Ns	L	T	A	M	F	I	Berry	Bacca	Yellow	Brown
Smilax cumanensis Humb. & Bonpl. ex Willd	24, 27	C3	Ns	L	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Smilax pittieriana Steyerm.	3, 17	C3	Ns	L	T	A	M	F	I	Berry	Bacca	Yellow	Brown
SOLANACEAE													
Capsicum rhomboideum (Dunal) Kuntze	1	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Red	Brown
Cestrum alternifolium (Jacq.) O.E. Schulz	1, 24	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Purple-black	Black
Cestrum bigibbosum Pittier	6, 7	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Cestrum megalophyllum Dunal	7, 21	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Cestrum microcalyx Francey	7	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Cestrum potaliifolium Dunal	7	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Red	Brown
Cestrum salicifolium Jacq.	7	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Purple-black	Brown
Datura inoxia Mill.	5, 9, 11	C3	Ns	Ah	T	A	D	D	D	Septifragal capsule	Septifragal capsule	Brown	Brown
Lycianthes sp.	5	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Yellow	Brown
Lycium nodosum Miers	5	C3	S	Sh	T	A	M	F	I	Berry	Bacca	Red	Brown
Nicotiana glauca Graham	1, 5	C3	Ns	Sh	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Brown
Solanum sect. Maurella	18	C3	Ns	Ah	T	A	D	F	I	Berry	Bacca	Purple-black	Brown

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Solanum americanum Miller	1, 5, 8	C3	Ns	Ah	T	A	D	F	I	Berry	Bacca	Purple-black	Brown
Solanum asperum Rich.	6, 7, 21	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Yellow	Brown
Solanum bicolor Willd. ex Roem. & Schult.	23, 27	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Green	Brown
Solanum brachycanthum Dunal	21	C3	Ns	Sh	T	A	M	F	I	Berry	Bacca	Yellow	Brown
Solanum campaniforme Roem. & Schult.	19	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Red	Brown
Solanum gardneri Sendtn.	1, 5	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Red	Brown
Solanum hazenii Britton	1	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Green	Brown
Solanum mammosum L.	27	C3	Ns	Ah	T	A	D	F	I	Berry	Bacca	Orange	Brown
Solanum ombrophilum S. Knapp	21	C3	Ns	Sh	T	A	D	F	I	Berry	Bacca	Green	Brown
Solanum stramoniifolium Jacq.	18, 20	C3	Ns	Ah	T	A	D	F	I	Berry	Bacca	Orange	Brown
STYRACACEAE													
Styrax pallidus A. DC.	7, 21	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Yellow	Brown
Styrax wurdackiorum Steyerm.	17	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Yellow	Brown
SURIANACEAE													
Suriana maritima L.	11, 13	C3	S	Sh	T	A	M	D	I	Agregate of achene	Achenetum	Brown	Brown
SYMPLOCACEAE													
Symplocos suaveolens Klotzsch	21	C3	S	Sh	T	A	M	F	I	Drupe	Drupe	Yellow	Brown
TALINACEAE													
Talinum paniculatum (Jacq.) Gaertn.	1	CAM	S	Ph	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Green	Black
Talinum triangulare (Jaqc.) Willd.	5	CAM	S	Ph	T	A	D	D	D	Septicidal capsule	Septicidal capsule	Brown	Black
THYMELAEACEAE													
Daphnopsis americana (Mill.) J.R. Johnst.	7, 21	C3	Ns	Tr	T	A	M	F	I	Drupe	Nuculanium	Green	Black
VELLOZIACEAE													
Vellozia tubiflora (A. Rich.) Kunth	16, 19	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
VERBENACEAE													
Citharexylum subthyrsoideum Pittier	1	C3	Ns	Sh	T	A	M	F	I	Drupe	Drupe	Orange	Brown
Lantana achyranthifolia Desf.	1, 24, 25	C3	Ns	Ph	T	A	D	F	I	Drupe	Drupe	Purple-black	Beige
Lantana armata Schauer var. Velutina Moldenke	1, 27	C3	Ns	Ph	T	A	D	F	I	Drupe	Drupe	Purple-black	Brown
Lantana camara L. subsp. moritziana (Otto & A. Dietr.) R.W. Sanders	13, 18, 21, 24	C3	Ns	Ph	T	HP	D	F	I	Drupe	Drupe	Purple-black	Beige

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Lantana canescens Kunth	1, 5, 9	C3	Ns	Ph	T	A	D	F	I	Drupe	Nuculanium	Brown	Brown
Lantana caracasana Turcz.	1	C3	Ns	Ph	T	A	D	F	I	Drupe	Nuculanium	Brown	Brown
Lantana involucrata L.	13	C3	Ns	Ph	T	A	M	F	I	Drupe	Drupe	Purple-black	Brown
Lantana trifolia L.	1	C3	Ns	Ph	T	A	D	F	I	Drupe	Drupe	Purple-black	Brown
Lippia oreganoides Kunth	5	C3	Ns	Sh	T	A	M	D	I	Schizocarp	Microbasarium	Brown	Brown
Phyla nodiflora var. reptans (Kunth) Moldenke	5	C3	Ns	Ph	T	A	D	D	I	Schizocarp	Microbasarium	Brown	Brown
Stachytarpheta cayenensis (Rich.) Vahl	1, 3	C3	Ns	Ah	T	A	D	D	I	Schizocarp	Microbasarium	Black	Brown
Stachytarpheta jamaicensis (L.) Vahl	21	C3	Ns	Ph	T	A	D	D	I	Schizocarp	Microbasarium	Black	Brown
Stachytarpheta mutabilis (Jacq.) Vahl	1, 2	C3	Ns	Ph	T	A	D	D	I	Schizocarp	Microbasarium	Black	Brown
Stachytarpheta trinitensis Moldenke	21	C3	Ns	Ph	T	A	D	D	I	Schizocarp	Microbasarium	Black	Brown
Verbena litoralis Kunth	21	C3	Ns	Ph	T	A	D	D	I	Schizocarp	Camarium	Brown	Beige
VIOLACEAE													
Hybanthus attenuatus (Humb. & Bonpl. ex Schult.) Schulze-Menz	1	C3	Ns	Ah	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Hybanthus calceolaria (L.) Oken	25	C3	Ns	Ph	T	A	D	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
VITACEAE													
Cissus alata Jaqc.	24	C3	S	L	T	A	D	F	I	Drupe	Drupe	Purple-black	Beige
Cissus erosa Rich.	3, 24, 25	C3	Ns	L	T	A	D	F	I	Drupe	Drupe	Purple-black	Beige
Cissus sicyoides L.	1, 2, 5	CAM	Ns	L	T	A	D	F	I	Drupe	Drupe	Purple-black	Beige
Cissus trifoliata (L.) L.	11-13	CAM	S	L	T	A	D	F	I	Drupe	Drupe	Purple-black	Beige
VOCHYSIACEAE													
Vochysia venezuelana Stafleu	3, 22, 27	C3	Ns	Tr	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
XIMENIACEAE													
Ximenia americana L.	1	C3	Ns	Tr	T	A	M	F	I	Drupe	Drupe	Yellow	Brown
XYRIDACEAE													
Abolboda acaulis Maguire	14, 17	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Abolboda macrostachya var. Robustior Steyerm.	14	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Orectanthe sceptrum (Oliver) Macguire	14	C3	S	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Brown
Xyris bicephala Gleason	14, 15	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Xyris fallax Malme	14	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Xyris involucrata Nees.	14-16	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black

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Xyris laxifolia Martius var. delta	26	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Xyris roraimae Malme	14	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Xyris savanensis Miq.	26	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Xyris setigera Oliver	14-17, 19	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Xyris seubertii Nilsson	16	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Xyris surinamensis Spreng.	14, 16	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
Xyris uleana Malme	14, 16	C3	Ns	Ah	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Brown	Black
ZINGIBERACEAE													
Renealmia nicolaioides Loes.	7	C3	Ns	Ph	T	A	M	D	D	Loculicidal capsule	Loculicidal capsule	Purple-black	Black+Red
ZYGOPHILLACEAE													
Bulnesia arborea (Jacq.) Engl.	2, 5	C3	Ns	Tr	T	A	M	D	I	Schizocarp	Samarium	Brown	Brown
Guaiacum officinale L.	5	C3	Ns	Tr	T	A	M	D	D	Septicidal capsule	Septicidal capsule	Yellow	Brown
Kallstroemia maxima (L.) Hook. & Arn.	1, 5	C4	Ns	Ah	T	A	D	D	I	Schizocarp	Camarium	Brown	Brown
Tribulus cistoides L.	11-13	C4	Ns	Ah	T	A	D	D	I	Schizocarp	Camarium	Brown	Brown

[1]Localities
1= Secondary dry forest, Caracas Valley. 10° 29´N; 66° 33´W
2= Riparian dry forest, Tuy Valley, Cua, Miranda State. 10° 09´ N; 66° 53´ W
3= Riparian wet forest, Cataniapo River. Amazonas State. 5° 36´N; 67° 6´W
4= Páramo, Andean High Mountain, La Culata National Park. Merida State. 8° 03´N; 70° 49'W
5= Xerophytic shrubland, Central Coastal Zone. Vargas State. 10° 36´N; 67° 2´W
6= Cloud forest, Coastal mountain range, Miranda State. 10° 20´ N; 66° 55´ W
7= Cloud forest, Coastal mountain range, Henri Pittier National Park. Aragua State. 10° 21´ N; 67° 36´ W
8= Sub-Páramo, High mountain shrubland, Pico Naiguatá, El Ávila National Park. Capital District. 10° 32´ N; 66° 47´ W
9= Littoral Meadow, Coastal Plain of Paraguaná. Falcón State. 11° 50´N; 69° 48´W
10= Mangrove, Coastal Plain of Paraguaná. Falcon State. 11° 40´N; 69° 49´W
11= Psamophilous Meadow, Coastal Plain of Paraguaná. Falcón State. 11° 40´N; 69° 49´W
12= Xerophytic shrubland, Coastal Plain of Paraguaná. Falcón State. 11° 40´N; 69° 49´W
13= Littoral Shrubland, Atolon, Morrocoy National Park. Falcon State. 10° 58´N; 68° 15´W
14= Broad-leaved meadow, Gran Sabana Plateau, Canaima National Park. Bolívar State. 5° 38´ N; 61° 22´W
15= Mesotermic shruland (Jardin), Gran Sabana Plateau, Canaima National Park. Bolívar State. 5° 38´ N; 61° 41´W
16= Mesotermic shruland (Liworiwo), Gran Sabana Plateau, Canaima National Park. Bolívar State. 5° 36´ N; 61° 29´W
17= Mesotermic shruland (Mareman), Gran Sabana Plateau, Canaima National Park. Bolívar State. 5° 44´ N; 61° 24´W
18= Secondary bushland, Gran Sabana Plateau, Canaima National Park. Bolívar State. 5° 40´ N; 61° 32´W
19= Savanna grassland, Gran Sabana Plateau, Canaima National Park. Bolívar State. 5° 42´ N; 61° 31´W
20= Secondary savanna, Fallow, Gran Sabana Plateau, Canaima National Park. Bolívar State. 5° 40´ N; 61° 32´W
21= Dwarf cloud forest, Insular montane forest, Cerro Copey National Park. Nueva Esparta State. 10° 59′ N; 63° 54′ W
22= Dry forest, Venezuelan Central Plain, Estacion Biologica de los Llanos. Guárico State. 8° 56´N; 67° 25´W
23= Disturbed grassland, Venezuelan Central Plain, Estacion Biologica de los Llanos. Guárico State. 8° 56´N; 67° 25´W
24= Ecotone Forest-Savanna, Venezuelan Central Plain, Estacion Biologica de los Llanos. Guárico State. 8° 56´N; 67° 25´W
25= Savanna with shrubs, Venezuelan Central Plain, Estacion Biologica de los Llanos. Guárico State. 8° 56´N; 67° 25´W
26= Palm swamp, Venezuelan Central Plain, Morichal Largo. Guárico State. 8° 56´ N; 67° 25´ W
27= Galery forest, Venezuelan Central Plain, Orituco River. Guárico State. 9° 47´ N; 67° 25´W
28= Paramo, San José de Sur, Merida State.
29= Dry forest, Aguas Termales Las Trincheras, Carabobo State. 10°18N; 68°04´W
30= Dry forest, Mision Nuestra Sra. del Carmen, Yaracuy State. 10°20´N; 68°41W
31=Xerophytic shrubland, Near San Juan de Lagunillas, Merida State. 8° 30´N; 71°21´W
32=Xerophytic shrubland, Mesa de Esnujaque, Trujillo State. 9°03´N; 70°42´W
33= Experimental Station, Barrancas, Barinas State. 8°46' N, 70°25'W
34= Dry forest, flooded plain of the Mene river, Zulia State. 10°27'N; 71°27'W
35=Mesotermic shruland (Kama fall), Gran Sabana Plateau, Canaima National Park. Bolívar State.
36= Montane Forest, Avila National Park, Capital District.
37= Dry premontane forest, Los Caracas, Distrito Federal, Estado Vargas. 10°37´N; 66°34¨W
38= Rain forest, Imataca Reserve, Bolívar State. 8°03´N; 61°39´W
39= Rain forest, near El Dorado, Bolívar State. 6°43´N; 61°37´W
40= Municipio Manrique, Road to La Sierra, Cojedes State.
41 = Municipio Romulo Gallegos, East to Las Vegas, Cojedes State.
42 = Disturbed area, Guanare-Mesa Cavacas road, Portuguesa State.
43 = Páramo, Andean High Mountain, El Zumbador, Tachira State
44 = Salazar town, To Chururú, Tachira State
45 = Road edge, Dabajuro-Maracaibo, Falcón State.
46 = Stream border, National Park, Cuevas de la quebrada, El Toro, Falcón State,
47 = Disturbed area, Maracay, Aragua State.
48 = Avocado plantation, Palo Negro, Aragua State.
49 = Road side Merida-Jaji, Las Correras, Merida State.
50 = Road Barinas-Santo Domingo, Barinas State.
[2]Succullence: S = Succulent, Ns = No succulent
[3]Life form: Tr = Trees, Sh = Shrubs, L = Lianas, Ph = Perennial herbs, Ah = Annual herbs
[4]Epiphytism: T = Terrestrials, E = Epiphytes
[5]Nutritional relation: A = Autotropics, I = Insectivores, P = Parasitics
[6]Successional stage: M = Mature, D = Disturbed
[7]Fruit texture: F = Fleshy, D = Dry
[8]Fruit dehiscence: D = Dehiscent, I = Indehiscent

Author Contributions

Nelson Ramírez: Contribution in the concept of the study; data collection; data analysis and interpretation; manuscript preparation; contribution to critical revision, adding intellectual content.

Yeni Barrios: Contribution to data collection; manuscript preparation; contribution to critical revision, adding intellectual content; data analysis and interpretation.

Herbert Briceño: Contribution to data collection; data analysis and interpretation; manuscript preparation.

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 ethic conflicts.

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Editorial

It's biodiversity, stupid!

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Paraphrasing James Carville, a strategist in Bill Clinton's successful 1992 presidential campaign, **"It's biodiversity, stupid!"**, the phrase we must shout out for the world to realize that the destruction of biodiversity and associated ecosystem services underlies both the SARS-Cov2 pandemic and the climate crisis.

Pandemics emerge from microbial diversity found in nature. Emerging diseases (e.g., Ebola, Zika, Dengue, Chikungunya) and almost all known pandemics (e.g., Influenza, HIV/AIDS, COVID-19) are zoonoses; that is, they are caused by microbes of animal origin. Mammals (mainly bats, rodents, primates) and some birds (such as waterfowl), as well as livestock (e.g., poultry), are the most important reservoirs of pathogens with pandemic potential (IPBES 2020)

Blaming biodiversity for the emergence of pandemics is wrong because the risk of a pandemic is driven by exponentially increasing anthropogenic changes. Land-use change, agricultural expansion and intensification, wildlife trade and consumption, overharvesting natural resources, pollution, among other unsustainable use of the environment, disrupt natural interactions among wildlife and their microbes, increase contact among wildlife, livestock, people, and their pathogens, and have led to almost all pandemics (IPBES 2020).

Currently, a pandemic preparedness strategy is non-existent and the world responds to a pandemic after it has emerged. Nonetheless, the IPBES Workshop Report on Biodiversity and Pandemics (IPBES 2020) identifies substantial knowledge that provides pathways to predict and prevent pandemics. Further, an increase in knowledge about microbial diversity and reducing the expansion of agribusiness, mining, and logging over pristine areas could allow us to prevent the development of yet another pandemic in a few years.

Research work that predicts geographic origins of future pandemics, identifies key host reservoirs and pathogens most likely to emerge, and demonstrates how environmental and socioeconomic changes correlate with disease emergence, is urgently needed. Pilot projects, often at a large scale, have demonstrated that such knowledge can be used to effectively target viral discovery, surveillance, and outbreak investigation. The major impact on the public health of COVID-19, of HIV/AIDS, Ebola, Zika, Influenza, SARS, and many other emerging diseases underlines the critical need for science-based policies that promote pandemic prevention (IPBES 2020). The public health crisis also calls for the implementation of policies leading to transformative changes (see IPBES 2019 and 2020 for these policy options).

Climate change has implications in disease emergence and will likely increase substantial future pandemic risk by driving movements of people, wildlife, host reservoirs, and pathogen vectors. Such movements will lead to new and increased contact among species and disrupt natural host-pathogen dynamics. Biodiversity loss associated with landscape degradation can lead to an increased risk of an emerging disease. This happens in cases in which species well adapted to human-dominated landscapes are also able to harbor pathogens that pose a high risk of zoonotic transmission. Pathogens of wildlife, livestock, and people can directly threaten biodiversity as well; they emerge via the same activities that drive disease risk in people (e.g., the emergence of chytridiomycosis in amphibians worldwide due to the wildlife trade).

> "Climate change and biodiversity loss are two of the most pressing issues of the Anthropocene. While there is recognition in both scientific and policy-making circles that the two are interconnected, in practice they are largely addressed in their own domains. The research community dedicated to investigating the climate system is somewhat, but not completely, distinct from that which studies biodiversity. Each issue has its own international Convention (the UN Framework Convention on Climate Change and the Convention on Biological Diversity), and each has an intergovernmental body that assesses available knowledge [the Intergovernmental Panel on Climate Change (IPCC) and the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES)]. This functional separation creates a risk of incompletely identifying, understanding, and dealing with the connections between the two. In the worst case, it may lead to taking actions that inadvertently prevent the solution of one or the other, or both issues. It is the nature of complex systems that they have unexpected outcomes and thresholds, but also that the individual parts cannot be managed in isolation from one another" (Pörtner et al 2021).

Impacts of climate change on biodiversity affect species geographical distribution, species phenology, population dynamics, community structure, ecosystem function, and, therefore, the ecosystem services they can provide. Although the Paris Agreement focuses on keeping the increase in global average temperature below 1,5ºC until de end of the century, most experts in climate change, when privately asked, agree that the best we will achieve is more like an increase of up to 3ºC (Tollefson, 2021)

The scientific community has been working for some time on the synergies and trade-offs between climate and biodiversity. Examples of synergy include an action taken to protect the biodiversity that simultaneously contributes to mitigating climate change and action to increase the capacity of species or ecosystems to adapt to climate change, which cannot be avoided. In contrast, negative trade-offs may also result. For instance, an action taken to mitigate climate change by using the land or ocean to absorb greenhouse gases may result in loss of biodiversity or other nature-based benefits that flow from the affected ecosystems. Only by considering climate and biodiversity as parts of the same complex problem – which also includes the actions, motivations, and aspirations of society – scientists and policymakers can advance in designing and implementing solutions that avoid maladaptation and maximize beneficial outcomes for climate and biodiversity and, consequently, for public health. Seeking such solutions is important if society wants to protect development gains and expedite the move towards a more sustainable, healthy, and equitable world for all. The role of science in addressing the current pandemic illustrates how science can inform policy and society for identifying possible solutions.

Connecting the climate and biodiversity spheres is especially crucial at this moment when the world seems to be gearing up for stronger actions on both. Urgent, timely, and targeted actions can minimize detrimental trends and counteract escalating risks while avoiding costly ones. Humankind has no time to lose, and we hope that this Editorial will support such urgent actions toward "The Future We Want". Biodiversity and associated ecosystem services loss and Climate Change are two sides of the same coin. Neither will be successfully resolved unless both are tackled together. What are the solutions to the multiple crises we leave? We would say "Its biodiversity coupled with reduction of fossil fuel, consumerism, waste, pollution, and deforestation, stupid!"

Author Contributions

Carlos A. Joly: 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.

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

Conflicts of Interest

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

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Inventory

Fish fauna of small-order streams of savannah and forest fragments landscape in the lower Tapajós River basin, Amazonia

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Abstract: To better understand the fish fauna of Amazonian streams, we assessed small streams in a landscape of forest fragments and savannah in the region of the lower Tapajós River, Brazil. We sampled the fish fauna using a well-tested active capture method during two dry seasons (October 2006 and 2018) and one rainy season (March to May 2018). Species richness was calculated using an abundance matrix and first-order jackknife estimator. Using qualitative and quantitative data, we present a cluster analysis in which each stream corresponds to a sampling unit. We collected 6,094 individuals of 43 species distributed in six orders. The sampling effort represents 73% of the estimated richness (58.69 ± 7.65). The most abundant species were *Copella nattereri, Iguanodectes variatus* and *Laimosemion dibaphus* that together represent almost half of the total sample (48.7%). The most frequent species were *Aequidens epae*, *Helogenes marmoratus* and *Laimosemion dibaphus*, which were collected in 11 of the 13 sampled streams. This is the first fish fauna list for small-order streams of savannah and forest fragments landscape in Amazonian Brazil. The richness of fish and the presence of many rare species underscore the contribution of small streams to the regional fish fauna composition, even in dynamic and spatially restricted landscapes.
Keywords: *Eastern Amazonia; Headwater streams; Neotropical fish; Riverscapes; Stream fish.*

Ictiofauna de riachos de pequena ordem de uma paisagem de savana e fragmentos florestais no baixo rio Tapajós, Amazônia

Resumo: Com o objetivo de aprimorar o conhecimento científico sobre a ocorrência da ictiofauna de riachos na Amazônia, acessamos pequenos riachos em uma paisagem composta por fragmentos florestais e savana, na região do baixo rio Tapajós. Amostramos a fauna de peixes com um método bem testado de captura ativa em duas estações secas, outubro de 2006 e 2018 e em uma estação chuvosa de março a maio de 2018. A riqueza de espécies foi calculada a partir da matriz de abundância com o estimador jackknife de primeira ordem. Usando dados qualitativos e quantitativos, apresentamos uma análise de agrupamento, onde cada riacho corresponde a uma unidade amostral. Coletamos 6094 indivíduos, de 43 espécies distribuídas em seis ordens. O esforço de amostragem representou 73% da riqueza estimada (58,69 ± 7,65). As espécies mais abundantes foram *Copella nattereri, Iguanodectes variatus* e *Laimosemion dibaphus*, representando em conjunto quase a metade do total amostrado (48,7%). As espécies mais frequentes foram *Aequidens epae*, *Helogenes marmoratus* e *Laimosemion dibaphus*, coletadas em 11 dos 13 riachos amostrados. Esta é a primeira lista de peixes de pequenos riachos em savana e fragmentos florestais da Amazônia brasileira. A riqueza de peixes e a presença de muitas espécies raras ressaltam a contribuição de riachos de pequena ordem para a composição regional da fauna de peixes, mesmo em paisagens dinâmicas e espacialmente restritas.
Palavras-chave: *Amazônia oriental; Paisagens de rios; Peixes neotropicais; Peixes de riachos; Riachos de cabeceira.*

Introduction

The Neotropical region has the most diverse freshwater fish fauna on the planet, with 5,160 described species for South America and over 9,100 estimated species (Reis et al. 2016). The Amazon basin contains more than 2,700 freshwater fish species, of which around 1,700 are endemic (Reis et al. 2016, Dagosta and de Pinna 2019; Oberdorff et al. 2019). More than half of its linear extension comprises small-order streams (Macedo and Castello 2015) that have an extraordinarily diverse fish fauna (Bührnheim & Cox-Fernandes 2003, Mendonça et al. 2005, de Oliveira et al. 2009, Barros et al. 2011, Silva-Oliveira et al. 2016, Leitão et al. 2017).

Fish fauna studies in the Amazon basin are widespread for upland rainforest streams but still incipient for savannah landscapes. This vegetation has a restricted spatial distribution representing only 3–4% of the basin area (Pires and Prance 1985) and, as expected, many endemic taxa (Barbosa et al. 2003, Plotkin & Riding 2011, De Carvalho & Mustikin 2017). The savannah and its surrounding forest fragments along the lower Tapajós River are drained by small streams that are used for recreation by local populations and are threatened by urban growth. Therefore, it is urgent to conduct studies about these streams and their biota. Our goal here is to present the first fish fauna list for small streams in a savannah and forest fragments landscape, which is based on a standardized and well-tested active capture method used for small Amazonian streams.

Material and Methods

1. *Study area*

Sampling sites were selected in a landscape comprising forest fragments and savannah vegetation connected to a continuous forest (Amaral et al. 2017), in the lower Tapajós River basin (Figure 1 and Table 1). The combined sampling sites represent a drainage area of 17,847 ha. Drainage flows into a main lake, Verde Lake, and smaller streams flow to the right margin of the Tapajós River. The drainage is poorly developed or branched, with sparse streams in the landscape (Figure 1 and 2). The streams have clear water, a natural condition that is attractive to local tourism (Fróis pers. obs. and Figure 1).

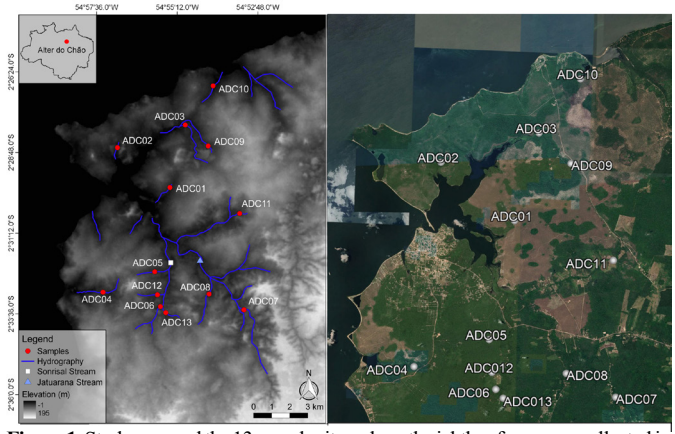


Figure 1. Study area and the 13 sample sites where the ichthyofauna was collected in small-order streams of savannah and forest fragments landscape in the lower Tapajós River (ADC is the code for Alter do Chão – the district name). The bigger streams at the study site are Jatuarana and Sonrisal, both third order streams. The image on the left represents elevation information from the SRTM radar, and on the right represents the vegetation in the study area (savannah = brown spots surrounding the ADC 01, 02, 03, 09, 10 and 11 samples). (SRTM 1 Arc-Second Global; Geographical Projection Lat-Long; Planimetric Datum WGS84; Database: IBGE/ANA).

The average annual precipitation is 1,991 mm and there are two well-defined climatic seasons: a dry period (precipitation <100 mm/month) between July and November and a rainy period (precipitation >100 mm) between December and June. The mean annual temperature is 25.9ºC, with a variation of 1.8 °C (Climate-data.org 2019). The vegetation is formed by semideciduous forest (IBGE 2012) surrounded by savannah. This savannah contains two dominant grass species, a shrub vegetation dominated by Melastomataceae and Myrtaceae species, and sparse, short- to medium-sized trees (Magnusson et al. 2008).

2. *Data collection*

We sampled the ichthyofauna in 13 first- and second-order streams (50-meter stretch per stream) using the standardized active capture method described in Mendonça et al. (2005). We carried out the first sampling in October 2006 at the peak of the dry season. We sampled the streams two more times in 2018, once in the rainy season (March to May) and once in the dry season (October).

The 50-meter stretches were blocked with fine-mesh nets (5 mm stretched mesh size) and the fish were sampled with two people/two hours of effort using seine net and hand nets. Collected specimens were euthanized with a 2% clove oil solution (Fernandes et. al 2017), fixed in a 10% formalin solution, transferred to 70% alcohol, and are deposited in the INPA Fish Collection (Table S1). We identified specimens using the literature (Géry 1977, Vari 1982, Kullander 1986). The taxonomic classification follows Fricke et al. (2020). We evaluated the sampling effort from an abundance matrix and a first-order *jackknife* richness estimator (Krebs 1999), with 1,000 randomizations and considering each stream stretch as an independent sample unit, using the software ESTIMATES version 9 (Cowell 2013). We calculated the fauna dissimilarity among sample units using the *Jaccard* distance for qualitative data (presence/absence) and *Bray-Curtis* distance for quantitative data, which is summarized as dendrograms drawn in PAST 3.20 (Hammer et al. 2001).

Results

We sampled 6,094 individuals, belonging to 43 species, eight orders and 22 families (Table 2). The streams had clear (mean turbidity = 1.3 NTU, range = 0.02-6.2) and acidic waters (mean pH = 4.5, range = 3.4-5.3), with low conductivity (mean = 15.4 µS/cm, range = 6.4-46.4) and relatively high temperature (mean = 27.3 °C, range = 25.2-29.4). Characiformes was the richest and most abundant order, with 19 species and 4,094 individuals, followed by Cichliformes with eight species and 542 individuals. Gymnotiformes had one more species than Siluriformes, but the latter had three times more individuals. Cyprinodontiformes was represented by two species and Gobiiformes, Perciformes and Synbranchiformes by one species each (Table 3). The most abundant species were *Copella nattereri* (1,181 individuals, 19.4% of total), *Iguanodectes variatus* (1,070, 17.4%) and *Laimosemion dibaphus* (728, 11.8%), which together accounted for almost half of the total individuals (2,958, 48.7%) (Figures 3 and 4). The most frequent species were *Aequidens epae*, *Helogenes marmoratus* and *L. dibaphus*, collected in 11 of the 13 sampled streams.

Thirty-two species were recorded during the first sampling (Dry season/2006), 29 species during the second sampling (Rainy season/2018) and 30 species during the third sampling (Dry/2018).

Table 1. Fish richness and total abundance for each stream sampled in savannah and forest fragments landscape in the lower Tapajós River basin.

Station	Remarks	Elevation	Coordinates	Richness (Abundance)
ADC01	Camarão Stream flows into the midwestern region of Verde Lake.	26 m	2°29'51.79"S 54°55'26.51"W	5 (74)
ADC02	Miritiapena Stream flows into the northern region of Verde Lake.	36 m	2°28'40.62"S 54°57'0.40"W	19 (768)
ADC03	Macaco Stream flows into the far northern region of Verde Lake.	26 m	2°28'0.23"S 54°54'59.22"W	13 (344)
ADC04	São Luíz Stream flows into Pindobal Lake.	30 m	2°32'58.63"S 54°57'26.10"W	7 (264)
ADC05	Heitor Stream is an affluent of Sonrisal Stream that flows into the far southern region of Verde Lake.	35 m	2°32'22.20"S 54°55'53.62"W	9 (813)
ADC06	Eugênia Stream is an affluent of Sonrisal Stream that flows into the far southern region of Verde Lake.	35 m	2°33'24.41"S 54°55'43.57"W	11 (616)
ADC07	São Pedro Stream is an affluent of Jatuarana Stream that flows into the far southern region of Verde Lake.	48 m	2°33'30.10"S 54°53'14.24"W	11 (439)
ADC08	São Raimundo Stream is an affluent of Jatuarana Stream that flows into the far southern region of Verde Lake.	32 m	2°33'1.94"S 54°54'16.49"W	11 (540)
ADC09	Aurélio Stream flows into the far northern region of Verde Lake.	31 m	2°28'37.74"S 54°54'18.29"W	8 (428)
ADC10	Taparí Stream flows into Taparí Lake.	18 m	2°26'50.39"S 54°54'9.47"W	29 (888)
ADC11	Areia Branca Stream flows into the far southern region of Verde Lake.	41 m	2°30'38.23"S 54°53'21.98"W	11 (317)
ADC12	Baroca Stream is an affluent of Sonrisal Stream that flows into the far southern region of Verde Lake.	36 m	2°33'3.24"S 54°55'48.94"W	3 (23)
ADC13	Laranjal Stream is an affluent of Sonrisal Stream that flows into the far southern region of Verde Lake.	44 m	2°33'35.17"S 54°55'34.00"W	11 (173)

Of the 43 species collected, 18 (41,9%) were recorded during all sampling periods. Species abundance did not vary among periods, except for *Copella callolepis* (Dry/2006: 14 individuals; Rainy/2018: 80; Dry/2018: 476), *C. nattereri* (677; 282; 201), *Hyphessobrycon heterorhabdus* (155; 11; 180) and *Helogenes marmoratus* (164; 44; 99) (Table 2). Some species distributions were related to a specific sample site or to a set of sample sites that were hydrographically related. *Copella callolepis* was present in a set of streams that drain into the southern border of Verde Lake (ADC 05, 06, 07, 08, 11 and 13). Its congeneric *C. nattereri* was present in the other sites (ADC 02, 03, 04, 09 and 10) and was never recorded in the same sample site. *Elachocarax junki* and *Pygopristis denticulata* were only sampled in the ADC 03 stream.

Species richness varied among streams. Sample sites ADC 02 and 10 had the greatest species richness (S = 19 and 28, respectively). Some of these species were considered occasional due to the variation between sampling periods (Table 2). In contrast, ADC 12 had the lowest species richness (3) (Table 1).

A faunistic analysis of similarity showed that stream ADC 12 was the most divergent sample followed by ADC 02 and 10, for both qualitative and quantitative data. A set of five streams formed a group with higher similarity (ADC 05, 06, 07, 08, 11 and 13) for the qualitative data, suggesting a geographical clustering for this subset of the whole fish assemblage (Figure 5).



Figure 2. Stretches from stream samples located in a savannah and forest fragments landscape in the lower Tapajós River basin.

Discussion

This inventory is the first to focus exclusively on small streams within a savannah and forest fragments landscape and our results reinforce the importance of spatial heterogeneity to the regional fish community composition. The species richness recorded (43) is considered high given the relatively small number of streams sampled (13) and that only active capture methods were used. Many studies of headwater streams in the Amazon basin, with different sampling efforts and capture methods, show comparable species richness numbers (Araújo-Lima et al. 1999, Bührnheim & Cox-Fernandes 2001, Mendonça et al. 2005, Espírito-Santo et al. 2009, Oliveira et al. 2009).

The first-order *jackknife* estimator showed that 73% of the expected species were sampled (58.69 ±7.65). This efficiency of the sampling effort used here was satisfactory for active collection sampling in first- and second-order streams. For sections with two times the sample length (100 m), Anjos et al. (2007) using similar collection methods and sampling effort obtained 71.4 to 94.1% of the estimated species richness in central Amazonia.

The recorded fish fauna is characterized by typical inhabitants of Amazonian upland forest streams (Santos & Ferreira 1999). There was a dominance of species that occupy the uppermost (surface) strata of the water column and were observed in habitats with stronger currents, such as *Iguanodectes variatus* (Iguanodectidae) and *Hyphessobrycon heterorhabdus* (Characidae), as well as species present in slow-flowing backwaters, such as *Copella* spp. (Lebiasinidae). In addition, abundant species associated with deeper and slow-flowing environments, such

Table 2. Ichthyofauna of small-order streams of savannah and forest fragments landscape in the lower Tapajós River basin.

	Sampling period		
TAXON	**2006/dry**	**2018/rainy**	**2018/dry**
CHARACIFORMES			
Acestrorhynchidae			
Acestrorhynchus falcirostris (Cuvier 1819)	-	3	-
Heterocharax virgulatus Toledo-Piza 2000	34	-	-
Characidae			
Charax condei (Géry & Knöppel 1976)	34	-	-
Moenkhausia copei (Steidachner 1882)	-	3	
Hemigrammus levis Durbin 1908	-	55	-
Hemigrammus ocellifer (Steindachner 1882)	68	11	130
Hemigrammus stictus (Durbin, 1909)	-	-	3
Hyphessobrycon heterorhabdus (Ulrey 1894)	155	11	180
Hemigrammus analis Durbin 1909	-	93	8
Crenuchidae			
Crenuchus spilurus Günther 1863	82	58	110
Elachocharax junki (Géry 1971)	8	-	5
Curimatide			
Curimatopsis evelynae Géry 1964	1	8	8
Erythrinidae			
Hoplias malabaricus (Bloch 1794)	4	14	5
Iguanodectidae			
Iguanodectes variatus Géry 1993	306	320	444
Lebiasinidae			
Copella nattereri (Steindachner 1876)	677	303	201
Copella callolepis (Regan 1912)	14	80	476
Nannostomus digrammus (Fowler 1913)	1	35	-
Nannostomus marginatus Eigenmann 1909	25	36	-
Serrasalmidae			
Pygopristis denticulata (Cuvier, 1819)	9	-	-
CICHLIFORMES			
Cichlidae			
Acarichthys heckelii (Müller & Troschel 1849)	-	8	-
Acaronia nassa (Heckel 1840)	-	3	7
Aequidens epae Kullander 1995	63	81	186
Apistogramma gephyra Kullander 1980	35	44	94
Dicrossus maculatus Steindachner 1875	-	-	1
Hypselecara coryphaenoides (Heckel 1840)	4	-	6
Mesonauta festivus (Heckel 1840)	-	2	-
Taeniacara candidi Myers 1935	6	-	2
CYPRINODONTIFORMES			
Fluviphylacidae			
Fluviphylax simplex Costa 1996	-	3	-
Rivulidae			
Laimosemion dibaphus (Myers 1927)	218	216	294

GOBIIFORMES			
Eleotridae			
Microphilypnus ternetzi Myers 1927	60	-	32
GYMNOTIFORMES			
Gymnotidae			
Gymnotus coropinae Hoedeman 1962	3	2	2
Gymnotus sp.1	1	-	-
Hypopomidae			
Microsternarchus bilineatus Fernández-Yépez 1968	22	30	29
Brachyhypopomus regani Crampton *et al*. 2017	8	10	30
Rhamphichthyidae			
Gymnorhamphichthys rondoni (Miranda Ribeiro 1920)	11	1	10
Hypopygus lepturus Hoedeman 1962	11	-	17
PERCIFORMES			
Polycentridae			
Monocirrhus polyacanthus Heckel 1840	-	1	1
SILURIFORMES			
Auchenipteridae			
Trachelyopterichthys taeniatus (Kner, 1858)	2	-	-
Cetopsidae			
Helogenes marmoratus Günther 1863	164	44	99
Doradidae			
Acanthodoras cataphractus (Linnaeus 1758)	1	-	-
Heptapteridae			
Brachyglanis microphthalmus Bizerril 1991	18	-	7
Trichomycteridae			
Potamoglanis hasemani (Eigenmann 1914)	109	6	56
SYNBRANCHIFORMES			
Synbranchidae			
Synbranchus madeirae Rosen & Rumney 1972	2	13	1
TOTAL	2156	1494	2444

as *Aequidens epae*, *Apistogramma gephyra* (Cichlidae) and *Helogenes marmoratus* (Cetopsidae), were also recorded in the present inventory, of which the latter is a common inhabitant of leaf-packed habitats under moderate to swift currents (Vari & Ortega 1986, Carvalho et. al 2013).

In the Neotropics, dominance in fish community composition (in descending order of richness) is generally by Characiformes and Siluriformes, together accounting for about 80% of the species (Lowe-McConnell 1999). Fish community composition studies of headwater streams throughout Amazonia show similar results regarding the distribution of species richness among taxonomic groups; usually Characiformes and Siluriformes are the most representative orders (Sabino & Zuanon 1998, Mendonça et al. 2005, Araújo et al. 2009). However, in the present inventory, Characiformes and Cichliformes were the richest, which is similar to the pattern observed by Silva-Oliveira et al. (2016) for small, non-flooded rainforest streams in the lower Tapajós River basin. Characidae and Cichlidae were the most representative and, in both inventories, Loricariidae was absent. This pattern may be related to the natural characteristics lacustrine (ria-lake) environments originating from the Tapajós River estuary and favor a greater diversity of cichlids, similar to the distribution pattern observed for the ichthyofauna in streams in Caxiuanã, along the lower Anapu River (Montag et al. 2008).

The fish community changes over time and space, with changes between streams in the same hydrographic basin or in spatially close basins, suggest that the fish assemblages can be influenced by local environmental characteristics of the streams in a small-scale context (Mendonça et al. 2005). Changes in fish assemblage's composition during sampling periods, as observed for the abundances of C. *nattereri* (677; 282; 201), *Hyphessobrycon heterorabdus* (155; 11; 180) and *Helogenes marmoratus* (164; 44; 99), may be related to seasonality (Espírito-Santo et al. 2009). Small streams do not present predictable variations in water level but respond quickly to local rainfall that affect streams' structural conditions and water physicochemical parameters in shorter and more frequent periods (Walker 1995).

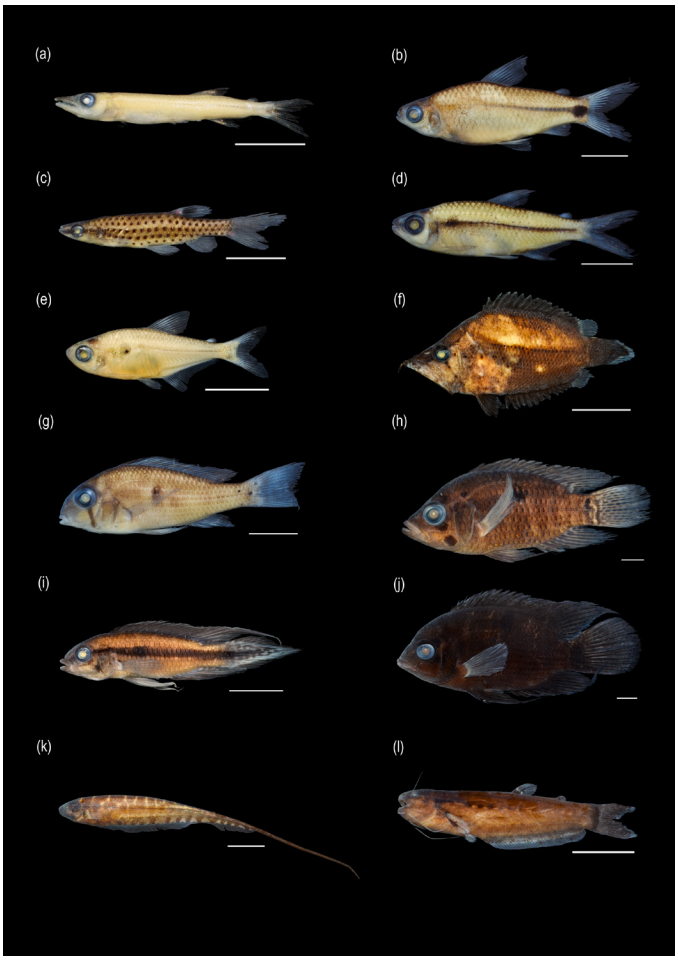


Figure 3. Photo of the most representative orders collected in small-order streams of savannah and forest fragments landscape in the lower Tapajós River basin. Scale: 1 cm. Characiformes: (a) *Acestrorhynchus falcirostris*; (b) *Curimatopsis evelynae*; (c) *Copella nattereri*; (d) *Moenkhausia copei*; (e) *Hemigrammus stictus*; Perciformes: (f) *Monocirrhus polyacanthus*; Cichliformes: (g) *Acarichthys heckelii*, (h) *Acaronia nassa*; (i) *Apistogramma gephyra*; (j) *Hypselecara coryphaenoides*; Gymnotiformes: (k) *Hypopygus lepturus* and Siluriformes; (l) *Helogenes marmoratus*. Color in alcohol.

Table 3. Fish richness and total abundance for each order for small-order streams of savannah and forest fragments landscape in the lower Tapajós River basin.

Order	Species (%)	Abundance (%)
Characiformes	19 (44.2%)	4018 (65.9%)
Cichliformes	8 (18.6%)	542 (8.9%)
Gymnotiformes	6 (13.6%)	187 (3.1%)
Siluriformes	5 (11.4%)	506 (8.3%)
Cyprinodontiformes	2 (4.5%)	731 (11.9%)
Gobiiformes	1 (2.3%)	92 (1.5%)
Perciformes	1 (2.3%)	2 (0.03%)
Synbranchiformes	1 (2.3%)	16 (0.3%)

Our data show low similarity with the fish fauna from first- to third-order upland rainforest streams in the Tapajós National Forest (TNF) (Silva-Oliveira et al. 2016), which is located on the same margin of the Tapajós River and nearly one hundred km away from our study area. We recorded only 18 species in common with the TNF inventory (23% similarity – *Jaccard* distance) among the 43 species collected in the present study and 53 species collected by Silva-Oliveira et al. (2016).

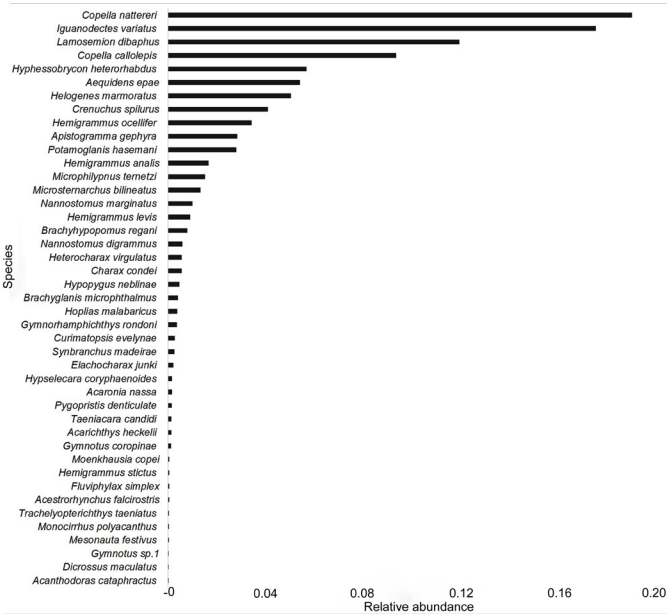


Figure 4. Species distribution using a relative abundance rank for 13 streams located in small-order streams of savannah and forest fragments landscape in the lower Tapajós River basin.

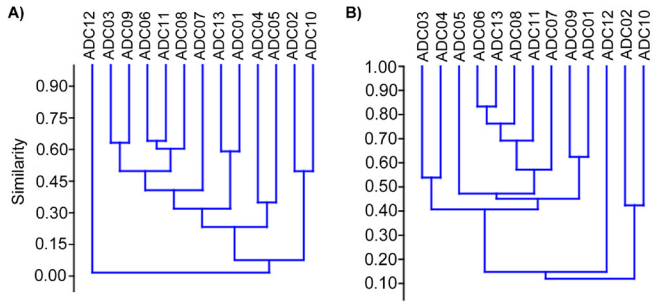


Figure 5. Similarity analysis for fish fauna sampled in small-order streams of savannah and forest fragments landscape in the lower Tapajós River basin. (A) Similarity based on *Bray-Curtis* distance (abundance); (B) Based on *Jaccard* distance (presence/absence) (Cophen. corr. 0.92 and 0.96, UPGMA method) for all sampling periods and for all 13 sampled streams.

The low species richness for stream ADC 12 could be related to local features, given its partially degraded condition resulting from direct human use for recreation, featuring large and shallow pools covered by litter and low dissolved oxygen concentration (1.4 mg/L). At this site, we collected juveniles of *Hoplias malabaricus*, *Laimosemion dibaphus* and *Synbranchus madeirae*, which are capable of surviving in these conditions due to their respiratory adaptations (Lowe-McConnell 1964, Val et al. 1998).

We identified a subset of streams that are remarkably similar in fish assemblage composition when compared to the other sampled streams. These streams are hydrographically connected at the southern border of Verde Lake and drain into the forest fragments vegetation, sharing characteristics that may function as environmental filters for fish species (Mendonça et al. 2005). Among them, ADC 05 is the least similar, which had one species (*Nanostomus marginatus*) exclusive to this sample site. Furthermore, this group of streams shares the presence of *Copella*

callolepis, whereas its congener *C. nattereri* was recorded only to the northern portion of the drainage. This separation may be due to the lake acting as a barrier or the result of different biological interactions occurring at the opposite portions of the lake's shore.

High species richness values observed in the ADC 02 and ADC 10 streams could be related to lake proximity, being more affected by the river flood pulse and therefore having a distinct fish fauna (Walker 1990). In the same stretches, we recorded *Acestrorhynchus falcirostris* and *Mesonauta festivus* juveniles, which shows that these streams can function as refuges and growth sites for lake-dwelling species (Goulding 1980, Meyer et al. 2007). These two streams have a greater fluctuation in species number among periods, with the occurrence of non-resident species in the channel that use the habitat during the rainy season, such as *Moenkhausia copei*, *Hemigrammus analis*, *H. levis*, *Acarichthys heckelii* and *Fluviphylax simplex*. This result highlights the contribution of small streams for maintaining the regional diversity of the fish fauna.

Species richness in this inventory is numerically comparable but taxonomically distinct from that of streams in other forested, non-floodable areas throughout Amazonia and represents an important component of the regional fish fauna diversity. Therefore, this study is also important because it improves our knowledge about the fish fauna of small-order streams of mixed savannah-forest fragments landscape. This landscape is spatially restricted and poorly known in Amazonia in regard to fish communities and their relationships with the environment. In addition, the presence of species exclusive to some sampling sites, even after three sampling periods, confirms the need to implement riverscape protection strategies that consider a greater number of headwater streams, which will ensure the maintenance of hydrological connectivity (Jézéquel et al. 2020) to safeguard the local fauna and regional diversity.

Supplementary Material

The following online material is available for this article:
Table S1 - Deposited material.

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Author Contributions

Each author's contributions were as follows:

Raul Fróis: substantial contribution to conception and design, data acquisition, identified specimens, analysis and interpretation and drafting of the manuscript.

Bruno Ribeiro: contribution to data acquisition.

Jansen Zuanon: identified specimens, substantial contribution to conception and design, data acquisition and critical revision for important intellectual content.

Amanda Mortati: substantial contribution to conception and design, data analysis and interpretation and drafting of the manuscript.

Conflicts of Interest

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

Ethics

The authors declare that they followed the code of ethics of the Brazilian Institute of Environment and Renewable Resources (IBAMA) for the collection of fish under license No. 62565-3 with due care for the sacrifice of animals using Eugenol anesthetic. This project is endorsed by the Animal Use Ethics Committee of the Federal University of Western Pará under the protocol No. 0220200088.

Data availability

The data is part of a Projeto Igarapés database linked to the Biodiversity Research Program (PPBio) and will be included in the Brazilian Biodiversity Information System (SiBBr).

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Morphological characterization and diversity of tadpoles (Amphibia: Anura) at Emas National Park and its surrounding, Goiás State, Brazil

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Abstract: Tadpoles are abundant in the environments in which they occur and remain in aquatic habitats for longer periods than adults, being relatively easier to collect. Despite the increase in tadpole research in the past decade, our understanding of its morphological diversity remains limited. Here, we provide morphological characterizations for larvae of 15 anuran species that occur at Emas National Park (ENP) and its surroundings, in Goiás, and compare them with descriptions available in the literature for other locations. We also present an update of the list of anuran species known to the ENP, based on tadpole sampling. We found tadpoles from 15 anuran species, of which five represent new records for the park. Many species showed variations in morphological characters when compared with descriptions available in the literature for other locations, reinforcing the importance of describing larvae from different populations. Through the exploration of morphological characters, it is possible to make inferences about the functional diversity of the larvae and questions related to the homology of characters, in addition to assisting in the identification and taxonomic distinction of species. Studies with tadpole communities can generate key information about the factors that drive the anurans' richness and distribution and can provide support for establishing more consistent conservation strategies and management plans.
Keywords: *External Morphology; Cerrado; Species survey; Conservation unity; Tropical anurans.*

Caracterização morfológica e diversidade de girinos (Amphibia: Anura) no Parque Nacional das Emas e seus arredores, estado de Goiás, Brasil

Resumo: Os girinos são abundantes nos ambientes que ocorrem e permanecem nos habitats aquáticos por períodos de tempo mais longos que os adultos, sendo relativamente mais fáceis de coletar. Apesar do aumento da pesquisa com girinos na última década, nossa compreensão sobre sua diversidade morfológica ainda permanece limitada. Aqui, fornecemos caracterizações morfológicas para larvas de 15 espécies de anuros que ocorrem no Parque Nacional das Emas (PNE), Goiás, e comparamos com descrições disponíveis na literatura para outras localidades. Apresentamos também uma atualização da lista de espécies de anuros conhecidos para o PNE, com base na amostragem de girinos. Encontramos larvas de 15 espécies de anuros, das quais cinco representam novos registros para o parque. Muitas espécies apresentaram variações nos caracteres morfológicos quando comparamos com descrições disponíveis na literatura para outras localidades, reforçando a importância da descrição de larvas de diferentes populações. Através da exploração de caracteres morfológicos é possível realizar inferências sobre a diversidade funcional das larvas e questões relativas à homologia de caracteres, além de auxiliar na identificação e distinção taxonômica das espécies. Estudos com comunidades de girinos podem gerar informações importantes sobre os fatores que impulsionam a riqueza e a distribuição dos anuros e, podem fornecer suporte para o estabelecimento de estratégias de conservação e planos de manejo mais consistentes.
Palavras-chave: *Morfologia externa; Cerrado; Levantamento de espécies; Unidade de conservação; Anuros tropicais.*

Introduction

The biphasic life cycle is one of the main characteristics that differentiate amphibians from the rest of terrestrial vertebrates. Most of the group's representatives have a larval phase, which for most species is aquatic, and an adult phase, usually terrestrial (Duelman & Trueb 1986). The numerous morphological and behavioral adaptations allow tadpoles to live in different types of habitat, such as puddles, phytotelmata, or streams (Altig & McDiarmid 1999). As anuran larvae need to remain in these environments until development is complete, their location may be more predictable and more accessible for capture than breeding adult frogs (Lips & Savage 1996, Altig & McDiarmid 1999, Silva 2010, Mascarenhas et al. 2016).

Despite the relative ease of collection, tadpoles are rarely targets for inventories conducted in the Neotropics, with most studies using the adult phase and acoustic information (Maladozzo et al. 2017). The main obstacle for the increase in the studies using anuran larvae is the difficulty of identification (Rossa-Feres & Nomura 2006, Provete et al. 2012). Although taxonomic keys are a tool that undoubtedly facilitates access to species diversity, the morphological characterizations of sampled populations have become increasingly necessary, as in addition to helping to identify larvae, it allows inferences to be made about phylogenetic relationships (Altig & McDiarmid 1999, Vences et al. 2010, Schulze et al. 2015, Gehara et al. 2014). Despite the importance, studies with this purpose still represent a gap for the tropical region, particularly for Brazil, where around 793 species of anurans with aquatic larvae are known (Rossa-Feres et al. 2015), but only 60% have the larval phase described (Provete et al. 2012).

The scenario worsens when considering the high morphological plasticity of the tadpoles. Adapting to the diverse selective pressures exerted by habitats requires tadpoles' high adaptive capacity and phenotypic plasticity (Lind & Johansson 2007, Marques & Nomura 2018, Marques et al. 2019). The phenotypic plasticity can cause a high variation in certain morphological traits in response to local environmental pressures, and consequently, can mislead the correct taxonomic identification of the anuran larvae. We must understand better how tadpoles' morphological diversity is affected by geographic variation and, to achieve this goal, we need to increase the number of anuran populations that have their larvae described, providing characterizations even for species that already have a formal description (Gehara et al. 2014).

Currently, in the Cerrado, about 212 anuran species are known (Valdujo et al. 2012), of which more than half are endemic (51%, Colli et al. 2002). However, the morphological characterizations for the species that occur in the biome are scarce, and even those that already have a formal description, are restricted to specific locations (e.g. northwest region of São Paulo, Rossa-Feres & Nomura 2006). The Emas National Park (ENP), located in the southwest region of Goiás, is considered one of the largest preservation areas in the Cerrado, where 25 anuran species are known (14 of them in larval phase, Kopp et al. 2010). However, morphological characterizations for larvae that occur in the park are currently unavailable.

Here, we provide morphological characterizations for larvae of 15 anuran species that occur at ENP and surrounding and compare them with descriptions already available in the literature. We also present an update of the list of anuran species known for the park, based only on tadpole sampling. We hope that the information provided by this study may assist in future research on the anurofauna of Cerrado and assist in understanding the morphological diversity of anuran larvae.

Material and Methods

Sampling was carried out at breeding sites located at Emas National Park and surrounding (17°49', 18°28'S and 52°39', 53°10'W), southwest of Goiás, Brazil (Figure 1). ENP harbors a variety of vegetation types such as "cerrado *sensu stricto*" (dense Savannah), "Murundu" fields (Termite mounds), "Veredas" (Palm swamps), Riparian and Seasonal Forests (Ramos-Neto & Pivello 2000). The study area also has a high heterogeneity of water body types that vary between lotic or lentic environments and permanent or temporary. The surroundings of ENP have been under constant pressure due to intense agricultural activities and the farming of soybean and sugarcane (IBDF 1981).

We visited 23 water bodies during the rainy seasons (October to March) from 2014-2015, 2015-2016, and 2016-2017 (see table S1 in supplementary material). Waterbody margins were sampled using a conical dip net (3 mm² mesh), sweeping the environment for an hour or until a complete turn in its perimeter was completed. Although this sampling method is one of the most used for collecting tadpoles, the physical structure of water bodies can affect their efficiency. In deep pools, for example, the reach of the dip net is often limited to only shallow and marginal portions of the pond (Silva 2010, Morais et al. 2011).

The collected tadpoles were anesthetized with 5% lidocaine solution and subsequently, fixed and preserved in 10% formalin solution. The identification of the specimens was made based on Rossa-Feres & Nomura (2006). This taxonomic key includes the most common anuran species found throughout the Cerrado. Species that were not found in this taxonomic key were identified by comparisons with published articles. Digital images of tadpoles were taken with a DFC550 lens coupled to a Leica M205A stereomicroscope. Taxonomic nomenclature followed Frost (2020). Testimony material was deposited at the Zoological Collection of the Federal University of Goiás (ZUFG, for more details, see Table S2 in supplementary material).

We used around 10 tadpoles between stages 34 and 40 to characterize species morphology (*sensu* Gosner 1960). The use of tadpoles at, or close to, the developmental stage 37 to characterize morphological variation reduces allometric differences (Grosjean 2005). Morphological description and terminology follow Altig & McDiarmid (1999) and Pezzuti (2011), the nomenclature of oral apparatus follows Altig (1970) and classification of ecomorphological guilds follows Altig & Johnston (1989). Coloration classification was made based on fixed specimens.

Estimated species richness and confidence intervals were calculated from a species accumulation curve generated from 5000 randomizations (Lande et al. 2000) in EstimateS 9.1.0 (Colwell 2016). A species accumulation curve records the total number of species collected over a sampling effort (Gotelli & Colwell 2001), so it can be used to indicate whether the sampling was sufficient to estimate the species number in a community (Cullen et al. 2012). A sample-based accumulation curve allows the calculation of confidence intervals for all points on the curve, facilitating comparisons between areas (Colwell et al. 2004). The first-order *Jackknife* estimator (*Jackknife 1*) was used to estimate and compare local and expected richness since it is the best method to simulate curves from empirical data (Walther & Morand 1998). The *Jackknife 1* estimates richness by adding the number of observed species to a parameter calculated from the number of rare species found in a given sample (*"singletons"*) and the total sample number (Colwell et al. 2004).

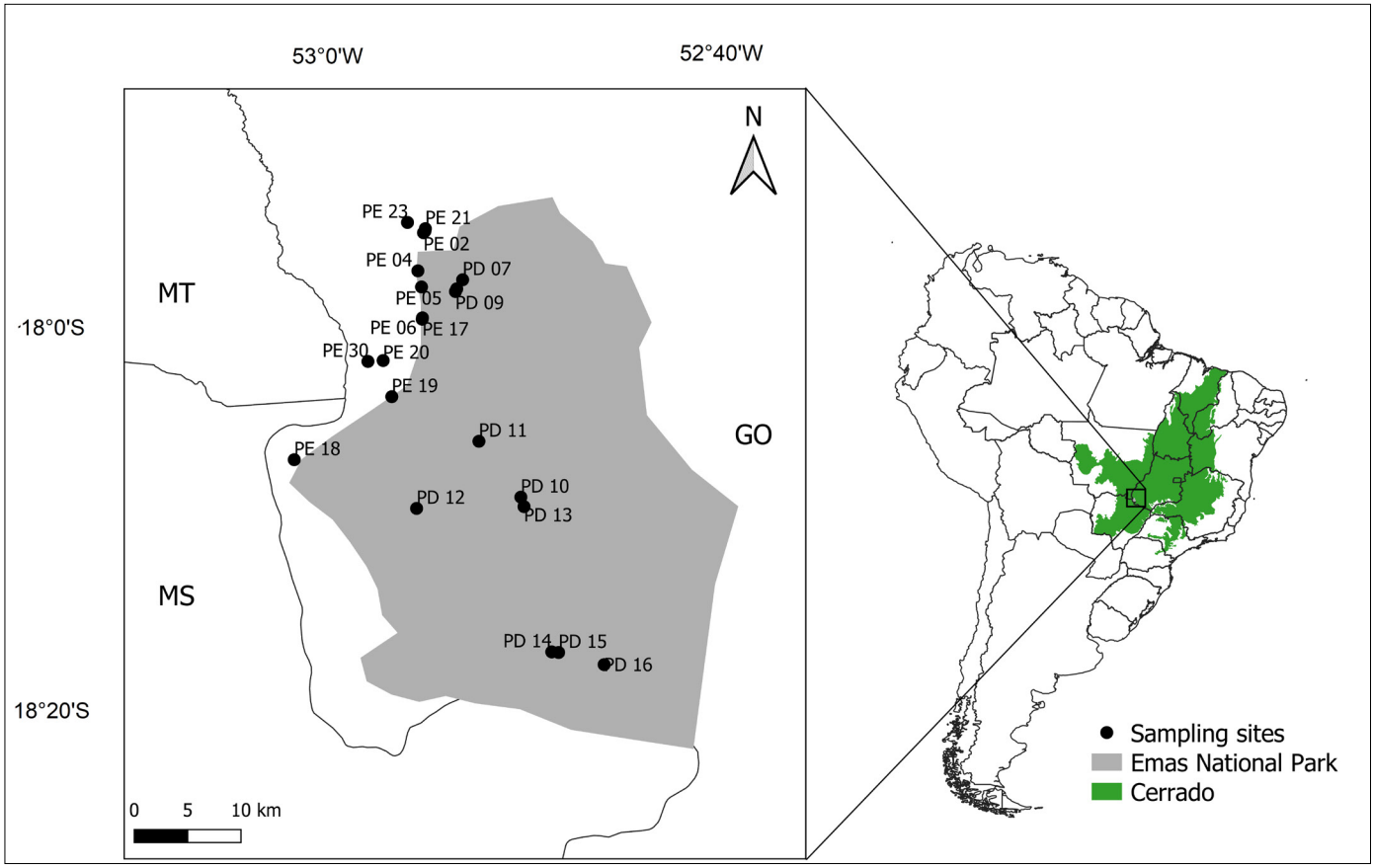


Figure 1. Location of sampled water bodies at ENP and surroundings, Goiás, Brazil. The green area represents the remnants vegetation cover of the Cerrado and the gray area represents the area of ENP, the black line is the border between the states of Goiás, Mato Grosso, and Mato Grosso do Sul and black dots are sampling sites PD refers to sampling points located within the ENP and PE to points located around the ENP.

Results

We collected 7.640 individuals of 15 anuran species distributed in six genera and three families (see Table S3 in supplementary material). We recorded five species not found previously and represent new records for the study area: *Dendropsophus nanus*, *Scinax* aff. *similis*, *Physalaemus marmoratus, Elachistocleis* sp. and *Elachistocleis cesarii*. The families with the largest number of species were Hylidae and Leptodactylidae (seven and six species, respectively). Microhylidae family presented only two species. The most abundant species was *Scinax* aff. *similis* with 3234 individuals, representing 42.32% of the total specimens collected.

Larvae were classified into five ecomorphological guilds (Figure 2), being represented by macrophagous tadpoles (*Dendropsophus nanus, Dendropsophus* sp.), benthic tadpoles (*Boana albopunctata, Leptodactylus fuscus, L. podicipinus, Physalaemus cuvieri, P. nattereri, P. marmoratus*), suspension feeder tadpole**s** *(Elachistocleis cesarii, Elachistocleis* sp.), carnivore tadpoles (*Leptodactylus labyrinthicus*) and nektonic tadpoles (*Scinax* aff. *similis, S. fuscomarginatus, S. fuscovarius, Dendropsophus minutus*).

Species accumulation curves for the study area showed a strong tendency to stabilize (Figure 3). However, as confidence intervals of observed and expected richness curves did not overlap, we infer that we have recorded fewer species than expected, which may be a consequence of using a single sampling technique to sampling anurans (only larval phase).

1. Morphological characterization and comments

Hylidae Rafinesque, 1815

Dendropsophus sp., figure (4A).

Specimens examined. 10 tadpoles, stages 34 to 39.

Characteristics. Body compressed, elliptical in dorsal view and depressed triangular in lateral view. Snout pointed in dorsal view and sloped in lateral view. Eyes lateral dorsolaterally directed. Nares circular laterally positioned with opening anterolaterally directed without projection. Spiracle lateroventral, sinistral posterodorsally directed and fully fused to the body wall. Vent tube dextral positioned at the origin of the ventral fin. Oral disc anteroventral modified to a protractile tube. Absence of emargination, marginal and submarginal papillaes. Tooth row formula absent. Absence of upper and lower jaw sheaths. Dorsal and ventral fins low with slightly convex margin emerging at ventral tube level. Coloration spotted or marbled with angular stains, muscle tail slightly crosslinked by melanophores, tail with coloration transparent.

Notes. This species has been referred to in other works as *Dendropsophus* sp. (gr. *microcephalus*) (e.g. Melo et al., 2013) and as *D. jimi* (Marques et al. 2019, supp. Information; Vaz-Silva et al. 2020). However, its distribution is not yet recognized in the Goiás State, although at least one population was reported in Brasília municipality (Frost, 2020). Tadpoles associated with *Dendropsophus* sp. have larger bodies, in comparison with the tail length, higher dorsal fins, and longer snouts than tadpoles of *D. nanus*.

Dendropsophus minutus (Peters 1872), figure (4B)

Specimens examined. 10 tadpoles, stages 34 to 38.

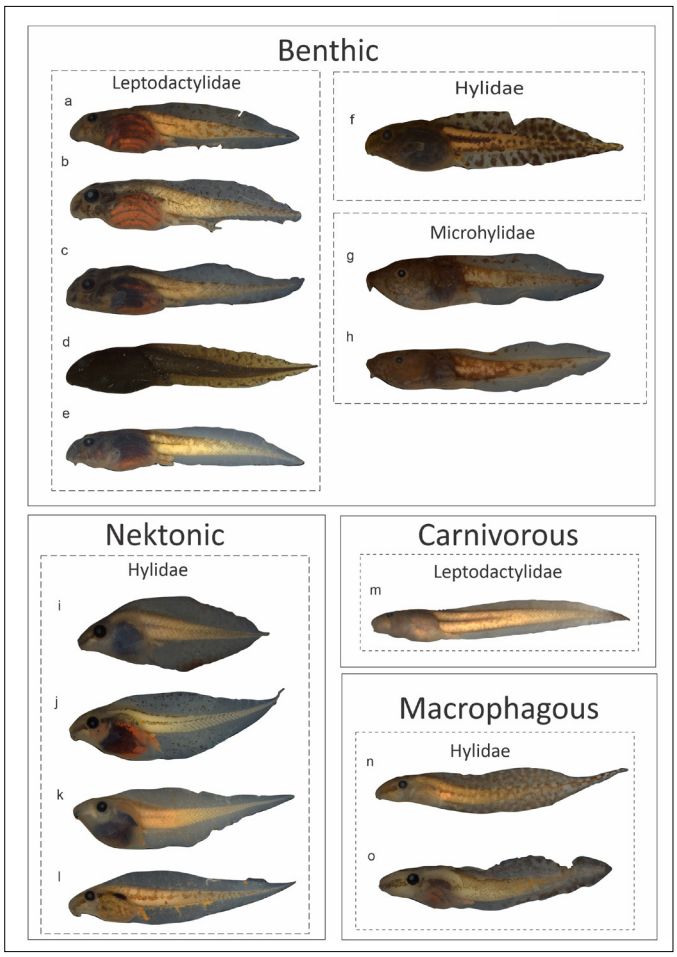


Figure 2. Ecomorphological guilds according to McDiamird & Altig (1999) for tadpoles found at ENP and its surroundings: a) *Physalaemus nattereri*; b) *Physalaemus cuvieri*; c) *Physalaemus marmoratus*; d) *Leptodactylus podicipinus*; e) *Leptodactylus fuscus*; f) *Boana albopunctata*; g) *Elachistocleis* sp.; h) *Elachistocleis cesarii*; i) *Dendropsophus minutus*; j) *Scinax* aff. *similis*; k) *Scinax fuscovarius*; l) *Scinax fuscomarginatus*; m) L*eptodactylus labyrinthicus*; n) *Dendropsophus nanus*; o) *Dendropsophus* sp.

Characteristics. Body compressed, ovoid in dorsal view and triangular in lateral view. Snout rounded in dorsal view and sloped in lateral view. Eyes lateral laterally directed. Nares circular dorsolaterally positioned with opening posterodorsally directed without projection. Spiracle lateroventral, sinistral, posterodorsally directed, centripetal wall present, fully fused to the body wall. Vent tube dextral, with a free distal edge. Oral disc anteroventral with keratinized structures, emargination absent, marginal papillae present and submarginal papillae absent. Tooth row formula 0/1. Upper jaw sheath "arc" shaped and lower jaw sheath "U" shaped. Dorsal and ventral fins high with convex margin emerging at ventral tube level. Coloration and muscle tail slightly crosslinked by melanophores, tail with coloration transparent.

Notes. The tadpoles we describe are similar to those described for other populations, differing in a few characters: body and snout shape, tooth row formula, and fin height. The population described by Dubeux et al. (2020), collected in the municipalities of Limoeiro de Anadia, Alagoas State, Brazil (stages 30 to 34) and Macaíba, Rio Grande do Norte State, Brazil (stage 35 to 39), had an elliptical elongated body in dorsal view and truncated snout in lateral view. The position of the oral disk is anterior, and the tooth row formula is 1/2. The tadpoles described by Rossa-Feres & Nomura (2006), collected in Nova Itapirema and Macaúbas, São Paulo State, Brazil (stages 37 to 40), had an oval body in dorsal view and nostrils positioned laterally, and a low dorsal fin inclination (<30°). The sampled population described by Schulze et al. (2015), collected in San Sebastian, Bolívia (stages 36 to 41), had a different tooth row formula, with tadpoles presenting LTRF 0/2.

Dendropsophus nanus (Boulenger 1889), figure (4C)

Specimens examined. 10 tadpoles, stages 34 to 39.

Characteristics. Body compressed, elliptical in dorsal view and depressed triangular in lateral view. Snout rounded in dorsal view and sloped in lateral view. Eyes lateral laterally directed. Nares oval laterally positioned with opening anterolaterally directed without projection. Spiracle lateroventral, sinistral, posterodorsally directed, centripetal wall present, fully fused. Vent tube dextral, positioned at the origin of the ventral fin. Oral disc ventral modified to a protractile tube, marginal and submarginal papillaes absent. Tooth row formula absent. Upper jaw sheath "arc" shaped and lower jaw sheath "V" shaped. Dorsal and ventral fins low with slightly convex margin emerging at vent tube level. Coloration spotted or marbled with rounded stains, muscle tail spotted or marbled with angular stains, tail with homogeneous coloration.

Notes. The tadpoles described by Rossa-Feres & Nomura (2006), collected in Nova Itapirema, São Paulo State, Brazil (stages 37 to 40), have some differences from the tadpoles characterized in this study. Those tadpoles had an oval body and a pointed snout in dorsal view, an anteroventral oral disc, and an obtuse dorsal fin, regarding its angle of emergence. The population collected in San Sebastian, Bolivia (stages 37 and 38) and described by Schulze et al. (2015) had a compressed body, ovoid body in dorsal view and a "tapered" snout in dorsal view.

Scinax aff. *similis* (Cochran 1952), figure (4D)

Specimens examined. 10 tadpoles, stages 34 to 38.

Characteristics. Body compressed, elliptical in dorsal view and triangular in lateral view. Snout truncate in dorsal view and sloped in lateral view. Eyes lateral laterally directed. Nares rounded/circular, dorsolaterally positioned with opening dorsolaterally directed without projection. Spiracle lateroventral, sinistral, with posterodorsally directed opening, centripetal wall fused with the body wall. Vent tube dextral, fused to the ventral fin. Oral disc anteroventral, with keratinized structures, emargination absent, marginal and submarginal papillaes present. Tooth row formula 2(1,2)/3(1). Upper jaw sheath "M" shaped and lower jaw sheath "V" shaped. Dorsal and ventral fins high with convex margin emerging anterior to the ventral tube. Coloration spotted or marbled with angular stains, muscle tail slightly crosslinked by melanophores, tail with coloration transparent.

Notes. The population described by Alves & Carvalho e Silva (1999), from the Rio de Janeiro State, Brazil (stage 37), had oval nostrils positioned dorsally and LTRF 2(2)/3(1). The tadpoles described by Rossa-Feres & Nomura (2006), from Nova Itapirema, São Paulo State, Brazil (stages 37 and 38), had a rounded snout in dorsal view, a spiracle positioned posterodorsally and tooth row formula 2(2)/3(1), while tadpoles from ENP had the nostril posterodorsally directed and the LTRF 2(1,2)/3(1). Populations of this species in the Goiás State have been treated as *Scinax* aff. *similis* by Frost (2021) and Vaz-Silva et al. (2020) because of the taxonomic uncertainty (N.N. Dias, pers. comm.).

Scinax fuscomarginatus (Lutz 1925), figure (4E)

Specimens examined. 10 tadpoles, stages 34 to 39.

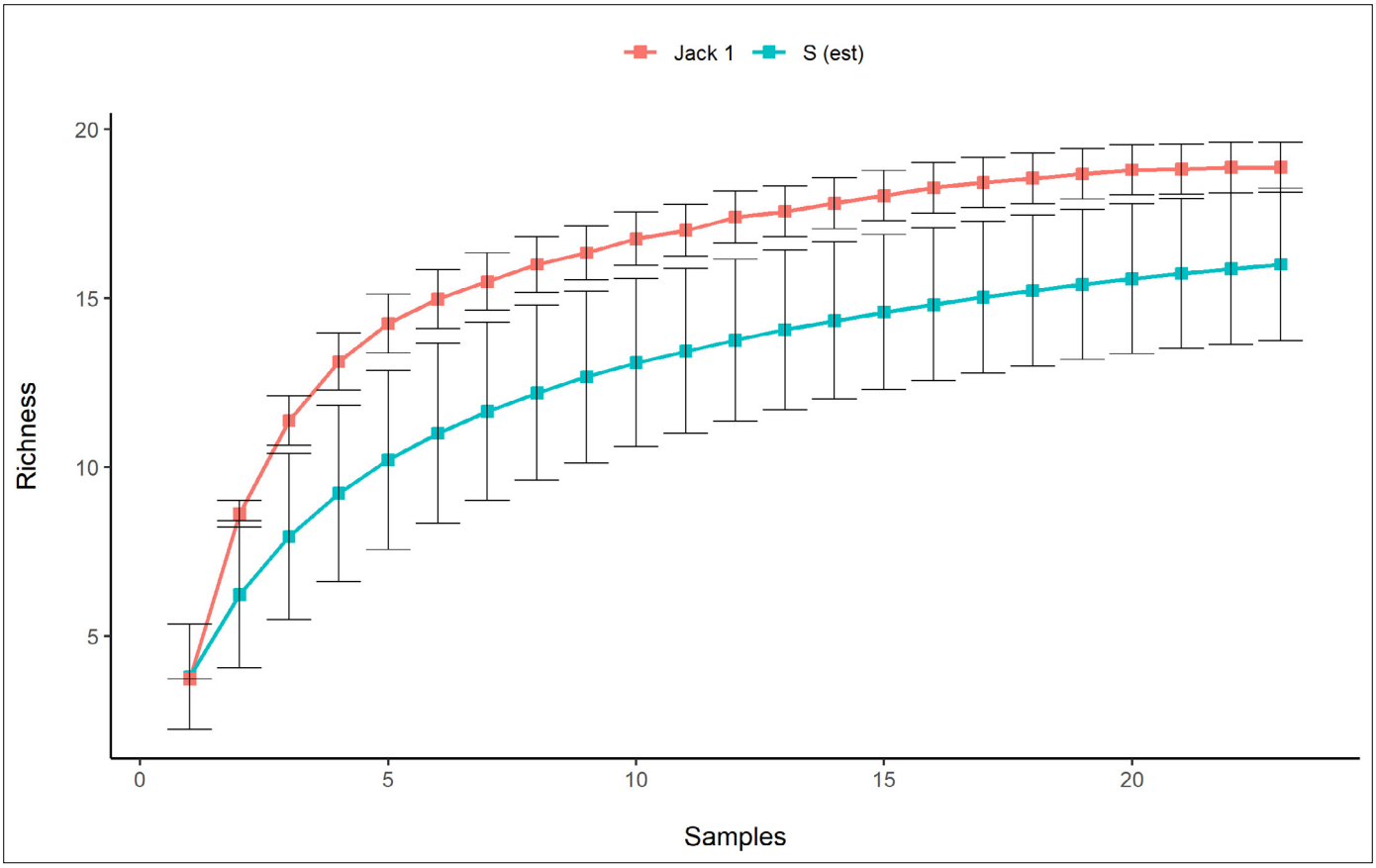


Figure 3. Species accumulation curve of anuran species at larval phase found at ENP. Vertical bars are confidence intervals at 95%.

Characteristics. Body compressed, rounded in dorsal view and depressed triangular in lateral view. Snout truncates in dorsal view and rounded in lateral view. Eyes lateral laterally directed. Nares circular dorsolaterally positioned with opening dorsolaterally directed without projection. Spiracle lateroventral, sinistral, posterodorsally directed; centripetal wall fused to the body wall. Vent tube dextral, fused to the ventral fin. Oral disc ventral, with keratinized structures, ventral emargination, marginal papillae present and submarginal papillae absent. Tooth row formula 2(2)/3(1). Upper jaw sheath "arc" shaped and lower jaw sheath "U" shaped. Dorsal and ventral fins medium with convex margin emerging anterior to the vent tube. Coloration slightly crosslinked by melanophores, muscle tail spotted or marbled with angular stains, tail with coloration transparent.

Notes. The population described by Rossa-Feres & Nomura (2006) from Nova Itapirema, São Paulo State, Brazil, had an oval body and a rounded snout in dorsal view, anteroventral oral disc, dorsal fin with an obtuse angle of emergence, originating in the anterior third of the body.

Scinax fuscovarius (Lutz 1925), figure (4F)

Specimens examined. 10 tadpoles, stages 35 to 38.

Characteristics. Body compressed, elliptical in dorsal view and triangular in lateral view. Snout rounded in dorsal view and sloped in lateral view. Eyes dorsal, dorsolaterally directed. Nares oval, dorsolaterally positioned with opening laterally directed without projection. Spiracle lateroventral, sinistral, posteriorly directed, centripetal wall fused to the body wall. Vent tube dextral, fused to the ventral fin. Oral disc anteroventral with keratinized structures, lateral emargination, marginal papillae present and submarginal papillae present. Tooth row formula 2(2)/3(1). Upper jaw sheath "arc" shaped and lower jaw sheath "V" shaped. Dorsal and ventral fins high with convex margin emerging at ventral tube level. Coloration and muscle tail slightly crosslinked by melanophores, tail with coloration transparent.

Notes. The tadpoles described by Rossa-Feres & Nomura (2006) from the northwest region of the São Paulo State, Brazil, differ from the population that we described by an oval body in dorsal view, eyes directed laterally and an upper "M" shaped sheath. The sampled population described by Schulze et al. (2015), collected in San Sebastián and Estancia Büchler, Bolívia (stages 32 to 38), had a body compressed, ovoid in dorsal view, eyes directed laterally, and a spiracle with directed posterodorsally.

Boana albopunctata (Spix 1824), figure (4G)

Specimens examined. 10 tadpoles, stages 34 to 40.

Characteristics. Body depressed, elliptical in dorsal view and depressed rounded in lateral view. Snout oval in dorsal view and rounded in lateral view. Eyes dorsal, dorsolaterally directed. Nares reniform, dorsally positioned with opening dorsolaterally directed with a large projection. Spiracle lateral, sinistral, posteriorly directed, centripetal wall present, large free end. Vent tube dextral, with a free distal edge. Oral disc ventral, with keratinized structures, ventral emargination, marginal papillae present and submarginal papillae absent. Tooth row formula 2(1,2)/ 3(1). Upper jaw sheath "arc" shaped and lower jaw sheath "U" shaped. Dorsal fin medium with slightly convex margin emerging at ventral tube level. Ventral fin low with margin parallel to the longitudinal axis of the tail muscle emerging at ventral tube level. Coloration spotted or marbled with rounded stains, muscle tail spotted or marbled with angular stains, tail with coloration transparent.

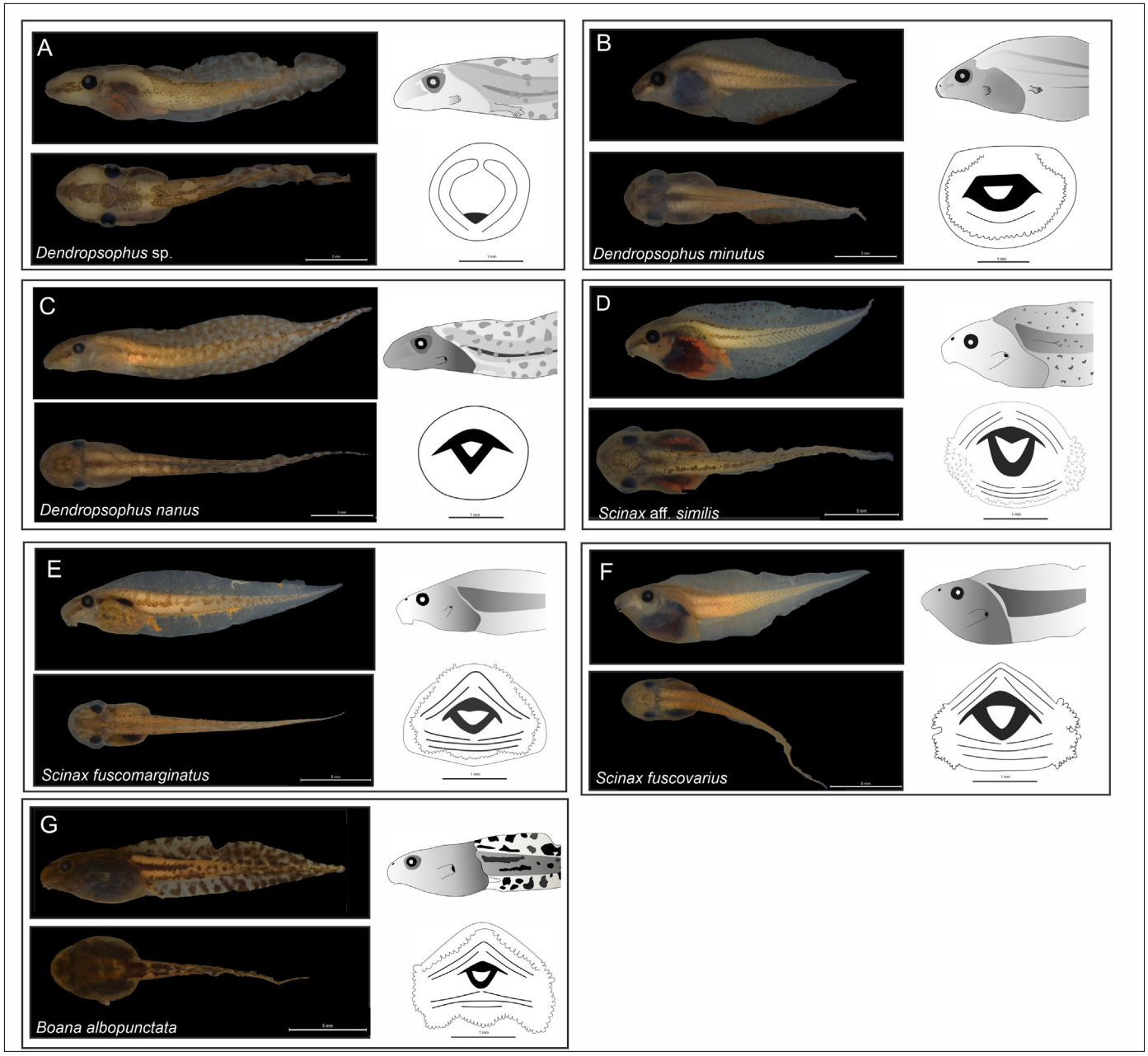


Figure 4. Lateral and dorsal view of hylid tadpoles that occur in the ENP. Schematic drawing to highlight the spiracle and oral disc of tadpoles.

Notes. Some characteristics vary among the populations already described for *Boana albopunctata*: the origin and height of the dorsal fin, the position of the oral disc, and the shape of the snout, body, and nostrils. The population described by de Sá (1995) presents a plane-convex body in lateral view, snout rounded in dorsal view, eyes directed laterally, and oval nostrils. Rossa-Feres & Nomura (2006) described a population collected in Nova Itapirema and Vitória Brasil, São Paulo State, Brazil. Those tadpoles differ from the tadpoles that we describe as they have an oval body in dorsal view, eyes directed laterally, nostrils shape oval, lower jaw sheath "V" shaped and dorsal fin with acute emergence angle originating from the tail-body junction. The tadpoles described by Dubeux et al. (2020) present an ovoid body in dorsal view, an acuminate snout in lateral view, eyes directed laterally and dorsal fin originating in the body-tail junction.

Leptodactylidae Werner, 1896

Leptodactylus labyrinthicus (Spix 1824), figure (5A)

Specimens examined. 10 tadpoles, stages 37 to 39.

Characteristics. Body depressed, elliptical in dorsal view and depressed rounded in lateral view. Snout oval in dorsal view and rounded in lateral view. Eyes dorsal dorsally directed. Nares oval dorsally positioned with opening dorsolaterally directed without projection. Spiracle lateroventral, sinistral, posterodorsally directed, centripetal wall present, fully fused to the body wall. Vent tube medial, with a free distal edge. Oral disc anterior, with keratinized structures, emargination and submarginal papillae absent and marginal papillae present. Tooth row formula 1/2(1). Upper jaw sheath "arc" shaped and lower jaw sheath "V" shaped. Dorsal and ventral fins are low with margin parallel to the longitudinal axis of the tail muscle emerging at

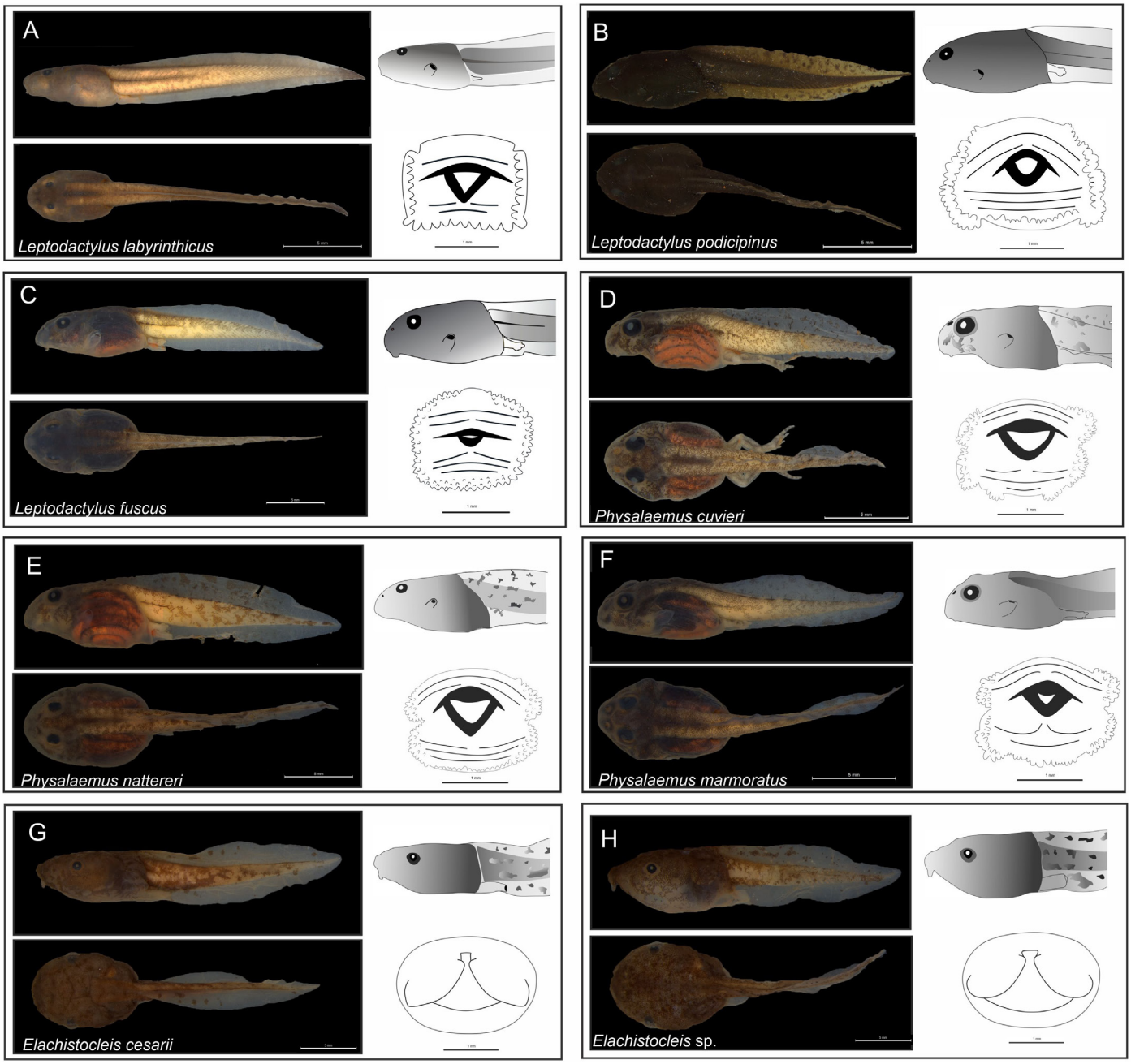


Figure 5. Lateral and dorsal view of leptodactylid and microhylid tadpoles that occur in the ENP. Schematic drawing to highlight the spiracle and oral disc of tadpoles.

ventral tube level. Coloration and muscle tail slightly crosslinked by melanophores, tail with coloration transparent.

Notes. Our tadpoles differ from those described by Rossa-Feres & Nomura (2006), from the municipality of Nova Itapirema, São Paulo State, Brazil, by the body globular-depressed in lateral view and oval in dorsal view, the rounded snout in dorsal view and the anteroventrally oral disc (stages 36 to 39).

Leptodactylus podicipinus (Cope 1862), figure (5B)

Specimens examined. 10 tadpoles, stages 35 to 40.

Characteristics. Body depressed, ovoid in dorsal view and depressed rounded in lateral view. Snout oval in dorsal view and rounded in lateral view. Eyes dorsal, anterolaterally directed. Nares oval, dorsally positioned with opening laterally directed, without projection. Spiracle lateroventral, sinistral, posterodorsally directed, centripetal wall fused to the body wall with the free distal edge. Vent tube medial fused to the ventral fin. Oral disc ventral, with keratinized structures, ventral emargination, marginal papillae present and submarginal papillae present. Tooth row formula 2(2)/3. Upper jaw sheath "arc" shaped and lower jaw sheath "V" shaped. Dorsal and ventral fins low with margin parallel to the longitudinal axis of the tail muscle emerging at ventral tube level. Coloration spotted or marbled with angular stains, muscle tail homogeneous coloring, tail with coloration homogeneous.

Notes. Tadpoles from Bolívia (stages 36 and 39, Schulze et al. 2015) had body compressed, elongated-ovoid in dorsal view, snout rounded in dorsal view and "slightly tapering" in lateral view, eyes dorsolaterally directed, and spiracle ventrolateral. The tadpoles (stage 37), described

by Rossa-Feres & Nomura (2006) from the northwestern region of São Paulo State, Brazil, had an oral disc positioned anteriorly, eyes positioned dorsolaterally and a sloped snout in view dorsal.

Leptodactylus fuscus (Schneider 1799), figure (5C)

Specimens examined. 10 tadpoles, stages 34 to 37.

Characteristics. Body depressed, elliptical in dorsal view and depressed rounded in lateral view. Snout oval in dorsal view and rounded in lateral view. Eyes dorsal dorsally directed. Nares oval dorsally positioned with opening laterally directed without projection. Spiracle lateroventral, sinistral, posterodorsally directed, centripetal wall present, fully fused to the body wall. Vent tube medial with a free distal edge. Oral disc ventral with keratinized structures, emargination absent, marginal and submarginal papillaes present. Tooth row formula 2(2)/3(1). Upper jaw sheath "arc" shaped and lower jaw sheath "V" shaped. Dorsal fin low with margin slightly convex emerging at ventral tube level. Ventral fin low with margin parallel to the longitudinal axis of the tail muscle emerging at ventral tube level. Coloration slightly crosslinked by melanophores, muscle tail spotted or marbled with angular stains, tail with coloration transparent.

Notes. The population from Nova Itapirema, São Paulo State, Brazil, described by Rossa-Feres & Nomura (2006), had a depressed globular body in lateral view, oval body in dorsal view, sloped snout in lateral view, eyes directed laterally and anteroventral oral disc. The tadpoles described by Dubeux et al. (2020), collected in the municipality of Macaíba, Rio Grande do Norte State, Brazil (stages 36 to 40), differ by the oval snout in lateral view and the oral disc positioned anteroventrally.

Physalaemus cuvieri Fitzinger 1826, figure (5D)

Specimens examined. 10 tadpoles, stages 34 to 38.

Characteristics. Body depressed, ovoid in dorsal view and depressed rounded in lateral view. Snout oval in dorsal view and rounded in lateral view. Eyes dorsal anterolaterally directed. Nares oval, dorsally positioned with opening dorsally directed, with a small projection. Spiracle lateral, sinistral, posterodorsally directed, centripetal wall absent. Vent tube medial, entirely fused to ventral fin. Oral disc ventral with keratinized structures, ventral and lateral emargination, marginal and submarginal papillaes present. Tooth row formula 2(2)/3(1). Upper jaw sheath "arc" shaped and lower jaw sheath "V" shaped. Dorsal fin medium with slightly convex margin emerging at ventral tube level, ventral fin low with margin parallel to the longitudinal axis of the tail muscle emerging at ventral tube level. Coloration and muscle tail slightly crosslinked by melanophores, tail with coloration transparent.

Notes. The tadpoles described by Rossa-Feres & Nomura (2006), collected in the northwest region of São Paulo State, Brazil (stages 37 to 39), differ from the larvae that we describe by the rounded snout in the dorsal view, dorsolateral eyes and dorsal fin with low inclination.

Physalaemus nattereri Steindachner 1863, figure (5E)

Specimens examined. 10 tadpoles, stages 35 to 38.

Characteristics. Body globular, elliptical in dorsal view and depressed rounded in lateral view. Snout oval in dorsal view and rounded in lateral view. Eyes dorsal anterolaterally directed. Nares circular, dorsally positioned with opening dorsally directed, without projection. Spiracle lateroventral, sinistral, posterodorsally directed, centripetal wall totally fused to the body wall. Vent tube dextral, fused to the ventral fin. Oral disc ventral, with keratinized structures, lateral emargination, marginal and submarginal papillaes present. Tooth row formula 2(2)/3(1). Upper jaw sheath "arc" shaped and lower jaw sheath "V" shaped. Dorsal fin low with margin slightly convex emerging at ventral tube level. Ventral fin low with margin parallel to the longitudinal axis of the tail muscle emerging at ventral tube level. Coloration and muscle tail spotted or marbled with angular stains, tail with coloration transparent.

Notes. The population we describe is very similar to that of two other descriptions, differing only in the shape of the body and snout, and in the direction of the eyes. The tadpoles described by Rossa-Feres & Nomura (2006), collected in Nova Itapirema, São Paulo State, Brazil (stages 35 to 39), had an ovoid body and pointed snout in dorsal view, sloped snout in lateral view, and dorsolateral eyes. The population described by Schulze et al. (2015), collected from San Sebastián and Caparú, Bolivia (stages 37 to 41), had a rounded snout in dorsal view and "slightly tapered" in lateral view.

Physalaemus marmoratus (Reinhardt & Lütken 1862), figure (5F)

Specimens examined. 10 tadpoles, stages 35 to 37.

Characteristics. Body depressed, ovoid in dorsal view and depressed rounded in lateral view. Snout oval in dorsal view and rounded in lateral view. Eyes dorsal, anterolaterally directed. Nares circular, dorsally positioned with opening dorsally directed. Spiracle lateroventral, sinistral, posterodorsally directed, centripetal wall fused to the body wall. Vent tube medial, fused to the ventral fin. Oral disc ventral with keratinized structures, ventral and lateral emargination, marginal and submarginal papillaes present. Tooth row formula 2(2)/2(1). Upper jaw sheath "arc" shaped and lower jaw sheath "V" shaped. Dorsal fin low with slightly convex margin emerging at anterior third of the tail. Ventral fin low with margin parallel to the longitudinal axis of the tail muscle emerging at ventral tube level. Coloration and muscle tail slightly crosslinked by melanophores, tail with coloration transparent.

Notes. Larvae of this species are very similar to those described by Nomura et al. 2003 and by Rossa-Feres & Nomura (2006), collected in Nova Itapirema, São Paulo State, Brazil (stages 37 to 40) when the species was still known as *Physalaemus fuscomaculatus*. The tadpoles differed only in the direction of the eyes, classified as dorsolateral by the authors and in the upper jaw sheath shape, which has an "M" shape.

Microhylidae Günther, 1858

Elachistocleis cesarii (Miranda-Ribeiro 1920), figure (5G)

Specimens examined. 9 tadpoles, stages 34 and 37.

Characteristics. Body globular, rounded in dorsal view and depressed rounded in lateral view. Snout rounded in dorsal view and truncate in lateral view. Eyes lateral laterally directed. Nares absent. Spiracle ventral with opening dorsally directed and centripetal wall fused to the vent tube. Vent tube ventral, entirely fused to ventral fin. Oral opening anterior with keratinized structures absent, dermal flap with pointed edges, emargination, marginal and submarginal papillaes. Tooth row formula absent. Upper and lower jaw sheath absent. Dorsal fin low with margin parallel to the longitudinal axis of the tail muscle emerging at ventral tube level, ventral fin low with slightly convex margin emerging at ventral tube level. Coloration slightly crosslinked by melanophores, muscle tail spotted or marbled with angular stains, tail with coloration transparent.

Notes. The tadpoles referred to as *Elachistocleis cesarii* in our study could be the same that were identified as *Elachistocleis* cf. *ovalis* in the previous survey carried out by Kopp et al. (2010). The tadpoles described by De Medeiros Magalhães et al. (2012) from the municipality

of Macaíba, Rio Grande do Norte State, Brazil, had an oval body in lateral and dorsal view. The tadpoles described by Dubeux et al. (2020), also for the municipality of Macaíba, are quite similar to the tadpoles from ENP, differing only in the body shape in lateral view that was considered depressed triangular by the authors.

Elachistocleis sp., Figure (5H)

Specimens examined. 10 tadpoles, stages 34 to 40.

Characteristics. Body globular, rounded in dorsal view and depressed rounded in lateral view. Snout rounded in dorsal view and truncate in lateral view. Eyes lateral laterally directed. Nares absent. Spiracle ventral, opening dorsally directed with centripetal wall fused to the vent tube. Vent tube ventrally fused to ventral fin with sinister opening and ventral wall longer than the dorsal wall. Oral opening without keratinized structures, dermal flap in front of the oral opening with rounded edges, emargination, marginal and submarginal papillaes absent. Tooth row formula absent. Upper and lower jaw sheaths absent. Dorsal fin low with margin parallel to the longitudinal axis of the tail muscle emerging at the body-tail junction. Ventral fin low with slightly convex margin emerging at ventral tube level. Coloration slightly crosslinked by melanophores, muscle tail spotted or marbled with angular stains, tail with coloration transparent.

Notes. The larvae of *Elachistocleis* sp. belong to a species not formally described yet (N. Maciel, comm. pers.). In our samples, this tadpole could be morphologically distinguished from the tadpole of *Elachistocleis cesarii* due to the vent tube opening ventrally, which had a sinistral opening in *Elachistocleis* sp., and because of the pointed projections in the dermal flap (rounded emarginate in the *Elachistocleis* sp).

Discussion

We present characterizations of the external morphology for larvae of 15 species of anurans and an updated list of anurans in the larval phase that occurs in the ENP. The tadpoles associated with the species *Leptodactylus sertanejo* was excluded from the study because we collected only one individual. Five species represent new records for the park. We found a high morphological diversity for tadpoles in ENP, with larvae represented in five of the 15 exotrophic ecomorphological guilds (*sensu* Altig & McDiarmid 1999): benthic, macrophagous, carnivore, suspension feeder, and nektonic tadpoles. Many species had variations in morphological traits when compared with descriptions available for other locations, reinforcing the importance of describing larvae from different populations.

1. *Morphological characterization*

Our knowledge about tadpoles' morphological diversity has advanced in the last 20 years, but there is still much more to explore. Several species remain with no formal description of the larval phase or the morphology, and the understanding of geographic, ontogenetic and metamorphic variation is still scarce, especially in the Neotropics (Altig & McDiarmid 1999; Provete et al. 2012). We found that the height of the fins, the direction of the eyes, and the shape of the body and nostrils were the morphological traits that had more variation among populations. The number of rows of denticles, the position of the spiracle, and the position of the vent tube varied for only a few species.

The microhabitat and environmental heterogeneity may explain part of the observed variation in the tadpoles' morphological traits that we found. Most of the articles that we used to compare external morphology among populations are from larvae collected in the Atlantic Forest (e.g. De Medeiros Magalhães et al. 2012, Dubeux et al. 2020). Thus, tadpoles exposed to specific selective pressures may present variations in morphological characteristics throughout the species distribution (Gatz 1979).

Conversely, the variation in the morphological traits found in species with wide distribution may denote a complex of cryptic species, as in the case of *Scinax* aff. *similis*. For this species, the number of denticle rows is considered a diagnostic character between species and relatively well maintained evolutionarily (Altig & McDiarmid 1999, Candioti 2007). These traits varied among all populations for which the tadpole's description is available.

2. *Species survey*

The species accumulation curve showed that we found fewer species than expected, which may be related to the use of only one sampling method for the survey. Kopp et al. (2010), for example, surveyed the anurofauna in the ENP region using sampling of adults and larvae and recorded 25 species (14 in the larval phase). Here, we only sampled anurans in the larval phase, which may explain the smaller number of species. Besides, our sampling was performed only in the rainy season, while Kopp et al. (2010) sampled both in the rainy and dry seasons, which increases the chance of sampling of anuran species that breed at different seasons of the year.

Although we collected anurans only in the larval phase, and we have limitations in our collection method related to sampling in the deepest portions of the ponds, we recorded for the first time the occurrence of *Dendropsophus nanus*, *Scinax* aff. *similis*, *Physalaemus marmoratus*, *Elachistocleis* sp. and *Elachistocleis cesarii* in the ENP. Among the larval anurans found by Kopp et al. (2010), we did not find *Rhinella schneideri* (Werner 1894), *Leptodactylus furnarius* Sazima & Bokermann, 1978, *Pseudopaludicola* aff. *falcipes* and *Pseudopaludicola* cf. *mystacalis*. The tadpoles' referred to as *Elachistocleis* sp. is the larval phase of a probably new species (N. Maciel, comm. pers.).

Larval sampling can increase the detectability of different species, as demonstrated in the following studies (Table 1). Considering species

Table 1. Faunistic surveys that registered anurans in adult and larval phases.

Study	Locality	Total species	Species only in larval phase	Number of aquatic environments sampled	Total months sampled
Kopp et al. 2010	Emas National Park	25	0	12	16
Garey et al. 2014	Serra da Bocaina National Park	46	4	14	18
Melo et al. 2013	Lago do Cedro Extractive Reserve	36	8	35	3
Morais et al. 2011	Southwestern region of the Goiás state	36	6	45	9
Batista & Bastos 2014	Transition zone Cerrado- Atlantic Forest	34	6	66	6

found exclusively in the larval phase, Melo et al. (2013) found eight of 36 species (Lago do Cedro Extractive Reserve), Morais et al. (2011) found six of 36 (southwestern region of Goiás State), Batista & Bastos (2014) found six of the 34 species (transition zone at the Cerrado-Atlantic Forest), while Garey et al. (2014), in the Atlantic Forest Biome (Serra da Bocaina National Park), found four of the 46 species registered. On the other hand, Kopp et al. (2010) found 25 anurans species at ENP, but none was found exclusively in the larval stage. Thus, surveys can potentially increase the detection of anurans and produce more accurate species lists, as long as they are combined with information obtained from surveys of adults, larvae and acoustic information (Silva 2010). In addition, we highlight the importance of standardizing the collection method and the sampling effort to facilitate the comparisons among surveys. For studies that focus on anuran tadpoles surveys, the sampling method must be well planned to overcome the challenges of finding the larval of anuran, as pond depth and vegetation association.

The sampling of tadpoles can provide important information both for delimiting the geographic distribution of anurans and for increasing understanding of their morphological diversity (Altig & McDiarmid 1999). Despite the increase in research on tadpoles in the last decade, information on distribution patterns, natural history, ecology and morphological diversity of the larvae are still scarce (Provete et al. 2012, Rossa-Feres et al. 2015). By investing in basic biodiversity research, we can generate more accurate models on the determinants of anurans' richness and distribution, and provide support for proposing more consistent conservation strategies and management plans.

Supplementary Material

The following online material is available for this article:

Table S1. Characterization of sites sampled at ENP and surroundings. High: vegetation cover ≥70%; Low: vegetation cover <70%. PD refers to the sites located within ENP. PE refers to sites located in the vicinity of ENP.

Table S2. Voucher number of anurans in larval phase registered from Emas National Park.

Table S3. Abundance and richness by sampling locality. Species abbreviations: *Dendropsophus minutus* (Dm), *Dendropsophus nanus* (Dn), *Dendropsophus* sp. (Dsp), *Elachistocleis cesarii* (Ec), *Elachistocleis* sp. (Esp), *Boana albopunctata* (Bal), *Leptodactylus fuscus* (Lf), *Leptodactylus labyrinthicus* (Ll), *Leptodactylus podicipinus* (Lp), *Physalaemus nattereri* (Pn), *Physalaemus cuvieri* (Pc), *Physalaemus marmoratus* (Pm), *Scinax fuscomarginatus* (Sfm), *Scinax fuscovarius* (Sf) and *Scinax* aff. *similis* (Saffs).

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Author Contributions

Gabriela Alves-Ferreira: 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.

Ingrid B. Ferreira da Paixão: 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.

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

Conflicts of interest

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

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Inventory

Checklist of the ichthyofauna of Mamirauá Sustainable Development Reserve, Middle Solimões, Amazonas, Brazil: high richness in a large protected area of Western-Central Amazonia

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Abstract: The present study reviews the records of occurrences of fish species found in the Mamirauá Sustainable Development Reserve (MSDR). The reserve is located in a large section of the middle Solimões River basin, in its interflow with Japurá River. For the elaboration of the list of fish species occurring in Mamirauá Reserve, we used a database of different studies on fish communities carried out in the area over the last three decades, in addition to the material deposited in the ichthyological collections of three scientific institutions, the National Institute for Amazon Research – INPA, the Mamirauá Sustainable Development Institute – IDSM and the Science and Technology Museum of the Catholic University of Rio Grande do Sul – PUCRS. The ichthyofauna of the MSDR is composed of 541 species, encompassing 45 families and 15 orders. These correspond to 20% of all valid species known for the entire Amazonia so far. As observed in other studies in the Neotropical Region, the more represented orders were Siluriformes (209 species) and Characiformes (185 species), followed by the Gymnotiformes (78 species). The results presented here demonstrate a considerable increase (86%) in the knowledge about the fish diversity found in Mamirauá Reserve, in relation to its first list of fish species, published in the 90's. This increase reflects not only the growth in number of studies on fish diversity in the area, with new surveys, but also the continuous taxonomic work on the collections, and descriptions of twenty-eight new species, with one hundred and ten type series. Further surveys are expected to take place in the Northwestern, more isolated areas of the Reserve, and will allow the identification of new occurrences, and may even unveil new fish species yet to be described to Science..
Keywords: *Amazon; Checklist; Distribution; First record; Neotropical; Taxonomy.*

Lista de verificação da ictiofauna da Reserva de Desenvolvimento Sustentável Mamirauá, Médio Solimões, Amazonas, Brasil: alto endemismo e riqueza em uma grande área protegida da Amazônia Centro-Ocidental

Resumo: Este estudo apresenta uma revisão dos registros de ocorrências das espécies de peixes encontradas na Reserva de Desenvolvimento Sustentável Mamirauá (RDSM), ampla área localizada na bacia do Médio Solimões, em seu interflúvio com o Rio Japurá. Para a elaboração da lista de peixes que ocorrem na Reserva Mamirauá foram utilizados os bancos de dados de diferentes estudos sobre comunidades de peixes realizados na área ao longo das últimas décadas, além de informações referentes ao material tombado nas coleções ictiológicas de três instituições científicas, o Instituto Nacional de Pesquisas da Amazônia- INPA,o Instituto de Desenvolvimento Sustentável Mamirauá – IDSM e o Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul – PUCRS. A ictiofauna da RDSM é composta por 541 espécies, incluindo 45 famílias e 15 ordens. Estes valores correspondem a cerca de 20% de todas espécies válidas conhecidas para toda a Amazônia até o momento. Assim como em outros estudos na região Neotropical as ordens que apresentaram as maiores riquezas

foram siluriformes (209 espécies) e Characiformes (185 espécies), seguidas de Gymnotiformes (78 espécies). Os resultados apresentados neste trabalho demonstram um aumento considerável (86%) no conhecimento sobre a diversidade de peixes encontrados na Reserva Mamirauá, em relação à primeira lista de peixes da RDSM, publicada na década de 1990. Este aumento reflete não apenas o crescimento no número de estudos sobre a diversidade de peixes na área, com a ocorrência de novos levantamentos, como também a intensificação dos trabalhos taxonômicos de classificação e descrição de vinte oito novas espécies com cento e dez séries tipos. Novos levantamentos deverão ocorrer nas áreas mais isoladas da Reserva, na sua porção noroeste. Estas atividades permitirão a identificação de novas ocorrências, e podem até revelar espécies novas a serem descritas..
Palavras-chave: *Amazônia; Lista de verificação; Distribuição; Primeiro registro; Neotropical; Taxonomia.*

Introduction

At the end of the XX century, an attempt to inventory the fish fauna of the Mamirauá Reserve was made, and produced a first list of 291 species (Crampton 1999). This first effort was limited by the lack of human and financial resources and did not encompassed a representative portion of the reserve. Seemingly, the problems that led to a limited list of fish species for the Mamirauá area are the same observed for the entire Amazon basin. The current knowledge on the Amazonian fish diversity is far from adequate, and the estimates on the number of existing fish species varies greatly (Malabarba et al., 1998; Carvalho et al. 2009; Albert et al. 2011; van der Sleen & Albert 2017; Dagosta & De Pina, 2019; Oberdorff et al., 2019). But it is widely accepted that there are approximately 2700 already described fish species living in the Amazon basin (Dagosta & De Pina, 2019). Nevertheless, a strikingly high number of fish species are being described for the Amazon every year (Valsecchi et al., 2017). Unfortunately, a relevant portion of the currently known fish fauna, like in other important megadiverse freshwater ecosystems of the World, is now threatened (Darwall et al, 2016; Arthington et al. 2016; IBAMA, 2018). Although some of the areas of the Central Amazonia and its floodplains have been intensively surveyed during the last half century (Correa et al., 2008; Freitas et al., 2014; Siqueira-Souza et al., 2016), some areas remain virtually unknown, or very poorly known, demonstrating the importance of inventory studies in the region. There is very few information available about the fish diversity of the middle Solimões region, a vast and biologically important part of the Western Brazilian Amazonia.

For many centuries the floodplain areas of the Amazon, annually inundated by white sediment-rich waters, have been visited and studied. Most of the material collected in these expeditions was sent to foreign institutions, mainly in Europe (Filho, 2009). The majority of the large cities and small towns in the Amazon are located in the várzea ecosystem, and almost all the commercial fisheries in the Amazon is carried out in várzea water bodies. The Amazonian varzea is a particular type of wetland, a seasonal floodplain forest inundated by whitewater rivers, with an intricate mosaic of waterbodies and annually flooded shores (Junk et al., 2011; Junk et al., 2014). Probably this is why we have the existing information about its fish fauna (Santos et al., 1991; Goulding et al. 1996; Saint-Paul et al., 2000; Zuanon et al., 2008). Records are, however, focused on the large-bodied species, most of commercial value, and a very few information is available about occurrence and distribution of the fish fauna in most parts of the Amazonian várzea. This information is usually originated in species lists from very restricted areas, tend to be taxonomically unreliable and not supported by voucher specimens deposited in the main scientific fish collections. Despite these limitations, it is generally recognized that the ichthyofauna found in the Solimões-Amazonas várzea is placed among the more diverse of the Amazon, especially at the Western parts of the Central Brazilian Amazon, upstream from Manaus, the capital city of Amazonas State. This várzea ecosystem holds at least 647 fish species, including areas from the borders with Peru and Colombia, and the mouth, in the Atlantic coast (Zuanon et al., 2008).

Fish surveys and other similar studies in the Middle Solimões region were intensified in the early 1990's through an intense research program implemented to support the regulation of the management for the newly created Mamirauá Sustainable Development Reserve – RDSM. The RDSM was the first protected area of this category implemented in Brazil. One of the main characteristics of this type of protected area, is the participatory management of natural resources by the local populations, combined with the scientific research to support their activities (Queiroz 2005). In this way, a large inventory was made for the Mamirauá Reserve area and its adjacent rivers, generating a first list of fish species (Crampton 1999). The vast majority of the material collected at that time was deposited in large national collections such as INPA, and also the Science and Technology Museum of Pontifical Catholic University of Rio Grande do Sul (PUCRS). Part of this material collected at Mamirauá Reserve was used to build a small reference collection at Mamirauá Institute, located in the town of Tefé, Amazonas State.

Subsequently, with the consolidation of the Mamirauá Sustainable Development Institute (IDSM), several other inventories were carried out in the region, generating new lists of fish species for the RDSM, and representing a considerable increase in the knowledge about the richness of the fish fauna of that protected area. The previous reference collection was greatly improved with new deposits from this reserve and other protected areas, and also from different parts of the Western Brazilian Amazonia, which became the current IDSM ichthyological collection. However, this recently generated information on the RDSM was never compiled in a single checklist. Therefore, the goal of the present paper, is to provide an updated list of the fish fauna that occur in the Mamirauá Sustainable Development Reserve.

Material and Methods

1. Study area

The fish collections were all conducted during field expeditions to the Mamirauá Sustainable Development Reserve (RDSM), in the Brazilian Central Amazon floodplain (Figure 1). Mamirauá is a wetland site of international importance listed under the UN Ramsar Convention, and the largest protected area of flooded forests in Brazil. The whole reserve's area (1,124,000 ha) if formed exclusively by the lowland floodplains of the Solimões and Japurá rivers, a complex mosaic of flooded forests interspaced by different types of water bodies; lakes, "canos" (channels), rivers and "paranãs" (river connections), each of them with particular physical and biological features, but connected at least once a year, since the entire reserve is completely flooded for 3 to 6 months annually (Henderson, 1999). The mosaic of forests (Wittmann et al. 2006) and water bodies, lakes and channels, at Mamirauá is typical of the *várzea* environment (Figure 2).

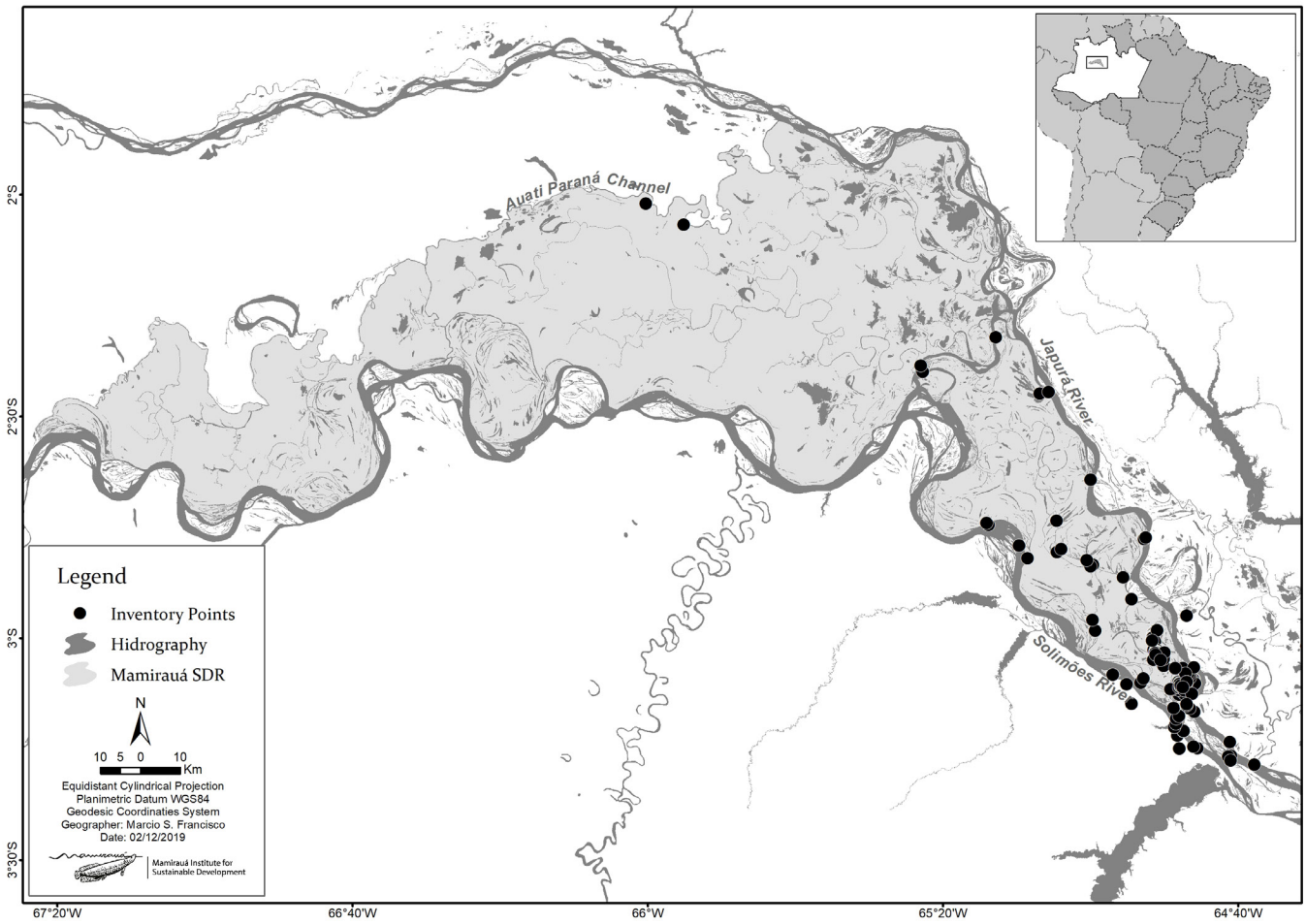


Figure 1. Map showing the Mamirauá Sustainable Development Reserve, Amazonas State, Brazil, with the geographical distribution of the points of distribution of fish sampling sites (black dots), and the main water bodies in the region (rivers, lakes and channels).

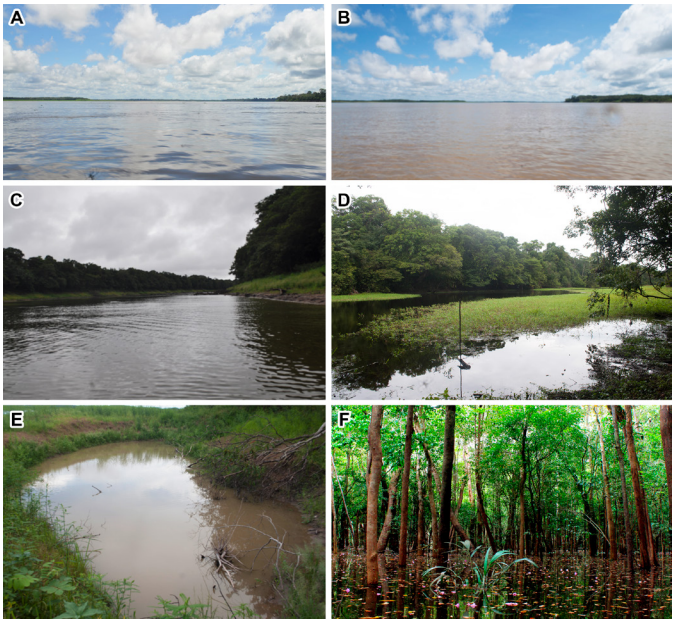


Figure 2. Examples of permanent and temporary aquatic environments sampled during the fish collections carried out at the Mamirauá Reserve: a) Japurá River; b) Solimões River; c) Mamirauá lake channel; d) Taracuazinho lake; e) Taxizal flood pool; f) Igapó (flooded forest) in Mamiraua system lake.

During a complete hydrological cycle, the water level in Mamirauá varies by more than 10 m (Ramalho et al. 2009), alternating wet and dry periods in a typical annual flood pulse (Junk et al., 1989). Four seasons can be identified, based on water level (Gaston & He, 2011). These are (i) high water season, from May until mid-July; (ii) falling water season, from mid-July to September; (iii) low water season, in the months of September, October and November; and (iv) rising water season, from December to April. These water bodies support a large fish fauna (Henderson & Crampton 1997), with diverse communities in each of the major aquatic habitats present (Henderson & Hamilton 1995).

The floodplain area in the confluence of Japurá and Solimões Rivers, where Mamirauá is located, is characterized by high atmospheric temperatures with average annual ranging from 28°C to 30°C, with maximum monthly ranging from 33°C to 35°C and minimum monthly ranging from 20°C to 22°C. The highest precipitations are concentrated between December and May (Ramalho et al., 2009) when it can reach 300 mm per month during the wettest years and the annual precipitation in the reserve is in average 3000 mm. The Japurá and Solimões Rivers consists of large white water rivers, carrying sediments from the erosion of the Andes, and forming large inundated habitats. Solimões River is one of the largest Amazonian rivers (discharge 53.3 x 10^3 m^3/second) and the main channel of the Amazon Basin, until it gets the discharge of blackwaters from the Negro River and creates the mighty Amazon River. Japurá River, on the other hand,

although smaller (discharge 14,5 x 10^3 m^3/second) is the Brazilian name for the Caquetá River, from Colombia. Successive erosion and deposition processes along the geological history of this floodplain created a complex mosaic of permanent and temporary waterbodies. The annual variation of water level responds for the various degrees of connectivity between those different waterbodies and the two main rivers. There are five main aquatic environments types in the Mamirauá Reserve relevant to the present work, since they were systematically surveyed over the years: the main rivers, lakes, canos and paranãs, flooded florest and the temporary pools formed inside the forest, when the water level recedes. The paranãs are channels connecting the main rivers, while the canos are channels that transport water from the rivers and from main channels to lower order aquatic environments within the floodplain, like smaller channels or lakes. Since canos are very shallow, some of them may dry completely during the low water periods. The lakes, on the other hand, may vary in shapes and sizes, and usually retain water during the entire hydrologic cycle. Therefore, lakes may retain a loose connection to the main channel during low water phase. During the high water period, all water bodies are connected and a direct communication is established among them all (Table 1).

2. *Data collection*

To prepare this checklist, a database was built with the information from different studies carried out mainly in the Southern, Eastern and Southeastern parts of the area (see black dots in Figure 1) over the last decades (Crampton, 1999; Chaves 2006; Santos 2007; Reis 2007). Whenever necessary, the collected material was revised in the fish collection of the IDSM. Additionally, we searched for all material collected at the RDSM in other important ichthyological collections in Brazil: Museum of Science and Technology (MCP) of the Pontifical Catholic University of Rio Grande do Sul, Museum of Zoology of the University of São Paulo (MZUSP), University of Campinas (ZUEC) and National Institute for Amazonian Research (INPA), available on SpeciesLink (www.specieslink.org.br). After the list was compiled, possible names and synonyms, and their occurrence, were confronted with information available in the Eschmeyer's Catalog of Fishes (Fricke et al.2020). To avoid possible synonymies between species cataloged by the many studies in the area, we applied the precautionary principle and remove all risks of double entries.

Results

Until the present, the ichthyofauna of the Mamirauá Sustainable Development Reserve is composed of 541 species, including 45 families and 15 orders (Table 2). These figures correspond to about 20% of all species valid for the Amazon (Dagosta and De Pinna 2019), and represent a 86% increase in relation to the first list produced for the RDSM, published in the end of the last century (Crampton, 1999). As detected in other studies and fish fauna surveys in Neotropical sites, the most represented orders were Siluriformes, with 209 species, and Characiformes, with 185 species (Beltrão and Soares 2018; Beltrão et al. 2019; Dagosta and De Pinna 2019). Together they represent more than 70% of the fish species richness at Mamirauá Reserve. Next in importance comes the Gymnotiformes, with 78 species. The gymnotids are remarkably diverse at the Mamirauá Reserve, where several new species have been described during the last two decades (Albert & Crampton 2001; Crampton et al. 2004; Crampton et al. 2005) (Figure 3f). At least, three new gymnotid species were recently discovered, two Apteronotids and one Hypopomids, and are under description. In the fourth place, the Cichliformes, with 40 species, is another species-rich order present. At Mamirauá we included in the checklist *Apistogrammoides pucallpaensis* Meinken, 1965, which had its first record for Brazil published recently (Oliveira et al. 2019) (Figure 3d).

The species richness at the family level also follows the general pattern found in the Neotropics. The five richest families are Characidae, with 61 species, Loricariidae with 55 species, Cichlidae with 37 species, Apteronotidae with 33 species and Auchenipteridae with 25 species. These numbers correspond to 39% of the total species richness at Mamirauá. Remarkably, family Characidae alone holds 11% of the total richness, demonstrating the diversity of this fish family at the protected area.

The richest aquatic environment present was the floodplain lakes (369 spp.), followed by the "canos" and paranás (301 spp.), and the rivers (261 spp.). In all aquatic environments Characiformes was the dominant order, followed by Siluriformes and Cichliformes. Such richness distribution among orders is expected for the Neotropical fish fauna, being reported from several prior studies (Queiroz et al., 2013; Sleen and Albert, 2018; Beltrão et al., 2019; Dagosta and De Pinna, 2019) (figure 4).

From the names included in the first fish species list published for Mamirauá Reserve (Crampton, 1999), we removed those identified only at the genus level, since they are not present in the material deposited in any known biological collection. They are *Saccoderma* sp.1, *Pimelodus* sp.1, *Pseudostegophilus* sp.1, *Hoplosternum* sp.1, *Plagioscion* sp.1 and "*Petalodoras* sp.1". We also removed *Knodus*

Table 1. Physical and chemical parameters of water quality for the water bodies at Mamirauá Reserve based on Henderson (1999), Affonso et al. (2011 and 2015) and Pedro et al. (2013).

	Solimões River		Japurá River		Várzea Lakes		Várzea Canos and Paranãs		Temp. Pools
Parameters	**High Water**	**Low Water**	**High Water**	**Low Water**	**High Water**	**Low Water**	**High Water**	**Low Water**	**Low Water**
Secchi (m)	1.2	0.6	1.35	0.56	1.7	0.43	1.7	0.40	0.30
pH	6.9	6.8	6.36	6.60	6.85	7.01	6.84	7.29	6.95
Eletr. Conduc. (µS.cm-1)	87.7	200.6	77.3	131.0	115.29	85.21	110.53	231.02	155.29
Turbidity (NTU)	57.74	62.21	23.82	28.75	6.33	43.19	6.97	51.93	-
Dis. Oxygen (mg.l-1)	0.6	0.2	0.77	0.34	2.59	5.12	2.3	6.12	0.18
Temperature (°C)	27.1	31.3	27.8	30.9	27.27	31.52	26.62	31.32	28.14

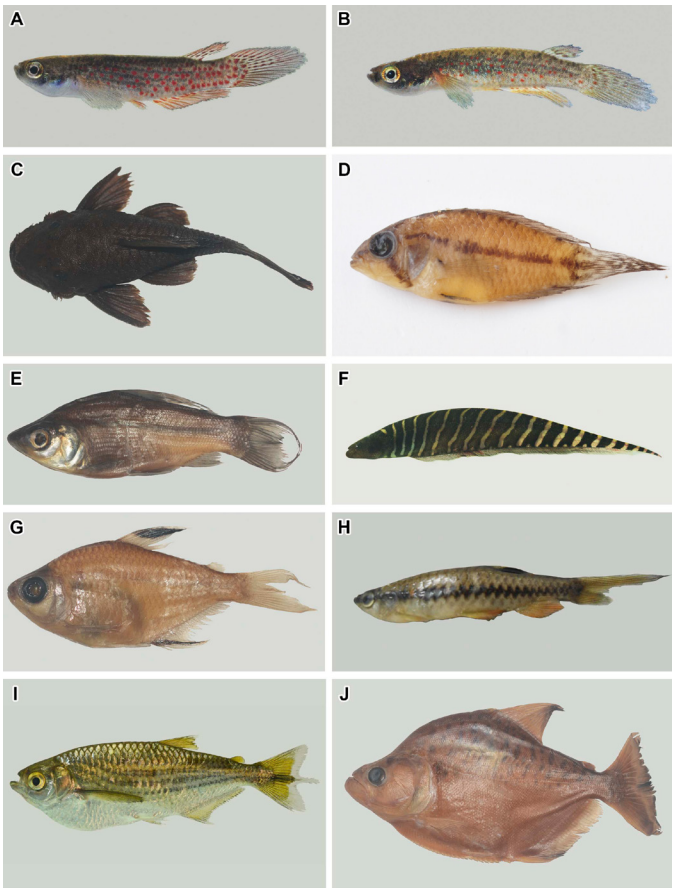


Figure 3. Representative individuals of some species collected at Mamiraua Reserve: a) *Anablepsoides* "mamiraua" sp.n ♂; b) *Anablepsoides* "mamiraua" sp.n ♀; c) *Ancistrus* cf. *hoplogenys*; d) *Apistogrammoides pucallpaensis*; e) *Curimatopsis microlepis*; f) *Gymnotus mamiraua*; g) *Moenkhausia hemigrammoides*; h) *Pyrrhulina zigzag*; i) *Triportheus angulatus*; j) *Serrasalmus* sp. n.

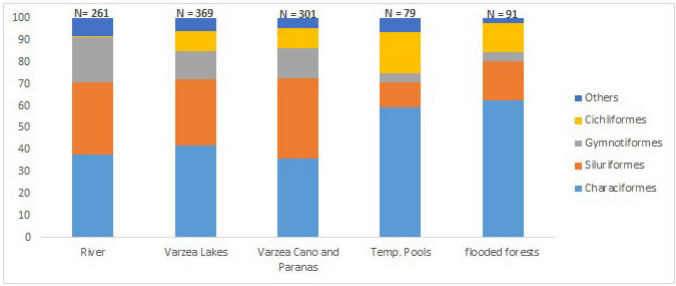


Figure 4. Ranking of richness by Orders and habitat of fish species found in the Mamirauá Sustainable Development Reserve (MSDR), N = Number of species.

sp.1 and *Tetragonopterus* sp.1, both included in a scientific report (M. Catarino, unpublished), informed as collected and identified only at the genus level. We found no correspondence with any material deposited in the collections consulted. Additionally, in the present version of the fish species list, we removed three names identified at the species level, mentioned in inventories and studies carried out at Mamirauá Reserve, but not deposited in any biological collection. They are *Microglanis carlae* Vera Alcaraz, da Graça & Shibatta, 2008, *Nannostomus harrisoni* (Eigenmann, 1909), *Crenicichla cametana* Steindachner, 1911 and *Lycengraulis grossidens* (Spix & Agassiz 1829). The decision to remove these four entries from the list was based on the consideration that *Microglanis carlae* has its distribution restricted to the Paraguay River basin; *Nannostomus harrisoni* has its distribution restricted to the Demerara river basin in Guyana, and that *Crenicichla cametana*, occurs only in the Xingu and Tocantins-Araguaia river basins (Dagosta and De Pinna 2019). *Lycengraulis grossidens* is a marine/estuarine species, with not confirmed records for freshwater habitats, and freshwater specimens identified. Consequently, it is more likely that these were misidentifications made by those responsible for the reports of the inventories consulted.

The miniature Crenuchidae *Elachocharax pulcher* Myers, 1927 (sensu Weitzman and Vari 1988; Toledo-Piza et al. 2014), and the hemiodontid *Hemiodus atranalis* (Fowler, 1940) were added to this list because they were recently captured at the Mamirauá Reserve, and we also included in our list three more species that just had their first records for the Solimões river basin, *Curimatopsis microlepis*, *Moenkhausia hemigrammoides* Géry, 1965 and *Pyrrhulina zigzag* Zarske & Géry, 1997 (Figures 3e; 3g; 3h).

Serrasalmus cf. *spilopleura* and *Mesonauta insignis* have their geographic distribution falling far from the Mamirauá Reserve area, and their occurrence can be questioned (Dagosta and De Pinna 2019; Kullander and Silfvergrip, 1991). A careful review of the identification of these species should be conducted in the near future.

Fifty-seven taxa in the list were not identified at the species level, and thus have an uncertain identification at this level. They were included in the list because there are deposited material in scientific collections to voucher for their names. Forty of them were identified only at the genus level, such as *Potamotrygon* sp.1, *Microcharacidium* sp.1, *Microschemobrycon* sp.1 and *Ancistrus* sp.1"mancha dorsal". Sixteen species were pre-determined with "cf.", such as *Metynnis* cf. *maculatus*, *Jupiaba* cf. *zonata* and *Ancistrus* cf. *hoplogenys* (Figure 3f). Eight species are new and are now under the process of description, listed here as *Characidium* sp. n., *Serrasalmus* sp. n., *Paravandellia* sp. n., *Plectrochilus* sp. n., *Brachyhypopomus* **sp.** n., *Adontosternarchus* sp. n., *Sternarchella* sp. n. and *Anablepsoides*"mamiraua" sp. n. (Figures 3a; 3b; 3c).

Discussion

The fish fauna found at the Mamirauá Reserve is typical of the Amazonian várzea ecosystem. Like other parts of the várzea (Zuanon et al. 2008), the more represented or richest families detected at RDSM fish fauna were Characidae, Loricariidae and Cichlidae. Species found at várzea lakes at the vicinity of the Solimões river (Saint-Paul et al., 2000; Freitas et al., 2014; Siqueira-Souza et al., 2016) are very similar to those found at lakes in Mamirauá. Similarly, the species found in floating meadows mattresses at the Eastern Peruvian Amazon (Correa et al., 2008) are also similar to those found in the floating meadows at Mamirauá. However, in all those previous accounts, species richness was not as high as the one found at Mamirauá Reserve and its aquatic environments. The study area is located in a part of the várzea considered exceptionally species-rich, and holding a set of important endemic species (Zuanon et al., 2008).

By any account, the Amazon basin has a superlative number of fish species. Available estimates vary greatly, but most of them suggest a number that may reach 3,500 species (Malabarba et al., 1998; Junk et al. 2007; Carvalho et al. 2009; Albert et al. 2011; van der Sleen & Albert 2017;

Dagosta & De Pina, 2019). However, some other authors suggest a significant upward trend, and that this number may reach up to 5,000 species in the next 70 years, if we maintain the current rate of description of new species (Ota et al. 2015). These values suggest that the Amazon fish fauna may represent about 15% of all freshwater fish species described in the world at the present (Oberdorff et al. 2019). The Congo River basin, in Africa, is considered the second most diverse river basin in the world, with less than half the number of fish species registered for the Amazon River basin (Snoeks et al. 2011).

Species richness in a particular area is the result of several processes operating at multiple spatial and temporal scales (Peláez & Pavanelli 2018), comprising numerous evolutionary lineages, resulting from the interaction of geological factors associated with vicariant and dispersion agents (Lundberg, 1998; Dagosta and de Pinna 2017). The distribution of fish species in the Amazonian sub-basins and adjacent drainage systems is complex, and amounts to numerous distribution overlaps and superlative degrees of biogeographic congruence (Dagosta and De Pinna 2017). The diversity patterns of this mega-fauna and the processes that generate these patterns are still only partially known (Dagosta and De Pinna 2019). However, recent studies suggest that the richness pattern of the Amazonian ichthyofauna is supported mainly by three factors: area, climate and energy availability (Oberdorff et al. 2019). The pattern shown here for Mamirauá fish species diversity is consistent with the recent predictions, but the pattern of fish endemism at Mamirauá is much higher than expected (Oberdorff et al., 2019).

The total number of species listed for the Mamirauá Reserve is considerably higher than in other studies, with the species richness at Middle Solimões basin reaching figures higher than those from other Amazonian sub-basins, such as the Tapajós River basin (with 529 species), the Xingu River basin (with 502 species), even though the study area of the Middle-Solimões corresponds to a small proportion of those two sub-basins. In addition, its known species richness reaches about 63% to 85% of the total species registered for the main channel of the Amazon River, depending on the source adopted (Zuanon et al., 2008; Dagosta and De Pinna 2019). This high value we found is probably the result of two combined factors. The first would be the high sampling effort applied during the last decades to the study area (Figure 5). The ichthyofauna of many Amazonian regions remain under-sampled, some of them are still nearly unknown to science, with no biological collection performed so far. Consequently, the differences in species richness found may simply reflect the difference in collection efforts (Queiroz et al. 2013). The two sub-basins under the greatest sampling effort are the same with the highest richness, the Negro River, with 1165 registered species (Beltrão et al. 2019), and the Madeira River, with 1062 species. Besides those two we have, of course, the main river channel, the Solimões-Amazonas, with 922 species recorded (Dagosta and De Pinna 2019).

The other explaining factor that may be responsible for the high species richness recorded would be the location of the Mamirauá Reserve and its environmental diversity. Located in the interflow of two great rivers, Solimões and Japurá, and in a large floodplain area, Mamirauá Reserve has a complex mosaic of bodies of water that are repeatedly connected and isolated, at least once a year. This type of ecosystem and the dynamics of its permanent or temporary aquatic environments provide several habitats and microhabitats that are distinct, and therefore can support a very high species richness (Figure 4). In this part of the Amazonian floodplains the water level rises annually around 11m (Ramalho et al., 2009), invading a mosaic of equally diverse array of forest types, and connecting and isolating all the local water bodies, sometimes for many consecutive months, probably with important implications for the richness of fish species in the area (Junk, et al. 1989; Arantes et al., 2017. In each part of the hydrological cycle, the aquatic environments present at the várzea can show a striking variation in water quality parameters (see Table 2). Besides that, Mamirauá Reserve lays at the confluence of the Japurá River, and the mouths of Tefé, Jutaí and Juruá Rivers are also very close, just few kilometers away. This high proximity to many other river basins and their fish faunas, with distinct levels of dissimilarity among them, could be another source of diversity and species richness. The distribution of the fish species in the Amazon sub-basins and adjacent drainage systems is complex, and amounts to numerous distributional

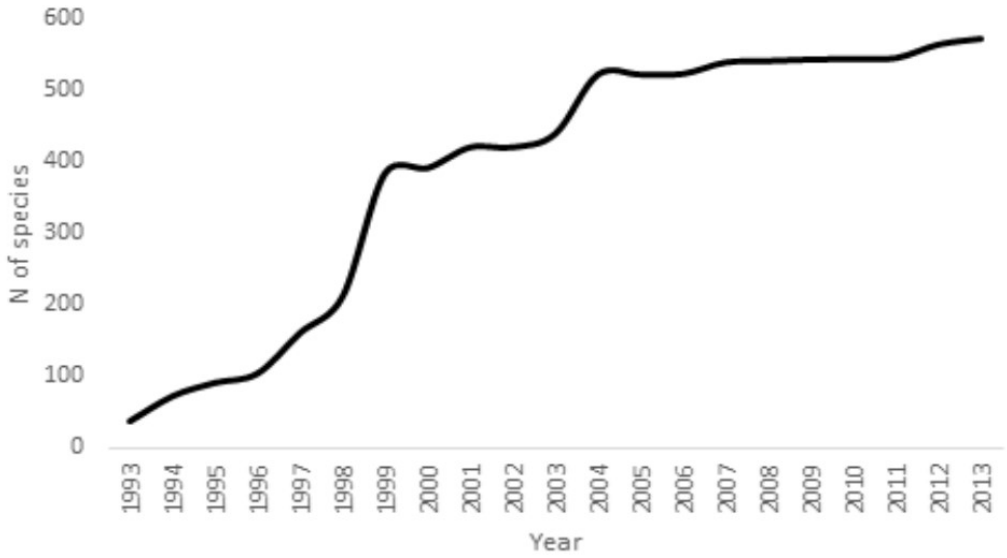


Figure 5. Species accumulation curve per year in the list of fish species recorded for Mamirauá Sustainable Development Reserve.

overlaps and superlative degrees of biogeographic congruence (Dagosta and de Pinna 2017). In the same way the high species richness of the Solimões River near Manaus can also be explained by its close proximity to the mouth of the Negro River (Zuanon et al., 2008).

None of the species recorded for the study area is listed as threatened of extinction, according with the International Union for Conservation of Nature (IUCN) and IBAMA (2018). Since the 2000's, several new species have been described for the area, almost all of them belonging to the Gymnotiformes, demonstrating a high species richness of this particular order at the Mamirauá Reserve, as in other várzea areas with habitats of similar diversity and structural complexity. This is probably due to the high number of taxonomic studies on this particular group of fish at Mamirauá (Albert & Crampton 2001; Crampton et al. 2004; Crampton et al. 2005; Correa et al. 2006; Albert and Crampton 2006; de Santana & Crampton 2007; de Santana & Crampton 2010; de Santana & Vari 2010; Lundberg et al. 2013; Sullivan et al. 2013; Carvalho & Albert 2015; Crampton et al. 2016; Evans et al. 2017).

It is expected that, as new undersampled areas are explored and surveyed, especially in the Northwestern part of Mamirauá Reserve, another significant increase in the fish species list will be achieved. As can be said for the whole Amazon, improvements in the sampling effort, together with continued taxonomic revision of the collected material, will result in the increase in the number of records, of new occurrences, and even in the description of new fish species for the study area. Recent studies on the Neotropical fish fauna have led to a significant improvement on the knowledge on fish diversity in the Amazon as never before (Sleen and Albert 2018; Dagosta and De Pinna 2019; Oberdorff et al. 2019), and we expect that this trend will be maintained or improved for the next decades.

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Author Contributions

Alexandre Pucci Hercos: elaboration of study's concept and design; data collection, analysis and preparation of manuscript.
Jonas Alves de Oliveira: elaboration of study's concept and design; data collection and analysis.
Jomara Cavalcante de Oliveira: elaboration of study's concept and design; data collection, analysis and preparation of manuscript.
Elizabeth Kathleen de Queiroz Rodrigues: elaboration of study's concept and design; data collection, analysis and preparation of manuscript.
Rita Louro Barbosa: data collection, analysis and preparation of manuscript.
Helder Lima de Queiroz: elaboration of study's concept and design; data collection, analysis and preparation of manuscript.

Table 2. List of fish species found at the Mamirauá Sustainable Development Reserve, during inventories, surveys and research on fish auto-ecology, biology and fish community ecology. * Paratype; **Holotype; ***Neotype. IDSM = Instituto de Desenvolvimento Sustentável Mamirauá; MCP = Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul; INPA = Instituto Nacional de Pesquisa da Amazônia; MZUSP = Museu de Zoologia da Universidade de São Paulo; ZUEC = Museu de Zoologia da Universidade Estadual de Campinas.

ESPÉCIE	FONTE
MYLIOBATIFORMES: Potamotrygonidae	
*Potamotrygon constellata (*Vaillant, 1880)	IDSM3017
Potamotrygon henlei (Castelnau, 1855)	MCP32907
Potamotrygon histrix (Müller & Henle, 1839)	IDSM3018
Potamotrygon motoro (Müller & Henle, 1841)	IDSM3019
Potamotrygon sp.1	MCP32891
OSTEOGLOSSIFORMES: Osteoglossidae	
Osteoglossum bicirrhosum (Cuvier, 1829)	IDSM254; IDSM1106; INPA-ICT18698
OSTEOGLOSSIFORMES: Arapaimidae	
Arapaima gigas (Schinz, 1822)	IDSM3020
CLUPEIFORMES: Engraulidae	
Anchoviella alleni (Myers, 1940)	INPA-ICT18808; MCP29620; MCP29621
Anchoviella guianensis (Eigenmann, 1912)	IDSM1918
Jurengraulis juruensis (Boulenger, 1898)	IDSM23; INPA-ICT19407; INPA-ICT18782
Lycengraulis batesii (Günther, 1868)	IDSM24; IDSM41; MCP29902; MCP29903
Lycengraulis cf. *figueiredoi*	MCP30002
CLUPEIFORMES: Pristigasteridae	

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Ilisha amazonica (Miranda Ribeiro, 1920)	IDSM1099; INPA-ICT19280
Pellona castelnaeana (Valenciennes, 1847)	IDSM53
Pellona flavipinnis (Valenciennes, 1837)	IDSM25; IDSM1837; IDSM2289; INPA-ICT18828
Pristigaster cayana Cuvier, 1829	IDSM43; IDSM1091; IDSM1836; MCP29649; MCP29650
Pristigaster whiteheadi Menezes, de & Pinna, 2000	INPA-ICT18718
CHARACIFORMES: Crenuchidae	
Characidium aff. *Zebra*	IDSM1932
Crenuchus spilurus Günther, 1863	IDSM3021
Characidium sp. *n.*	IDSM3016
Microcharacidium sp.*1*	MCP29347; MCP29348; MCP29349; MCP29350; MCP29436; MCP29437; MCP29438; MCP29439
CHARACIFORMES: Erythrinidae	
*Erythrinus erythrinus (*Bloch & Schneider, 1801)	IDSM116; IDSM167; IDSM328; INPA-ICT19242; MCP29924; MCP29925; MCP29926; MCP29927
Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)	IDSM117; INPA-ICT19246
Hoplias malabaricus (Bloch, 1794)	IDSM196; IDSM214; IDSM238; IDSM285; IDSM1135; IDSM2653; MCP32755; MCP32756; MCP32757; MCP32759; MCP32760
CHARACIFORMES: Cynodontidae	
Cynodon gibbus Spix & Agassiz, 1829	IDSM397; IDSM1965; MCP29921
Hydrolycus scomberoides (Cuvier, 1819)	IDSM1104; IDSM1966; IDSM35; IDSM137
Rhaphiodon vulpinus Spix & Agassiz, 1829	MCP30586
CHARACIFORMES: Serrasalmidae	
Colossoma macropomum (Cuvier, 1818)	IDSM2996
Metynnis altidorsalis Ahl, 1923	IDSM1394; IDSM1395; IDSM1396; IDSM1397; IDSM1398; IDSM1399; IDSM1400; IDSM1401; IDSM1402; IDSM1403; IDSM1473
*Metynnis hypsauchen (*Müller & Troschel, 1844)	In the process of cataloging
Metynnis luna Cope, 1878	IDSM1467; IDSM1468; IDSM1470; IDSM1471; IDSM1472; IDSM1517; IDSM1727; IDSM1521; MCP31637
*Metynnis maculatus (*Kner, 1858)	IDSM1739
Myloplus asterias (Müller & Troschel, 1844)	IDSM1453; IDSM1454; IDSM1455; IDSM1456; IDSM1457; IDSM1459; IDSM1460; IDSM1461; IDSM1462; IDSM1463; IDSM1464; IDSM1465; IDSM1466; IDSM1516
Myloplus rhomboidalis (Cuvier, 1818)	In the process of cataloging
Myloplus rubripinnis (Müller & Troschel, 1844)	IDSM1732; IDSM1452; MCP31638
Myloplus schomburgkii (Jardine & Schomburgk, 1841)	In the process of cataloging
Myloplus torquatus (Kner, 1858)	IDSM1093
Mylossoma aureum (Spix & Agassiz, 1829)	IDSM233; IDSM1014; IDSM1518; IDSM1519; IDSM1689; IDSM1505; IDSM1514; IDSM1695; IDSM1696; IDSM1703; IDSM1704; IDSM1733; IDSM1737; IDSM1740; IDSM1741; IDSM1742; MCP31679; MCP31681
Mylossoma albiscopum (Cope 1872)	IDSM194; IDSM232; IDSM283; IDSM1035; IDSM1504; IDSM1506; IDSM1507; IDSM1508; IDSM1509; IDSM1510; IDSM1511; IDSM1513; IDSM1530; IDSM1645; IDSM1690; IDSM1692; IDSM1693; IDSM1694; IDSM1697; IDSM1698; IDSM1699; IDSM1700; IDSM1701; IDSM1702; IDSM1705; IDSM1706; IDSM1707; IDSM1708; IDSM1709; IDSM1710; IDSM1711; IDSM1712; IDSM1714; IDSM1715; IDSM1726; IDSM1728; IDSM1729; IDSM1730; IDSM1731; IDSM1734; IDSM1735; IDSM1736; IDSM1738; IDSM1743; MCP31654; MCP31656
Piaractus brachypomus (Cuvier, 1818)	IDSM205; IDSM1120; IDSM1691
Pristobrycon calmoni (Steindachner, 1908)	MCP29976; MCP29977; MCP29978; MCP29979; MCP29980; MCP29981; MCP29982; MCP29983
Pristobrycon striolatus (Steindachner, 1908)	IDSM1412; IDSM1421; IDSM1422; IDSM1423; IDSM1424; IDSM1425

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Pristobrycon sp.*1*	MCP33149
Pygocentrus nattereri Kner, 1858	IDSM127; IDSM234; IDSM1114; IDSM1426; IDSM1427; IDSM1428; IDSM1429; IDSM1430; IDSM1431; IDSM1432; IDSM1433; IDSM1434; IDSM1435; IDSM1436; IDSM1437; IDSM1438; IDSM1439; IDSM1440; IDSM1441; IDSM1442; IDSM1443; IDSM1444; IDSM1445; IDSM1446; IDSM1448; IDSM1449; IDSM1450; IDSM1451; IDSM1520; IDSM1522; IDSM1523; IDSM1524; IDSM1526; IDSM1527; IDSM1528; MCP32747; MCP32748; MCP32749
Serrasalmus cf. *altipinis*	MCP33213; MCP33214;
Serrasalmus eigenmanni Norman, 1929	IDSM1416; IDSM1417; IDSM1418; IDSM1419; IDSM1420; IDSM163; IDSM1414
Serrasalmus elongatus Kner, 1858	IDSM136; IDSM235; IDSM1406; IDSM1515; IDSM2308; MCP31652; MCP32900; MCP32901; MCP32902; MCP32904
Serrasalmus maculatus Kner, 1858	IDSM1407; IDSM1408; IDSM1411; IDSM1883
Serrasalmus medinai Ramírez, 1965	IDSM2302; IDSM256; IDSM1713
Serrasalmus rhombeus (Linnaeus, 1766)	IDSM261; IDSM333; IDSM113; IDSM1251; IDSM1405; IDSM1409; IDSM1481; IDSM1482; IDSM1483; IDSM1484; IDSM1485; IDSM1486; IDSM1487; IDSM1489; IDSM1490; IDSM1492; IDSM1494; IDSM1495; IDSM1496; IDSM1497; IDSM1498; IDSM1499; IDSM1500; IDSM1501; IDSM1502; IDSM1503; IDSM1512; IDSM1716; IDSM1717; IDSM2299; IDSM2300; IDSM2301; IDSM2304; IDSM2305; IDSM2307; IDSM2309; IDSM2310; IDSM1744; IDSM255; MCP32905
Serrasalmus serrulatus (Valenciennes, 1850)	MCP33038
Serrasalmus sp. *n.*	IDSM1474; IDSM1475; IDSM1476; IDSM1477; IDSM1478; IDSM1479; IDSM1480
Serrasalmus sp.*1*	MCP31677; MCP31678; MCP32753; MCP32754; MCP32894; MCP32895; MCP32897; MCP32909; MCP33198; MCP33200; MCP33201; MCP33202; MCP33203; MCP33205; MCP33206; MCP33207; MCP33209
Serrasalmus aff. *spilopleura* Kner, 1858	MCP33032
CHARACIFORMES: Hemiodontidae	
Anodus elongatus Agassiz, 1829	IDSM2202; MCP30042
Hemiodus gracilis Günther, 1864	In the process of cataloging
Hemiodus argenteus Pellegrin, 1908	In the process of cataloging
Hemiodus atranalis (Fowler, 1940)	IDSM3063
Hemiodus immaculatus Kner, 1858	MCP31710
Hemiodus microlepis Kner, 1858	IDSM3064
Hemiodus unimaculatus (Bloch, 1794)	IDSM3015
CHARACIFORMES: Anostomidae	
Abramites hypselonotus (Günther, 1868)	IDSM1046; IDSM1652; IDSM1796; IDSM1828
Anostomoides atrianalis Pellegrin, 1909	IDSM3022
Laemolyta proxima (Garman, 1890)	INPA-ICT18852; INPA-ICT18853; IDSM91
Laemolyta taeniata (Kner, 1859)	IDSM1105; IDSM1955; IDSM1964; IDSM1970
Leporinus agassizi Steindachner, 1876	IDSM151; IDSM334; IDSM1033; INPA-ICT19293
Leporinus cf. *niceforoi*	IDSM1971; IDSM1973; INPA-ICT18805
Leporinus fasciatus (Bloch, 1794)	IDSM1971; IDSM1973; INPA-ICT18805
*Leporinus friderici (*Bloch, 1794)	IDSM29; IDSM152; IDSM226; IDSM1878; INPA-ICT19347; INPA-ICT19346; INPA-ICT19341; INPA-ICT19340; INPA-ICT19339; INPA-ICT19338; INPA-ICT19335; INPA-ICT19333; INPA-ICT19332; INPA-ICT19330; INPA-ICT19329; INPA-ICT19327; INPA-ICT19326; INPA-ICT19325; INPA-ICT19324; INPA-ICT19319; MCP31647 MCP32810; MCP32811; MCP32812; MCP32813; MCP32814; MCP32815

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Leporinus jamesi Garman, 1929	MCP33034; MCP33121
Megaleporinus trifasciatus Steindachner, 1876	IDSM149; IDSM153; IDSM1884; IDSM2103; INPA-ICT19351; INPA-ICT19350; INPA-ICT19349; INPA-ICT19348; MCP29754; MCP29755; MCP29756
Pseudanos gracilis (Kner, 1858)	IDSM2997
Pseudanos trimaculatus (Kner, 1858)	IDSM1084; INPA-ICT19309; INPA-ICT19308
Rhytiodus argenteofuscus Kner, 1858	IDSM259; IDSM1073; INPA-ICT19306; MCP32935
Rhytiodus microlepis Kner, 1858	IDSM125; IDSM154; IDSM165; IDSM1054; INPA-ICT19289; *INPA-ICT19288; MCP29923*
Schizodon fasciatus Spix & Agassiz, 1829	IDSM1638; IDSM1972; IDSM155; IDSM198; IDSM1638; *INPA-ICT19546; INPA-ICT18712; MCP29992; MCP29993; MCP29994; MCP29995*
CHARACIFORMES: Chilodontidae	
Caenotropus labyrinthicus (Kner, 1858)	IDSM30; MCP33026; MCP33027
Caenotropus sp.*1*	IDSM1143; IDSM2118
Chilodus punctatus Müller & Troschel, 1844	IDSM3065
CHARACIFORMES: Curimatidae	
Curimata incompta Vari, 1984	IDSM2204
Curimata knerii Steindachner, 1876	MCP30627
Curimata vittata (Kner, 1858)	IDSM105; IDSM1121
Curimatella alburna (Müller & Troschel, 1844)	IDSM146; IDSM330; IDSM1077; IDSM1891; IDSM1949; INPA-ICT19264
Curimatella dorsalis (Eigenmann & Eigenmann, 1889)	In the process of cataloging
Curimatella meyeri (Steindachner, 1882)	MCP29607; MCP30621
Curimatopsis evelynae Géry, 1964	IDSM1865
Curimatopsis macrolepis (Steindachner, 1876)	IDSM1079
Curimatopsis microlepis Eigenmann & Eigenmann, 1889	IDSM2998
Cyphocharax abramoides (Kner, 1859)	IDSM1859
Cyphocharax festivus Vari, 1992	IDSM103; IDSM108; INPA-ICT19262
Cyphocharax plumbeus (Eigenmann & Eigenmann, 1889)	MCP33043
Cyphocharax gouldingi Vari, 1992	IDSM2999
Cyphocharax spiluropsis (Eigenmann & Eigenmann, 1889*)*	MCP29543; MCP29545; IDSM3000
Potamorhina altamazonica (Cope, 1878)	IDSM27; IDSM1900; MCP29381
Potamorhina latior (Spix & Agassiz, 1829)	IDSM26; IDSM1103; IDSM1818; IDSM1899; MCP32936
Psectrogaster amazonica Eigenmann & Eigenmann, 1889	IDSM225; IDSM3001
Psectrogaster essequibensis (Günther, 1864)	IDSM1946
Psectrogaster rutiloides (Kner, 1858)	IDSM135; IDSM1806; IDSM1846; MCP29795; MCP29796
Steindachnerina bimaculata (Steindachner, 1876)	MCP33140
Steindachnerina hypostoma (Boulenger, 1887)	IDSM1851; IDSM1847; MCP29931
Steindachnerina leucisca (Günther, 1868)	IDSM28; IDSM1061; IDSM1947; IDSM1948; MCP33141 MCP33142; MCP33143; MCP33144
CHARACIFORMES: Prochilodontidae	
Prochilodus nigricans Spix & Agassiz, 1829	IDSM99; IDSM223; IDSM1137; IDSM1803; MCP29711; MZUSP27925.0
Semaprochilodus insignis (Jardine, 1841)	IDSM1804; IDSM1108; IDSM204
Semaprochilodus taeniurus (Valenciennes, 1821)	IDSM224
CHARACIFORMES: Lebiasinidae	
Copeina guttata (Steindachner, 1876)	IDSM3002
Copella gr. *nattereri*	IDSM3038
Copella callolepis (Regan, 1912)	IDSM1138; IDSM1906; IDSM2657

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Nannostomus eques Steindachner, 1876	IDSM1908; IDSM1957
Nannostomus unifasciatus Steindachner, 1876	IDSM1907; IDSM1956
Nannostomus trifasciatus Steindachner, 1876	In the process of cataloging
Pyrrhulina australis Eigenmann & Kennedy 1903	IDSM2658
Pyrrhulina brevis Steindachner, 1876	IDSM222
Pyrrhulina filamentosa Valenciennes, 1847	In the process of cataloging
Pyrrhulina semifasciata Steindachner, 1876	IDSM183; IDSM207; IDSM1122; IDSM1905; IDSM2654
Pyrrhulina vittata Regan, 1912	IDSM3003
Pyrrhulina zigzag Zarske & Géry, 1997	IDSM2607; IDSM2671; IDSM2672; IDSM2673
CHARACIFORMES: Ctenoluciidae	
Boulengerella maculata (Valenciennes, 1850)	IDSM3066
Boulengerella cuvieri (Spix & Agassiz, 1829)	MCP32767
CHARACIFORMES: Chalceidae	
Chalceus erythrurus (Cope, 1870)	IDSM1083; IDSM1653; IDSM1890; INPA-ICT18619; INPA-ICT19286
CHARACIFORMES: Triportheidae	
Agoniates anchovia Eigenmann, 1914	IDSM31; IDSM1038; IDSM1549; IDSM1759; IDSM1936; IDSM2137; INPA-ICT19531; INPA-ICT19529; MCP29799; MCP29801; MCP29804
Triportheus albus Cope, 1872	IDSM1102; IDSM1931; MCP29940; MCP29941; MCP299942
Triportheus angulatus (Spix & Agassiz, 1829)	IDSM1755; IDSM1789; IDSM1053; INPA-ICT19303; INPA-ICT18767; MCP29943***; MCP29944; MCP29945; MCP29947
Triportheus auritus (Valenciennes, 1864)	IDSM1100; IDSM1756
CHARACIFORMES: Gasteropelecidae	
Carnegiella marthae Myers, 1927	IDSM2622; IDSM2660; IDSM1118; IDSM1825
Carnegiella strigata (Günther, 1864)	IDSM2627
Gasteropelecus sternicla (Linnaeus, 1758)	IDSM237; IDSM997; INPA-ICT18821
Thoracocharax stellatus (Kner, 1858)	IDSM55; IDSM1060; IDSM1101; IDSM1758; IDSM1791; IDSM1830; IDSM1838; IDSM1839; IDSM1852; IDSM1860; IDSM1937; IDSM2136; IDSM2625; INPA-ICT18816; MCP29568; MCP29569
CHARACIFORMES: Bryconidae	
Brycon amazonicus (Spix & Agassiz, 1829)	INPA-ICT19118; INPA-ICT19108; INPA-ICT19107; MCP29758; IDSM0111; IDSM228; MZUSP27924.0
Brycon falcatus Müller & Troschel, 1844	IDSM176
Brycon melanopterus (Cope, 1872)	In the process of cataloging
CHARACIFORMES: Iguanodectidae	
Bryconops melanurus (Bloch, 1794)	In the process of cataloging
Iguanodectes geisleri Géry, 1970	IDSM1911; IDSM2133
Iguanodectes purusii (Steindachner, 1908)	IDSM3005
*Iguanodectes spilurus (*Günther, 1864)	IDSM1126; MCP30630
Piabucus dentatus (Koelreuter, 1763)	IDSM3006
CHARACIFORMES: Acestrorhynchidae	
Acestrorhynchus abbreviatus (Cope, 1878)	IDSM1968; INPA-ICT19179; INPA-ICT19178; INPA-ICT19177; MCP29973
Acestrorhynchus falcatus (Bloch, 1794)	IDSM213
Acestrorhynchus falcirostris (Cuvier, 1819)	IDSM114; INPA-ICT18833; MCP29558; MCP29559
Acestrorhynchus microlepis (Schomburgk, 1841)	IDSM115; MCP30588; MCP30590
Acestrorhynchus nasutus Eigenmann, 1912	IDSM3007
Gnathocharax steindachneri Fowler, 1913	IDSM3008
CHARACIFORMES: Characidae	
Aphyocharax gr. *dentatus*	IDSM2290

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Aphyocharax pusillus Günther, 1868	IDSM44; IDSM45; IDSM1037; IDSM1130; IDSM1667; IDSM1787; IDSM1809; IDSM1933; MCP29551; MCP29552; MCP29553; MCP29580; MCP29581; MCP32769
Astyanax sp.*1*	IDSM2188; IDSM2212
Astyanax bimaculatus (Linnaeus, 1758)	IDSM3024
Boehlkea fredcochui Géry, 1966	IDSM1141
Brachychalcinus copei (Steindachner, 1882)	IDSM1930; IDSM2162
Charax condei (Géry & Knöppel, 1976)	IDSM3025
Charax gibbosus (Linnaeus, 1758)	INPA-ICT18779
Charax tectifer (Cope, 1870)	IDSM1843
Chrysobrycon sp.*1*	IDSM2159
Ctenobrycon hauxwellianus (Cope, 1870)	IDSM2171
Ctenobrycon spilurus (Valenciennes, 1850)	IDSM1136; IDSM1525; IDSM1566; IDSM1781; IDSM1896; IDSM1951; IDSM2624; INPA-ICT18793
Galeocharax gulo (Cope, 1870)	IDSM1082; IDSM1919; IDSM2186
Gymnocorymbus thayeri Eigenmann, 1908	IDSM1864; IDSM2184; IDSM2185; IDSM2606; IDSM2644
Hemigrammus belottii (Steindachner, 1882)	IDSM3009
Hemigrammus analis Durbin, 1909	IDSM1912
Hemigrammus haraldi Géry 1961	IDSM193; IDSM1945; IDSM2111; IDSM1858
Hemigrammus hyanuary Durbin, 1918	IDSM3010
Hemigrammus levis Durbin, 1908	IDSM1915
Hemigrammus luelingi Géry, 1964	IDSM2656
Hemigrammus ocellifer (Steindachner, 1882)	IDSM1617; IDSM1139; IDSM2626
Hemigrammus rodwayi Durbin, 1909	IDSM1914
Hemigrammus unilineatus (Gill, 1858)	IDSM1124; IDSM1824; IDSM1897; IDSM2189; IDSM2623; IDSM2630
Hemigrammus aff. *worderwinkleri*	IDSM3026
Hyphessobrycon bentosi Durbin, 1908	IDSM3027
Hyphessobrycon copelandi Durbin, 1908	In the process of cataloging
Jupiaba cf. zonata	IDSM150
Microschemobrycon sp.*1*	IDSM039
Moenkhausia ceros Eigenmann, 1908	IDSM2569
Moenkhausia chrysargyrea (Günther, 1864)	In the process of cataloging
Moenkhausia collettii (Steindachner, 1882)	IDSM1823; IDSM2655
Moenkhausia collettii "alta"	In the process of cataloging
Moenkhausia comma Eigenmann, 1908	In the process of cataloging
Moenkhausia cotinho Eigenmann, 1908	IDSM1096
Moenkhausia dichroura (Kner, 1858)	IDSM229; IDSM1095; IDSM1913; IDSM1765; IDSM1888; IDSM1895; IDSM1954; IDSM1969; IDSM1974; INPA-ICT18703; INPA-ICT18702
Moenkhausia gracilima (Eigenmann, 1908)	IDSM1921; IDSM1938
Moenkhausia grandisquamis (Müller & Troschel, 1845)	In the process of cataloging
Moenkhausia hemigrammoides Géry, 1965	IDSM1909
Moenkhausia intermedia Eigenmann, 1908	IDSM85; IDSM1782; IDSM1040; IDSM1885; INPA-ICT18701; *INPA-ICT18700; INPA-ICT18699*
Moenkhausia lata Eigenmann, 1908	IDSM2567
Moenkhausia lepidura (Kner, 1858)	IDSM1065; IDSM1953; IDSM2092
Moenkhausia megalops (Eigenmann, 1907)	In the process of cataloging
Moenkhausia melogramma Eigenmann, 1908	IDSM1075; IDSM1866; IDSM1910; IDSM2209; IDSM2659
Moenkhausia cf. *naponis*	IDSM1762; IDSM1784; IDSM1934; IDSM2101

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Moenkhausia oligolepis (Günther, 1864)	IDSM1123; INPA-ICT18721; INPA-ICT18723
Odontostilbe fugitiva Cope, 1870	IDSM2573; IDSM2574
Paragoniates alburnus Steindachner, 1876	MCP29612; MCP29850
Phenacogaster pectinatus (Cope, 1870)	IDSM3028
Phenacogaster sp.*1*	In the process of cataloging
Poptella compressa (Günther, 1864)	IDSM1134; IDSM1532; IDSM1780; IDSM2196
Prionobrama filigera (Cope, 1870)	IDSM1557
Prodontocharax alleni Böhlke, 1953	MCP29863; MCP31917
Prodontocharax melanotus Pearson, 1924	IDSM54; IDSM1760; IDSM1792; IDSM1795; IDSM1810; IDSM1849; IDSM1854; IDSM2571; IDSM2572
Protocheirodon pi (Vari, 1978)	*IDSM1808; IDSM2591*
Roeboides affinis (Günther, 1868)	IDSM1564; IDSM1935; IDSM1920; IDSM1840; IDSM999; IDSM1845; INPA-ICT19543; INPA-ICT19540; INPA-ICT19539; INPA-ICT19538; MCP29988
Roeboides myersii Gill, 1870	IDSM76; IDSM86; IDSM230; IDSM231; IDSM260; IDSM1036; IDSM1805; INPA-ICT19521; INPA-ICT9520; INPA-ICT19519; INPA-ICT19518; INPA-ICT19517; INPA-ICT19516; INPA-ICT18736; MCP30577; MCP30578; MCP30580; MCP30581; MCP30582; MCP30583; MCP30584
Serrapinnus gr. *gracilis*	IDSM998; IDSM1898
Stethaprion erythrops Cope, 1870	IDSM2126; IDSM2170; INPA-ICT19564; MCP29909; MCP29910
Stichonodon insignis (Steindachner, 1876)	IDSM1080
Tetragonopterus argenteus Cuvier, 1816	IDSM75; IDSM282; IDSM1783; IDSM1802; IDSM1844; IDSM1967; IDSM2105; INPA-ICT18693; INPA-ICT18692
Tetragonopterus chalceus Spix & Agassiz, 1829	INPA-ICT18707
GYMNOTIFORMES: Apteronotidae	
Adontosternarchus balaenops (Cope, 1878)	IDSM2175; IDSM2293; IDSM1820; IDSM211; IDSM1003; INPA-ICT18272; INPA-ICT18271; INPA-ICT18270; INPA-ICT18269; INPA-ICT18268; INPA-ICT18266; INPA-ICT11520; MCP33386; MCP33387; MCP33390; MCP39314; MCP39315; MCP39316; MCP39317; MCP39318; MCP39319; MCP39320; MCP39321; MCP39322; MCP39323; MCP39324; MCP39325; MCP39326; MCP39327; MCP39328; MCP39329
Adontosternarchus clarkae Mago-Leccia, Lundberg & Baskin, 1985	IDSM1004; IDSM1801; IDSM1799; IDSM1829; IDSM1877; IDSM2076; IDSM2639; IDSM785; IDSM289; IDSM2096; INPA-ICT18230; INPA-ICT18229; INPA-ICT15809; INPA-ICT9971; MCP39330; MCP39331; MCP39332; MCP39333; MCP39334; MCP39335; MCP39336; MCP39337; MCP39338; MCP39339; MCP39340; MCP39341; MCP39342
Adontosternarchus sachsi (Peters, 1877)	IDSM279; INPA-ICT18278; INPA-ICT15808; INPA-ICT11519; MCP39352; MCP39353; MCP39354; MCP39355
Adontosternarchus nebulosus Lundberg & Cox Fernandes 2007	INPA-ICT17311*
Adontosternarchus sp. *n.*	MCP39302*; MCP39303*; MCP39304**; MCP39305*; MCP39306*; MCP39307*; MCP39308*; MCP39309*; MCP39310; MCP39311; MCP39312; MCP39313
Apteronotus albifrons (Linnaeus, 1766)	IDSM828; IDSM1066; IDSM1867; INPA-ICT18179
Apteronotus apurensis Fernández-Yépez, 1968	INPA-ICT18298; INPA-ICT18256; INPA-ICT18255; INPA-ICT18254; INPA-ICT18156; INPA-ICT15834; INPA-ICT15811; INPA-ICT15803
Apteronotus bonapartii (Castelnau, 1855)	IDSM744; IDSM745; IDSM775; IDSM776; IDSM994; IDSM1798; IDSM1822; IDSM1826; IDSM1868; IDSM1944; IDSM2061; IDSM2070; IDSM2174; IDSM2082; IDSM2031; IDSM2032; IDSM2033; IDSM2034; INPA-ICT09970
Compsaraia compsa (Mago-Leccia, 1994)	In the process of cataloging
Compsaria samueli Albert & Crampton, 2009	IDSM276
Pariosternarchus amazonensis Albert & Crampton, 2006	MCP34916**; MCP34917*

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Parapteronotus hasemani (Ellis, 1913)	IDSM1001; IDSM59; IDSM637; IDSM746; IDSM754; IDSM758; IDSM2047; IDSM002056; IDSM002057; IDSM002095; IDSM002129; IDSM002147; IDSM002173; IDSM001869; INPA-ICT018315; INPA-ICT018314; INPA-ICT018313; INPA-ICT018312; INPA-ICT 018310; INPA-ICT018309; INPA-ICT018308; INPA-ICT018307; INPA-ICT018305; INPA-ICT018302; INPA-ICT018258; INPA-ICT018257; INPA-ICT015807; INPA-ICT9969; MCP33437; MCP33438; MCP33439; MCP33440; MCP33441; MCP33442
Platyurosternarchus macrostomus (Günther, 1870)	IDSM1986; IDSM2183; INPA-ICT15828; MCP41660
Porotergus duende de, Santana & Crampton, 2010	MCP37360*
Porotergus gimbeli Ellis, 1912	IDSM1006; INPA-ICT15804; MCP37523; MCP37524; MCP37525; MCP37526; MCP37527; MCP37529; MCP37530; MCP37531
Porotergus gymnotus Ellis, 1912	IDSM2291
Sternarchella calhamazon Lundberg, Cox Fernandes, Campos, da, Paz & Sullivan, 2013	MCP49414; MCP49415; MCP49416; MCP49417; MCP49418; MCP49419; MCP49420; MCP49421; MCP49422*
Sternarchella duccis (Lundberg, Cox Fernandes & Albert, 1996)	INPA-ICT15818
Sternarchella raptor (Lundberg, Cox Fernandes & Albert, 1996)	IDSM60; INPA-ICT15819; MCP33291; MCP33292
Sternarchella rex Evans, Crampton & Albert 2017	MCP49422**; MCP49423*
Sternarchella schotti (Steindachner, 1868)	IDSM2177; IDSM2634; IDSM1873; IDSM2132; IDSM295; IDSM1050; IDSM1797; IDSM2148; IDSM2298; IDSM1942; INPA-ICT18264; INPA-ICT18263; INPA-ICT 18262; INPA-ICT18261; INPA-ICT18260; INPA-ICT18191; INPA-ICT15801; INPA-ICT09979; MCP33371; MCP33372; MCP33373; MCP33389; MCP49424; MCP49425; MCP49426; MCP49427; MCP49428; MCP49429; MCP49430; MCP49431; ZUEC-PIS12339
*Sternarchella terminalis (*Eigenmann & Allen, 1942)	IDSM275; INPA-ICT18150; ZUEC-PIS12340; MCP33370; MCP49432; MCP49433; MCP49434; MCP49435; MCP49436
Sternarchella sp. *n*.	ZUEC-PIS12337*; ZUEC-PIS12338*
Sternarchogiton nattereri (Steindachner, 1868)	IDSM2176; IDSM2632; IDSM2146; IDSM2131; IDSM1800; IDSM1761; IDSM996; IDSM278; INPA-ICT18297; INPA-ICT18178; INPA-ICT18177; INPA-ICT15799; INPA-ICT11522; MCP38306
Sternarchogiton porcinum Eigenmann & Allen, 1942	MCP37532; MCP37533; MCP37534; MCP37535; MCP37536; MCP37537; MCP37539; MCP37540; MCP37541; MCP37542
Sternarchogiton sp.*1*	MCP33311; MCP37543
Sternarchorhamphus muelleri (Steindachner, 1881)	IDSM290; INPA-ICT18259; INPA-ICT15823; MCP33461; MCP33462; MCP33463; MCP33464; MCP33465; MCP33466; MCP41652; MCP41653; MCP41655; MCP41656; MCP41657; MCP41658
Sternarchorhynchus cramptoni de, Santana & Vari, 2010	MCP41637*; MCP41638*
Sternarchorhynchus curvirostris (Boulenger, 1887)	IDSM2130
Sternarchorhynchus mormyrus (Steindachner, 1868)	MCP33285; MCP41640; MCP41641; MCP41642
Sternarchorhynchus oxyrhynchus (Müller & Troschel, 1849)	IDSM1879; INPA-ICT18274; INPA-ICT18194; MCP33382; MCP33383; MCP33384; MCP33391
Sternarchorhynchus sp.*1*	MCP41639; MCP41643; MCP41645; MCP41646; MCP41647; MCP41648; MCP41649; MCP41650; MCP41651
Tenebrosternarchus preto (de Santana & Crampton, 2007)	INPA-ICT15806*; INPA-ICT18164*; MCP37548*; MCP37549*; MCP37550*; MCP37554*; MCP37555*; MCP37556*; MCP37557*
GYMNOTIFORMES: Sternopygidae	
Distocyclus conirostris (Eigenmann & Allen, 1942)	IDSM1876; IDSM2190; IDSM2150; IDSM2172; IDSM995; INPA-ICT18301; INPA-ICT18300 INPA-ICT18299; INPA-ICT18031; INPA-ICT15812; INPA-ICT11517; MCP33286; MCP33287; MCP33288; MCP33289; MCP33290
Eigenmannia limbata (Schreiner & Miranda Ribeiro, 1903)	IDSM98; IDSM128; IDSM732; IDSM778; IDSM779; IDSM1111; IDSM2051; IDSM2052; IDSM2097;INPA-ICT18684; INPA-ICT18683; INPA-ICT18681; INPA-ICT18288; INPA-ICT18287; INPA-ICT18286; INPA-ICT18285; INPA-ICT18282; INPA-ICT18281; INPA-ICT18202; INPA-ICT9976
Eigenmannia macrops (Boulenger, 1897)	IDSM96; IDSM1052; IDSM1870; IDSM2090; IDSM2098; IDSM2179; IDSM288
Eigenmannia gr. *trilineata* López & Castello, 1966	INPA-ICT15795

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Eigenmannia virescens (Valenciennes, 1842)	IDSM404; IDSM407; IDSM780; IDSM781; IDSM786; IDSM787; IDSM859; IDSM860; IDSM861; IDSM1005; IDSM1874; IDSM1848; IDSM2060; INPA-ICT35171; MCP33293; MCP33294; MCP33295; MCP33296; MCP33297
Eigenmannia sp.*1*	MCP47752
Rhabdolichops caviceps (Fernández-Yépez, 1968)	IDSM274; INPA-ICT15791; INPA-ICT9981; MCP35999; MCP36000; MCP36001; MCP36002; MCP36004; MCP36005; MCP36006; MCP36007; MCP36008; MCP36010; MCP36011; MCP36022
Rhabdolichops eastwardi Lundberg & Mago-Leccia, 1986	IDSM2180; IDSM273; INPA-ICT18220; INPA-ICT18218; INPA-ICT18217; INPA-ICT18212; INPA-ICT018211; INPA-ICT011518; MCP36012: MCP36013; MCP36014; MCP36015; MCP36018; MCP36019; MCP36020; MCP36023; MCP36024; MCP36025
Rhabdolichops electrogrammus Lundberg & Mago-Leccia, 1986	MCP36027; MCP36028; MCP36029
Rhabdolichops lundbergi Correa, Crampton & Albert, 2006	*IDSM1010; INPA-ICT18226; INPA-ICT18222; INPA-ICT25254*; MCP36031*; MCP36032*; MCP36033*; MCP36034*; MCP36035*; MCP36036*; MCP36037**; MCP36038*; MCP36039*; MCP36040*; MCP36042*; MCP36043*; MCP36044*; MCP36051*
Rhabdolichops navalha Correa, Crampton & Albert, 2006	*IDSM2094; IDSM2149; IDSM2182; IDSM1116; IDSM1872; IDSM1816*
Rhabdolichops nigrimans Correa, Crampton & Albert, 2006	*IDSM294; IDSM1007; IDSM1850; IDSM1871; IDSM1943; INPA-ICT18371; INPA-ICT18370; INPA-ICT18369; INPA-ICT18239; INPA-ICT18225; INPA-ICT18224; INPA-ICT18223; INPA-ICT18221; INPA-ICT15794*
Rhabdolichops troscheli (Kaup, 1856)	INPA-ICT18162; INPA-ICT9973; MCP36055; MCP36057; MCP36058
Sternopygus branco *Crampton, Hulen & Albert, 2004*	INPA-ICT18166; INPA-ICT15786*; MCP32241*; MCP32242*; MCP32243*; MCP32244*; MCP32245*; MCP32246*; MCP32451**
Sternopygus macrurus (Bloch & Schneider, 1801)	IDSM728; IDSM755; IDSM757; IDSM769; IDSM771; IDSM181; IDSM849; IDSM1011; IDSM1763; IDSM1976; IDSM2035; IDSM2036; IDSM2037; IDSM2038; IDSM2039; IDSM2040; IDSM2041; IDSM2042; IDSM2043; IDSM2044; IDSM2045; IDSM2053; IDSM2054; IDSM2055; IDSM2109; IDSM2128; INPA-ICT18316; INPA-ICT18190; INPA-ICT15802; INPA-ICT9974; MCP032247; MCP32248; MCP32250; MCP32251; MCP32252; MCP32258; MCP33374; MCP33375
GYMNOTIFORMES: Gymnotidae	
Electrophorus varii de Santana, Wosiacki, Crampton, Sabaj, Dillman, Mendes-Júnior & Castro e Castro, 2019	IDSM143; IDSM2667; IDSM2670; INPA-ICT57626; INPA-ICT15820
Gymnotus arapaima Albert & Crampton, 2001	IDSM142; IDSM800; IDSM765; IDSM773; IDSM804; IDSM805; IDSM806; IDSM808; IDSM2046; IDSM2048; IDSM2049; IDSM2050; INPA-ICT18391; INPA-ICT18390; INPA-ICT18389; INPA-ICT15833*; INPA-ICT14532*; INPA-ICT9963*; MCP33298; MCP33365; MCP33434; MCP33435; MCP33436; MCP49987*; MZUSP75166.0 MZUSP75167.0; MZUSP75179.0
Gymnotus carapo Linnaeus, 1758	IDSM1788; IDSM734; IDSM801; IDSM1008; IDSM1978; IDSM809
Gymnotus jonasi Albert & Crampton, 2001	IDSM122; IDSM217; IDSM802; IDSM810; IDSM811; INPA-ICT18318; INPA-ICT 11513; INPA-ICT15830*; MCP33331; MCP33332; MCP33334; MCP33335; MCP33336; MCP33337; MCP33338; MCP033339; MCP33340; MCP33341; MCP33342; MCP33343; MCP33366; MCP46931
Gymnotus mamiraua Albert & Crampton, 2001	IDSM191; IDSM218; IDSM219; IDSM733; IDSM764; IDSM766; IDSM767; IDSM772; IDSM803; IDSM807; IDSM812; IDSM869; IDSM870; IDSM871; IDSM872; IDSM873; IDSM874; IDSM1009; IDSM1861; IDSM1982; IDSM2114; IDSM2651; IDSM2665; IDSM2666; INPA-ICT18421; INPA-ICT18420; INPA-ICT18419; INPA-ICT18418; INPA-ICT18417; INPA-ICT18416; INPA-ICT18415; INPA-ICT18414; INPA-ICT18413; INPA-ICT18412; INPA-ICT18411; INPA-ICT18410; INPA-ICT18409; INPA-ICT18408; INPA-ICT18407; INPA-ICT18406; INPA-ICT18405; INPA-ICT18404; INPA-ICT18403; INPA-ICT18402; INPA-ICT 18401; INPA-ICT18400; INPA-ICT18399; INPA-ICT18398; INPA-ICT18397; INPA-ICT18396; INPA-ICT18395; INPA-ICT18394; INPA-ICT18393; INPA-ICT18392; INPA-ICT27577; INPA-ICT18159; INPA-ICT14537; INPA-ICT13504; INPA-ICT15832*; INPA-ICT9962*; INPA-ICT13503**; MCP29805; MCP33282; MCP33283; MCP33284; MCP33348; MCP33349; MCP33350; MCP33351; MCP33352; MCP33353; MCP33354

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Gymnotus melanopleura Albert & Crampton, 2001	INPA-ICT9966*
Gymnotus obscurus Crampton, Thorsen & Albert,2005	IDSM2636; MZUSP60604.0; MZUSP60605.0; MZUSP60606.0
Gymnotus onca Albert & Crampton, 2001	INPA-ICT11512**
Gymnotus varzea Crampton, Thorsen & Albert, 2005	IDSM000797; IDSM798; IDSM281; INPA-ICT18424*; INPA-ICT18423*; INPA-ICT018422*; MZUSP60601.0; MZUSP60602.0; MZUSP60603.0; MZUSP75158.0*; MZUSP75159.0*; MZUSP75160.0*; MZUSP75161.0*; MZUSP75162.0*; MZUSP75163.0*; MZUSP75164.0*
GYMNOTIFORMES: Hypopomidae	
Brachyhypopomus batesi Crampton, de, Santana, Waddell & Lovejoy, 2016	IDSM2065
Brachyhypopomus beebei (Schultz, 1944)	IDSM120; IDSM739; IDSM814; IDSM816; IDSM863; IDSM864; IDSM2074; IDSM2083; IDSM2091; INPA-ICT18341; INPA-ICT18338; INPA-ICT18337; INPA-ICT18336; INPA-ICT18335; INPA-ICT9943; MCP45313; MCP45342; MCP45343; MCP45344; MCP45358; MCP45361; MCP45380; MCP45381; MCP45382; MCP45383; MCP45385; MCP45387; MCP45420; MCP45421; MCP45422; MCP45424; MCP45427; MCP45428; MCP45450
Brachyhypopomus belindae Crampton, de, Santana, Waddell & Lovejoy, 2016	MCP45267*; MCP45430*; MCP45431*; MCP47867*; MCP45360**
Brachyhypopomus bennetti Sullivan, Zuanon, Cox & Fernandes, 2013	IDSM174; IDSM220; IDSM729; IDSM730; IDSM736; IDSM741; IDSM742; IDSM748; IDSM749; IDSM1987; IDSM1988; IDSM1989; IDSM1990; IDSM1991; IDSM1992; IDSM1993; IDSM1994; IDSM1995; IDSM1996; IDSM1997; IDSM1998; IDSM1999; IDSM2000; IDSM2001; IDSM2002; IDSM2003; IDSM2004; IDSM2005; IDSM2006; IDSM2007; IDSM2008; IDSM2009; IDSM2010; IDSM2011; IDSM2012; IDSM2013; IDSM2014; IDSM2015; IDSM2016; IDSM2017; IDSM2018; IDSM2019; IDSM820; IDSM821; IDSM788; IDSM789; IDSM830; IDSM825; IDSM827; IDSM2025; IDSM2026; IDSM2027; IDSM2028; IDSM2029; IDSM2030; IDSM2064; IDSM2022; IDSM2089; IDSM836; IDSM837; IDSM840; IDSM866; IDSM867; IDSM868; IDSM843; IDSM1128; IDSM1766; IDSM2069; IDSM2072; IDSM2073; IDSM1863; IDSM2077; MCP33278; MCP33280; MCP33281; MCP45251; MCP45252; MCP45253; MCP45254; MCP45255; MCP45256; MCP45257; MCP45315; MCP45316; MCP45330; MCP45345; MCP45346; MCP45347; MCP45348; MCP45359; MCP45384; MCP45388; MCP45389; MCP45390; MCP45391; MCP45392; MCP45394; MCP45399; MCP45400; MCP45401; MCP45429; MCP45451; MCP45465; MCP46934; MCP47021; MZUSP75152.0*; MZUSP75153.0*; MZUSP75154.0*; MZUSP75155.0*; MZUSP75156.0*; MZUSP75157.0*
Brachyhypopomus brevirostris (Steindachner, 1868)	IDSM121; IDSM774; IDSM743; IDSM822; IDSM835; IDSM845; IDSM1110; IDSM1132; IDSM1928; IDSM1767; IDSM2600; IDSM1984; IDSM1886; IDSM2211; IDSM2108; INPA-ICT18252; INPA-ICT18251; INPA-ICT18250; INPA-ICT18249; INPA-ICT18248; INPA-ICT18247; INPA-ICT18343; INPA-ICT18342; MCP33367; MCP44758; MCP45259; MCP45260; MCP45261; MCP45262; MCP45317; MCP45318; MCP45319; MCP45323; MCP45326; MCP45331; MCP45362; MCP45363; MCP45386; MCP45395; MCP45396; MCP45402; MCP45403; MCP45404; MCP46927; MCP46930; MCP46935;
Brachyhypopomus flavipomus Crampton, de, Santana, Waddell & Lovejoy, 2016	IDSM123; IDSM124; IDSM126; IDSM203; IDSM815; IDSM824; IDSM838; IDSM2020; IDSM2021; IDSM2062; IDSM2161; IDSM2079; IDSM2080; IDSM2084; IDSM2085; IDSM2646; MCP45264; MCP45265*; MCP45266*; MCP45329; MCP45349*; MCP45350*; MCP45364; MCP45365; MCP45367*; MCP45368; MCP45405*; MCP45406*; MCP45425*; MCP45453
Brachyhypopomus hendersoni Crampton, de, Santana, Waddell & Lovejoy, 2016	IDSM844
Brachyhypopomus hamiltoni Crampton, de, Santana, Waddell & Lovejoy, 2016	MCP45268; MCP45269*; MCP45482**
Brachyhypopomus pinnicaudatus (Hopkins, Comfort, Bastian & Bass, 1990)	IDSM731; IDSM737; IDSM738; IDSM792; IDSM175; IDSM215; IDSM248; IDSM464; IDSM817; IDSM826; IDSM829; IDSM832; IDSM839; IDSM853; IDSM2063; IDSM1129; IDSM1977; MCP45275; MCP45276; MCP45277; MCP45278; MCP45279; MCP45280; MCP45281; MCP45328; MCP45351; MCP45370; MCP45398; MCP45409; MCP45410; MCP45433; MCP45435; MCP45436; MCP45437; MCP45438; MCP45455; MCP46928

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Brachyhypopomus walteri Sullivan, Zuanon, Cox & Fernandes, 2013	IDSM221; IDSM833; IDSM834; IDSM1927; IDSM1881; IDSM1768; IDSM1140; IDSM2023; IDSM2024; IDSM2087; MCP33368; MCP33369; MCP44607; MCP44649*; MCP44742; MCP45290; MCP45291; MCP45292; MCP45293; MCP45295*; MCP45320*; MCP45321; MCP45327; MCP45412*; MCP45413; MCP45441; MCP45443; MCP45444*; MCP45445; MCP45458*; MCP45487; MCP45488*; MCP45490; MCP46933
Brachyhypopomus regani Crampton, de, Santana, Waddell & Lovejoy, 2016	IDSM740; IDSM2075; IDSM2288; IDSM2597; IDSM2598; IDSM2601; IDSM2618; IDSM2192; IDSM2156; IDSM858; IDSM865; MCP45282; MCP45283; MCP45284; MCP45285; MCP45286; MCP45333*; MCP45334*; MCP45335*; MCP45411*; MCP45439*; MCP45446*; MCP45456; MCP45473; MCP45484*; MCP47022**
Brachyhypopomus sp. n.	MCP33279; MCP44744*; MCP44760; MCP45324*; MCP45459; MCP46021
GYMNOTIFORMES: Rhamphichthyidae	
Hypopygus lepturus Hoedeman, 1962	IDSM855
Steatogenys elegans (Steindachner, 1880)	IDSM761; IDSM253; IDSM793; IDSM993; IDSM1757; IDSM1794; IDSM1827; IDSM1880; IDSM2099; IDSM2115; INPA-ICT18231; INPA-ICT18171; INPA-ICT18169; INPA-ICT18168; INPA-ICT18167; INPA-ICT9957; MCP31923; MCP31929; MCP31930; MCP31931; MCP31936; MCP31937; MCP31938; MCP31939; MCP31941; MCP31942; MCP31943; MCP31944; MCP31945; MCP31948
Gymnorhamphichthys rondoni (Miranda Ribeiro, 1920)	In the process of cataloging
Gymnorhamphichthys hypostomus Ellis, 1912	IDSM3031
Rhamphichthys heleios Carvalho & Albert, 2015	INPA-ICT18332*; INPA-ICT18323*
Rhamphichthys lineatus Castelnau, 1855	INPA-ICT18276; MCP33456; MCP33457; MCP44757
Rhamphichthys marmoratus Castelnau, 1855	IDSM542; IDSM735; IDSM750; IDSM794; IDSM1980; IDSM1985; IDSM2100; IDSM2178; MCP33380; MCP33381; MCP33450; MCP33452; MCP33454; MCP33455; MCP44604; MCP46929; MCP46932
Rhamphichthys rostratus (Linnaeus, 1766)	IDSM1807; MCP33444; MCP33446
Rhamphichthys sp.1	MCP33378; MCP47019
SILURIFORMES: Trichomycteridae	
Apomatoceros sp.*1*	MCP33162; MCP33163; MCP33164; MCP33165
Homodiaetus sp.*1*	MCP29342
Henonemus punctatus (Boulenger, 1887)	IDSM2138; IDSM2152; IDSM2181
Megalocentor echthrus de Pinna & Britski, 1991	IDSM2198; MCP29548; MCP30637; MCP30646;
Paravandellia sp. *n*.	MCP29562*
Pareiodon microps Kner, 1855	MCP29949; MCP29950
Plectrochilus machadoi Miranda Ribeiro, 1917	IDSM2153
Plectrochilus wieneri (Pellegrin, 1909)	IDSM2635
Plectrochilus sp. *n*.	MCP29560*; MCP31629
Pseudostegophilus nemurus (Günther, 1869)	IDSM132; IDSM2151; MCP30010; MCP30013; MCP30015
Potamoglanis hasemani (Eigenmann, 1914)	In the process of cataloging
Stegophilus septentrionalis Myers, 1927	MCP29554; MCP29557
Tridensimilis sp.*1*	In the process of cataloging
Vandellia cirrhosa Valenciennes, 1846	MCP30643
Vandellia sanguinea Eigenmann, 1917	MCP30633
Vandellia sp.*1*	MCP29343; MCP29344; MCP29561
SILURIFORMES: Callichthyidae	
Callichthys callichthys (Linnaeus, 1758)	IDSM168; IDSM2652; IDSM2640; IDSM2112; MCP33116; MCP33117; MCP33118; MCP33119
Corydoras acutus Cope, 1872	In the process of cataloging
Corydoras ambiacus Cope, 1872	In the process of cataloging

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Corydoras elegans Steindachner, 1876	IDSM2603; IDSM2604; IDSM2123
Corydoras latus Pearson, 1924	IDSM2617
Corydoras leopardus Myers, 1933	IDSM1777
Corydoras multiradiatus (Orcés V., 1960)	In the process of cataloging
Corydoras pygmaeus Knaack, 1966	IDSM2605; IDSM2631
Corydoras splendens (Castelnau, 1855)	In the process of cataloging
Corydoras gr. *zygatus*	In the process of cataloging
Dianema longibarbis Cope, 1872	IDSM145; IDSM1979; IDSM2168; IDSM2650
Hoplosternum littorale (Hancock, 1828)	IDSM147; IDSM286; IDSM1983; MCP29443; MCP29444; MCP29445; MCP29446; MCP29447; MCP29448; MCP29449; MCP29450; MCP29450; MCP29451; MCP29452; MCP29453; MCP29454; MCP29455; MCP29456; MCP29457
Lepthoplosternum altamazonicum Reis, 1997	MCP29317; MCP29319; MCP29320; MCP29321; MCP29322; MCP29323; MCP29324; MCP29325; MCP29326; MCP29327; MCP29328; MCP34561; MCP34562
Lepthoplosternum pectorale (Boulenger, 1895)	IDSM177; IDSM247; IDSM2674; IDSM2677; IDSM2678
Lepthoplosternum ucamara Reis & Kaefer, 2005	MCP29316; MCP29318; MCP29329; MCP29582
Megalechis picta (Müller & Troschel, 1849)	IDSM185; IDSM1; IDSM1131; IDSM2110; IDSM2167
Megalechis thoracata (Valenciennes, 1840)	IDSM2675; IDSM2676; MCP32940; MCP32941; MCP32943; MCP32944; MCP32945; MCP32946
SILURIFORMES: Loricariidae	
Acanthicus hystrix Spix & Agassiz 1829	IDSM2122
Ancistrus dolichopterus Kner, 1854	IDSM1030; IDSM1158; IDSM1745; IDSM1751; IDSM1752
Ancistrus hoplogenys (Günther, 1864)	MCP29784; IDSM1227
Ancistrus sp.*1* "mancha dorsal"	IDSM1170; IDSM1226; IDSM1244; IDSM1383; IDSM1384; IDSM1386; IDSM1167; IDSM1031; IDSM1159; IDSM1191; IDSM1197
Ancistrus sp.2 "robusto"	IDSM1245
Ancistrus sp.3	MCP29730; MCP29736
Aphanotorulus emarginatus (Valenciennes, 1840)	IDSM1023; IDSM1169; IDSM1229; IDSM1192; IDSM1318; IDSM1684; INPA-ICT19490; INPA-ICT19489; MCP30623; MCP30627; MCP33268; MCP33269; MCP33270; MCP33272; MCP33273
Aphanotorulus cf. *emarginatus*	IDSM1317; IDSM1247; IDSM1180
Dekeyseria amazonica Rapp Py-Daniel, 1985	IDSM1076; IDSM1258; IDSM1259; IDSM1260; IDSM1261; IDSM1262; IDSM1263; IDSM1264; IDSM1265; IDSM1266; IDSM1267; IDSM1268; IDSM1269; IDSM1270; IDSM1271; INPA-ICT19496; INPA-ICT19495; INPA-ICT19494; MCP29765
Dekeyseria scaphirhyncha (Kner, 1854)	INPA-ICT37654
Farlowella amazonum (Günther, 1864)	MCP29738
Farlowella gr. *gracilis*	IDSM1117
Farlowella henriquei MirandaRibeiro, 1918	MCP29769
Farlowella nattereri Steindachner, 1910	IDSM1153; IDSM1165; MCP29714; MCP29713; MCP29714; MCP29715; MCP29716; MCP29718
Farlowella oxyrryncha (Kner, 1853)	IDSM1026
Farlowella rugosa Boeseman, 1971	IDSM1629
Hemiodontichthys acipenserinus (Kner, 1853)	IDSM1670; IDSM1068; MCP29790; MCP29791; MCP29792; MCP29793; MCP29794
Hypoptopoma bianale Aquino & Schaefer, 2010	MCP29584; MCP29591; MCP33115
Hypoptopoma brevirostratum Aquino & Schaefer, 2010	MCP29592

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Hypoptopoma gr. *gulare* Cope, 1878	IDSM1027; IDSM1045; IDSM1160; IDSM1194; IDSM1195; IDSM1199; IDSM1202; IDSM1272; IDSM1273; IDSM1274; IDSM1275; IDSM1276; IDSM1277; IDSM1278; IDSM1279; IDSM1280; IDSM1281; IDSM1282; IDSM1283; IDSM1284; IDSM1285; IDSM1286; IDSM1287; IDSM1288; IDSM1289; IDSM1290; IDSM1291; IDSM1292; IDSM1293; IDSM1294; IDSM1295; IDSM1296; IDSM1297; IDSM1298; IDSM1299; IDSM1301; IDSM1302; IDSM1303; IDSM1304; IDSM1305; IDSM1724; IDSM1725; IDSM2680; IDSM2681; IDSM1234; INPA-ICT19065; INPA-ICT19064; INPA-ICT19062; MCP33106; MCP33107; MCP33108; MCP33109; MCP33112; MCP33113; MCP33114
Hypoptopoma psilogaster Fowler, 1915	IDSM1775
Hypoptopoma thoracatum Günther, 1868	IDSM1204; IDSM1043; IDSM1155; IDSM1171; IDSM1237
Hypostomus aff. *plecostomus*	IDSM402; IDSM1224; IDSM1243; IDSM2140
Hypostomus carinatus (Steindachner, 1881)	IDSM482; IDSM1161; IDSM1168; IDSM1230; IDSM1238; IDSM1310
Hypostomus cf. *hoplonites*	IDSM118
Hypostomus gr. *pyrineusi*	IDSM1018; IDSM1142
Limatulichthys griseus (Eigenmann, 1909)	INPA-ICT19090; INPA-ICT19089; IDSM1150
Limatulichthys sp.*1*	MCP29814; MCP29818
Loricaria cataphracta Linnaeus, 1758	INPA-ICT19087; INPA-ICT19086; INPA-ICT19085
Loricaria simillima Regan, 1904	IDSM1357; IDSM1658
Loricaria sp.*1*	MCP30613; MCP31668; MCP31669; MCP31670; MCP31672; MCP31673; MCP31674
Loricariichthys acutus (Valenciennes, 1840)	IDSM240; IDSM138; INPA-ICT18926; MCP29706; MCP29709
Loricariichthys maculatus (Bloch, 1794)	IDSM139; IDSM1074; IDSM1313; IDSM1355; IDSM1356; IDSM1358; IDSM1366; IDSM1369
Loricariichthys nudirostris (Kner, 1853)	IDSM1314; IDSM140; MCP29779; MCP29780; MCP29781
Loricariichthys stuebelii (Steindachner, 1882)	INPA-ICT18967; INPA-ICT18966
Loricariichthys sp.*1*	IDSM1315
Otocinclus vestitus Cope, 1872	IDSM1776
Oxyropsis carinata (Steindachner, 1879)	IDSM1149; IDSM1175; IDSM1183; IDSM1184; IDSM1185; IDSM1186; IDSM1188; IDSM1190; IDSM1196; IDSM1198; IDSM1200; IDSM1201; IDSM1203; IDSM1206; IDSM1209; IDSM1210; IDSM1211; IDSM1212; IDSM1300; IDSM1306; IDSM1307; IDSM1308; IDSM1309; IDSM1235; MCP29577
Oxyropsis wrightiana Eigenmann & Eigenmann, 1889	MCP29615; MCP30639
Peckoltia brevis (La Monte, 1935)	IDSM1024; IDSM1189; IDSM1225; IDSM1232; IDSM1236; IDSM2620
Peckoltichthys bachi (Boulenger, 1898)	IDSM1025; IDSM2594; IDSM2621; IDSM1205; MCP33228
Pseudorinelepis genibarbis (Valenciennes, 1840)	IDSM1371; IDSM1320; IDSM1321; IDSM1322; MCP29674; MCP29675; MCP29789; MCP30624
Pterosturisoma microps (Eigenmann & Allen, 1942)	MCP33231
Pterygoplichthys gibbiceps (Kner, 1854)	IDSM1223; IDSM1241; IDSM1319; IDSM1718; IDSM2682; IDSM1679
Pterygoplichthys pardalis (Castelnau, 1855)	IDSM303; IDSM1375; IDSM1239; IDSM1240; IDSM1242; IDSM87; IDSM1022; IDSM1172; IDSM1179; IDSM239; IDSM1176; IDSM1207; IDSM1193; IDSM1219; IDSM1220; IDSM1221; IDSM1222; IDSM1228; IDSM1231; IDSM1252; IDSM1253; IDSM1254; IDSM1255; IDSM1256; IDSM1257; IDSM1380; IDSM1311; IDSM1312; IDSM1316; IDSM1719; IDSM1720; IDSM1721; IDSM1722; IDSM1723; INPA-ICT18862; MCP31698; MCP31699; MCP31700; MCP31701; MCP31702
Rinelocaria cf. *fallax*	IDSM1029; IDSM1187; IDSM1337; IDSM1338; IDSM1328; IDSM1344; IDSM1345; IDSM1349; IDSM1350; IDSM1351; IDSM2207; IDSM1364; IDSM1561
Rineloricaria castroi Isbrücker & Nijssen, 1984	IDSM717; INPA-ICT18674; INPA-ICT18673; MCP29749; MCP29823; MCP29822; MCP33249; MCP33250; MCP33251

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Rineloricaria formosa Isbrücker & Njissen, 1979	IDSM262; IDSM264; IDSM1144; IDSM1325; IDSM1327; IDSM1330; IDSM1331; IDSM1332; IDSM1334; IDSM1335; IDSM1336; IDSM1340; IDSM1341; IDSM1359; IDSM1360; IDSM2642; IDSM1778
Rineloricaria cf. *formosa*	In the process of cataloging
Rineloricaria hasemani Isbrücker & Njissen, 1979	In the process of cataloging
Rineloricaria lanceolata (Günther, 1868)	IDSM1028; IDSM1348
Rineloricaria phoxocephala (Eigenmann & Eigenmann, 1889)	IDSM2647; IDSM2613; INPA-ICT18670; INPA-ICT18667; INPA-ICT18665; MCP29825; MCP29827; MCP33229; MCP29833
Rineloricaria sp.*1*	MCP29830
Spatuloricaria sp.*1*	IDSM2690
Sturisoma aff. *brevirostre*	IDSM1248; IDSM1086
SILURIFORMES: Cetopsidae	
Cetopsis coecutiens (Lichtenstein, 1819)	IDSM298; MCP32816
Cetopsis sp.*1*	MCP33235; MCP33253
Cetopsis sp.*2*	MCP30622; MCP33252; MCP33254;
SILURIFORMES: Aspredinidae	
Bunocephalus aleuropsis Cope, 1870	MCP29654
Bunocephalus coracoideus (Cope, 1874)	IDSM162; IDSM1067; IDSM1078; IDSM1875; IDSM2102; IDSM2117; IDSM2119; IDSM2679; MCP29643
Bunocephalus verrucosus (Walbaum, 1792)	IDSM1087; IDSM2637; IDSM2649
Pterobunocephalus depressus (Haseman, 1911)	MCP29622; INPA-ICT18725; MCP29842; MCP29843
SILURIFORMES: Auchenipteridae	
Ageneiosus intrusus Ribeiro, Rapp Py-Daniel & Walsh, 2017	MCP32961; MCP32962; MCP32965
Ageneiosus inermis (Linnaeus, 1766)	IDSM1058; IDSM186; IDSM718; IDSM292; IDSM1929; IDSM1811
Ageneiosus lineatus Ribeiro, Rapp Py-Daniel & Walsh, 2017	MCP29895; MCP29897; MCP29899
Ageneiosus ucayalensis Castelnau, 1855	IDSM293; IDSM2633; INPA-ICT18922; MCP29898; MCP32832; MCP32833; MCP32834; MCP32960; MCP32967
Ageneiosus uranophthalmus Ribeiro, Rapp & Py-Daniel, 2010	MCP32963
Ageneiosus vittatus Steindachner, 1908	IDSM680; IDSM3
Auchenipterus ambyiacus Fowler, 1915	IDSM2206; MCP29402; MCP29403; MCP29404; MCP29406; MCP29407
Auchenipterichthys coracoideus (Eigenmann & Allen, 1942)	IDSM2593; MCP29217; MCP29219; MCP29220; IDSM000157
Auchenipterus nuchalis (Spix & Agassiz, 1829)	MCP29882; MCP29884; MCP29885; MCP30602
Centromochlus existimatus Mees, 1974	IDSM134; INPA-ICT19031; INPA-ICT19029; MCP29838; MCP29839; MCP29840; MCP29841
Centromochlus heckelii (De Filippi, 1853)	IDSM38; IDSM2154; MCP29618; MCP29619
Epapterus dispilurus Cope, 1878	IDSM36; IDSM268; IDSM271; IDSM2157; MCP29331; MCP29332; MCP29333
Pseudepapterus hasemani (Steindachner, 1915)	MCP029606
Tatia intermedia (Steindachner, 1877)	IDSM2599
Trachelyopterus galeatus (Linnaeus, 1766)	IDSM89; IDSM95; IDSM178; IDSM187; IDSM241; IDSM1771; IDSM1773; IDSM2579; MCP29412; MCP29354; MCP29412; MCP32804; MCP32805; MCP32809; MCP32809
Trachelyopterus sp. "placa larga"	IDSM1113; IDSM2576; IDSM2577
Trachycorystes porosus Eigenmann & Eigenmann, 1888	IDSM1002; IDSM1680; IDSM2210; IDSM2578
Trachycorystes trachycorystes (Valenciennes, 1840)	IDSM158
Tympanopleura atronasus (Eigenmann & Eigenmann, 1888)	IDSM37; IDSM269; IDSM1041; IDSM1857; INPA-ICT18986; INPA-ICT18983; MCP33178; MCP33179
Tympanopleura brevis Steindachner, 1881	IDSM682; IDSM683; IDSM2586
Tympanopleura longipinna Walsh, Ribeiro, Rapp & Py-Daniel, 2015	MCP29602; MCP29603

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Tympanopleura piperata (Eigenmann, 1912)	IDSM1047; IDSM1814
Tympanopleura rondoni (Miranda Ribeiro, 1914)	INPA-ICT18962; INPA-ICT18961; INPA-ICT18960; INPA-ICT18959; MCP29874; MCP29875; MCP29876; MCP29877
Tympanopleura cf. *brevis*	IDSM3034
Tympanopleura sp.*1*	MCP33177; MCP33180; MCP33183; MCP33184; MCP33185; MCP33186
SILURIFORMES: Doradidae	
Acanthodoras cataphractus (Linnaeus, 1758)	IDSM3035; IDSM3036
Agamyxis pectinifrons (Cope, 1870)	IDSM129; IDSM1032; IDSM1960; IDSM1855; IDSM2093; MCP33150; MCP33151; MCP33152; MCP33153; INPA-ICT19104
Amblydoras affinis (Kner, 1855)	IDSM1950; IDSM1959
Anadoras grypus (Cope, 1872)	IDSM1882; IDSM1926; IDSM1963; IDSM2664; IDSM1109; IDSM1770; INPA-ICT19581; INPA-ICT19579; INPA-ICT19578; INPA-ICT19577; INPA-ICT19576; INPA-ICT19569; INPA-ICT19568; MCP29526; MCP29527; MCP29529; MCP29530
Anadoras weddellii (Castelnau, 1855, 1908)	IDSM3037
Astrodoras asterifrons (Kner, 1853)	IDSM169
Centrodoras brachiatus (Cope, 1872)	MCP29380
Hassar cf. *wilderi*	IDSM3039
Hemidoras morrisi Eigenmann, 1925	IDSM131; IDSM296; IDSM015; IDSM2135; INPA-ICT19253; MCP29660; MCP32996; MCP32998; MCP33005
Hemidoras stenopeltis (Kner, 1855)	IDSM1016; IDSM1545; IDSM1841; IDSM1939; IDSM2155; IDSM2195; IDSM2197; INPA-ICT19371; INPA-ICT19365; MCP29887; MCP29891; MCP29892; MCP29893
Leptodoras gr. *Acipenserinus*	IDSMI265
Lithodoras dorsalis (Valenciennes, 1840)	IDSM3040
Megalodoras uranoscopus (Eigenmann & Eigenmann, 1888)	IDSM172; IDSM107; IDSM1051; IDSM1901; IDSM1769; IDSM2295; MCP33195; MCP33197
Nemadoras elongatus (Boulenger, 1898)	IDSM2134; INPA-ICT19273; INPA-ICT19272; MCP33125; MCP33126; MCP41546
Nemadoras hemipeltis (Eigenmann, 1925)	MCP33122; MCP33124
Nemadoras humeralis (Kner, 1855)	IDSM1055; INPA-ICT37004; INPA-ICT18889; INPA-ICT18886; INPA-ICT18883; INPA-ICT18882; INPA-ICT18881; INPA-ICT18880; INPA-ICT18878; INPA-ICT18877; MCP29531; MCP29532; MCP29534; MCP29535; MCP29536; MCP29538; MCP29539; MCP29541; MCP29542; MCP29646
Opsodoras boulengeri (Steindachner, 1915)	IDSM1817
Opsodoras morei (Steindachner, 1881)	INPA-ICT19254; INPA-ICT19252
Opsodoras stuebelii (Steindachner, 1882)	IDSM2160; IDSM1819; IDSM1981; INPA-ICT19251; INPA-ICT19250
Opsodoras sp.*1*	MCP32997
Ossancora asterophysa Birindelli, Sabaj & Pérez, 2011	MCP29644; MCP29645; MCP29668
Ossancora fimbriata (Kner, 1855)	MCP29786; MCP32956
Ossancora punctata (Kner, 1855)	IDSM173; IDSM1772; IDSM2187; IDSM1856; IDSM2648; INPA-ICT18737; MCP29662; MCP29663; MCP29665; MCP29666; MCP29667; MCP29806; MCP29807; MCP29808
Oxydoras niger (Valenciennes, 1821)	IDSM88; IDSM266; MCP29463
Platydoras armatulus (Valenciennes, 1840)	IDSM170; IDSM2104; MCP33193
Platydoras hancockii (Valenciennes, 1840)	IDSM3041
Pterodoras granulosus (Valenciennes, 1821)	IDSM94; IDSM267; IDSM2116; INPA-ICT19486; INPA-ICT19484; INPA-ICT19480; INPA-ICT19478; INPA-ICT19477; INPA-ICT19476; INPA-ICT19475; INPA-ICT18735; MCP31686; MCP31687; MCP31688; MCP31691; MCP31692

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Rhynchodoras xingui Klausewitz & Rössel, 1961	IDSM3042
Scorpiodoras heckelii (Kner, 1855)	In the process of cataloging
Tenellus ternetzi (Eigenmann, 1925)	IDSM2145; IDSM133; IDSM141; IDSM291; IDSM2205
Tenellus trimaculatus (Boulenger, 1898)	IDSM48; IDSM49; IDSM50; IDSM1059; IDSM2194; INPA-ICT19369; INPA-ICT19367; MCP29834; MCP29835; MCP29836; MCP29837
Trachydoras brevis (Kner, 1853)	INPA-ICT36472
Trachydoras microstomus (Eigenmann, 1912)	IDSM3043
Trachydoras nattereri (Steindachner, 1881)	IDSM1017; INPA-ICT19100
Trachydoras steindachneri (Perugia, 1897)	IDSM2; IDSM1020; IDSM1813; IDSM1831; IDSM2638; INPA-ICT19459; MCP29231; MCP29233; MCP29235; MCP29236; MCP29687
SILURIFORMES: Heptapteridae	
Brachyrhamdia marthae Sands & Black, 1985	MCP49174
Brachyrhamdia meesi Sands & Black, 1985	MCP29849
Cetopsorhamdia sp.1	IDSM2592
Gladioglanis conquistador Lundberg, Bornbusch & Mago-Leccia, 1991	In the process of cataloging
Goeldiella eques (Müller & Troschel, 1849)	IDSM159
Imparfinis stictonotus (Fowler, 1940)	MCP29575
Pimelodella altipinnis (Steindachner, 1864)	IDSM3045
Pimelodella cristata (Müller & Troschel, 1849)	IDSM1062; IDSM1125; IDSM2165; IDSM1962; MCP33256; MCP33258; MCP33259; MCP33262; MCP33264
Pimelodella geryi Hoedeman, 1961	In the process of cataloging
Pimelodella aff. *eigenmanni*	IDSM219
Pimelodella sp.*1*	MCP29858; MCP29859; MCP29900
Rhamdia quelen (Quoy & Gaimard, 1824)	IDSM2164; IDSM144
SILURIFORMES: Pimelodidae	
Brachyplatystoma filamentosum (Lichtenstein, 1819)	IDSM57; IDSM2294
Brachyplatystoma vaillantii (Valenciennes, 1840)	IDSM3046
Brachyplatystoma juruense (Boulenger, 1898)	IDSM3047
Brachyplatystoma platynemum Boulenger, 1898	IDSM3048
Brachyplatystoma rousseauxii (Castelnau, 1855)	IDSM3049
Calophysus macropterus (Lichtenstein, 1819)	IDSM74; IDSM208; IDSM1069; IDSM1835; IDSM2641; INPA-ICT18937; INPA-ICT18936; INPA-ICT18935; INPA-ICT18934; INPA-ICT18933; INPA-ICT18932; INPA-ICT18931; INPA-ICT18930; INPA-ICT18929; MCP32762; MCP32763; MCP32764; MCP32765; MCP32766;
Cheirocerus eques Eigenmann, 1917	IDSM1070; IDSM1832; IDSM2193; IDSM2139
Cheirocerus goeldii (Steindachner, 1908)	IDSM1056; IDSM1790; IDSM1833; IDSM1940; MCP29578; MCP29911; MCP29915
Duopalatinus peruanus Eigenmann & Allen, 1942	INPA-ICT19038
Exallodontus aguanai Lundberg, Mago-Leccia & Nass, 1991	MCP24733; MCP29624
Hemisorubim platyrhynchos (Valenciennes, 1840)	IDSM1107; INPA-ICT19447; MCP29783
Hypophthalmus edentatus Spix & Agassiz, 1829	IDSM2201
Hypophthalmus fimbriatus Kner, 1858	IDSM3050
Hypophthalmus marginatus Valenciennes, 1840	IDSM39; IDSM58; IDSM1834; IDSM2158; MCP33160
Leiarius marmoratus (Gill, 1870)	IDSM83
Leiarius pictus (Müller & Troschel, 1849)	IDSM3051
Megalonema sp.*1*	MCP29854; MCP29855
Phractocephalus hemioliopterus (Bloch & Schneider, 1801)	IDSM148

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Pimelodina flavipinnis Steindachner, 1876	MCP30046; MCP30047; MCP30048; MCP30049; MCP30052
Pimelodus albofasciatus Mees, 1974	IDSM2163
Pimelodus altissimus Eigenmann & Pearson, 1942	IDSM297; MCP29869;
Pimelodus blochii Valenciennes, 1840	IDSM90; IDSM242; IDSM252; IDSM1000; MCP29222; MCP29223; MCP29224; MCP29458; MCP29460
Pimelodus pictus Steindachner, 1876	MCP29853
Pimelodus ornatus Kner, 1858	In the process of cataloging
Pinirampus pirinampu (Spix & Agassiz, 1829)	IDSM209; IDSM51; IDSM2191; IDSM1013; MCP32910; MCP32911; MCP32912; MCP32913; MCP32914
Platysilurus mucosus (Vaillant, 1880)	IDSM1019; IDSM1812; IDSM1821; IDSM2166; INPA-ICT19050; MCP29878; MCP29879; MCP29881
Platynematichthys notatus (Jardine, 1841)	IDSM3053
Platystomatichthys sturio (Kner, 1858)	IDSM1071; MCP31695
Propimelodus caesius Parisi, Lundberg & DoNascimiento, 2006	MCP29918; MCP29919; MCP29920
Propimelodus sp.1	MCP29870
Pseudoplatystoma punctifer (Castelnau 1855)	IDSM3054
Pseudoplatystoma tigrinum (Valenciennes, 1840)	IDSM161; IDSM1764; IDSM1952; MCP29886
Sorubim elongatus Littmann, Burr, Schmidt & Isern, 2001	IDSM1637; MCP30575
Sorubim lima (Bloch & Schneider, 1801)	IDSM327; IDSM1021; INPA-ICT18855
Sorubim maniradii Littmann, Burr & Buitrago-Suarez, 2001	INPA-ICT26636
Sorubimichthys planiceps (Spix & Agassiz, 1829)	IDSM3055
Zungaro zungaro (Humboldt, 1821)	IDSM1941; IDSM2213; INPA-ICT19498
SILURIFORMES: Pseudopimelodidae	
Batrochoglanis raninus (Valenciennes, 1840)	IDSM1112; IDSM2127; IDSM2169; INPA-ICT28580
Batrochoglanis villosus (Eigenmann, 1912)	IDSM1127; INPA-ICT18795
Microglanis poecilus Eigenmann, 1912	IDSM2292
Microglanis sp. *1*	IDSM180; MCP29625; MCP29626; MCP29627; MCP29629
Pseudopimelodus sp.*1*	MCP29845
SYNBRANCHIFORMES: Synbranchidae	
Synbranchus lampreia Favorito, Zanata & Assumpção, 2005	MCP29363; MCP29364; MCP29365; MCP29366; MCP29367; MCP29368; MCP29369; MCP29370; MCP29371; MCP29372; MCP29373; MCP29374; MCP29375; MCP32915; MCP33025
Synbranchus madeirae Rosen &Rummey, 1972	IDSM1085; IDSM1862; IDSM1887; INPA-ICT18912; INPA-ICT18911; INPA-ICT18868
Synbranchus sp.1	IDSM189; IDSM1089; IDSM1779; IDSM1925; INPA-ICT18867; INPA-ICT18866; INPA-ICT18865; INPA-ICT18869; INPA-ICT52853; MCP33007; MCP33008; MCP33009; MCP33010; MCP33011; MCP33012; MCP33013; MCP33014; MCP33015; MCP33127; MCP33128; MCP33129
CICHLIFORMES: Cichlidae	
Acarichthys heckelii (Müller & Troschel, 1849)	IDSM102; IDSM287
Acaronia nassa (Heckel, 1840)	IDSM164; IDSM250; IDSM346; MCP29335; MCP29336; IDSM3057
Aequidens tetramerus (Heckel, 1840)	IDSM8
Apistogramma agassizii (Steindachner, 1875)	IDSM2619
Apistogramma bitaeniata Pellegrin, 1936	IDSM3011
Apistogramma cacatuoides Hoedeman, 1951	IDSM2611; IDSM2615
Apistogramma eunotus Kullander, 1981	IDSM3012
Apistogramma pertensis (Haseman, 1911)	IDSM1565
Apistogramma regani Kullander, 1980	IDSM2121

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Apistogrammoides pucallpaensis Meinken, 1965	IDSM202; IDSM2616
Astronotus ocellatus (Agassiz, 1831)	IDSM97; IDSM190; IDSM243; IDSM2668
Biotodoma cupido (Heckel, 1840)	IDSM3058
Bujurquina sp.*1*	IDSM3014
Chaetobranchus flavescens Heckel, 1840	IDSM216
Chaetobranchus semifasciatus Steindachner, 1875	IDSM249; MZUSP27926.0
Cichla monoculus Spix & Agassiz, 1831	IDSM201; IDSM246
Cichlasoma amazonarum Kullander, 1983	IDSM84; IDSM244; IDSM245; IDSM199; IDSM795; IDSM1639; MCP33135; MCP33137; MCP33138
Crenicara punctulata (Günther, 1863)	IDSM3013
Crenicichla cincta Regan, 1905	MCP29338
Crenicichla inpa Ploeg, 1991	INPA-ICT19388; MCP32986; MCP32987; MCP32988; MCP32989; MCP32990; MCP32991; MCP33187; MCP331188; MCP33189; MCP33190; MCP33191; MCP33192
Crenicichla lugubris Heckel, 1840	In the process of cataloging
Crenicichla regani Ploeg, 1989	MCP29608; MCP29611
Crenicichla reticulata (Heckel, 1840)	IDSM40; IDSM2602; INPA-ICT19201; MCP33039; MCP33040
Crenicichla proteus Cope, 1872	INPA-ICT18790; INPA-ICT18788
Crenicichla sp.*1*	MCP38632
Geophagus proximus (Castelnau, 1855)	IDSM3060
Geophagus cf. *altifrons*	In the process of cataloging
Heros efasciatus Heckel, 1840	IDSM455; IDSM15; MCP32920; MZUSP27929.0
Hypselecara temporalis (Günther, 1862)	IDSM1894
Laetacara thayeri (Steindachner, 1875)	IDSM101; IDSM2662; MCP29595; MCP29596; MCP29597; MCP29598
Mesonauta insignis (Heckel, 1840)	IDSM14
Pterophyllum leopoldi (Gosse, 1963)	IDSM13; IDSM2141
Pterophyllum scalare (Schultze, 1823)	IDSM2142
Satanoperca acuticeps (Heckel, 1840)	In the process of cataloging
Satanoperca jurupari (Heckel, 1840)	MCP32818
Satanoperca sp.*1*	MCP32819; MCP32820;
Symphysodon tarzoo Lyons, 1959	IDSM3061
CYPRINODONTIFORMES: Rivulidae	
Anablepsoides micropus (Steindachner, 1863)	IDSM272; IDSM1916; IDSM2612; IDSM2628; IDSM2661;
Anablepsoides ornatus Garman, 1895	IDSM1904
Anablepsoides sp.*1*	IDSM796*; INPA-ICT58224*; INPA-ICT58223**
CYPRINODONTIFORMES: Fluviphylacidae	
Fluviphylax cf. *pygmaeus*	IDSM3062
BELONIFORMES: Belonidae	
Potamorrhaphis guianensis (Jardine, 1843)	IDSM1958; INPA-ICT19000
Pseudotylosurus microps (Günther, 1866)	IDSM1098; IDSM1853; IDSM1923; MCP30038
TETRAODONTIFORMES: Tetradontidae	
Colomesus asellus (Müller & Troschel, 1849)	IDSM1064; IDSM1662; MCP33033
PERCIFORMES: Scianidae	
Plagioscion montei Soares & Casatti, 2000	MCP30598; MCP32750
Plagioscion squamosissimus (Heckel, 1840)	INPA-ICT19002; INPA-ICT19001; MCP31705
GOBIIFORMES: Eleotridae	
Microphilypnus sp.*1*	MCP30631; MCP30638
PLEURONECTIFORMES: Achiridae	
Hypoclinemus mentalis (Günther, 1862)	IDSM2688; IDSM1049
CERATODONTIFORMES: Lepidosirenidae	
Lepidosiren paradoxa Fitzinger, 1837	IDSM1088; IDSM2113; IDSM2645; INPA-ICT18697; INPA-ICT18696; INPA-ICT18695; INPA-ICT18694

Conflicts of Interest

The authors declare that there are no conflicts of interests related to the publication of this manuscript.

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Short Communication

Length-weight relationship and diet of the catfish *Cambeva guareiensis* (Siluriformes; Trichomycteridae)

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Abstract: The length-weight relationship (LWR) and diet of a small trichomycterid catfish, *Cambeva guareiensis*, was studied based on 58 specimens captured in Corrente stream, Guareí River basin, São Paulo, Brazil. LWR analyses showed values of *a* ranged from 0.0097 to 0.0149 and *b* from 2.858 to 3.250. The analysis of the diet showed that high amounts of aquatic insects (93.75% of total items) were consumed by the species. In addition, we found no statistically significant differences when comparing the diet between the dry and rainy periods. Our study contributes to the knowledge on populational biology and feeding ecology of trichomycterid fishes in Brazilian streams.

Keywords: *Chironomidae; Functional trait; Populational biology; Stomach content; Stream fish; Upper Paraná basin.*

Relação peso-comprimento e dieta do bagre *Cambeva guareiensis* (Siluriformes; Trichomycteridae)

Resumo: A relação peso-comprimento (RPC) e dieta de um pequeno bagre trichomycterídeo, *Cambeva guareiensis*, foi estudada com base em 58 espécimes capturados no riacho Corrente, bacia do rio Guareí, São Paulo, Brasil. As análises de RPC mostraram valores de *a* variando entre 0,0097-0,0149 e de *b* entre 2,858-3,250. A análise da dieta mostrou que altas quantidades de insetos aquáticos (93,75% do total de itens) foram consumidas pela espécie. Além disso, não encontramos diferenças estatisticamente significativas quando comparamos a dieta entre os períodos seco e chuvoso. Nosso estudo contribui para o conhecimento da biologia populacional e ecologia alimentar de peixes trichomicterídeos em riachos brasileiros.

Palavras-chave: *Bacia do Alto Paraná; Biologia populacional; Conteúdo estomacal; Peixe de riacho; Traço funcional.*

Introduction

The Trichomycteridae family—comprising siluriforms of freshwater ecosystems—holds a wide geographic distribution in South America; occurring, for example, from Andean to Brazilian waterbodies (e.g., Fernández & Vari 2009; Reis et al. 2019; Katz & Costa 2020). Most species are known to occur in surface waters (epigean), but some are found in hypogean environments (Rizzato et al. 2011; Castellanos-Morales 2010). In Brazil's freshwaters, most species occur in first to third order streams (e.g., Azevedo-Santos et al. 2020a). In the southeast of the country, many species of *Cambeva* and *Trichomycterus* have been reported (e.g., Casatti 2002; Lima et al. 2008; Barbosa & Azevedo-Santos 2012; Katz et al. 2018; Cetra et al. 2020; Reis et al. 2020; Costa & Katz 2021).

The genus *Cambeva* was recently proposed by Katz et al. (2018) based on *Pygidium davisi* Haseman, 1911. According to a recent compilation (Fricke et al. 2021), *Cambeva* holds over thirty described species. In just the Paranapanema River system (Upper Paraná River, Brazil), for instance, there were reported *C. davisi* (Haseman, 1911), *C. diabola* (Bockmann, Casatti & de Pinna, 2004), *C. guareiensis* Katz & Costa, 2020, *C. pascuali (*Ochoa, Silva, Silva, Oliveira & Datovo, 2017), and *C. perkos* (Datovo, Carvalho, & Ferrer, 2012) (Katz & Costa 2020). *Cambeva guareiensis*, in particular, occurs exclusively in small tributaries of sub-basins of the Paranapanema River system (Katz & Costa 2020; Azevedo-Santos et al. 2020a; Lisboa et al. 2020).

Scientific data (e.g., biology) is scarce for most *Cambeva* species. For *C. guareiensis*, there are studies only recording its distribution in streams (e.g., Azevedo-Santos et al. 2020a) and describing a case of albinism (Azevedo-Santos et al. 2020b). Data on population biology and feeding ecology of the species need to be available in the scientific literature. This is justifiable especially by the eminent growth of functional studies that need basic information. For example, knowing the diet of species may be a useful trait for future investigations about anthropic impacts on fish assemblages.

Here we provide the length-weight relationship of *C. guareiensis*. In addition, we described and compared the diet of the species in different periods (dry and rainy).

Material and Methods

1. *Study area*

The Corrente stream, where the collections were performed, is a tributary of the Guareí River, which, in turn, flows to the Paranapanema River (upper Paraná River system; Azevedo-Santos et al. 2020a). The source of the Corrente stream is located at approximately 700 meters above sea level in the region of "Mineiros" (~23°24'9.44"S, 48°23'42.21"W), in Angatuba municipality, São Paulo, Brazil. Fish were sampled above the waterfall of Corrente stream (~23°26'5.31"S, 48°23'18.78"W).

2. *Methods*

Sampling was done in September 2020 (dry season) and February 2021 (rainy season), and with the permission of the Brazilian Institute of Environment and Natural Resources (license number: SISBio 76135-1). Fish were caught with a hand net (1 mm mesh), in a stretch of ~ 200 meters of the Corrente stream. Sampling activity lasted ~ 50 minutes in both seasons. The collected specimens were euthanized with eugenol (exposed for more than 10 minutes - lethal dose) and fixed (with formalin 10%). Specimens were identified based on the original description provided by Katz & Costa (2020). Vouchers (10 specimens that were transferred to alcohol 70 %) were deposited at the UFRJ (Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil).

2.1. Length-weight relationship

The specimens were removed from formaldehyde, washed in water and then weighed (0.1 g) and measured (standard length; 0.1 mm). Later they were transferred to alcohol (70%) for diet analysis.

For the calculation of the length-weight relationship (LWR, hereafter), we considered together specimens collected in dry and rainy seasons. For the analyses, we used a linear regression "log$W$ = log$a$ + $b$log$L$" (Froese 2006; p. 243). Through a plot (i.e., log-log) the outliers for *Cambeva guareiensis* were excluded (*sensu* Froese 2006).

2.2. Diet

For stomach content analysis, we made an incision in all specimens from the anus to the isthmus to remove the stomachs. The stomach contents were placed in Petri dish and examined using a stereomicroscope (Stemi 305).

The animal content present in the stomach of the trichomycterids was identified only to the level of Order or Family based on Costa et al. (2006) and Mugnai et al. (2010) because they were often in an advanced state of digestion (preventing the determination at lower levels). Sometimes contents could only be identified as terrestrial insects. Pieces of plant leaves and roots were also found (vegetal fragments). We used the abundance of the food items found in the stomach of the trichomycterids as the variable to quantify the diet of the species.

With the data obtained, we built a matrix with the abundance of each item consumed by each specimen. Individuals without content, or with an advanced digestion process, were not included in the analyses. From the constructed matrix, we compared the food of the individuals in both sampling seasons (dry vs. rainy), in order to verify possible seasonal variations. With data converted to log (x+1), we used a permutational multivariate analysis of variance (PERMANOVA), with 9999 permutations, and Bray-Curtis distance. For analysis, we used the software PRIMER 6.1.13 PERMANOVA+ 1.0.3 (Clarke & Gorley 2006). Lastly, we also described the diet of the species using stomach contents during the studied period.

Results

1. *Length-weight relationship*

There were collected 58 individuals of *Cambeva guareiensis* (UFRJ 12717). The standard length of the specimens ranged from 24.0-62.5 millimeters and the weight from 0.18-3.70 grams. All sampled specimens were examined in the LWR (see Table 1).

2. *Diet*

Of the 58 specimens examined, 26 individuals sampled during dry season and 12 during rainy season had empty stomachs. The species ingested high amounts of aquatic insects (Figure 1), with predominance of Diptera of the families Chironomidae (56% of consumed items) and Simuliidae (14%). They also consumed aquatic insects of Trichoptera, comprising 12% of items, and vegetal fragments (5.8% of items). The PERMANOVA did not indicate a significant difference in species diet between dry and rainy seasons (Pseudo-F = 1.614, p = 0.159).

Table 1. Length-weight relationship of *Cambeva guareiensis* based on 58 individuals captured in Corrente stream, São Paulo, Brazil. The *a* and *b* refer to equation used (see Material and Methods section) ranging 95% of confidence limits; and R^2 refers to the correlation coefficient

***a* (95% CI)**	***b* (95% CI)**	**R^2**
0.0123 (0.0097-0.0149)	3.054 (2.858-3.250)	0.946

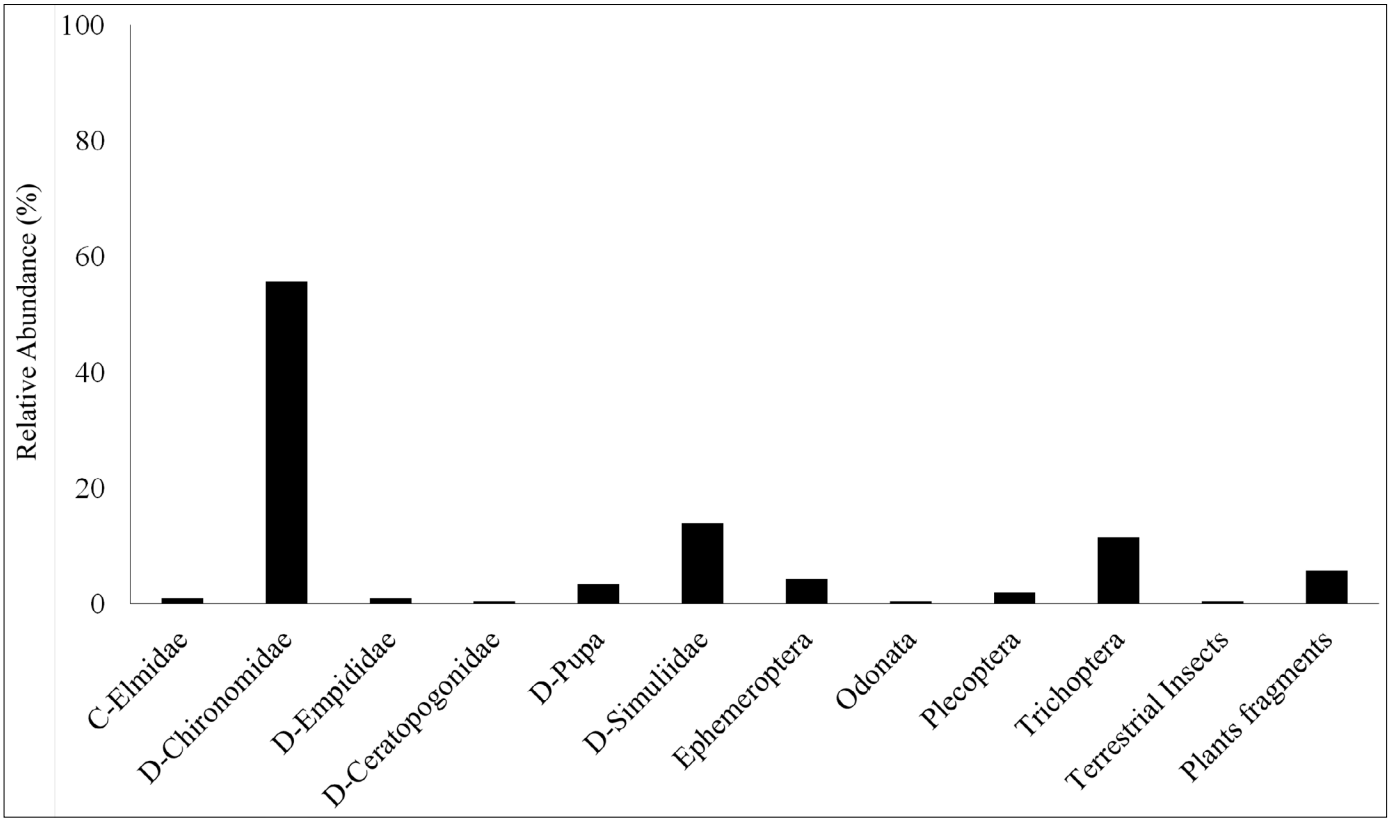


Figure 1. Relative abundance (%) of insects and vegetal fragments consumed by the analyzed fish in the dry and rainy seasons. C-Coleoptera and D-Diptera.

Discussion

1. Length-weight relationship

The value of *b* found for *Cambeva guareiensis* was 3.054 (2.858-3.250). Other species of the family Trichomycteridae, such as *Trichomycterus candidus* (Miranda Ribeiro, 1949), *T. pirabitira* Barbosa & Azevedo-Santos, 2012, and *T. piratymbara* Katz, Barbosa & Costa, 2013 (identification corrected herein to *T. sainthilairei* Katz & Costa, 2021, UFRJ 12719), had similar patterns (Azevedo-Santos et al. 2018). In fact, many stream fish species are expected to have *b* values in a similar range as that found for *C. guareiensis* and other trichomycterids (Froese 2006).

2. Diet

Insects were the main food item found in the stomach contents of the individual examined, especially aquatic insects. Other studies (e.g., Casatti 2002; Chará et al. 2006; Scott et al. 2007; Manoni et al. 2009; Rondineli et al. 2009) showed that other species of the same family or genus that *C. guareiensis* also feed on this group. The low prevalence of vegetal items, when compared with insects, and the morphology of the digestive system of *C. guareiensis*, suggests that leaves and roots were accidentally ingested during prey capture or that plants are not an important item in the diet of this species. However, only with the analysis of the diet—without observations in situ of the feeding behavior of the *C. guareiensis* (e.g., Casatti 2002)—, is impossible to confirm the first possibility suggested.

We found no statistically significative differences in the diet of *C. guareiensis* between different seasons (i.e., dry *vs.* rainy). Similar results were found by Manoel & Uieda (2019) for other species of the genus *Cambeva* in one impacted stream. A possible explanation is that Corrente stream has a similar characteristic such as those reported by these authors. Another explanation is that the availability of insects in the aquatic ecosystem may modulate the presence of this item in the diet of trichomycterids (*sensu* Scott et al. 2007). Therefore, the absence of seasonal changes in the diet of *C. guareiensis* may be related to low or no seasonal variation in the availability of aquatic insects in the stream, which was the predominant group among the food items. Both lines of investigation deserve attention in futures studies in Guareí River basin.

Here we contribute to the knowledge about the biology (LWR) and feeding ecology of *C. guareiensis*. These baseline data are extremely important, for example, for future studies on functional diversity. Trichomycteridae is a large and varied family of fishes (see de Pinna & Wosiacki 2003 with numerous species with little or no biological and ecological data. Therefore, studies in both fields should be encouraged for other species of the family.

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Author Contributions

Felipe H. N. P. Ribeiro: Collected the trichomycterids, led the writing, analyzed data, and collaborated with the writing.

Maria E. P. Bonan: Collected the trichomycterids, led the writing, analyzed data, and collaborated with the writing.

José Lucas Dias da Silva: Collected the trichomycterids and collaborated with the writing.

Valter M. Azevedo-Santos: Collected the trichomycterids, identified them, analyzed data, and collaborated with the writing.

Pedro S. Manoel: Analyzed the stomachs, analyzed data, and collaborated with the writing.

Eduardo M. Brambilla: Analyzed data and collaborated with the writing.

Carolina V. Silva: Idealized the work, collected the trichomycterids, analyzed the stomachs, analyzed data, and collaborated with the writing.

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

Fish fauna in low-order streams of the Piquiri River, Upper Paraná River basin, Brazil

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Abstract: The South America ichthyofauna encompasses the highest diversity of the world, however is highly threatened by anthropogenic actions. The fish fauna of nine low-order streams, tributaries of the Piquiri River and impacted by aquaculture, agriculture and urbanization were sampled in the present study. Samplings were done quarterly from December 2017 to September 2018 at three sites in each stream, using a portable electric fishing device in 50-meter segments. A total of 14,507 individuals were collected, belonging to six orders, 20 families, 46 genera, and 70 species. The highest richness and abundance were found for the orders Characiformes and Siluriformes. In this study, nine species that had not been recorded were found, totaling 163 for the basin. In addition, 14 non-native species were captured. The presented list of species contributes to the existing database of ichthyofauna distribution in Neotropical streams, denoting that it is underestimated in the region, mainly in low-order tributaries. The present study reinforces the importance of inventories and monitoring in environments with high biodiversity and sensitive to anthropogenic actions.
Keywords: *Biodiversity; Streams; Land use.*

Fauna de peixes em riachos de pequena ordem do rio Piquiri, bacia do alto rio Paraná, Brasil

Resumo: A ictiofauna sul-americana abrange a maior diversidade do planeta, no entanto, encontra-se altamente ameaçada pela ação antrópica. Nesse estudo, a fauna de peixes de nove riachos de pequena ordem foi amostrada. Esses riachos são afluentes do Rio Piquiri e afetados pela atividade aquícola, agrícola e urbanização. As coletas foram realizadas trimestralmente de dezembro/2017 a setembro/2018 em três pontos amostrais de cada riacho, utilizando-se equipamento portátil de pesca elétrica em segmentos delimitados de 50 metros. Foram coletados 14.507 indivíduos, pertencentes a seis ordens, 20 famílias, 46 gêneros e 70 espécies. Os maiores valores de riqueza e de abundância foram obtidos nas ordens Characiformes e Siluriformes. Neste estudo, foram encontradas nove espécies ainda não registradas, totalizando 163 para a bacia. Além disso, 14 espécies não-nativas foram capturadas. Ressalta-se que a lista de espécies apresentada contribui com o banco de dados existente sobre os padrões de distribuição da ictiofauna em riachos Neotropicais e demonstra como a mesma ainda pode ser subestimada na região, principalmente em tributários de pequena ordem. Esse estudo reforça a importância de inventários e do monitoramento em ambientes altamente diversos e sensíveis à ação antrópica.
Palavras-chave: *Biodiversidade; Riachos; Uso do solo.*

Introduction

South America has the highest fish diversity of the world, which encompasses more than nine thousand described species and approximately one third of all freshwater fish species (Reis et al. 2016). However, the conservation of the continental ichthyofauna of South America is an increasing challenge because of continuous losses of habitats caused by anthropogenic changes resulted from different soil uses, such as urbanization, agriculture, mining and hydroelectric dams (Pelicice et al. 2017), as well as overfishing and introduction of non-native species (Rios-Touma & Ramírez 2019). Therefore, the rate of species extinction can be higher than the actual information of number of species and their geographical distribution. Thus, ichthyofauna inventories are essential for a significant analysis of the biodiversity, especially in environments that have no significant sampling of their fauna, such as low-order streams (Frota et al. 2019).

The Piquiri River basin comprises a drainage area of 31,000 km² in the Upper Paraná Ecoregion (Abell et al. 2008), its sources are located in the São João Mountains and it runs 485 km before reaching the Paraná River, forming the third largest hydrographic basin in the State of Paraná, Brazil. The Piquiri River is one of the last tributaries free of damming in the Upper Paraná River basin, which reinforces its ecological importance (Agostinho et al. 2004a, Affonso et al. 2015) and makes it an important environment for migratory species (Gubiani et al. 2010). Considering its importance for the conservation of the Brazilian continental ichthyofauna and the occurrence of 152 fish species in this river basin in research developed by Cavalli et al. (2018), and 154 according to Reis et al. (2020), studies on low-order streams are necessary, mainly because of their importance for freshwater biodiversity, role in contributing to ecosystem service and sensitivity and vulnerability to anthropogenic disturbances (Biggs et al. 2017).

Rivers and streams of the region are intensely affected by the increased environmental degradation resulted from human activities, such as agricultural production (intensive crop production, livestock, and aquaculture) and urbanization (industrial and household effluents, and habitat changes) (Gubiani et al. 2010, Pereira et al. 2014). Thus, a continuous monitoring and inventorying of their ichthyofauna are essential for the development of a database that contributes to a better understanding of the species distribution in changed environments, and assists in defining and implementing practices for biodiversity management and conservation.

Thus, the objective of the present study was to survey the ichthyofauna of nine low-order streams (second and third orders; Strahler, 1957) that compose the Piquiri River basin (Upper Paraná Ecoregion) and are affected by agricultural, aquaculture and urbanization activities, and to inventory the occurring fish species in these environments to contribute to the improvement of information about the biodiversity of the region.

Material and Methods

1. *Study area*

The study was conducted in nine second and third-order streams that compose the Piquiri River basin and are located in the West and Northwest of the state of Paraná, South of Brazil (Figure 1). These regions comprise an area of 47,000 km² (23% of the total area of the state) and encompass 111 municipalities (IPARDES 2019). The regions have a humid subtropical climate, and its soil was classified as dystrophic Typic Hapludox (Latossolo Vermelho-Escuro; EMBRAPA - SNLCS 1984), which has good fertility and is highly favorable to agriculture (Pereira et al. 2014). The main economic activity in the regions is agriculture, but aquaculture is also an important activity. The West region is the main aquaculture production center of the state (Marengoni et al. 2007) and one of the three highest national aquaculture production regions (Becker et al. 2015). The main produced species in this region is *Oreochromis niloticus* L. (1758) (Nile tilapia). The aquaculture is less expressive in the Northwest region (SEAB 2018).

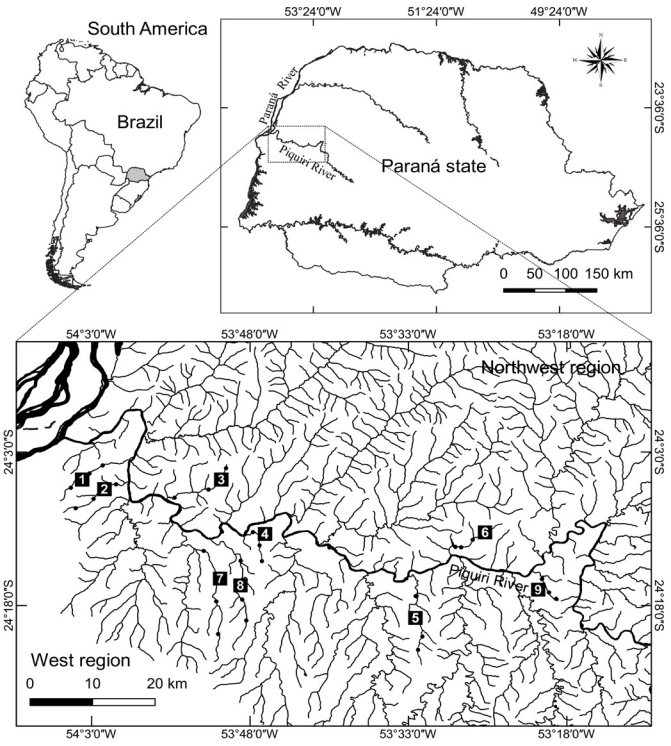


Figure 1. Sampled streams in the Piquiri River basin, Paraná, Brazil: 1) Córrego Tapera; 2) Córrego Taquari; 3) Rio do Bagre; 4) Sanga 16 de Janeiro Stream; 5) Rio Baiano; 6) Rio das Antas; 7) Arroio Santa Fe; 8) Arroio Pioneiro; and 9) Córrego Tatu. Dots indicate local of samplings over the longitudinal gradient of the streams (headwater, middle and mouth).

2. *Ichthyofauna sampling and data analysis*

The ichthyofauna was sampled quarterly from December 2017 to September 2018 at three sites of each stream in their longitudinal gradient (headwater, middle and mouth – Table 1). Fish assemblages were sampled using an electrofishing equipment (portable generator of alternating current of 2.5 kW, 400 V, 2A) in 50-meter segments delimited by multifilament nets f 0.5-centimeter mesh. Three successive downstream-to-upstream catches were established in each segment (Esteves & Lobón-Cerviá 2001).

The captured specimens were anesthetized in a eugenol solution (100 mg. L^{-1}) and fixed in a 10% formalin solution. The fishes were identified in a laboratory, according to Ota et al. (2018). Sample specimens were preserved in 70% alcohol and deposited in the ichthyological collection of the Nucleus of Research in Limnology, Ichthyology and Aquaculture (NUPELIA) of the State University of Maringá, Paraná State, Brazil. The sampling of the biological material was authorized by the Chico Mendes Institute for Conservation of

Biodiversity (ICMBIO; License no. 24680-1). The sampling protocol used in the present study was subjected to a process of ethical review and approved by the Ethics Committee on the Use of Animals of the Federal University of Paraná (CEUA – UFPR), in Palotina, PR, Brazil, under the Protocol no. 01/2018.

The sampling efficiency was evaluated based on data of total abundance, using the Chao 1 and Jackknife 1 richness estimators, which consider the actual number of species richness based on rare species shared between groups of samples. Subsequently, species accumulation curves were developed. All analyses were made in the Estimates 9.0 program (Colwell 2013).

Results

A total of 14,507 individuals were collected in the nine streams evaluated. Specimens were from six orders, 20 families, 46 genera, and 70 species (Table 2). The highest species richness was found for the orders Characiformes (34 species) and Siluriformes (21 species), which represented 80% of the total species sampled in the streams evaluated. The families that presented higher species richness were Characidae (18 species), Loricariidae (nine species), and Heptapteridae (seven species), representing 49% of the total species richness (Figure 2).

The streams with higher species richness were the Córrego Tapera (48 species), followed by the Córrego Taquari and Rio do Bagre, both presenting 42 species. Low species richness was found in the Córrego Tatu and Rio das Antas (16 species each). Among the species collected, six were captured in all streams evaluated, while 11 were found exclusively in one of the streams (Table 2).

The highest abundances were found for the orders Siluriformes (42%) and Characiformes (37%). *Pimelodella avanhandavae* and *Psalidodon* aff. *paranae* were the most representatives, with approximately 23% of the total abundance found. *Psalidodon* aff. *paranae* and *Phalloceros harpagos* were more abundant in the Rio das Antas, presenting 51% and 25% total abundance found, respectively. *Pimelodella avanhandavae* represented 61% of the total abundance found in the Arroio Pioneiro Stream, whereas *Poecilia reticulata* represented 66% of the abundance in the Córrego Tatu. *Hypostomus* cf. *tietensis* represented 27% of the abundance in Córrego Santa Fé. All species found in the others streams presented relative abundances lower than 24%.

Nine species identified in the samplings of the present study had not yet been recorded in the basin by other studies, namely *Aequidens plagiozonatus, Apteronotus* cf. *caudimaculosus, Coptodon rendalli, Erythrinus erythrinus, Hoplias misionera, Moenkhausia australe, M. bonita, Pyrrhulina australis* and *Steindachnerina brevipinna.*

Table 1. Geographic coordinates and abiotic variables of sampling sites in low-order streams of the Piquiri River, Upper Paraná River basin, Paraná, Brazil.

Stream	Site	Latitude	Longitude	Depth (m)	Width (m)	Flow (m/s)	Canopy (%)
Tapera	Headwater	24°06'29.9"S	54°04'58.6"W	0.43	4.30	0.7	48
	Middle	24°05'05.8"S	54°03'12.2"W	0.30	3.79	1.3	17
	Mouth	24°04'18.4"S	54°01'57.3"W	0.44	4.18	1.1	7
Taquari	Headwater	24°08'29.8"S	54°04'30.7"W	0.30	1.60	0.2	99
	Middle	24°07'34.7"S	54°02'49.1"W	0.42	3.71	0.6	65
	Mouth	24°06'09.8"S	54°00'41.5"W	0.57	3.50	1.9	25
Bagre	Headwater	24°04'35.0"S	53°50'16.3"W	0.19	2.15	0.7	78
	Middle	24°06'40.4"S	53°51'56.0"W	0,41	4.52	0.8	51
	Mouth	24°07'28.2"S	53°55'08.9"W	0.57	6.21	1.0	53
16 de Janeiro	Headwater	24°13'39.9"S	53°46'52.5"W	0.19	1.13	0.4	76
	Middle	24°12'07.4"S	53°47'06.1"W	0.24	4.23	0.6	98
	Mouth	24°10'49.8"S	53°47'43.2"W	0.34	4.74	0.6	55
Baiano	Headwater	24°22'20.4"S	53°32'5.5"W	0.39	4.04	0.5	100
	Middle	24°21'01.8"S	53°31'40.6"W	0.55	4.80	0.4	100
	Mouth	24°17'03.9"S	53°32'13.9"W	0.78	5.24	1.0	57
Antas	Headwater	24°11'34.6"S	53°26'54.8"W	0.48	3.61	1.0	100
	Middle	24°12'18.6"S	53°28'00.2"W	0.46	4.43	1.0	99
	Mouth	24°12'16.4"S	53°28'33.3"W	0.32	4.80	0.7	12
Santa Fé	Headwater	24°20'47.7"S	53°51'01.3"W	0.25	5.42	1.1	92
	Middle	24°17'36.2"S	53°51'11.6"W	0.37	6.98	1.2	100
	Mouth	24°12'40.0"S	53°52'23.3"W	0.77	5.89	0.7	100
Pioneiro	Headwater	24°19'27.9"S	53°48'21.2"W	0.32	2.90	0.5	99
	Middle	24°17'25.3"S	53°48'44.8"W	0.48	3.95	1.1	99
	Mouth	24°13'37.5"S	53°48'53.2"W	0.70	6.25	0.75	100
Tatu	Headwater	24°17'21.0"S	53°19'01.1"W	0.17	1.12	<0.1	100
	Middle	24°16'43.6"S	53°19'41.2"W	0.22	3.82	0.4	100
	Mouth	24°15'25.0"S	53°20'21.4"W	0.52	3.10	0.4	100

*Abiotic variables represent mean values of data collections

Table 2. List of species, total abundances and origin of fishes collected in low-order streams of the Piquiri River, Upper Paraná River basin, Paraná, Brazil. 1) Sanga 16 de Janeiro; 2) Rio das Antas; 3) Rio do Bagre; 4) Rio Baiano; 5) Arroio Pioneiro; 6) Arroio Santa Fé; 7) Córrego Tapera; 8) Córrego Taquari; and 9) Córrego Tatu. One asterisk (*) represents non-native species from the Upper Paraná River basin. Two asterisks (**) represent possible non-native species (Ota et al. 2018).

TÁXON	1	2	3	4	5	6	7	8	9	VOUCHER
ACTINOPTERI										
CHARACIFORMES										
Anostomidae										
Leporinus friderici (Bloch, 1794)	3							4		NUP22551, 22475
Characidae										
Characinae										
Galeocharax gulo (Cope, 1870)							1			NUP22361
Cheirodontinae										
Serrapinnus notomelas (Eigenmann, 1915)			24	6	10	4	24	53		NUP22525, 22415, 22382, 22484
Stethaprioninae										
Astyanax lacustris (Lütken, 1875)	281		30	30	129	68	85	188	46	NUP22534, 22494, 22391, 22570, 22348, 22454, 22418
*Moenkhausia australe (*Eigenmann, 1908)**	2						13			NUP22552, 22368
Moenkhausia bonita Benine, Castro, Sabino, 2004							2	21		NUP22369, 22476
Moenkhausia cf. *gracilima* Eigenmann, 1908							1			NUP22370
Moenkhausia sanctaefilomenae (Steindachner, 1907)			2				5	4		NUP22516, 22371, 22477
Oligosarcus paranensis Menezes, Géry, 1983			5				8			NUP22517, 22372
Oligosarcus pintoi Amaral Campos, 1945					1	2	17	6		NUP22373, 22478
Psalidodon bockmanni (Vari, Castro, 2007)		3	1				1			NUP22493, 22347
Psalidodon aff. *fasciatus* (Cuvier, 1819)	53		48	63	15	168	260	102		NUP22532, 22491, 22389, 22569, 22345, 22452
Psalidodon aff. *paranae* (Eigenmann, 1914)	7	1095	20	17	5	34	5	10		NUP22533, 22434, 22492, 22390, 22559, 22453
Stevardiinae										
Bryconamericus coeruleus Jerep, Shibatta 2017				1						NUP22393
Bryconamericus exodon Eigenmann, 1907*	34		34	5			186	442		NUP22535, 22496, 22394, 22349, 22455
Bryconamericus aff. *iheringii* (Boulenger, 1887)			32	10	6	37	15			NUP22495, 22392, 22571, 22346
Bryconamericus turiuba Langeani, Lucena, Pedrini, Tarelho- Pereira, 2005	156		168	13	197	14	192	198		NUP22536, 22497, 22395, 22560, 22350, 22456
Piabarchus stramineus (Eigenmann, 1908)			33	9	33	18	7	4		NUP22522, 22412, 22587, 22378, 22480
Piabina argentea Reinhardt, 1867			50	2						NUP22523, 22413
Crenuchidae										
Characidium gomesi Travassos, 1956							20			NUP22355
Characidium aff. *zebra* Eigenmann, 1909	7	28	31	3			38	110		NUP22539, 22436, 22501, 22398, 22354, 22461

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Curimatidae										
Cyphocharax modestus (Fernández-Yépez, 1948)	1				4		3	1		NUP22542, 22563, 22358, 22464
Steindachnerina brevipinna (Eigenmann, Eigenmann, 1889)*	1						3			NUP22383
Steindachnerina insculpta (Fernández-Yépez, 1948)	1				2	2		10		NUP22558, 22592, 22485
Erythrinidae										
Erythrinus erythrinus (Bloch, Schneider, 1801)*	8		5	1			1	2	1	NUP22543, 22505, 22400, 22359, 22466, 22421
Hoplias mbigua Azpelicueta, Benitez, Aichino, Mendez, 2015*	5	5	3		1	1	1	3	5	NUP22546, 22441, 22509, 22577, 22471, 22424
Hoplias misionera Rosso, Mabragaña, González-Castro, Delpiani, Avigliano, Schenone, Días de Astarloa, 2016	1	5	7		7	3	3	2	6	NUP22547, 22442, 22510, 22565, 22578, 22365, 22472, 22425
Hoplias sp.2			2	1						NUP22511, 22404
Lebiasinidae										
Pyrrhulina australis Eigenmann, Kennedy, 1903							1			NUP22380
Parodontidae										
Apareiodon affinis (Steindachner, 1879)			1					3		NUP22490, 22450
Apareiodon cf. *piracicabae* (Eigenmann, 1907)	22		11	6	1		9	76		NUP22530, 22489, 22387, 22342, 22449
Apareiodon vladii Pavanelli, 2006	4							1		NUP22531
Parodon nasus Kner, 1859	7		1	2			19	20		NUP22554, 22519, 22410, 22375
Prochilodontidae										
Prochilodus lineatus (Valenciennes, 1837)						5		2		NUP22482
GYMNOTIFORMES										
Apteronotidae										
Apteronotus aff. *albifrons* (Linnaeus, 1766)**							1			NUP22343
Apteronotus cf. *caudimaculosus* Santana, 2003**				1			1	16		NUP2388, 22344, 22451
Gymnotidae										
Gymnotus inaequilabiatus (Valenciennes, 1839)	71	134	39	125	135	61	36	65	35	NUP22544, 22438, 22506, 22401, 22362, 22468, 22422
Gymnotus pantanal Fernandes, Fernandes, Albert, Daniel-Silva, Lopes, Crampton, Almeida-Toledo, 2005*	33	1	17	5	13	14	8	18	14	NUP22545, 22439, 22507, 22402, 22564, 22576, 22363, 22469, 22423
Gymnotus sylvius Albert, Fernandes-Matioli, 1999		35	6	7	3		13	27		NUP22440, 22508, 22403, 22364, 22470
Sternopygidae										
Eigenmannia trilineata López, Castello, 1966			1					3		NUP22504, 22465
Sternopygus macrurus (Bloch, Schneider, 1801)			9					6		NUP22526, 22486

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SILURIFORMES										
Auchenipteridae										
Tatia neivai (Ihering, 1930)			6				2			NUP22528, 22385
Callichthyidae										
Callichthys callichthys (Linnaeus, 1758)	1		5		6		3	3		NUP22537, 22498, 22561, 22351, 22457
Corydoras aeneus (Gill, 1858)	247		7	8		8	16	59	154	NUP22540, 22502, 22399, 22573, 22356, 22462, 22419
Cetopsidae										
Cetopsis gobioides Kner, 1858			1	1				1		NUP22396, 22459
Heptapteridae										
Cetopsorhamdia iheringi Schubart, Gomes, 1959	10		51	3	11	5	92	32		NUP22538, 22500, 22397, 22353, 22460
Imparfinis mirini Haseman, 1911	1									NUP22549
Imparfinis schubarti (Gomes, 1956)	11		31	27	155	7	338	284		NUP22550, 22515, 22408, 22582, 22367, 22474
Pimelodella avanhandavae Eigenmann, 1917	169				1903	10	47	70		NUP22556, 22588, 22379, 22481
Pimelodella gracilis (Valenciennes, 1835)					4		1			
Phenacorhamdia tenebrosa (Schubart, 1964)			18	8	11	9	7	2		NUP22521, 22411, 22377, 22479
Rhamdia quelen (Quoy, Gaimard, 1824)	130	78	75	14	40	83	44	79	30	NUP22557, 22446, 22524, 22414, 22590, 22381, 22483, 22431
Loricariidae										
Hypostominae										
Ancistrus sp.						1				NUP22568
Hypostomus ancistroides (Ihering, 1911)	52	88	179	65	22	36	60	58	37	NUP22548, 22443, 22512, 22405, 22366, 22473, 22426
Hypostomus sp.1						1				NUP22581
Hypostomus sp.2			8	16	45	264			14	NUP22514, 22407, 22580, 22427
Hypostomus cf. *tietensis* (Ihering, 1905)			58	6	110	347				NUP22513, 22406, 22579
Loricariinae										
Farlowella hahni Meinken, 1937*							6	12		NUP22360, 22467
Loricariichthys platymetopon Isbrücker, Nijssen, 1979*						7				NUP22583
Rineloricaria latirostris (Boulenger 1900)					9	15				NUP22567, 22591
Otothyrinae										
Otothyropsis polyodon Calegari, Lehmann A., Reis, 2013			71				3			NUP22518, 22374
Trichomycteridae										
Cambeva aff. *davisi* (Haseman, 1911)		29	73			15	5	2		NUP22435, 22499, 22572, 22352, 22458
SYNBRANCHIFORMES										
Synbranchidae										

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Synbranchus marmoratus Bloch, 1795	2	10	11	115	20	19	8	32	2	NUP22447, 22527, 22416, 22593, 22384, 22487, 22432
CICHLIFORMES										
Cichlidae										
Aequidens plagiozonatus Kullander, 1984*	4	82	13	4	7	3	6	7	2	NUP22529, 22433, 22488, 22386, 22341, 22448, 22417
Coptodon rendalli (Boulenger, 1897)*		11			1					NUP22437, 22562
Crenicichla britskii Kullander, 1982	12		10		12	4	23	14	10	NUP22541, 22503, 22574, 22357, 22463, 22420
Geophagus iporangensis Haseman, 1911						11				NUP22575
Oreochromis niloticus (Linnaeus, 1758)*	29	2		5	210	18			6	NUP22553, 22444, 22409, 22566, 22584, 22428
CYPRINODONTIFORMES										
Poeciliidae										
Phalloceros harpagos Lucinda, 2008	2	530	4			3	22		2	NUP22429, 22445, 22520, 22584, 22376, 22429
Poecilia reticulata Peters, 1859*						9			712	NUP22589, 22430
Total abundance	1367	2136	1201	579	3128	1306	1662	2052	1076	
Richness	32	16	42	31	32	35	48	42	16	

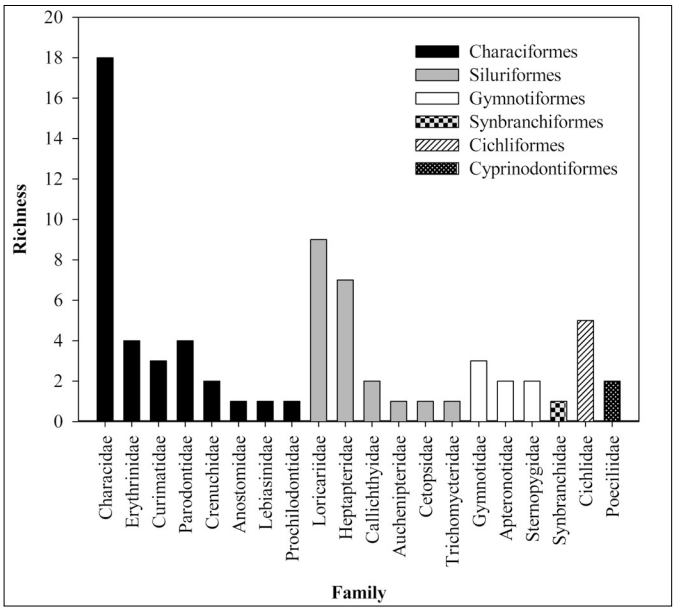


Figure 2. Richness of species by order and family identified in the nine sampled streams of the Piquiri River basin, Paraná, Brazil.

Regarding the origin of the ichthyofauna studied, 14 species were classified as non-native to the Piquiri River basin (Table 2), which represented 14% of the total abundance found. *Poecilia reticulata*, *Bryconamericus exodon*, *Oreochromis niloticus*, *Aequidens plagiozonatus* and *Gymnotus pantanal* presented the highest abundances among these non-native species.

The estimators of richness used indicated a good sampling efficiency, presenting similar values to those found in the samplings (Figure 3).

Discussion

The non-parametric richness estimators indicated a good efficiency in the samplings, since the estimated values of richness approximate the real number of species recorded in each stream. These estimators, despite being sensitive to changes in the distribution of abundance and despite providing estimates of the lower limit of richness at a local scale, consider environmental heterogeneity (Gotelli & Chao 2013, Gwinn et al. 2016, Bevilacqua et al. 2017). This is an important factor in the present study, given the number of sampling sites and the fact that they have different watershed land uses. In this way, nine species identified in the present study had not yet been recorded in the Piquiri River basin, even considering recent studies that updated the ichthyofauna composition of this basin and reported the occurrence of 152 (Cavalli et al. 2018) and 154 fish species (Reis et al. 2020). This indicates that the ichthyofauna diversity of the Piquiri River basin is underestimated, especially that of its low-order tributaries**,** and denotes a need for continuous researches in these environments. Although the information about ichthyofauna diversity in Neotropical streams has been improved over the years, several species are still unknown to science (Ota et al. 2015, Frota et al. 2019, Mezzaroba et al. 2021).

Neotropical streams in South America are characterized by the occurrence of a high fish diversity due to the geographic isolation of this continent and its drainage basins, and the high diversity of habitats over its longitudinal gradient, with predominance of species from the orders Characiformes and Siluriformes (Lowe-McConnell 1999, Agostinho et al. 2007). The predominance of these orders has been recorded for the Upper Paraná Ecoregion (Langeani et al. 2007, Cavalli et al. 2018), as found in the present study.

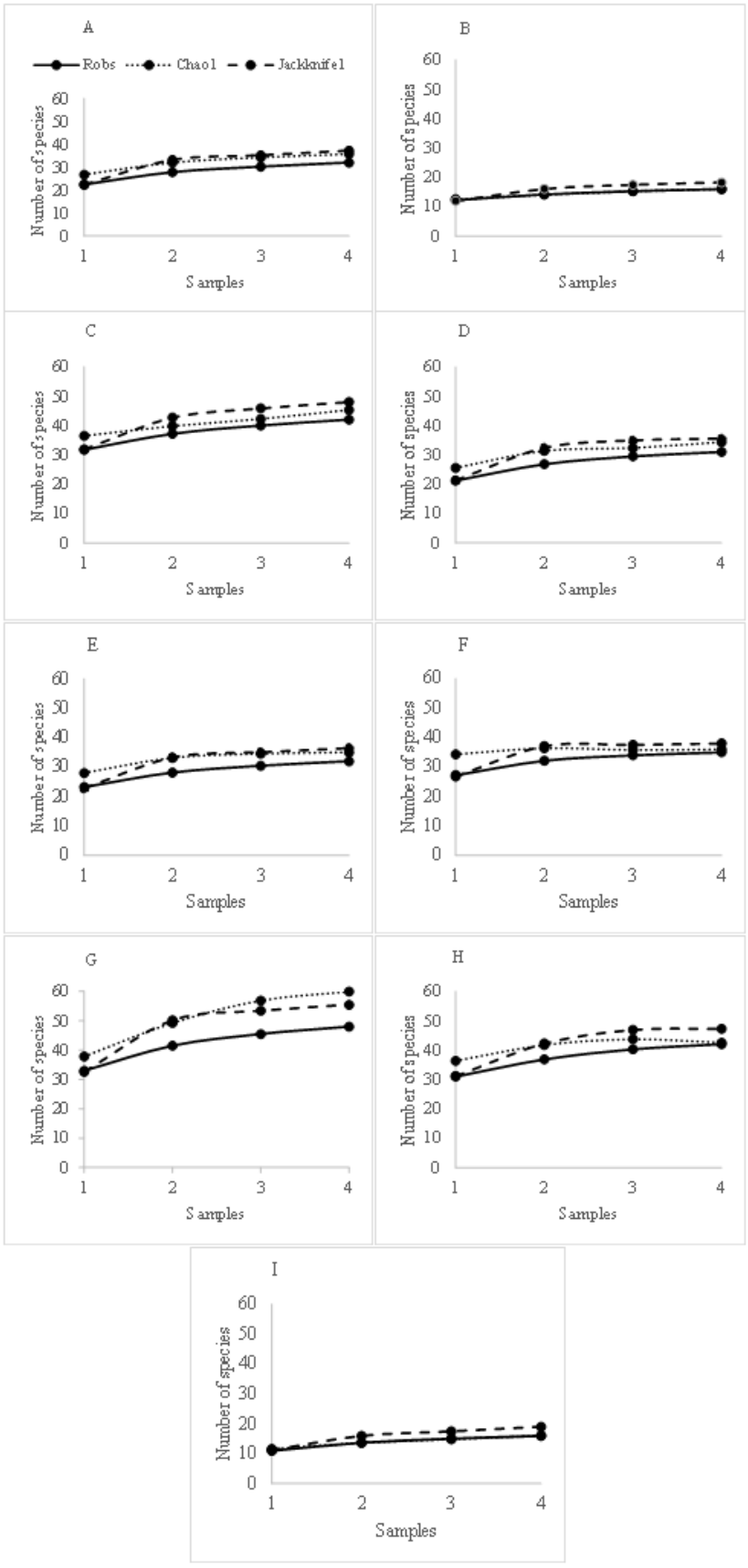


Figure 3. Species accumulation curves (Robs) and richness estimations (Chao 1 and Jackknife 1) for fish samples collected quarterly in streams of the Piquiri River basin, Paraná, Brazil, from December 2017 to September 2018. Sanga 16 de Janeiro (A); Rio das Antas (B); Rio do Bagre (C); Rio Baiano (D); Arroio Pioneiro (E); Arroio Santa Fé (F); Córrego Tapera (G); Córrego Taquari (H); and Córrego Tatu (I).

Regarding the order Characiformes, a high occurrence of small-size species from Characidae was observed, which is highly distributed in freshwater environments, encompasses a large proportion of stream fish species, and presents diverse feeding and reproductive habits (Britski 1972, Lowe-McConnell 1999). The predominance of species of the order Siluriformes is related to habitat characteristics, such as presence of riffles and boulders in the stream bed substrate, which favor the occurrence of Loricariidae and Heptapteridae. The latter is associated with environments near rapids and that have submersed marginal vegetation and cracks between rocks (Bockmann and Guazzelli 2003, Pagotto et al. 2011).

The predominance of the *Psalidodon* aff. *paranae* and *Phalloceros harpagos* in the Rio das Antas, whose was dammed to supply water for aquaculture systems, indicates the plasticity of these species in modified habitats by human actions. *Phalloceros harpagos* and species of *Psalidodon* are common in streams of the Upper Paraná River basin (Langeani et al. 2007, Gubiani et al. 2010) and their wide plasticity allows them to explore efficiently changed habitats (Monaco et al. 2014, Pereira et al. 2014). The predominance of the non-native species *Poecilia reticulata* in the Córrego Tatu, where environmental changes occurred due to urbanization near the headwater reach, denotes the plasticity of this species to explore changed environments. Previous studies indicate similar patterns, with predominance of *P. reticulata* in environments that were affected by urbanization (Cunico et al. 2006, Gubiani et al. 2010). Urban development is one of the main factors for biodiversity changes in streams because it fragments natural landscapes, changing hydrological regimes, matter flow, and nutrient cycling. It is associated with the establishment of non-native species that can increase their abundance and dominance under adverse environmental conditions (Cunico et al. 2012).

The occurrence of the non-native *Oreochromis niloticus* and *Coptodon rendalli* is related to the intense aquaculture activity in the region. Aquaculture is the main vector for introducing non-native species into environments around the world (Lima et al. 2018), and highly frequent introductions have great potential of negatively effects on the diversity of native species and the ecosystem services (Pelicice et al. 2017). The high abundance of *O. niloticus* and occurrence of *C. rendalli* found in the streams evaluated are due to escapes from ponds used for aquaculture activities, denoting the need for efficient escape containment mechanisms (Nobile et al. 2019). The occurrence of non-native species due to aquaculture activities is also reported by others studies on the region and can be attributed to the low distances between fish ponds and streams, which allows escapes through effluent waters under inadequate management, rupture or overflow in rainy periods, and intentional releases (Orsi & Agostinho 1999, Forneck et al. 2016, Ribeiro et al. 2018, Casimiro et al. 2018, Forneck et al. 2020).

Other non-native species were found in the present study due to different vectors of species introduction in the basin. The occurrence of *Bryconamericus exodon* is associated with the transposition channel of the Itaipu Hydroelectric Power Plant, which connects the downstream region of the reservoir to the upstream region of the dam (Ota et al. 2018). The presence of the *Gymnotus pantanal* is probably because of accidental introductions due to use of live baits for fishing, and floods in biogeographic barriers, as in the Salto de Sete Quedas, which resulted from the formation of the Itaipu reservoir. The presence of *Aequidens plagiozonatus* is possibly because of the ornamental fish trade. This species is found in the Upper Parana River basin since 2014 (Ota et al. 2018) and was found in all streams evaluated in the present study.

Regarding the native species found, *Prochilodus lineatus* and *Leporinus friderici* stand out. These species are abundant in the Upper Paraná River basin, present ecological and economical importance, and are long-distance migratory species that move from feeding areas to breeding areas (Agostinho et al. 2004b, Agostinho et al. 2007, Makrakis et al. 2012, Silva et al. 2015, Bido et al. 2018). The presence of juveniles of these species in the sampled streams reinforces the need to maintain the Piquiri River basin free from hydroelectric dams, since these barriers hinder migration routes, preventing those juveniles of these species access environments where migratory species breed and grow (Agostinho et al. 2008, Silva et al. 2015).

In view of the results obtained and in agreement with other researches carried out recently in the basin (Cavalli et al. 2018, Reis et al. 2020), 163 fish species are recorded in the Piquiri River basin. Regarding the number of non-native species, it is worth mentioning that Cavalli et al. (2018) recorded 30 species among the 152 sampled and that Reis et al. (2020) recorded 41 species among the 154. Despite the high number already registered, in the present study, five of the nine new records are of non-native species, totaling 48 in the referred basin, which reinforces the importance of knowledge and monitoring of streams that are under strong anthropogenic pressure.

The list of species found in the present study contributes to the existing database of ichthyofauna distribution in Neotropical streams, considering that it shows the presence of species that had been not yet registered for the Piquiri River basin, and a high occurrence of non-native species in the basin. The study basin is in the last stretch free from hydroelectric dams of the Upper Paraná River basin, which is essential for the integrity of biological processes in this environment. Therefore, this study reinforces the importance of inventories and monitoring of highly sensitive environments to anthropogenic changes.

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Author Contributions

Mariele P. Camargo: 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.

Sandra C. Forneck: 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.

Fabrício M. Dutra: Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Leonardo B. Ribas: Contribution to data collection; Contribution to data analysis.

Almir M. Cunico: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data

analysis and interpretation and 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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Erratum

Erratum: Checklist of mammals from Goiás, central Brazil

In the article "Checklist of mammals from Goiás, central Brazil", with the DOI code number: https://doi.org/10.1590/1676-0611-BN-2020-1173, published at Biota Neotropica 21(3): e20201173, on:

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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Article

Spider (*Arachnida-Araneae*) diversity in an amazonian altitudinal gradient: are the patterns congruent with mid-domain and rapoport effect predictions?

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Abstract: The Mid-Domain Effect (MDE) and the Rapoport (RE) effect are two biogeographical theories that make predictions about biogeogaphic patterns. MDE predicts higher richness in the central portions of a gradient if it is within a bounded domain. RE predicts a positive relation between altitude and species range size along an altitudinal gradient. Our aim was to document the distribution of spider species richness along an altitudinal gradient in the Brazilian Amazon, and to test the influence of MDE and RE on the diversity patterns. Our study was conducted at the Pico da Neblina (Amazonas state, Brazil), and we sampled spiders at six different altitudes using two methods: nocturnal hand sampling and a beating tray. We obtained 3,140 adult spiders from 39 families, sorted to 529 species/morphospecies. Richness declined continuously with an altitude increase, but the fit with the MDE richness estimates was very weak and was not significant. Range size was not related to altitude, i. e., no RE. Finally, the abundance distribution within each species range varied more specifically, which prevented the occurrence of a RE at the community level. The influence of MDE was extremely low, a consequence of our community characteristics, formed mostly by small range size species. Short and medium range species were located at all altitudes, preventing a significant relation between range size and altitude. The distribution of abundance within a species range varied specifically and do not support a RE hypothesis.
Keywords: *Arachnology, geometric constraints, mountain ecology, environmental gradients, biodiversity, Amazon.*

Diversidade de aranhas (*arachnida-Araneae*) em um gradiente altitudinal na amazônia. seriam os padrões congruentes com o esperado pelo efeito do dominio central e pelo efeito rapoport?

Resumo: O Efeito do Domínio Central (MDE) e o Efeito Rapoport (ER) são duas teorias biogeografias que fazem previsões sobre a distribuição da diversidade ao longo de gradientes. O MDE prevê maior riqueza nas porções centrais de um gradiente, se este estiver dentro de um domínio fechado. O ER prevê uma relação positiva entre altitude e tamanho da distribuição ao longo do gradiente altitudinal. Nosso objetivo foi o de registrar a distribuição de uma comunidade de aranhas ao longo de um gradiente altitudinal na Amazônia Brasileira, e testar se há uma influência do EDC e do ER sobre os padrões de diversidade da comunidade. Nosso estudo foi feito no Parque Nacional do Pico da Neblina (AM, Brasil), e nós amostramos aranhas em seis altitudes diferentes. Nós coletamos 3.140 exemplares adultos de 39 famílias, que foram divididos em 529 espécies/morfoespécies. A riqueza declinou com o aumento de altitude, mas o padrão não mostrou ajuste com as previsões feitas pelo EDC. O tamanho da distribuição altitudinal também não esteve relacionado ao previsto pelo ER. Por fim, a distribuição de abundância ao longo da distribuição altitudinal das espécies variou de maneira específica, o que impediu a ocorrência de um ER nos padrões da comunidade. A influência do EDC sobre os padrões observados foi baixíssima, uma consequência de características de nossa comunidade, já que esta é formada por espécies com pequena distribuição altitudinal. Espécies de distribuição altitudinal médias e grandes ocorreram em todas as partes do gradiente o que impediu

a ocorrência de um ER. Por fim, o ER também não foi observado na distribuição de abundância das espécies ao longo do gradiente, já que essa variou de maneira específica.

Palavras-chave: *Aracnologia, restrições geométricas, ecologia de montanhas, gradientes ambientais, biodiversidade, Amazônia.*

Introduction

Altitudinal gradients have always attracted the attention of scientists, from eighteenth and nineteenth century naturalists to modern ecologists and biogeographers. Partially relegated for a certain period (Lomolino 2001), the study of altitudinal gradients has been experiencing a recovery of interest, especially during the last decade, with richness patterns being increasingly well documented, for a larger range of taxa and environments (e.g., McCain 2005, 2009a, 2010, Dunn et al. 2006, Grau et al. 2007, Liew et al., 2010, Scheibler et al. 2014,Transpurger et al. 2017, Thormann et al. 2018). Richness usually decreases with altitude, either monotonically, or after low altitude plateau of high richness, but it may also present a unimodal pattern, peaking at mid altitudes, which is frequently observed (Rahbek 2005, McCain 2009a, Dong et al. 2017).

In the last decade, two new biogeographical theories became a recurring subject for empirical studies on altitudinal gradients, the mid-domain effect (MDE) (Colwell & Lees 2000a) and Rapoport's rule (RE) (Stevens 1989). MDE represented a new and original approach to explain peaks of species richness at mid altitudes (or latitude, or any other gradient). Colwell & Lees (2000a) demonstrated through simulations that the reshuffling of species range inside a domain delimited by hard boundaries (*i. e*., limits from which no species can expand its range) results in a larger overlap of species ranges around the center of the domain, producing a richness distribution pattern very similar to those observed in some empirical studies. This process was also referred to as the effect of geometric constraints in the placement of species ranges on a bounded domain.

By explaining observed patterns while dispensing the influence of any ecological or environmental gradients, the MDE aroused a lot of interest and has been the subject of a thorough scrutiny (Colwell et al. 2005, Romdal et al. 2005, Zapata et al. 2005, Storch et al. 2006, Letten et al. 2013, Pan et al. 2016). Criticisms range from the methodologies employed to test it to its assumptions (Laurie & Silander 2002, Zapata et al. 2003, Hawkins et al. 2005, Currie & Kerr 2008), but other studies still advocate its validity as an explanatory hypothesis for certain gradients in species richness (Carranza et al. 2008, Grytnes et al. 2008, VanDerWal et al. 2008), although maybe restricted to some limited situations (Dunn et al. 2007).

Rapoport's rule is a positive relation between range size and latitude and was proposed as an explanation for latitudinal gradients of species richness (Stevens 1989). It was hypothesized that species from higher latitude have broader environmental tolerance, due to greater climatic variation, and thus could expand their range at lower latitudes, increasing the local richness at these latitudes. But the opposite would not be possible, due to the narrow environmental tolerance of species from lower latitudes. Stevens (1989) also proposed that the large range expansion observed for high latitude species would happen through a rescue effect (Brown & Kodric-Brown 1977), *i. e*. the maintenance of populations at unsuitable places through a continuous migration of individuals from source populations located at places with more adequate conditions for its existence.

Rapoport's rule was later extended to altitudinal and bathymetric gradients (Stevens 1992, 1996), and also raised an intense debate on its validity, causes and consequences. Although the support to the role of Rapoport's rule as a driver of species richness gradient is very weak (Rohde 1996, Colwell & Lees 2000, Willig et al. 2003, Bhattarai & Vetaas 2006), the positive association between range size and latitude/altitude/depth was actually detected in several studies (Stevens 1992, Fleishman et al. 1998, Fortes & Absalão 2004, Brehm et al. 2007, Chettri et al. 2010). Nonetheless, since a considerable number of studies failed to observe this relation, the rule was called into question, which led Blackburn & Gaston (1996) state that the humbler term "effect" would be more appropriate to describe this phenomenon.

The Rapoport rescue effect has been much less investigated, although it was proposed as the mechanism responsible for the Rapoport effect (Stevens 1989). The only study that directly tried to verify Steven's prediction, by investigating the relative abundance of species at each altitude, revealed a pattern opposite to what could be expected by the theory. Large ranged species were more abundant at lower altitudes and expanded their range upwards (Almeida-Neto et al. 2006), which the authors called the "alternative rescue effect".

Information about spiders along altitudinal gradients is scarce. Most of the few studies about spiders along altitudinal gradients are from temperate localities, usually for a subset (guilds or families) of the spider community (Otto & Svensson 1982, Bosmans et al. 1986, Olson 1994, Russel-Smith & Stork 1994, Chatzaki et al. 2005), and most reported a mid-altitudinal richness peak. Only Chatzaki et al. (2005) tested, and supported a Rapoport effect, in a study on the family Gnaphosidae at Cretan mountains, but Otto & Svensson (1982) also reported larger altitudinal ranges for species from higher altitudes.

Given the large literature available on species richness patterns on altitudinal gradients, spiders are clearly underrepresented, if we consider their high diversity (> 49,000 species – World Spider Catalog, 2021) and ecological importance as a top invertebrate predator (Coddington et al. 1991). Our focal group is understory and forest floor spiders.

In this study, we investigated a spider community along an altitudinal gradient in Brazilian Amazonia. Our study area - Pico da Neblina (AM - Brazil) is the highest mountain in Brazil, and is renowned for its botanical diversity and endemism levels (Berry & Riina 2005), while its fauna is less know (see Willard et al. 1991 and McDiarmid & Donnelly 2005). Moreover, it is located in a remote area still mainly covered by forest at a very large scale, which guarantees an unusual conservation level even at lower altitudes, rarely observed in studies on altitudinal gradients (Nogués-Bravo et al. 2008).

Our objectives are: 1 - to record the pattern of spider species distribution along the altitudinal gradient at the Pico da Neblina and

to assess the relation of this pattern with altitude and with MDE predictions, 2 - to test for the occurrence of a Rapoport effect, 3 - to investigate the existence of a rescue effect, and 4 - contribute to the knowledge of spider diversity in tropical mountains, expecting high diversity and endemism.

Material and Methods

1. Study area

The study was carried out at the Pico da Neblina (00°48'07" N e 66°00'40" W) (Figure 1), the highest Brazilian mountain with 2,994 m.a.s.l. (IBGE, 2004). Located in the municipality of São Gabriel da Cachoeira, north of the Amazonas state, Brazil, the study sites belongs to the Pico da Neblina National Park, with 2,260,344 ha, and also overlapped with the Yanomami Indigenous Land. The Pico da Neblina lies within a mountainous region that represents the boundary between Brazil and Venezuela (RADAM, 1978). It is also one of the southern components of the Guayana Region, a region of very old geological origin (mostly Precambrian rocks) famous for its sandstone mountains with vertical cliffs and table tops, the tepuis (Steyermark, 1986), as well as for its diverse and endemic biota (Rull, 2005). Although the Pico da Neblina is also formed by sandstone rocks and harbours extensive high altitude plateaus (2,000 to 2,400 m), it does not present the typical tepui shape.

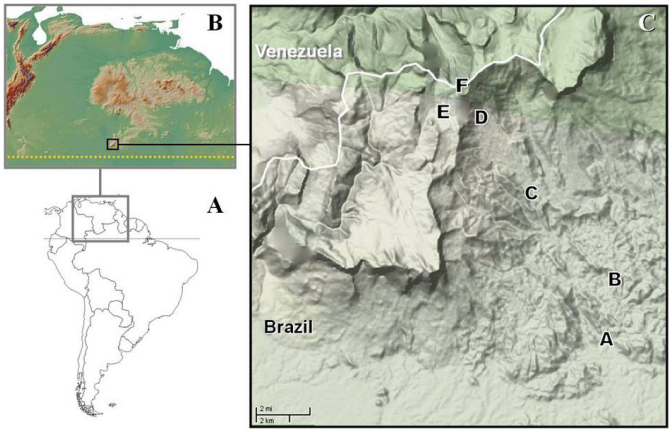


Figure 1. Study area.. A) South America; B) Northern South America (rectangle of map A enlarged). The mountain range at the left of the map represents the northern part of the Andes, and the mountainous region in the center of the map is the Guayana Shield, showing the study area in its southern part. The dotted yellow line represents the equator; C) Closer view of the study area (rectangle of map B enlarged), the Pico da Neblina. Letters represent the altitudes sampled: A - 100 m, B - 400 m, C - 860 m, D - 1,550 m, E - 2,000 m, F - 2,400 m.

According to a division proposed for the Guayana region, the study area can be divided in three main physiographic units according to the temperature and altitude. Lowlands, up to 500 m and macrothermic climate (> 24°C annual average); uplands, from 500 to 1,500 m and submesothermic climate (18° - 24°C); and highlands, from 1,500 to 2,994, with mesothermic (12° - 18°C) and submicrothermic climate (8° - 12°C) (Huber 1995, Nogués & Rull 2007). At the Pico da Neblina, the annual average rainfall in the lowlands is 3,000 mm/year, without a dry season, and the humidity is about 85-90% (RADAMBRASIL 1978). Rainfall increases with altitude until around 1800 m, being gradually replaced by a constant mist, and the average humidity reaches almost 100% (RADAMBRASIL 1978).

Vegetation in the lowlands is composed by a tall, evergreen forest. Uplands are covered by montane forests, which present decreasing biomass and tree size, especially when declivity is accentuated, leading to shallower soils (Pires & Prance 1985). In the highlands, forests are replaced by more open types of vegetation like high altitude scrublands and broad leave meadows, which grow on organic peat soils and on rocky substrates. At the Neblina, forests formation occurs up almost to 2,000 m, and their high altitude formations stand out for their diversity and endemism (Berry & Riina 2005). Species from the families Bromeliaceae, Rapateaceae and Theaceae are among the most characteristics elements of this flora. Detailed information on the geology and vegetation of the region can be found at Berry et al. (1995) and Berry & Riina (2005).

2. Sampling and identification

Spiders were collected with two traditional methods in spider inventories (Coddington et al., 1991): beating tray and manual active search. In the first method the understory vegetation was sampled through the beating of leaves, branches, vines and other parts of the vegetation with a stick, while holding a 1 m^2 tray under it. The spiders falling in the tray were collected, and the sampling unit consisted of 20 of those beating events, in different plants, randomly located along a 30 m long transect.

In the second method spiders from the forest floor and from the understory were directly collected with the help of tweezers and/or plastic vials. The sampling unit represents one hour of search within an approximate area of 300 m^2 (30 x 10 m).

The first method was employed during the day, from 08.00 h to 11.00 h, and the second at night from 19.30 h to 23.00 h. All spiders collected with both methods were immediately preserved in 70% ethanol.

Sampling was carried out by three collectors at six altitudes, 100, 400, 860, 1,550, 2,000 and 2,400 m. At each altitude we investigated three sites, about 100 m apart from each other. In each of those three sites, the three collectors sampled gathered three samples with the beating tray technique, durint the morning, and three samples by manual active seach during the night, totaling nine samples of each method by site. This correspond to a total sampling effort of of 54 samples by altitude (27 of each method) 324 samples (162 of each method) for the whole gradient. We also measured the temperature at each sampling site, at the beginning and at the end of nocturnal sampled. The sampling expedition occurred from 22 September to 13 October 2007, period considered as dry season locally.

Only adult spiders were identified. Specimens were sorted into morphospecies usually by the first author and then identified until the lowest taxonomic level by specialists. Voucher specimens were deposited at the collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), at Manaus (AM), and duplicates were deposited at the Instituto Butantan (IBSP), São Paulo (SP) and at the Museu Paraense Emílio Goeldi (MPEG), Belém (PA).

3. Richness measures

The species richness for each altitude was calculated as the total number of species collected in the three sites at each altitude, pooling data from both sampling methods. We interpolated richness estimates

in all analysis, for all taxonomic levels. Interpolation assumes that a species occurs in all altitudes between its maximum and minimum altitudinal record, and represents a common procedure in studies on species richness on altitudinal gradients (Stevens 1992, Sanders 2002, Almeida-Neto et al. 2006, Bhattarai & Veetas 2006, Grau et al. 2007). It is based on the assumption that the sampling of biological communities is usually incomplete, which is certain for a community of tropical arthropods (Coddington et al. 2009), and that altitudinal ranges are continuous. So we believe that the increase in richness provided by the interpolation represents a realistic contribution to our data, although it may enhance or even create mid-altitude peaks (Grytnes & Vetaas 2002).

We also compare interpolated richness with other richness measures calculated for each altitude: observed richness, rarefied richness (coverage-based rarefaction) and the exponential of Shannon-Wiener index, or numbers equivalents (D). D was selected as a measure of diversity because it take into account the relative abundance of species. Its use over raw diversity indices has been recommended for allowing a more intuitive interpretation (Jost 2006), as it possess the doubling propriety (Hill 1973), *i. e*. if two equal sized, completely distinct communities with a diversity D = X are combined, their diversity will be D = 2X.

To calculate the rarefied richness we used a coverage-based rarefaction (Chao & Jost 2012). This technique compares communities not by equaling all of then to the lowest abundance recorded, as is done in individual-based rarefaction, but by the same level of inventory completeness. This is calculated based on the proportion of species that are still missing, which is calculated according to richness estimatives. This technique also compares the richness of different communities by extrapolation, when necessary, and it also allow us to produce rarefaction curves with richness estimators and 95% confidence intervals.

Shannon-Wiener index values were obtained with the software Paleontological Statistical (PAST, Hammer et al. 2001), and their exponential in a excel sheet.. The rarefaction analyzes were performed in R Cran Project software 4.0.5 (2021), using packages vegan (Oksanen et al. 2020), iNEXT (Hsieh et al. 2020) e ggplot2 (Wickham, 2016).

4. *Geometric constraints*

The software RangeModel (Colwell 2006) was used to estimate the spiders communities richness along a dimensional gradient under the assumption of geometric constraints.,The gradient is represented by all the altitudes sampled,and the lower and highest altitudes represent the limits of the domain, wich no range can extend beyond. This null model places the empirical altitudinal ranges of each species randomly along the gradient,without replacement, and richness at each sampling site is counted. This procedure was repeated 1,000 times, without replacement, and the mean estimated richness and its 95% confidence intervals were calculated.

Species recorded in just one altitude represent a problem, since their range is restricted to a single point, the altitude in which it was recorded. This decreases drastically the chance of those species being recorded during the randomization process, leading to an underestimation of richness. A simple solution is to expand the altitudinal range of the species upslope and downslope (Bhattarai & Veetas 2006, Brehm et al. 2007), usually to half the distance from the nearest sampling site. In our study, however, the distance between our sampling sites was too uneven to allow this procedure.

To overcome this problem, we used the discrete domain model, developed by Dunn et al. (2006) available at RangeModel. In the discrete model the domain is divided into discrete, ordered sampling points, and each empirical species range encompasses the distance from the first to the last sampling point where that species was recorded. Additional information required is the 'fill', which is the number of sites at which each species was actually recorded. To perform the analysis, we just filled the gaps in the fill input data to represent complete interpolation. The discrete model may be less realistic, since different distances among sampling sites are artificially standardized. Moreover, probably in order to avoid this situation, it was recommended for use with datasets gathered at evenly or approximately evenly sampling sites (Dunn et al. 2006, Colwell 2008). However, by this approach we were able to obtain simulations without missing any record and, more important, we believe that we maintained the main principle of geometric constraints models, which is to randomize observed ranges along a bounded domain.

5. *Analyses*

We analyzed the variation in interpolated species richness along the gradient through an ordinary least squares (OLS) multiple regression with mean richness estimates predicted by a MDE simulation and altitude as explanatory variables. We used the AICc (small sample corrected Akaike Information Criterion) to select the best model. We used altitude as an environmental variable because it is usually strongly correlated with other environmental factors, as temperature and vegetation type (Dunn et al. 2007), and could be used as a surrogate for environmental variation along the gradient (Bateman et al. 2010). The temperature measured at our sampling sites was indeed closely related to altitude ($R^2 = 0.99$, $p < 0.001$). We tested this relationship for richness at the species, genus and family level. Geometric constraints are stronger on large ranged taxa (Colwell & Lees 2000, Dunn et al. 2006), so we expect that MDE predictions will present a better fit with increasingly higher taxonomic levels, since the range of the analyzed taxa will greatly increase, especially at the family level. We analyzed the residuals of the regression through Moran's I correlogram to assess the occurrence of spatial autocorrelation, but no significant trend was found, which allowed us to keep our analysis design with OLS regression (Diniz-Filho et al. 2003). The analysis was performed with Spatial Analysis Macroecology (SAM) software (Rangel et al. 2010).

Rapoport effect was investigated with an OLS regression between recorded range size and the altitudinal midpoint of each species. We calculated the range as the difference between upper and lower altitudinal limits, and the midpoint was the average altitude between the range extremities, *i. e*., a geometric midpoint. We added 200 m to each ranges, since otherwise species recorded at just one altitude would have an altitudinal range of 0, which is not very realistic. However, this approximation does not have any influence in the analyses, unlike what is observed in the geometric constraints simulations for this study. We also tested the Rapoport effect for a subset of the community based on a minimum abundance criterion. Most species from our dataset are rare, represented by just a few individuals. They thus have a large probability of being recorded in just one altitude, but this may be simply due to undersampling rather than a genuine narrow distribution. Thus, we removed all species represented by just one or two individuals to perform another OLS regression between range size and midpoint for the species represented by at least three individuals (243 species or 46% of total richness), an arbitrary criterion. This allows us to keep in the analysis species

present in just one altitude, but whose distribution is more reliable due to the larger number of individuals.

We investigated the occurrence of a rescue effect by the following procedure. First we calculated the weighted average midpoint (WAM) (Almeida-Neto et al. 2006) for each species. The WAM is obtained by multiplying the number of individuals present at each altitude by the corresponding altitude, summing up those products from all altitudes and dividing it by the total abundance of the species. Assuming that a species attains its maximum abundance in optimal environmental conditions (Whitaker 1967, Brown 1984) the WAM can represent more accurately the actual altitudinal preference of a species than the midpoint. Then we checked the relation between the midpoint and the WAM through an OLS regression with the midpoint as independent variable. We inspected the graph and considered that any species placed outside of the 95% CI of its WAM presented a significant rescue effect, *i. e*., its WAM presented a significant deviation from its midpoint. We included only species with large ranges (defined here as those present in at least four altitudes), since both Rapoport and Alternative rescue effect are attributed to large range species.

Finally, we present the RSFD (range size frequency distribution) and the altitudinal range profile of the community. We produced the RSFD by plotting the range size of each species, ordered by range size. In the altitudinal range profile, species are represented by their range and WAM and are ordered by their WAM in an increasing manner. Due to the large number of species, we divided the altitudinal range profile in three groups, according to the range size: short (present at just one altitude), medium (two to three altitudes), and large (four to six altitudes).

Results

1. *Richness patterns and sampling completeness*

We obtained a total of 3,140 adult spiders, which were sorted to 529 morphospecies, representing 196 genera and 39 families. A complete list is presented in Nogueira et al. (2014).

The species richness of spiders decreased with increasing altitude. The decrease was monotonic and was observed for all four richness and diversity measures employed (Table 1). While the observed and rarefied richness and D showed a more or less gradual decline, the interpolation greatly increased the number of species of the second altitude (400 m), which became only slightly lower than the richness of the first altitude (Figure 2). The remaining richness measures declined monotonically. Abundance also decreased along the gradient but the decline was not monotonic. Notably, the second altitude presented a relatively low number of individuals. Nonetheless, abundance remained quite high until the fourth altitude (1,550 m), and then presented a steep decrease, although remaining similar between the two highest altitudes.

The rarefied richness values indicate a monotonic decline in richness (Figure 3), but the rarefaction curves also allow us to evaluate the diversity pattern of the community. It is possible to see that the two first altitudes, the most species-rich, possess a very similar diversity pattern, and there is an overlap of those two altitudes confidence interval.

Richness declines more in the two following altitudes, but the fifth altitude, at 2,000 m, presents a considerable diversity, and its confidence intervals overlap with the interval from the altitude below, at 1,550. Even though the richness obtained at 2,000 is much lower than that of the preceeding altitude, the slope of the curve indicates that this is more due to the low spider abundance at this altitude.The last altitude sampled presented a much smaller richness, and the value and shape of the rarefaction curve, beginning to stabilize, show that it represents a much less diverse community.

Richness at higher taxonomic levels presented a similar pattern to that observed for species, with decreasing richness along the gradient, but there is an inversion between the two first altitudes, and a slightly higher number of genera and families is found at 400 m than at 100 m. This is an effect of interpolation, which had already greatly increased species richness at the second altitude, although not enough to overcome richness at 100 m. It indicates that the broader distribution of genus and families along the gradient, based on a increasingly higher number of individuals enhance the possibility of interpolation, in addition to reduce the differences in richness along the gradient, which make the decrease in richness less steep than that observed for specific level.

2. *Richness predictors – MDE and altitude*

The variation of spider species richness across the gradient (Figure 4) was negatively related to altitude, and the contribution of MDE to the observed pattern was negligible (Table 2). The Altitude model was able to explain 97.9% of the variation, with the lowest AICc. The MDE model had an extremely weak and non-significant fit with spider species richness. Altitude was also selected as the best model for genera and family richness, but the explained variation decrease with increasing taxonomic level, although remaining quite large (Table 2).

Table 1. Abundance and richness by altitude. For species we present the observed richness (S obs), interpolated richness (S int), numbers equivalents (D) and rarefied richness (Raref). For genera and families we present observed and interpolated richness.

		Genera				Families			
Altitude	**N**	**S obs**	**S int**	**D**	**Raref**	**S obs**	**S int**	**S obs**	**S int**
100	687	225	224	142.74	377.1	116	116	30	30
400	591	194	223	98.59	302.7	107	125	29	32
860	713	171	185	82.02	271.3	87	96	25	28
1550	597	115	120	61.68	197,1	71	79	23	25
2000	295	69	71	26.31	115,9	45	49	17	18
2400	257	24	24	6.10	34.1	22	22	11	11
Total	3140	528				196		39	

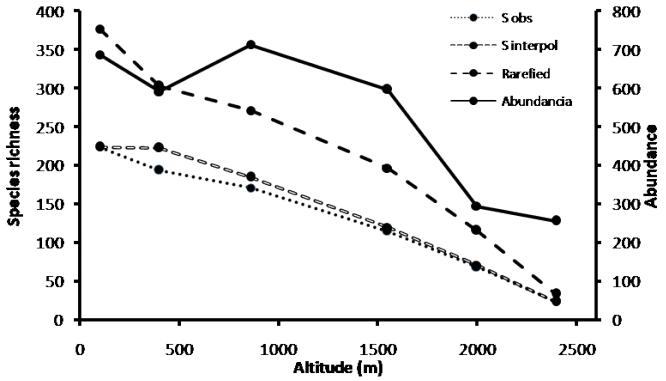


Figure 2. Abundance, observed, interpolated and rarefied species richness of spiders along the gradient of altitude at the Pico da Neblina.

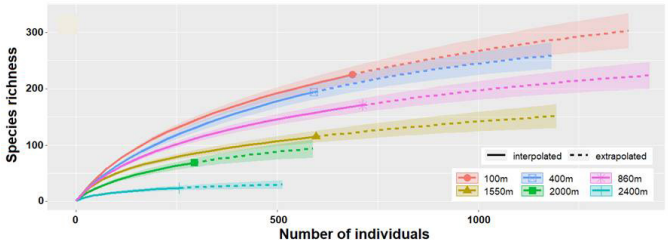


Figure 3. Rarefaction curves of spider species richness for six altitudes sampled at the Pico da Neblina. The full line represents the interpolated richness and the dotted line the richness calculated by extrapolation. The colored band surrounding the richness lines represents 95% confidence intervals.

3. *RSFD and Rapoport effect*

Most of the species (63%) had small ranges, occurring in just one altitude (Figure 5), while only 25 species, 5% of the total, had large ranges, encompassing at least half of the domain. The decrease in species number with increasing altitude for the three range sizes is visible in the range profile (Figure 5). Small range species peaked at the first altitude (100 m), and maintained a relatively high number of species until the fourth altitude (1,550 m). With increasing range size it is possible to see that the richness of mid altitude sites is largely determined by species from low altitudes. There is little overlap between species from the upper half of the gradient and those from the much more diverse lower part.

The test of the Rapoport effect showed that range size was not related to altitude ($R^2 = 0.003$, $p = 0.189$). The largest range species are situated at the center of the domain, and they decrease towards the gradient edges. The relation between range size and altitude performed for the 243 species represented by at least three individuals were also very weak and not significant ($R^2 < 0.001$, $p = 0.666$).

4. *Abundance distribution along the range*

The WAM and the midpoint presented a significant positive relation ($R^2 = 0.473$, $p < 0.001$). The WAM of almost half (12) of the 25 large range species presented a significant deviation from its midpoint. Among them, seven had a WAM smaller than the midpoint (upwards range expansion) and five had a WAM larger than the midpoint (downwards range expansion).

Discussion

The results revealed that spider species richness declined monotonically along the altitudinal gradient at the Pico da Neblina. The estimated richness

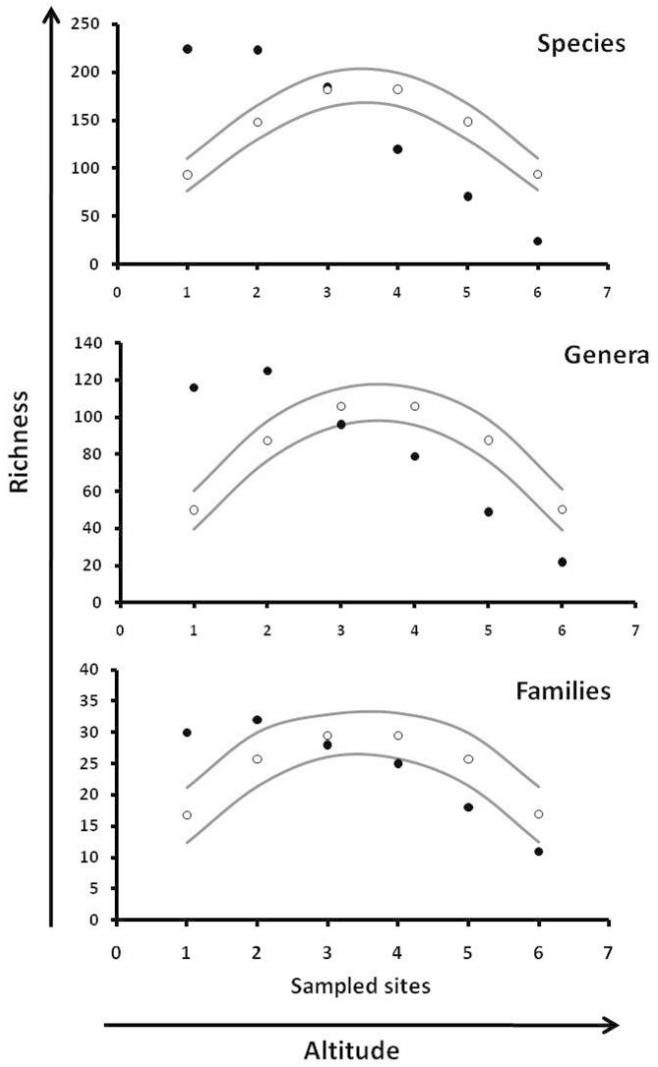


Figure 4. Observed richness (closed circles) and mean richness estimated by the MDE (open circles) based on 1000 randomization, with 95% confidence intervals (grey lines). Data include all the spiders sampled at Pico da Neblina.

values produced by the coverage-based rarefaction reveal some interesting patterns. The values calculated to the first two altitudes predicts a community composed by hundreds of species, a richness similar to that obtained in other spider inventories from lowland Amazonian terra-firme forests (Dias & Bonaldo 2012, Bonaldo & Dias 2010, Höfer & Brescovit 2001).

The rarefaction/extrapolation curves also helped to highlight the relative high diversity recorded at the 5th altitude, at 2,000 m. Even though the richness obtained at this altitude is much lower than that of the preceeding altitude, the slope of the curve indicates that this is more due to the low spider abundance. So, during the transition from montane forest to high-altitude open habitats, the abundance of the community presented a larger decrease than the diversity itself. Only at the highest altitude sampled the richness really droped, and since the curve shows signs of stabilization the number of species still to be detected is probably not very large.

The negative relation with altitude and the lack of any apparent influence of the MDE on the richness patterns points that the species distribution along the gradient is not explained by random processes, and the lower altitudes represent a more favorable environment for most species, resulting in higher richness and abundance.

Table 2. Results of the multiple regression performed amongspider richness and three explanatory models, altitude, richness estimated by the MDE simulations, and Altitude + MDE. We present the Akaike Information criterion (AICc), Delta AICc, coefficient of determination and probability in F test for the three models to the specifc, generic and familiar level. Models are ordered according to the AICc.

	Model	AICc	Delta AICc	R^2	p
Species	Altitude	63,676		0.979	< 0.001
	MDE + Altitude	80.318	16.642	0.998	< 0.001
	MDE	86.847	23.171	0.022	0.777
Genus	Altitude	61.148		0.941	0.001
	MDE	77.811	16.664	0.05	0.669
	MDE + Altitude	84.061	22.913	0.982	0.002
Family	Altitude	46.069		0.883	0.005
	MDE	58.176	12.107	0.117	0.507
	MDE + Altitude	62.588	16.52	0.988	1

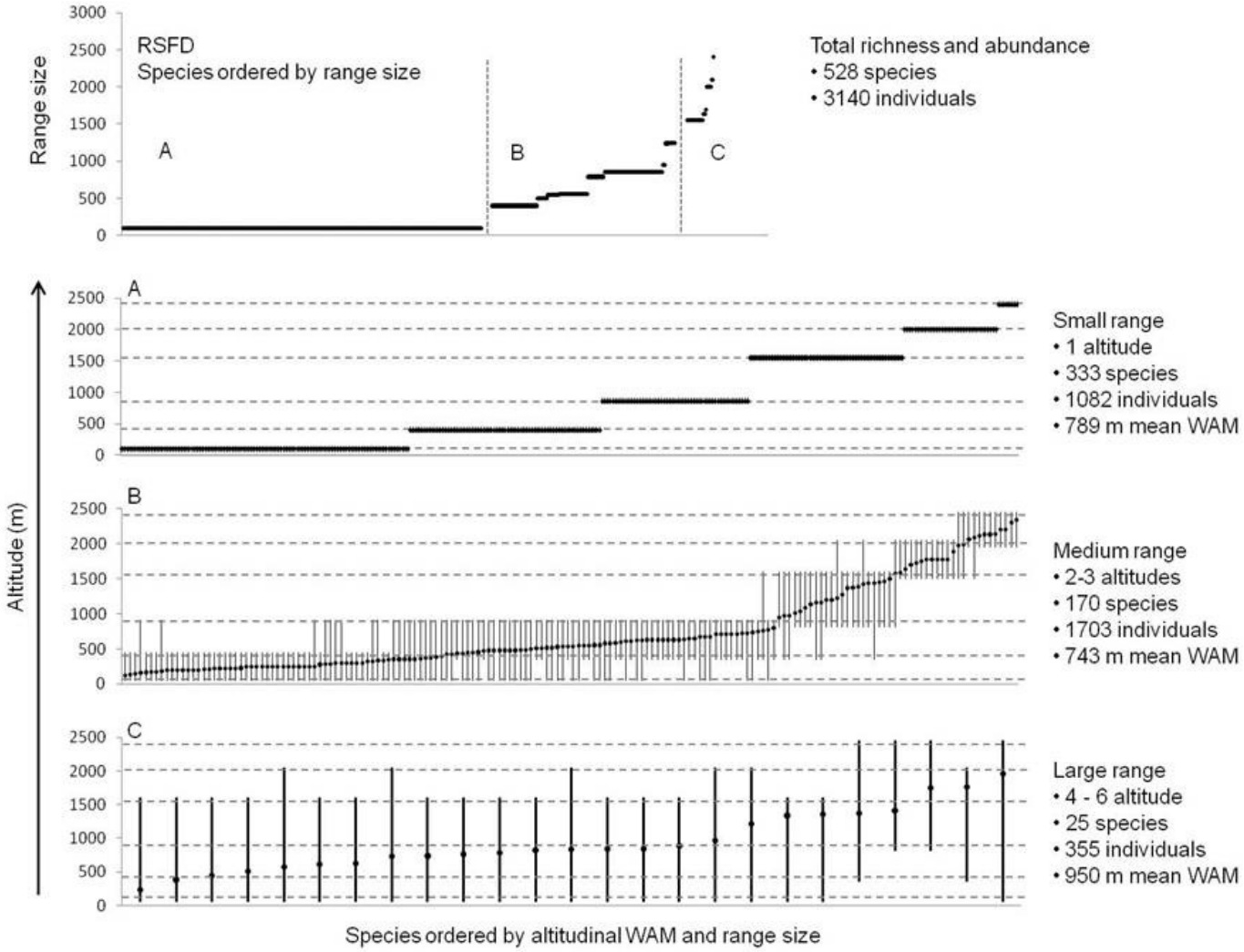


Figure 5. Range size frequency distribution (RSFD) of the spider community sampled at Pico da Neblina, and range profile of the species for three range size categories. Species in the RSFD graphic are represented by points and are ordered by increasing range size. Ranges are represented by vertical bars in graphs A, B and C, and their WAMs (weighted average midpoints) are represented by closed circles. Species are ordered according to the values of their WAMs and then by range size. Dotted lines at graphs A, B and C represent the six altitudes sampled.

1. *Spider species richness at altitudinal gradients*

Our results differ from most information available on spiders at altitudinal gradients (Olson 1994, Bosmans et al. 1986, Olson 1994, Chatzaki et al. 2005). However, differences in important factors, as sampling design, climate or target group demand a cautious approach when comparing the results. Some studies were performed on tropical mountains, but focused only on a subset of the community, like orb-weavers (Ferreira-Ojeda & Flórez-D. 2007) or canopy spiders (Russel-Smith & Stork 1994), or, in one case, on the fauna of an irrigated rice ecosystem (Sebastian et al. 2005). Moreover, they were not designed *a priori* to investigate altitudinal trends in a detailed manner, sampling as few as three altitudes or presenting very unbalanced designs, biased towards low altitude sites. As a consequence the high variability observed in the results, reporting a richness peak from the lowest, mid and even highest altitudes sampled, may be difficult to interpret.

More detailed studies reported a richness peak at mid-altitude sites. Some of them focused on litter-dwelling spider (Otto & Svensson 1982, McCoy 1990, Olson 1994) and this pattern was suggested to be an indirect consequence of optimal environmental conditions at those altitudes for herbivorous arthropods (Olson 1994), since precipitation often peaks at mid-altitudes (McCain 2007). Mid-altitude richness peak are also characteristics of studies from temperate localities (Otto & Svensson 1982, Bosmans et al. 1986, Chatzaki et al. 2005) which may indicate a different and more tolerant response of the temperate fauna to the decrease in temperature than that of the tropical fauna from our study, or to be a reflex of the greater environmental zonation at tropical mountains (Wiens & Graham, 2005, Ghalambor, 2006, McCain, 2009b). Additionally, the lower richness at lower altitudes may also be a consequence of human disturbance (McCoy 1990, Chatzaki et al. 2005), a problem already highlighted in others studies (Wolda 1987, Sanders 2002, McCain 2009a). Finally, mid-altitude richness peak could, of course, be due to geometric constraints, but this seems unlikely, as is exposed above.

2. *Geometric constraints and richness predictors*

The accumulation of information in the literature and its organization in recent reviews has challenged the importance of geometric constraints as a driver of richness patterns. Performance of MDE models as richness predictors has proven poor in several situation for several taxa (reviews in McCain 2007a, b, 2009a, Currie & Kerr 2008), and seems to be restricted to certain situations. Basically, the importance of geometric constraints increases at biome and regional levels (Jetz & Rahbek, 2001, Bellwood et al. 2005, Dunn et al. 2007, but see Rangel & Diniz-Filho 2005) and for large ranged species (Colwell et al. 2004, Dunn et al. 2007, VanDerWal et al. 2008).

Moreover, altitudinal gradients possess some characteristics that may make then inadequate to test MDE predictions. First, altitude is more closely related to area and temperature than latitude (Dunn et al. 2007). Moreover, environmental changes along altitudinal gradients are notoriously steep, exhibiting drastic changes over relatively small spatial scales, which may reduce average range size and, as a consequence, the influence of geometric constraints (Colwell et al. 2009). Finally, and more important, the very essence of geometric constraints theories, a domain delimited by hard boundaries, may be very questionable for altitudinal gradients. Lower limits of altitudinal domains, unless located at the sea border or small islands, actually lack any evident geographic barrier.

Mountains from arid localities present a sharp climatic transition from dry lowlands to more humid places at mountain slopes, which may represent an environmental barrier at the base of the gradient. However, in mountains from humid, tropical localities, as the Pico da Neblina, the base is covered by the very same lowland forest that surrounds the gradient (in our case in a very large scale), what was termed as a "soft" (and ineffective) barrier (Colwell & Hurtt 1994). Moreover, while simulations clearly show that richness effectively decrease at the border of domains delimited by hard boundaries (Colwell & Hurtt 1994, Grytnes & Vetaas 2002, Rangel & Diniz-Filho 2005), models assuming soft boundaries at the gradient base with an underlying decreasing richness trend generates a pattern of monotonic decrease very similar to that observed in our study (Colwell & Hurtt 1994 – hybrid model, Grytnes & Vetaas 2002 – model III).

The application and effectiveness of the assumption of hard boundaries had already been scrutinized in several aspects (Laurie & Silander 2002, Zapata et al. 2005), but critics didn't include the asymmetry of boundaries in altitude gradients, although this characteristic was already highlighted when geometric constraints models were presented (Colwell & Hurtt 1994). Curiously, it hasn't been much take into account since then and is not usually mentioned as one of the causes of poor performance of MDE models when richness decreases along the gradient (Almeida-Neto et al. 2006, Sanders et al. 2007, Liew et al. 2010, McCain 2010, but see Chettri et al. 2010). Given the above exposed, the lack of fit of MDE with our data, obtained from a small range community species (average range represents only 15% of domain size) on an altitudinal gradient on a local scale seems perfectly logical, and geometric constraints can be discarded as a meaningful driver of species richness pattern for our community.

Richness at higher taxonomic levels presented a small, low altitude, unimodal richness peak, due to interpolation. It indicates that the broader distribution of genus and families along the gradient, based on a increasingly higher number of individuals enhances the possibility of interpolation, in addition to reducing the differences in richness along the gradient, which makes the decrease in richness less steep than that observed for species level.

Concerning geometric constraints, it is possible to see in Figure 4 a gradual approach to the MDE prediction as taxonomic levels increase, although the relation remains small and not significant. This is a consequence of the great increase in range size (mean average range size in relation to domain size: genus – 29.1%, family – 55.1%) but it is also a final evidence of the lack of influence of geometric constraints on our richness patterns, given the already mentioned positive relation between range size and fit to MDE predictions. This is an unequivocal evidence of the influence of some strong environmental or historical gradient on our community.

Actually, our data indicates an intimate relation with temperature, an environmental factor that continuously decline with altitude (McCain 2007b, and references therein). The importance of climatic factors has obviously already been explored in numerous studies and its influence on altitudinal gradients was synthesized in the climate model proposed by McCain (2007b). Based on water availability and temperature, it predicts richness peaks at mid-altitudes in mountains located at arid environments and decreasing richness at mountains from

wet environments, which was corroborated by our study. Temperature was also exerted the most positive influence on ant species richness (Sanders et al. 2007).

Our richness patterns results are from the combined influence of several factors, and some hypothesis offer theoretic support for these, for example species-area relationship (SAR). One of the oldest patterns reported by ecologists (Hawkins 2001), SAR predicts a positive relation between area size and richness (Rosenzweig 1995), and has often be used as an explanatory factor with several positive results. However, recent studies failed to find significant area effects for several taxa at altitudinal gradients (Fu et al. 2006, Kluge et al. 2006, McCain 2007a, 2009a 2010, Beck & Chey 2008), and SAR also seems to have a larger influence on richness patterns at regional rather than at local scales (Lomolino 2001, McCain 2005, Romdal & Grytnes 2007). This suggests that an eventual bias in our data due to area effects is probably not very important.

3. Rapoport effect, rescue effect and RSFD

Our data didn't support a Rapoport effect, as range size was not related to altitude. The triangular pattern of our data is a product of the geometric constraints on range size (Colwell & Hurtt 1994). As range size increases it has fewer possibilities of location and is constrained to have its midpoint near the center of the domain. This pattern will necessarily arise whenever large ranges encompass the whole domain. As a consequence, a RE may only be possible in the absence (or occurrence in a proportionally very small number) of short or/and medium range species at higher and even mid altitudes, or when ranges are small in relation to the domain, which reduces the geometric restrictions on their location.

Evidence of RE at altitudinal gradient is variable. As observed in relation to its application on the latitudinal gradient (Gaston et al. 1998, Ribas & Schoereder 2006), a considerable number of studies failed to find a significant positive relation between range size and altitude (Vetaas & Grytnes 2002, Grau et al. 2007, Liews et al. 2010), which reinforces the impression that it is not a general pattern. Other works, in contrast, presents evidences in its support (Fleishman et al. 1998, Sanders 2002, McCain 2009a), including the only study that verified its occurrence for spiders, more precisely, for ground dwelling spiders of the family Gnaphosidae in Cretan mountain ranges (Chatzaki et al. 2005). The authors attributed the results to the high environmental tolerance of this family, as several species, most of them from lowlands, occupied a large portion of the gradient. At the Pico da Neblina, on the other hand, most of the spiders had small ranges. This may reflect intrinsic differences between communities from tropical and temperate environments (although it is observed that Gnaphosidae seems particularly tolerant) and also may offer evidence of higher biological zonation on tropical mountains than on temperate ones. This would lead to narrower altitudinal ranges for tropical species, an old theory (Janzen 1967) that has recently received empirical support (Ghalambour et al. 2006, McCain 2009b).

The only study that assessed Rapoport effect for tropical arachnids investigated the altitudinal distribution of harvestman (Opiliones) from mountains of the Brazilian Atlantic coastal forest (Almeida-Neto et al. 2006), with positive results. Most of the large range species were from low altitudes, but, as their range encompassed most of the domain they also presented most of the highest midpoints, which produced the positive relation between range size and altitude. At the Pico da Neblina, most of the large range species were also present at low altitudes (only four of the 25 large ranged species were not recorded at the first altitude), but an important number of short and medium range species were recorded at all altitudes, preventing a Rapoport effect. Logically, the different result may reflect differences in the biology of spiders and harvestman, such as dispersal capacity, notoriously poor for the latter group (Mestre & Pinto-da-Rocha 2004, Pinto-da-Rocha et al. 2005), among many other factors that vary between the studies. But we can further hypothesized that the lower height of mountains sampled at the Atlantic Forests (gradient extent of 950 m, against 2,400 m for the Pico da Neblina) allowed a proportionally larger range expansion from lowland species as well as preventing, with few exceptions, the existence of high altitude specialists (Almeida-Neto et al. 2006).

Although almost half of the large range species presented an important range expansion based on the form of individual abundance patterns, interpreted as an evidence of rescue effect, the number of species expanding their range downwards and upwards was similar. This suggests a more specific variation in the response of species to the environmental changes along the altitudinal gradient, instead of a rescue effect at the community level, as predicted by both rescue hypotheses. This result contrasts with those observed for harvestman of the Atlantic forest (Almeida-Neto et al. 2006) and Gnaphosidae from Crete (Chatzaki et al. 2005). In both cases results signaled a predominant upwards range expansion (alternative rescue effect), which may be a consequence of the fact that most of these communities were formed by lowland species, as mentioned above.

There were no important downwards range expansions either, as expected by a Rapoport rescue effect. Nonetheless, daily temperature variations at high altitude tropical sites can be comparable to seasonal temperature variations at higher latitudes (Ghalambour et al. 2006, McCain 2009b), characterizing the environmental conditions theoretically responsible for the occurrence of Rapoport rescue effect as well as Rapoport effect itself. In our case, a characteristic of our study area may have prevented the occurrence of these phenomena. Forest formations that occupy the gradient up until around 1,800 m are abruptly replaced by open formations from 2,000 m, representing a very different kind of environment. This may lead to a higher degree of specialization of the spider fauna from these habitats (2,000 and 2,400 m), as they may be thus unable to expand their range significantly to lower, forested altitudes. An evidence of this is that most of the species with medium and large range present at the high altitude sites are more abundant at lower altitudes. If true, it may offer evidence that broader thermal tolerance does not necessarily leads to a broad environmental tolerance in a more general way. Instead, broader climatic tolerance could have evolved at the cost of competitive ability to face species from lower altitudes (Ghalambor et al. 2006), or it could represent just another requirement to the specialization for these high altitude formations.

Although our data supported neither Rapoport effect nor a strong rescue effect, positive results observed in other studies and the evidence that high altitude environments demands a broad thermal tolerances indicates that theories based on rescue effects should be tested more often, as they may clarify the mechanisms responsible for RE. We suggest that the calculation of the weighted altitudinal midpoint (WAM) (Almeida-Neto et al. 2006) may represent a useful and easily accessible tool for this purpose, as abundance data can be easily obtained in studies based on sampling at different altitudes.

Conclusions

Our study represents the most complete spider inventory performed along an altitudinal gradient on a tropical mountain. Richness declined monotonically with increasing altitude, suggesting a strong positive relation with temperature, while the influence of geometric constraints was extremely low. We claim that our results seems in accordance with the current state of knowledge on richness patterns along altitudinal gradients, and the poor performance of MDE models is a consequence of the inadequacy of altitudinal gradients (at least at humid tropical sites) to test geometric constraints hypothesis, which also seem to be supported by the literature. Our data didn't corroborate a RE either. Actually, most of the species with large ranges were mainly located from low to mid altitudes, but any significant relation between range size and altitude was prevented by the fact that medium and small range species, the vast majority of our community, occurred in all altitudes. Finally, we couldn't observe any strong rescue effect at the community level, which means that the direction of range expansion varied more specifically, and was not related to range size or altitude. By focusing on an important albeit little studied group, our study represents a contribution to the knowledge of species richness distribution along altitudinal gradient, which is important to test the universality of the models proposed to predict and explain richness patterns observed in mountains.

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Authors Contributions

André do Amaral Nogueira: lead the sampling trip, material identification, data analysis and writing.

Antonio D. Brescovit: helped in the identification of the material and provided resources and facilities to help this process.

Gilmar Perbiche-Neves: helped with submission and reviewing process.

Eduardo Martins Venticinque: conceptualized the study and assisted the first author in all the steps of the study, as well as providing financial and logistical resources.

Conflict of interest

The authors declare no conflict of interest

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Inventory

Streams fish from Upper Araguaia and Middle Rio da Mortes basin, Brazil: generating subsidies for preservation and conservation of this critical natural resource

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Abstract: The Araguaia River basin has the highest fish biodiversity within the Cerrado biome (Brazilian savannah), with many endemic and threatened species by human activities. Despite growing efforts to catalog Neotropical freshwater fish biodiversity, many regions are still undersampled. Our objective is to complement the information about stream fish in two hydrographic basins in the Cerrado. We sampled 72 streams with 50 m stretch in the Upper Araguaia (n = 32) and Middle Rio das Mortes (n = 40) basins. We collected 14,887 individuals distributed in 137 species, 81 genera, 30 families, and six orders. Characidae, Loricariidae, and Cichlidae were the families richer in species. We found a high diversity of rare fish species in the streams sampled, ca. 71.5% of the species had at least five individuals collected, and 18 species had only one collected specimen. The most frequent species were *Astyanax* cf. *goyacensis, Knodus* cf. *breviceps*, and *Characidium* cf. *zebra*. Both basins shared around 43% of the species. We caught 76 species in Upper Araguaia and 120 species in Middle Rio das Mortes. Seventeen exclusive fish species occurred in Upper Araguaia, whereas 61 were found in the Middle Rio das Mortes basin. Our analysis showed lower diversity of fish in Upper Araguaia than in the Middle Rio das Mortes basin. Considering the exclusive fish species of both basins, the human threats in those regions, and the few existent protected areas, we need a better look at the aquatic biodiversity conservation of this ecosystem.
Keywords: *Biodiversity; Cerrado; Freshwater; Neotropical fishes; Headwaters.*

Peixes de riachos das bacias do alto rio Araguaia e médio Rio das Mortes, Brasil: gerando subsídios para preservação e conservação desse importante recurso natural

Resumo: A bacia do rio Araguaia apresenta a maior diversidade de peixes no bioma Cerrado, muitas dessas são endêmicas e ameaçadas pelas atividades antropogênicas. Apesar dos crescentes esforços para catalogar a diversidade de peixes neotropicais muitas regiões ainda permanecem subamostradas. O objetivo do nosso estudo é complementar a informação sobre peixes de riachos para duas importantes bacias hidrográficas no Cerrado. Amostramos um total de 72 trechos de 50 metros em riachos nas bacias alto rio Araguaia (n = 32) e médio Rio das Mortes (n = 40). Coletamos um total de 14.887 indivíduos distribuídos em 137 espécies, 81 gêneros, 30 famílias e seis ordens. As famílias Characidae, Loricariidae e Cichlidae foram as tiveram maior número de espécies. Encontramos uma grande raridade de espécies de peixes nos riachos amostrados, cerca de 71,5% das espécies apresentaram ao menos até cinco indivíduos coletados e 18 espécies tiveram apenas um único exemplar. As espécies com maior ocorrência nos riachos foram, *Astyanax* cf. *goyacensis Knodus* cf. *breviceps* e *Characidium* cf. *zebra*. As duas bacias compartilham aproximadamente 43% das espécies de peixes coletadas. Encontramos 76 espécies para o alto rio Araguaia e 120 espécies para médio Rio das Mortes. Observamos 17 espécies exclusivas para a bacia do alto rio Araguaia e 61 espécies exclusivas para bacia do Médio Rio das Mortes. Nossas análises mostraram que a diversidade de peixes é menor na bacia do alto rio Araguaia quando comparada a bacia do médio Rio das Mortes. Considerando as ameaças antrópicas, o baixo número unidades de conservação e o elevado número de espécies exclusivas presentes em ambas as bacias, existe uma necessidade urgente concentrar esforços na conservação desses ecossistemas.
Palavras-chave: *Biodiversidade; Cerrado; Água doce; Peixes Neotropicais; Riachos de Cabeceiras.*

Introduction

The Cerrado is a Brazilian biome considered one of the global biodiversity *hotspots* due to its high species riches, endemic rates, and human threats to its biodiversity (Myers et al. 2000). The origins of large South American rivers (Amazonica, Tocantins-Araguaia, Paraná, and São Francisco basin) are inserted into this biome, which is informally entitled the Brazilian "berço das águas" (water cradle). The water bodies of Cerrado (e.g., rivers, lakes, and streams) harbor about 1200 cataloged fish species (ICMBio 2020), corresponding to 25% of South American freshwater fish species. It is important to highlight that many of the Cerrado fishes are endemic and represent more than 42% (n = 131) of the threatened Brazilian fish species (Latrubesse et al. 2019). Among the river basins originating within the Cerrado, the Araguaia River basin harbors more considerable fish diversity (Dagosta et al. 2020), with more than 320 currently described species and many with a restricted distribution that mainly occupies the headwaters (first to third order) (Latrubesse et al. 2019). Unfortunately, the Araguaia River basin landscape is undergoing a rapid transformation. Agriculture plantations or pastures replace native vegetation, and water bodies are being dammed for hydropower dam construction and agricultural irrigation intensification (Coe et al. 2011, Latrubesse et al. 2019).

The high number of fish species with restricted distribution and the human-caused environmental degradation in these basins are significant challenges for fish biodiversity conservation (Nogueira et al. 2010, Latrubesse et al. 2019, Dagosta et al. 2020). Therefore, actions addressed to preserve this biodiversity should consider the wide variation in fish community composition among the catchment systems since many of these restricted-distribution fish species are exclusive from streams (Lima 2019).

Stream fish are among the most threatened aquatic organisms (Nogueira et al. 2010, Castro 1999, Castro & Polaz 2020), and one of their main threats concerns habitat degradation (Barletta et al. 2010, Castro & Polaz 2020). The riparian vegetation removal (i.e., the watercourse adjacent buffer zone) is the leading habitat homogenization cause (Casatti, Ferreira & Carvalho 2009, Teresa & Casatti 2012, Zeni et al. 2019). Consequently, the resulting eutrophication and silting of the river channel (Teresa & Casatti 2012) also contribute to biodiversity homogenization. Besides habitat change, the streams fish suffer other kinds of threats, such as introducing non-native species, highway and dam construction, agricultural pesticides, and fertilizer intensification (Winemiller et al. 2008, Reid et al. 2019).

Unfortunately, scientific ecological investigations advance more slowly than changes in natural ecosystems. Thus, many species can be extinct, even before they are formally described by science. Besides, there is data scarcity to fill distinct information gaps for many organisms (Hortal et al. 2015) regarding species proper identification (Linnean shortfalls) and the spatial distribution of the species (Wallacean shortfalls). It is essential to highlight that the Linnean shortfall is the most significant data gap to be solved because it directly affects all other biodiversity knowledge gaps (for more details, see Hortal et al. 2015). Furthermore, due to the growing and constant threat to streams, actions seeking to synthesize information about these ecosystems to guide research and conservation measures are needed (Dudgeon et al. 2006, Barletta et al. 2010, Cetra et al. 2020). Thus, our goal was to complement the information about stream fish in two important hydrographic basins in the Cerrado biome.

Materials and Methods

1. *Study Area*

We sampled a total of 72 streams ranging from first to fourth order (scale 1:10000 IBGE) according to Strahler's (1957) classification in the Upper Araguaia and Middle Rio das Mortes basin, belonging to the Tocantins–Araguaia ecoregion (Figure 1, Table 1). The Araguaia River is a major fluvial system of the Cerrado, draining 375,000 km^2 and with an average annual streamflow of 6,500 m^3.s^{-1} (Morais et al. 2008, Latrubesse et al. 2009). The Araguaia River sources in slopes of the "Caiapós" mountain, on the boundaries of Goiás and Mato Grosso states, at 850 m elevation above sea level and travels 2110 km up to its confluence with the Tocantins River. Thus, the Araguaia basin can be divided into three stretches: upper, middle, and lower (for more details about division, see Latrubesse & Stevaux 2002, Aquino et al. 2010). The Upper Araguaia River stretch, where a portion of our sampling sites are found, has an approximate extension of 450 km and is located between its source and the "Registro do Araguaia" district, draining an approximate area comprising 375,000 km^2 (Latrubesse & Stevaux 2002, Latrubesse et al. 2009).

The Rio das Mortes source is near to the "São Jerônimo" mountain, in the Mid-Southern Mato Grosso region at 808 m above sea level, flowing the northwest direction of the state for approximately 1,070 km until it flows into the middle section of the Araguaia River, near of São Félix do Araguaia city. The Rio das Mortes is the main tributary river of the Araguaia River basin, with a drainage area of approximately 61,684 km^2 and an average annual flow of roughly 891.53 m^3.s^{-1} (ANA 2020). The initial portion basin is inserted into a landscape with intensive agriculture activity, whereas the native vegetation is restricted to the hydrographic network margins . While in the middle stretch, where a portion of our sampling sites are located, the mainland use activity is livestock. However, due to indigenous lands (TIs) and the sharp slope of relief at the edges of the "Alcantilados" plateau, it is still possible to find relatively sizable native vegetation areas in this stretch (Lima 2009).

Our study area is localized in the upper and middle stretches of the Araguaia and Rio das Mortes basins, respectively. The climate of the region is *Aw,* according to the Köppen classification (Alvares et al. 2013), with two seasonal periods: (i) rainy from October to April and (ii) dry from May to September. The annual mean precipitation ranges from 1200 to 1900 mm, and the yearly average temperature is approximately 24 ºC, with higher temperatures in the rainy period (INMET 2020).

2. *Data Sampling*

Using geography information systems (GIS) tools, we chose 32 streams in the Araguaia River and 40 in the Rio das Mortes basin, totaling 72 stretches of streams to be sampled. The sites were selected based on the independence between them and accessibility criteria. We used the collection sampling method modified from the Biodiversity Research Program (PPBIO), which consisted of sampling a 50-meter stream stretch (Mendonça et al. 2005). We collected in each stream environmental variables related to the limnological conditions and structural variables related to the environmental characterization of the streams. We measured the limnological conditions (i.e., conductivity, dissolved oxygen, pH, turbidity, and water temperature) of the streams only once at the beginning of the sample stretch using a portable multiparametric probe (Horiba U-50). We divided each sampled

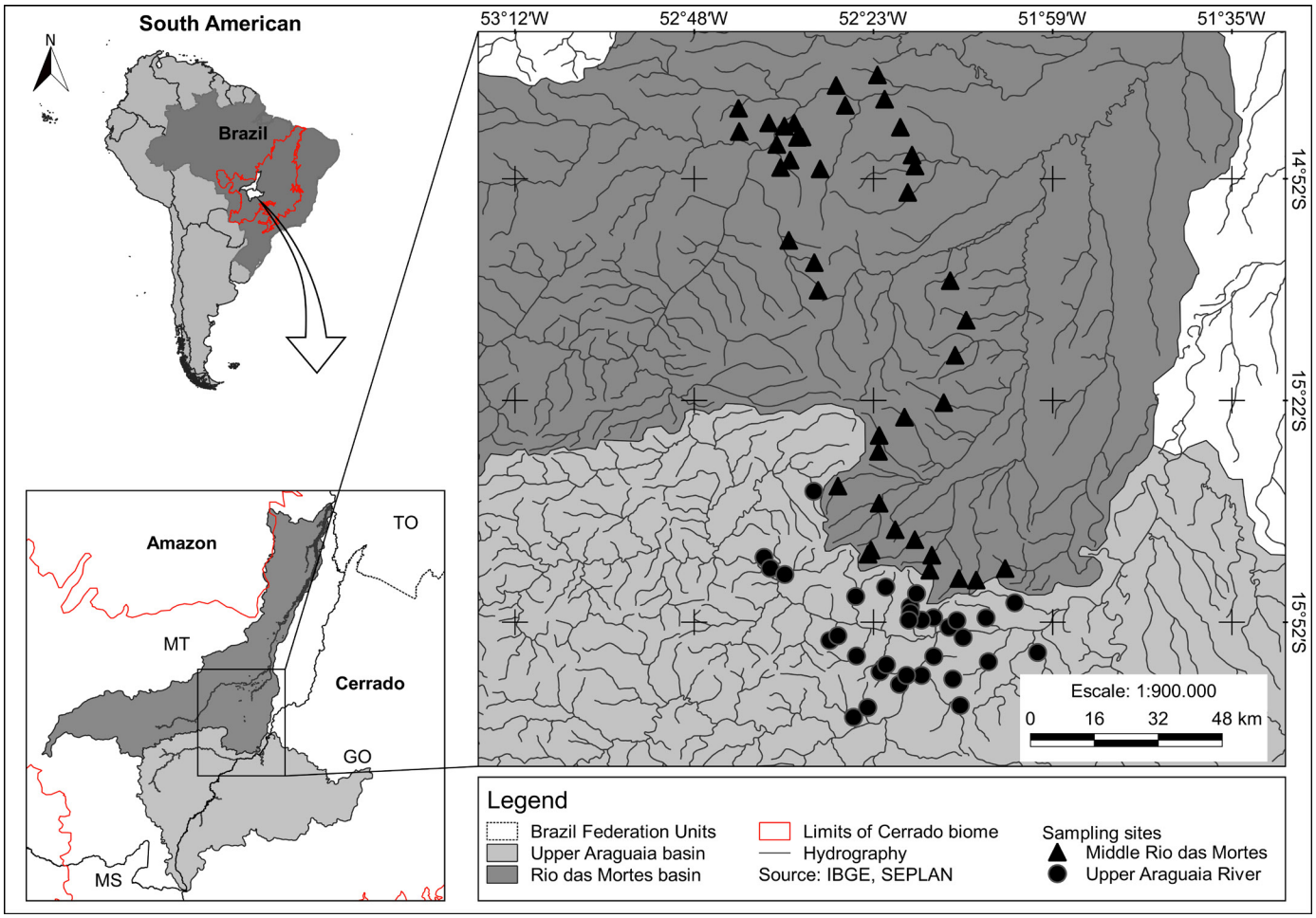


Figure 1. Localization of 72 streams sampled in the Upper Araguaia and Middle Rio das Mortes basin, Tocantins-Araguaia ecoregion.

stretch-50 m into six equidistant transects and recorded the following structural variables, representing the average values of each one of the measured variables in each transect: width, depth obtained from five measurements from one margin to the other, surface water velocity using the method fluctuate material (Teresa & Casatti 2012), and the proportion of substrate structure (i.e., sand, gravel, pebbles, rock, slab, and silt). In addition, we visually quantified the presence of trunks, leaf-litter, and margin structure variables (i.e., thin roots, thick roots, and grass banks) (Cummins 1974, Teresa & Casatti 2012).

We sampled the fish of the streams during the dry periods (May to September) between 2014 – 2017 for more catching efficiency and reduced seasonality effects on collections (Ueida & Castro 1999, Pease et al. 2012). Before initializing the sampling, we blocked the sample stretch limits with 5-mm mesh nets to prevent fish escape. Then, we sampled the fish through the standardized active collection, which consisted of employing four people for approximately one hour. Later, we sampled 35 streams stretch during the day using seine nets (3.0 × 1.5 m × 5.0 mm mesh) and dip nets (0.5 × 0.45 m × 5.0 mm mesh). Next, we used the electrofishing method (Honda EG1000 generator – 220 V, CA) with a single passage downstream, upstream, lasting approximately one hour to sample the other 37 streams. After the sampling, the individuals were anesthetized with benzocaine and sacrificed according to the Federal Council of Veterinary Medicine (in Portuguese CFMV 2012). In the laboratory, we measured the standard length (cm), weighted (g), and identified all specimens collected until the lowest taxonomic level possible using specialized bibliography (Venere & Garutti 2011), and to elaborate the taxonomic list using the Catalogue of Fishes (Fricke et al. 2021).

The Instituto Chico Mendes de Conservação da Biodiversidade(ICMBio; Permit Nº. 45316-1) and the Animal Use Ethics Committee of the Universidade Federal de Mato Grosso (CEUA / UFMT – Nº. 23108.152116) authorized our field collections. We stored the fish collected in the Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos at the Universidade Federal de Mato Grosso, Campus Araguaia, Pontal do Araguaia, Mato Grosso.

3. *Data Analysis*

We used a principal component analysis (PCA) to summarize the environmental characteristics of the streams. After running the PCA, we standardized all environmental variables (except pH) to zero mean and unit variances (z transformation). Next, we analyzed the richness values (number of species) and abundance (total number of individuals by species) of the fish communities using descriptive statistics. We considered as exclusive species those that occurred only within one basin and as unique species those that occurred only in one stream reach, and singletons those with only one specimen (Novotný & Basset 2000). Finally, we evaluated the species richness differences and the efficiency of the sampling effort within both basins using the rarefaction

Table 1. The list of sampled sites in the Upper Araguaia River (UAR) and Middle Rio das Mortes (MRM) basin, Tocantins-Araguaia ecoregion.

Sites	Name	Latitude	Longitude	Order	Width (m)	Depth (cm)	Collection method	Elevation
MRM01	Salgadinho stream	14º40'46.20"S	52º21'53.64"W	Third	4.04	15.78	Electrofishing	263
MRM02	Unnamed stream	14º46'54.48"S	52º36'26.64"W	Second	2.95	15.52	Electrofishing	279
MRM03	Queixada stream	14º44'25.80"S	52º35'25.08"W	Second	3.55	36.39	Electrofishing	273
MRM04	Unnamed stream	14º43'59.52"S	52º34'5.16"W	Second	12.81	21.72	Electrofishing	276
MRM05	Voadeira stream	14º41'35.88"S	52º27'11.88"W	Third	7.23	19.58	Electrofishing	269
MRM06	Unnamed stream	14º45'9.36"S	52º41'30.48"W	Second	2.28	33.65	Electrofishing	322
MRM07	Unnamed stream	14º43'58.80"S	52º37'32.16"W	Third	3.72	21.12	Electrofishing	295
MRM08	Barreira stream	14º38'53.16"S	52º28'26.40"W	Third	2.80	15.68	Electrofishing	277
MRM09	Affluent of the Piau stream	14º42'0.36"S	52º41'36.24"W	Third	2.11	39.65	Electrofishing	334
MRM10	Bacaba stream	14º53'26.16"S	52º18'46.44"W	Third	3.62	22.18	Electrofishing	298
MRM11	Cachoeirinha stream	14º49'50.88"S	52º17'47.40"W	Third	3.67	32.28	Electrofishing	288
MRM12	Duas Pontes stream	14º48'20.88"S	52º18'11.52"W	Fourth	5.66	35.38	Electrofishing	285
MRM13	Estilac stream	14º37'27.84"S	52º22'51.60"W	Second	3.18	30.53	Electrofishing	298
MRM14	Duas Pontes stream	15º5'24.72"S	52º13'2.64"W	Fourth	7.60	29.48	Electrofishing	301
MRM15	Pindaibinha stream	15º10'46.92"S	52º10'53.40"W	Fourth	3.72	32.37	Electrofishing	315
UAR01	Avoadeira stream	15º51'13.32"S	52º15'17.28"W	Third	3.33	30.60	Hand net and Dip net	521
UAR02	Peixinho stream	15º51'32.76"S	52º16'55.20"W	First	3.25	13.62	Hand net and Dip net	373
UAR03	Pitomba stream	15º51'14.76"S	52º8'12.48"W	Third	3.32	12.48	Hand net and Dip net	322
UAR04	Ouro Fino stream	15º49'12.00"S	52º4'19.56"W	Third	3.93	38.14	Hand net and Dip net	335
UAR05	Águas Quentes stream	15º52'31.80"S	52º13'12.36"W	First	3.32	12.88	Hand net and Dip net	325
MRM16	Areia stream	15º44'45.24"S	52º15'47.52"W	First	10.61	23.25	Hand net and Dip net	396
UAR06	Lontra stream	15º49'43.32"S	52º18'25.56"W	First	1.99	12.56	Hand net and Dip net	349
UAR07	Unnamed stream	15º50'33.3"S	52º18'24.9"W	First	6.31	9.36	Hand net and Dip net	345
UAR08	Unnamed stream	15º51'33.48"S	52º18'37.08"W	First	1.99	7.17	Hand net and Dip net	355
MRM17	Grande stream	15º44'31.20"S	52º5'37.68"W	Third	2.90	45.33	Hand net and Dip net	348
MRM18	Grande stream	15º35'39.48"S	52º22'38.28"W	Fourth	7.92	32.57	Hand net and Dip net	355
MRM19	Cava Funda stream	15º39'14.76"S	52º20'27.96"W	Third	5.01	19.20	Hand net and Dip net	398
MRM20	Taquaral stream	15º40'36.48"S	52º17'48.84"W	Third	7.77	43.92	Hand net and Dip net	369
MRM21	Fogaça stream	15º46'4.80"S	52º9'32.40"W	Third	2.66	9.30	Hand net and Dip net	397
MRM22	Ínsula stream	15º45'52.20"S	52º11'52.80"W	Third	3.68	13.27	Hand net and Dip net	388
MRM23	Taquaralzinho stream	15º42'42.48"S	52º15'31.32"W	Third	4.53	37.62	Hand net and Dip net	369
UAR09	Fundo stream	15º47'56.76"S	52º17'35.52"W	Fourth	5.00	21.82	Hand net and Dip net	343
UAR10	Portão stream	15º34'2.64"S	52º31'26.76"W	Second	4.98	27.57	Hand net and Dip net	427
MR24	Capa stream	15º33'19.44"S	52º28'11.64"W	Fourth	4.60	51.30	Hand net and Dip net	421
UAR11	Cambaúva stream	15º43'1.92"S	52º38'9.60"W	First	3.69	56.60	Hand net and Dip net	387
UAR12	Índios stream	15º44'30.84"S	52º37'20.28"W	Third	7.81	31.10	Hand net and Dip net	326
UAR13	Affluent of the Bateia stream	15º45'21.24"S	52º35'21.84"W	First	2.61	17.15	Hand net and Dip net	337
UAR14	Ponte Queimada stream	15º48'20.52"S	52º25'47.64"W	Fourth	5.99	30.70	Hand net and Dip net	377
UAR15	Affluent of the Monte Negro stream	15º58'33.96"S	52º22'30.72"W	First	1.51	22.97	Hand net and Dip net	379
UAR16	Buritirana stream	15º57'37.08"S	52º21'39.60"W	First	2.14	27.70	Hand net and Dip net	360
UAR17	Marimbondo stream	15º54'19.08"S	52º29'17.88"W	Second	3.03	41.00	Hand net and Dip net	344
UAR18	Mangabeira stream	15º53'40.56"S	52º28'12.00"W	Third	2.18	39.30	Hand net and Dip net	326
UAR19	Babilônia stream	15º56'25.44"S	52º25'41.16"W	Fourth	4.49	30.93	Hand net and Dip net	330
UAR20	Buritirana stream	5º51'36.72"S	52º12'8.64"W	Second	6.37	31.27	Hand net and Dip net	338
UAR21	Ribeirão das Mulas stream	15º55'57.00"S	52º1'15.60"W	Fourth	5.23	20.57	Hand net and Dip net	299
UAR22	Ribeirão Capivara stream	15º57'12.60"S	52º7'53.40"W	Fourth	3.99	29.80	Hand net and Dip net	319
UAR23	Affluent of the Avoadeira stream	15º47'3.84"S	52º21'44.64"W	Second	2.70	27.57	Hand net and Dip net	360

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UAR24	Grande stream	15º53'54.24"S	52º11'18.24"W	Third	5.07	14.40	Hand net and Dip net	302
UAR25	Areia stream	15º59'4.20"S	52º16'55.20"W	Fourth	6.33	26.80	Hand net and Dip net	300
UAR26	Jaraguá stream	15º56'29.04"S	52º15'15.48"W	Third	3.52	10.67	Hand net and Dip net	303
MRM25	Sucuri stream	15º15'33.12"S	52º12'23.04"W	Third	4.20	35.35	Electrofishing	338
MRM26	Matrinxã stream	15º21'59.04"S	52º13'55.20"W	Third	5.04	38.30	Electrofishing	363
MRM27	Água Limpa stream	15º23'57.84"S	52º19'12.72"W	Third	4.63	22.47	Electrofishing	415
MRM28	Mineiro stream	15º26'26.16"S	52º22'37.92"W	Third	2.96	22.27	Electrofishing	413
MRM29	Papagaio stream	15º28'35.76"S	52º22'43.32"W	Fourth	6.08	22.28	Electrofishing	388
UAR27	Caixão stream	16º4'45.12"S	52º26'4.92"W	Fourth	3.05	24.05	Electrofishing	320
UAR28	Cambaúva stream	16º3'25.56"S	52º24'10.80"W	Fourth	1.94	11.60	Electrofishing	336
UAR29	Cervo stream	16º0'17.28"S	52º19'53.40"W	Third	2.15	22.54	Electrofishing	326
UAR30	Grota Funda stream	15º59'3.48"S	52º18'56.52"W	Third	4.28	19.28	Electrofishing	332
MRM30	Unnamed stream	14º49'1.20"S	52º34'38.64"W	First	2.03	17.73	Electrofishing	422
MRM31	Unnamed stream	14º45'56.88"S	52º33'39.60"W	First	1.05	41.20	Electrofishing	395
MRM32	Unnamed stream	14º45'53.28"S	52º33'1.80"W	Second	3.23	28.40	Electrofishing	425
MRM33	Chupador stream	14º50'13.92"S	52º30'35.64"W	Second	1.83	27.33	Electrofishing	437
MRM34	Unnamed stream	14º44'34.08"S	52º19'46.20"W	First	6.93	9.57	Electrofishing	306
MRM35	Unnamed stream	15º6'42.84"S	52º30'51.84"W	Second	1.22	46.23	Electrofishing	616
MRM36	Unnamed stream	15º2'58.20"S	52º31'22.80"W	First	1.32	41.80	Electrofishing	575
MRM37	Unnamed stream	14º59'56.40"S	52º34'49.80"W	Second	2.10	65.68	Electrofishing	490
MRM38	Unnamed stream	14º50'2.76"S	52º35'55.32"W	First	1.71	30.92	Electrofishing	353
MRM39	Unnamed stream	15º42'34.92"S	52º24'7.92"W	First	1.34	10.55	Electrofishing	719
MRM40	Unnamed stream	15º42'1.08"S	52º23'43.44"W	First	1.30	16.35	Electrofishing	671
UAR31	Volta stream	16º3'9.72"S	52º11'41.64"W	Second	2.72	29.97	Electrofishing	339
UAR32	Unnamed stream	15º59'33.36"S	52º12'41.40"W	First	1.03	11.68	Electrofishing	356

and extrapolation (R/E) method (Colwell et al. 2012). We based our analyses on incidence data derived from the Hill number series with a 95% confidence interval obtained with the bootstrap method (Hill 1973, Chao et al. 2014, Colwell et al. 2012) using the *iNEXT* function from the *iNEXT* package (Hsieh et al. 2016). We performed all analyses and descriptive statistics with *R* software *version 3.6.1* (R Core Team 2019). We used the *vegan* package (Oksanen et al. 2018) to perform PCA and package *ggplot2* (Wickham 2009) to visualize the results.

Results

In general, the studied streams had low conductivity water (mean = 59.79 µS/cm), high dissolved oxygen levels (mean = 8.02 mg/l), slightly acidic (mean = 5.87 pH), low turbidity (mean = 2.38 NTU), and substrates with sand predominance (mean = 45.58%) and gravel (mean =16.95%). The first two PCA axes explained 27.76% of the environmental variation features in the streams (Figure 2). The first axis explained 16.57% of the variation and was positively associated with water temperature, silt, and grass banks and negatively associated with trunks and leaf-litters (Figure 2). The second axis accounted for 11.19% of the variation and was negatively associated with depth and sand (Figure 2). The first axis distinguished streams with a high proportion of grass banks in margins structures from streams with a high presence internal habits structure (Figure 2). The second axis differentiated streams with a higher proportion of pools and a higher proportion of unconsolidated substrates (sand) from streams with a high proportion of consolidated substrates (rocks) (Figure 2).

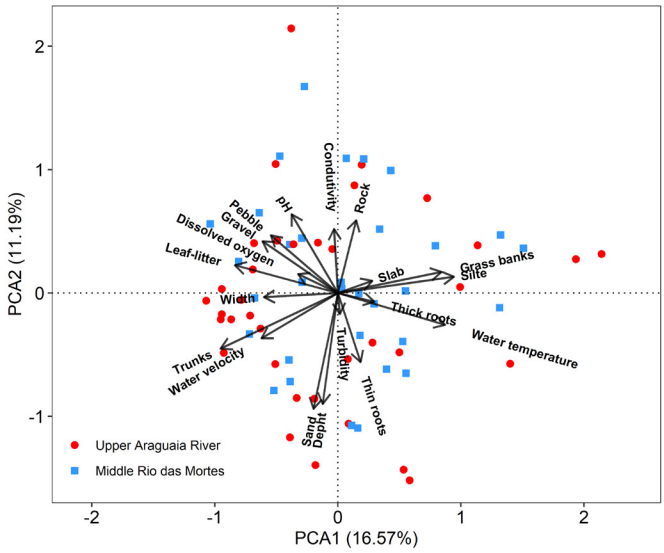


Figure 2. Biplot for principal components analysis (PCA) representing the main environmental variability in the sampling sites in the Upper Araguaia River and Middles Rio das Mortes basin, Tocantins-Araguaia ecoregion.

We collected a total of 14,887 individuals distributed in 137 species, 81 genera, 30 families, and six orders (Figure 3). The most species-rich families were Characidae, Loricariidae, and Cichlidae (40, 25, and 12 species, respectively). More than half of the individuals we sampled were concentrated in eight species (*Astyanax* cf. *goyacensis*, *Psalidodon xavante, Hyphessobrycon* aff. *tenuis*, *Knodus* cf. *breviceps*,

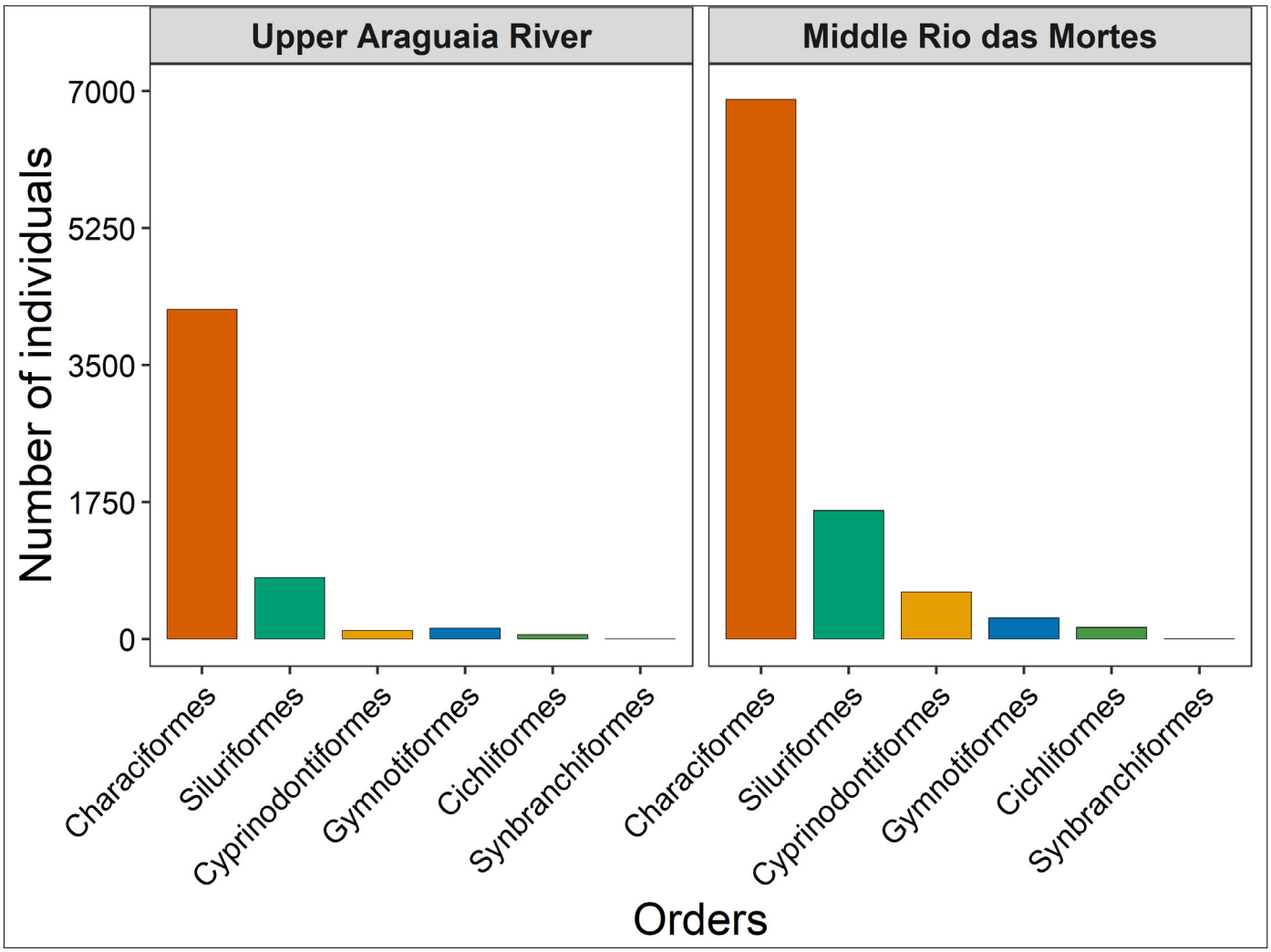


Figure 3. The individual abundance of six orders collected in the Upper Araguaia and Middle Rio das Mortes basins, Tocantins-Araguaia ecoregion.

Odontostilbe sp., *Phenacogaster* sp., *Aspidoras poecilus*, *Melanorivulus zygonectes*) (Table 2, Figure 4). The remaining 98 species (71.5%) had at least five individuals collected, and 18 species were considered singletons. The average richness per stream was 15.5 species (*SD* = 11). The species richness ranged from streams with only one species to streams with 48 species. The most frequent species in our sampled streams were *Astyanax* cf. *goyacensis* (*n* = 51), *Knodus* cf. *breviceps* (*n* = 43), *Characidium* cf. *zebra* (*n* = 40), *Imparfinis mirini* (*n* = 40), and *Moenkhausia oligolepis* (*n* = 40). We found 36 unique species, and 45 species identified only genera level. The *Hypostomus* and *Ancistrus* genera are the richer genera, showing the largest number of species identified up to the genera level.

The basins shared approximately 43% (*S* = 59) of the collected species. When we analyzed the species richness by basin, we found 76 species for Upper Araguaia and 120 in the Middle Rio das Mortes basin. We found 17 exclusives to Upper Araguaia and 61 species exclusive to the Middle Rio das Mortes basin. The rarefaction analysis showed that fish diversity in both Hill diversity series was lower in the Upper Araguaia River compared to the Middle Rio das Mortes basin (Figure 5a). The sampling effort analysis showed that the species richness for both basins was well represented, with a percentage of sample coverage greater than 93% of the estimated species (Figure 5bc). We sampled more than 93% of the Upper Rio Araguaia basin's estimated species richness, and 95% of the Middle Rio das Mortes basin's estimated species richness (Figure 5c).

Discussion

The predominance of the orders and families found in our study aligns with the expected patterns for Neotropical fishes in streams (Castro 1999, Lowe-McConnell 1999, Winemiller et al. 2008, Castro & Polaz 2020). The species richness and abundance of Characiformes, Siluriformes, and Cichliformes recorded in our study also follow the pattern reported in other studies with fish streams to some basins in the Cerrado biome (Leal et al. 2014, Barbosa et al. 2019). This pattern can be explained by the dominance of those orders in the Neotropical region (Lowe-McConnell 1999, Albert et al. 2011, Reis et al. 2016). The predominance of the Characidae family in the studied streams could be because this group is the richest in the Characiformes order, containing over 550 species (Albert et al. 2011) and displaying an extraordinary variation in morphological forms, feeding behaviors, and reproductive strategies (Melo et al. 2004, Winemiller et al. 2008). Such variety allows this group of fish to occur in the most diverse aquatic habitats. In turn, the predominance of Loricariidae fish can be due to the high species

Table 2. Species list with your respective abundance in Upper Araguaia River (UAR) and Middle Rio das Mortes (MRM), Tocantins-Araguaia ecoregion.

	Basin		
ORDER/Family/Species	**UAR**	**MRM**	**Total**
CHARACIFORMES			
Parodontidae			
Apareiodon sp.1		2	2
Apareiodon sp.2	88		88
Parodon pongoensis (Allen, 1942)	6	18	24
Curimatidae			
Curimatella immaculata (Fernández-Yépez, 1948)		1	1
Cyphocharax gouldingi Vari, 1992	25	131	156
Steindachnerina amazonica (Steindachner, 1911)	310	26	336
Prochilondotidae			
Prochilodus nigricans Spix & Agassiz, 1829		7	7
Anostomidae			
Leporinus friderici (Bloch, 1794)	2	2	4
Leporinus klausewitzi Géry, 1960	1	3	4
Leporinus sp.1	10	19	29
Leporinus venerei Britski & Birindelli, 2008		5	5
Erythrinidae			
Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)		32	32
Hoplias cf. *malabaricus* (Bloch, 1974)	17	58	75
Lebiasinidae			
Pyrrhulina australis Eigenmann & Kennedy, 1903	5	15	20
Gasteropelecidae			
Thoracocharax cf. *stellatus* (Kner, 1853)		107	107
Acestrorhynchidae			
Acestrorhynchus falcatus (Bloch, 1794)		4	4
Acestrorhynchus microlepis (Jardine, 1841)		9	9
Serrasalmidae			
Serrasalmus spilopleura Kner, 1858		1	1
Characidae			
Aphyocharax alburnus (Günther, 1869)	5	2	7
Aphyocharax sp.1		20	20
Astyanax argyrimarginatus Garutti, 1999	165		165
Astyanax cf. *goyacensis* Eigenmann, 1908	482	601	1083
Astyanax elachylepis Bertaco & Lucinda, 2005	15	124	139
Astyanax sp.		272	272
Bryconamericus novae Eigenmann & Henn, 1914		56	56
Creagrutus figueiredoi Vari & Harold, 2001	39	61	100
Creagrutus menezesi Vari & Harold, 2001	99		99
Creagrutus seductus Vari & Harold, 2001	70		70
Hemigrammus aff. *levis* Durbin, 1908	6	8	14
Hemigrammus cf. *rodwayi* Durbin, 1909	253	132	385
Hyphessobrycon aff. *tenuis* Géry, 1964	220	403	623
Hyphessobrycon sp.	261		261

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Jupiaba acanthogaster (Eigenmann, 1911)	18	146	164
Jupiaba elassonaktis Pereira & Lucinda, 2007		39	39
Jupiaba polylepis (Günther, 1864)		141	141
Knodus cf. *breviceps* (Eigenmann, 1908)	600	1233	1833
Knodus sp.		91	91
Microschemobrycon sp.1		8	8
Microschemobrycon sp.2	1		1
Moenkhausia aurantia Bertaco, Jerep & Carvalho, 2011	82	224	306
Moenkhausia cf. *comma* Eigenmann, 1908		27	27
Moenkhausia dichroura (Kner, 1858)		2	2
Moenkhausia lepidura (Kner, 1858)		137	137
Moenkhausia oligolepis (Günther, 1864)	102	234	336
Moenkhausia pyrophthalma Costa, 1994		1	1
Moenkhausia sp.		4	4
Moenkhausia venerei Petrolli, Azevedo-Santos & Benine 2016	46	192	238
Odontostilbe sp.	523	1031	1554
Phenacogaster cf. *pectinata* (Cope, 1870)		48	48
Phenacogaster sp.	11	622	633
Psalidodon xavante Garutti & Venere, 2009	511		511
Roeboexodon geryi Myers, 1960		28	28
Serrapinnus cf. *piaba* (Lütken, 1875)		16	16
Tetragonopterus chalceus Spix & Agassiz, 1829		6	6
Tetragonopterus sp.		9	9
Thayeria boehlkei Weitzman, 1957		4	4
Bryconidae			
Brycon falcatus Müller & Troschel, 1844	1	10	11
Iguanodectidae			
Bryconops alburnoides Kner, 1858		51	51
Bryconops giacopinii (Fernández-Yépez, 1950)	12	170	182
Bryconops melanurus (Bloch, 1794)	2	37	39
Crenuchidae			
Characidium cf. *zebra* Eigenmann, 1909	225	262	487
Characidium mirim Netto-Ferreira, Birindelli & Buckup, 2013		2	2
Characidium sp.1		2	2
Characidium sp.2		1	1
SILURIFORMES			
Auchenipteridae			
Trachelyopterus galeatus (Linnaeus, 1758)		2	2
Pimelodidae			
Pimelodus ornatus Kner, 1858		1	1
Pseudopimelodidae			
Microglanis sp.	49		49
Pseudopimelodus cf. *pulcher* (Boulenger, 1887)	1	23	24
Heptapteridae			
Cetopsorhamdia sp.	6		6
Cetopsorhamdia sp.2		1	1
Imparfinis mirini Haseman, 1911	213	237	450

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Imparfinis sp.	3	9	12
Mastiglanis asopos Bockmann, 1994		38	38
Phenacorhamdia somnians (Mees, 1974)	47	37	84
Pimelodella sp.		1	1
Pimelodella sp.1	11	72	83
Pimelodella sp.2		4	4
Pimelodella sp.3	49	50	99
Rhamdia quelen (Quoy & Gaimard, 1824)	4	25	29
Cetopsidae			
Cetopsis coecutiens (Lichtenstein, 1819)	1	11	12
Cetopsis sp.	2	2	4
Asprendinidae			
Bunocephalus sp.	1	7	8
Trichomycteridae			
Ituglanis macunaima Datovo & Landim, 2005	2		2
Stegophilus sp.	1		1
Callichthyidae			
Aspidoras poecilus Nijssen & Isbrücker, 1976	177	381	558
Callichthys callichthys (Linnaeus, 1758)	3	6	9
Corydoras araguaiaensis Sands, 1990		52	52
Corydoras maculifer Nijssen & Isbrücker, 1971		18	18
Loricariidae			
Ancistrus sp.1	3	118	121
Ancistrus sp.2		28	28
Ancistrus sp.3		1	1
Aphanotorulus emarginatus Valenciennes, 1840	1		1
Farlowella aff. *oxyrryncha* (Kner, 1853)		64	64
Farlowella aff. *schreitmuelleri* Arnold, 1936		28	28
Hisonotus sp.		19	19
Hypoptopoma gulare Cope,1878		2	2
Hypostomus aff. *cochliodon* Kner, 1854		1	1
Hypostomus cf. *atropinnis* (Eigenmann & Eigenmann, 1880)	14		14
Hypostomus faveolus Zawadzki, Birindelli & Lima 2008		10	10
Hypostomus sp.1	27	136	163
Hypostomus sp.2	1		1
Hypostomus sp.3	71	61	132
Hypostomus sp.4	37	1	38
Hypostomus sp.5	3		3
Loricaria sp.1	2	4	6
Loricaria sp.2	23	38	61
Loricaria sp.3		5	5
Otocinclus sp.	1		1
Parancistrus sp.		1	1
Parotocinclus britskii Boeseman, 1974	10	47	57
Parotocinclus sp.		39	39
Rineloricaria hasemani Isbrücker & Nijssen, 1979	18	62	80
Sturisoma nigrirostrum Fowler, 1940	6	2	8

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GYMNOTIFORMES			
Sternopygidae			
Eigenmannia trilineata Lópes & Castello, 1966	89	64	153
Sternopygus macrurus (Bloch & Schneider, 1801)	3	33	36
Apteronotidae			
Apteronotus albifrons (Linnaeus, 1766)	5	28	33
Apteronotus leptorhynchus (Ellis, 1912)		2	2
Rhamphichthyidae			
Gymnorhamphichthys petiti Géry & Vu, 1964	5	124	129
Gymnotidae			
Electrophorus electricus (Linnaeus, 1766)		1	1
Gymnotus cf. *carapo* Linnaeus, 1758	36	11	47
Gymnotus sp.	2	9	11
CYPRINODONTIFORMES			
Rivulidae			
Melanorivulus zygonectes (Myers, 1927)	110	599	709
Plesiolebias lacerdai Costa, 1989		2	2
Poeciliidae			
Pamphorichthys araguaiensis Costa, 1991	1	2	3
SYNBRANCHIFORMES			
Synbranchidae			
Synbranchus marmoratus Bloch, 1795	3	7	10
CICHLIFORMES			
Cichlidae			
Aequidens tetramerus Heckel, 1840	38	83	121
Apistogramma sp.		10	10
Biotodoma aff. *cupido* Heckel, 1840		2	2
Cichlasoma sp.	1		1
Crenicichla labrina (Spix & Agassiz, 1831)	18	20	38
Crenicichla reticulata (Heckel, 1840)		7	7
Crenicichla sp.		5	5
Heros aff. *efasciatus* Heckel, 1840		1	1
Laetacara araguaiae Ottoni & Costa, 2009		8	8
Retroculus lapidifer (Castelnau, 1855)		10	10
Retroculus sp.	2	6	8
Satonoperca jurupari (Heckel, 1840)		3	3
Total	5313	9574	14887

richness and diversity of the family in the Neotropical region (over 830 described species). Species in this family feed mainly on detritus and algae (Lujan et al. 2012). Detritus are abundant resources in tropical streams and are fundamental to ecosystem function (Bowen 1983), allowing those streams to support the high abundance and richness of detritivores fishes (Bowen 1983, Power 1983). In addition, the loricariid catfishes have an extraordinary variation in mouth morphologies, allowing them to forage detritus and periphyton in different types of habitat structures (e.g., rocks, trunks, sands, margins, and fast-water environments) presents in the headwater streams (Power 1983, Lujan et al. 2012).

Although the fish orders and families of the basin are well known, this pattern is not proper to species. We identified approximately 30% of the collected species only at the genera level. Many still need more detailed taxonomic and molecular studies (e.g., *Characidium* cf. *zebra*, *Hoplias* cf. *malabaricus* and *Gymnotus* cf. *carapo*). The significant number of species identified only at the genera level shows the need for further taxonomic studies in this basin. Considering the high fish species endemicity within these basins, there is a significant likelihood that many of these species identified only up to the genera level are new species. Previous studies on stream fish in these basins have also found similar patterns, with a great number of species not yet described

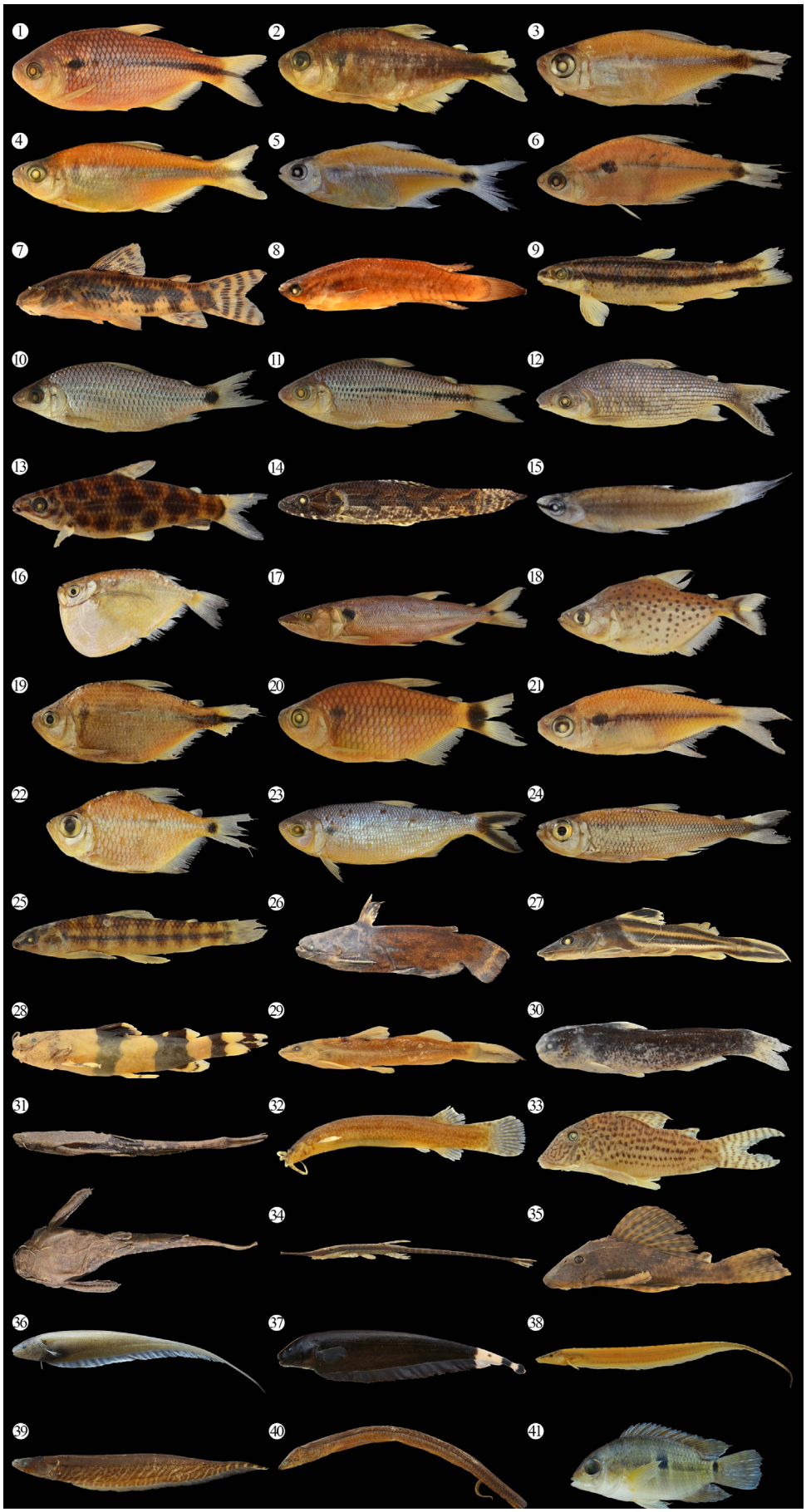

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Figure 4. The eight most abundant sampled species in the Upper Araguaia and the Middle Rio das Mortes basin and representative species of each family. Some families can have more than one more species represented. The total lengths mean are presented after the names of species. 1) *Astyanax* cf. *goyacensis*, 58.9 mm; 2) *Psalidodon xavante*, 45.9 mm; 3) *Hyphessobrycon* aff. *tenuis*, 31.4 mm; 4) *Knodus* cf. *breviceps*, 36.6 mm; 5) *Odontostilbe* sp., 30.9 mm; 6) *Phenacogaster* sp., 36.9 mm; 7) *Aspidoras poecilus*, 31.5 mm; *8) Melanorivulus zygonectes*, 29.6 mm. **Parodontidae** – 9) *Parodon pongoensis*, 64.6 mm; **Curimatidae** – 10) *Cyphocharax gouldingi*, 71.3 mm, 11) *Steindachnerina amazonica*, 105.7 mm; **Prochilondotidae** – 12) *Prochilodus nigricans*, 262.0 mm; **Anostomidae** – 13) *Leporinus* sp.1, 85.7 mm; **Erythrinidae** – 14) *Hoplias* cf. *malabaricus*, 106.3 mm; **Lebiasinidae** – 15) *Pyrrhulina australis*, 37.0 mm; **Gasteropelecidae** – 16) *Thoracocharax* cf. *stellatus*, 58.3 mm; **Acestrorhynchidae** – 17) *Acestrorhynchus falcatus*, 207.5 mm; **Serrasalmidae** – 18) *Serrasalmus spilopleura*, 63.9 mm; **Characidae** – 19) *Moenkhausia aurantia*, 57.3 mm, 20) *Moenkhausia oligolepis*, 57.8 mm, 21) *Moenkhausia venerei*, 34.3 mm, 22) *Tetragonopterus chalceus*, 50.0 mm; **Bryconidae** – 23) *Brycon falcatus*, 250.3 mm; **Iguanodectidae** – 24) *Bryconops giacopinii*, 56.3 mm; **Crenuchidae** – 25) *Characidium* cf. *zebra*, 35.2 mm; **Auchenipteridae** – 26) *Trachelyopterus galeatus*, 112.0 mm; **Pimelodidae** – 27) *Pimelodus ornatus*, 150.5 mm; **Pseudopimelodidae** – 28) *Pseudopimelodus* cf. *pulcher*, 48.5 mm; **Heptapteridae** – 29) *Imparfinis mirini*, 52.3 mm; **Cetopsidae** – 30) *Cetopsis coecutiens*, 57.1 mm; **Asprendinidae** – 31) *Bunocephalus* sp., 79.9 mm; **Trichomycteridae** – 32) *Ituglanis macunaima*, 47.5 mm; **Callichthyidae** – 33) *Corydoras maculifer*, 50.0 mm; **Loricariidae** – 34) *Farlowella* aff. *oxyrryncha*, 102.6 mm, 35) *Hypostomus* sp.3, 53.6 mm; **Sternopygidae** – 36) *Sternopygus macrurus*, 197.6 mm; **Apteronotidae** – 37) *Apteronotus albifrons*, 139.4 mm; **Rhamphichthyidae** – 38) *Gymnorhamphichthys petiti*, 143.9 mm; **Gymnotidae** – 39) *Gymnotus* cf. *carapo*, 150.7 mm; **Synbranchidae** – 40) *Synbranchus marmoratus*, 166.4 mm; **Cichlidae** – 41) *Aequidens tetramerus*, 63.2 mm.

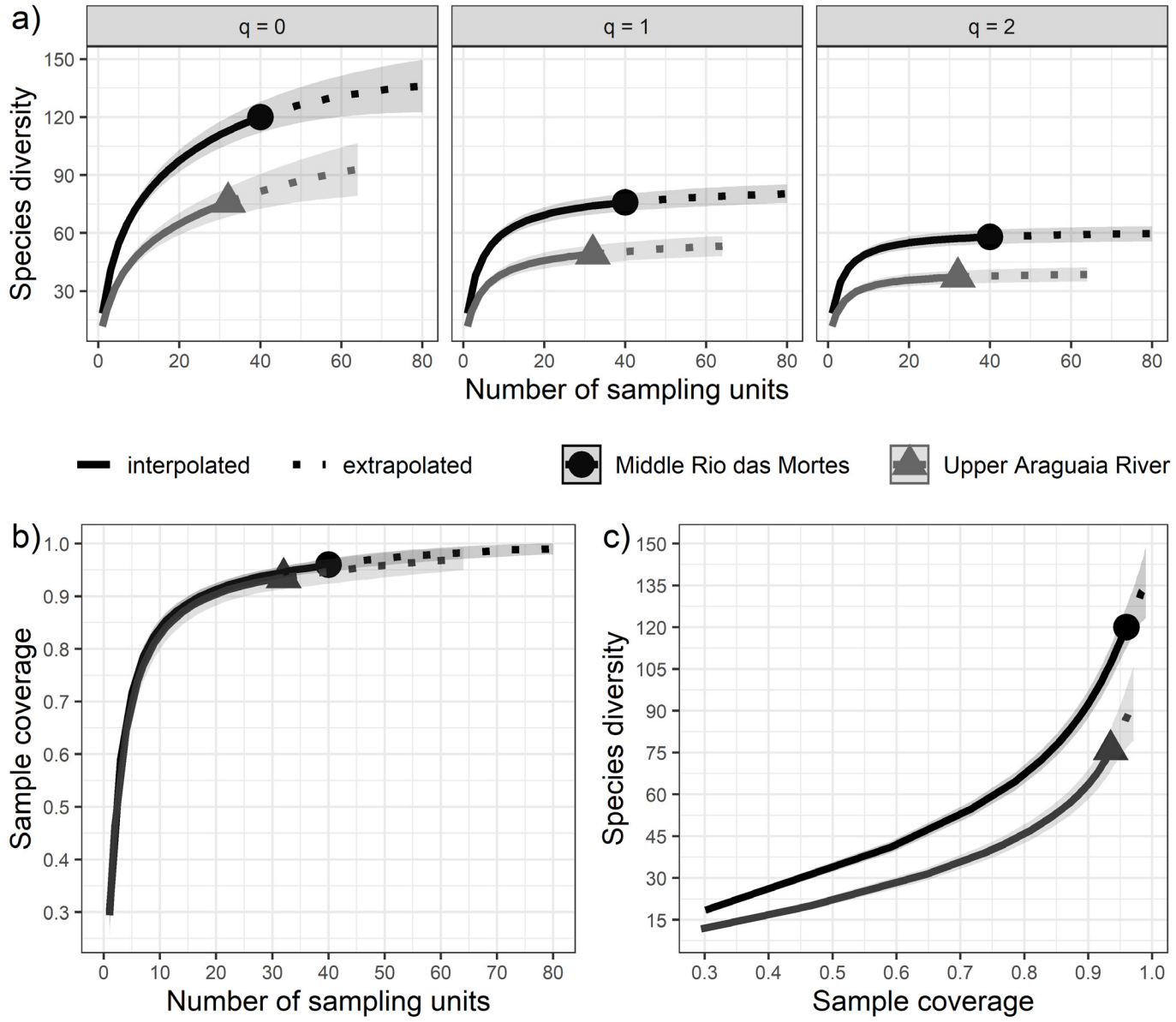


Figure 5. Sampling effort effectiveness for the Upper Araguaia River and the Middle Rio das Mortes basin, using the rarefaction method (solid line) and extrapolation (dotted line) based on Hill's numbers. (a) Incidence-based species accumulation curves, separated by order of diversity: q = 0 (Species richness), q = 1 (Shannon diversity) and q = 2 (Simpson diversity). (b) Sample completeness curves based on the number of sampling sites (c) coverage-based sampling curves based on species richness. We plotted all extrapolation curves to double the sample size, and the shaded area in all figures (a-b) denotes a confidence interval at 95% obtained from a bootstrap method with 999 replications.

(Melo et al. 2004, Matos et al. 2013, Jarduli et al. 2014, Oliveira et al. 2020). This large number of species to be described is one of the most important knowledge gaps in biodiversity (Linnean shortfalls) that needs to be addressed (Hortal et al. 2015). Even after two decades after the first studies with stream fish in the studied region, we still have a long way to know the actual diversity of stream fish in these basins. Although the number of researchers working with stream fish has increased, this advance is based less on taxonomic research than on other stream fish research (Junqueira et al. 2020, Lima 2021).

The average stream fish species richness observed in our study streams was 15 species, like the value found in other stream fish studies in this ecoregion (Melo et al. 2004, Matos et al. 2013, Barbosa et al. 2019, Oliveira et al. 2020). However, our data showed a wide variance in the number of species per stream. We sampled streams with one species and streams with up to 48 species. We believe that such variation in species richness between streams can be explained by environmental heterogeneity and hydrographic network size (Lowe-McConnell 1987, Tedesco et al. 2008, Vieira et al. 2018). The water physicochemical characteristics and habitat structures can vary spatially between nearby streams. This condition increases local environmental heterogeneity and makes fish diversity vary between streams (Benda et al. 2004). Besides, streams with more extensive drainage networks should support more diverse communities than streams with smaller drainage networks (Zbinden & Matthews 2017).

In our study, species with wide distribution (species that occurred in more than 50% of the sites) over the sampled streams belonged to groups of fish with more diversified feeding behaviors and reproductive strategies (Winemiller 1989). For the species present in our samples, we highlight the nektonic omnivores characids that feed on materials drifting in the water column and have split spawning (*Astyanax* cf. *goyacensis*; *Knodus* cf. *breviceps*, and *Moenkhausia oligolepis*), the benthic invertivores with fusiform bodies (*Characidium* cf. *zebra*), and the benthic omnivores catfish (*Imparfinis mirini*).

The species abundance patterns we found in this study are like those observed in streams with lower environmental degradation (Ferreira & Casatti 2006, Casatti, Ferreira & Langeani 2009). The species rarity of our samples is relatively high, with approximately 71.5% of them having at least five individuals collected and 18 having only one sampled specimen. The rare species patterns in ecological communities vary in abundance, where few species are common, some have intermediate abundance, and many are rare (Magurran & Henderson 2003). The number of rare species can vary from site to site because of natural variations in species abundance distributions or anthropogenic stressors (Preston 1948, Magurran & Henderson 2011). It is important to highlight that the rarity pattern for some species found in our study differs between the basins; for example, *Gymnorhamphichthys petiti* was rare in Upper Araguaia, but was abundant in the Middle Rio das Mortes basin. On the other hand, *Hypostomus* sp.4 was abundant in Upper Araguaia and rare in the Middle Rio das Mortes basin. Furthermore, the significant number of exclusive species in each basin shows distinct fish communities between them. Considering that the Araguaia River and Rio das Mortes belong to the same ecoregion (Abell et al. 2008), we assume that species dispersion (capacity for colonizing new habitats) and environmental filters are the main drivers responsible for the differences observed.

In this study, we did not find the fish species endangered. This finding can indicate a good ecological integrity of streams once the most sampled streams still have relatively preserved environmental conditions (Lima 2019). However, this scenario can change in the future. There is a series of threats to fish biodiversity within the basin's streams, mainly due to deforestation and the planned hydropower dams (Coe et al. 2011, Latrubesse et al. 2019, Dagosta et al. 2020, Pelicice et al. 2021). Considering the exclusive fish species of both basins, the human threats in those regions, and the few existent protected areas, we need a better look at this ecosystem's aquatic biodiversity conservation. This study contributes to filling one critical biodiversity knowledge gap (i.e., geographic distribution—Wallacean shortfalls) for fish species in streams in the Araguaia River and Rio das Mortes basins.

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Author Contributions

Luciano B. Lima**:** Substantial contribution in the concept and design of the study; contribution to data collection; contribution to data analysis and interpretation; contribution to manuscript preparation.

Fagner Junior M. Oliveira**:** Substantial contribution in the concept and design of the study; contribution to data collection; contribution to manuscript preparation; contribution to critical revision, adding intelectual content.

Fernando V. Borges**:** Substantial contribution in the concept and design of the study; contribution to data collection; contribution to manuscript preparation.

Fabiano Corrêa**:** Substantial contribution in the concept and design of the study; contribution to manuscript preparation; contribution to critical revision, adding intelectual content.

Dilermando P. Lima-Junior**:** Substantial contribution in the concept and design of the study; contribution to data collection; contribution to manuscript preparation; contribution to critical revision, adding intelectual content.

Conflicts of interest

All authors declare no competing interests.

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Article

Yeasts in native fruits from Brazilian neotropical savannah: occurrence, diversity and enzymatic potential

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Abstract: Cerrado is the second largest phytogeographic domain in Brazil, with a huge ethnobotany variety, including fruit species that stand out for their economic, industrial, biotechnological and medicinal potential. The objective of this study was to characterize the diversity of culturable yeasts and their potential for the production of hydrolytic enzymes in fruits of 13 species of native plants of the Cerrado in Brazil. Sequencing the 26S rRNA gene identified the isolates. The enzymatic potential was evaluated using specific substrates for the enzymes amylases, cellulases, proteases, and pectinases. Nine of the 13 fruit species analyzed showed yeast growth, totaling 82 isolates, identified in 26 species. The phylum Ascomycota predominated over Basidiomycota. The fruits of *Butia capitata* presented the highest species richness. *Candida* and *Meyerozyma* were the most frequent genera. About 57% of the isolates were able to produce at least one of the enzymes analyzed. The species *Papiliotrema flavescens, Hanseniaspora meyeri, Meyerozyma guilliermondii*, and *Rhodotorula mucilaginosa* produced all the enzymes tested. The results were found to expand the knowledge about the yeast communities present in fruits of the Cerrado native plants, evidencing the presence of species shared among the plants, and their potential for biotechnological use in the future.
Keywords: *hydrolytic enzymes;* Candida*; Cerrado domain;* Meyerozyma*; fruit pulp.*

Leveduras em frutos nativos do Cerrado: ocorrência, diversidade e potencial enzimático

Resumo: O Cerrado é o segundo maior domínio fitogeográfico do Brasil, com grande variedade etnobotânica, incluindo espécies frutíferas que se destacam por seu potencial econômico, industrial, biotecnológico e medicinal. O objetivo deste trabalho foi caracterizar a diversidade de leveduras cultiváveis e seu potencial para a produção de enzimas hidrolíticas em frutos de 13 espécies de plantas nativas do Cerrado brasileiro. O sequenciamento do gene 26S rRNA identificou os isolados. O potencial enzimático foi avaliado utilizando substratos específicos para as enzimas amilases, celulases, proteases e pectinases. Nove das 13 espécies de frutos analisadas apresentaram crescimento de levedura, totalizando 82 isolados, identificados em 26 espécies. O filo Ascomycota predominou sobre Basidiomycota. Os frutos de *Butia capitata* apresentaram a maior riqueza de espécies. *Candida* e *Meyerozyma* foram os gêneros mais frequentes. Cerca de 57% dos isolados foram capazes de produzir pelo menos uma das enzimas analisadas. As espécies *Papiliotrema flavescens, Hanseniaspora meyeri, Meyerozyma guilliermondii* e *Rhodotorula mucilaginosa* produziram todas as enzimas testadas. Os resultados encontrados ampliam o conhecimento sobre as comunidades de leveduras presentes nos frutos das plantas nativas do Cerrado, evidenciando a presença de espécies compartilhadas entre as plantas, e seu potencial para uso biotecnológico no futuro.
Palavras-chave: *Enzimas hidrolíticas;* Candida*; Domínio Cerrado;* Meyerozyma*; Polpa de frutas.*

Introduction

The Cerrado is the second largest phytogeographic domain in Brazil occupying about 2 million km^2 with phytophysiomic formations of tropical fields, savannah, and seasonal forest (Klink, 2005; Buzatti et al. 2018). This biome is considered a biodiversity hotspot characterized by having a high number of endemic vascular plant species (Souza et al. 2016; Buzatti et al. 2018). It is estimated that there are more than 4.400 plants native to this biome and, among this huge ethnobotanical variety, fruit species stand out for their economic, industrial, biotechnological, and medicinal value (Wantzen et al. 2012; Machado et al. 2014; Costas et al. 2018).

Among the native fruit species of the Brazilian Cerrado, some of the most studied and used for economic and biotechnological purposes are the *Anacardium humile* A.St.-Hil (Cerrado cashew) (Silva et al. 2013; Araújo et al. 2018), *Caryocar brasiliense* Cambess (pequi) (Paz et al. 2014) and *Mauritia flexuosa* Lf (buriti) (Castro et al. 2014; Garcia et al. 2015; Pratulea et al. 2019). The fruits of these plant species, besides being rich in nutritional values, are known to present molecules with anti-inflammatory, antioxidant, antimicrobial, thickening, and aromatic properties (Silva et al. 2013; Costas et al. 2018). In addition, to be known for their nutraceutical characteristics, the Cerrado fruits have great economic importance for small farmers and extractivists in the Northwest region of the state of Minas Gerais - Brazil, like the cooperative "Copabase" (www.copabase.org), whose main objective is the commercialization of family and artisanal production products, such as fruit pulps, sweets, cakes, and other food products from the Cerrado fruits (Souza et al. 2018).

Several microbial communities have the ability to colonize the interior of plant organs, known as endophytic microorganisms. The term endophytic concerns to all microorganisms that inhabit the interior of organs, tissues and in the inter-and intracellular space of plant cells in a mutualistic way, and may play crucial roles for the maintenance of plant health or producing plant growth regulators (Liu et al. 2019) and alkaloids that act in the protection of plant tissues against herbivores (Felber et al. 2016). Among these microorganisms, the presence of yeasts in the Cerrado native fruits has been attracting attention because they are important sources of new biotechnological resources (Moreira et al. 2015; Sperandio, et al. 2015; Vale, et al. 2015).

Yeasts represent a portion of the natural microbiota of the plant phyllosphere (leaves, stems, shoots, flowers, and fruits) (Vadkertiová et al. 2012; Ling et al. 2019; Piombo et al. 2020) and more recently has been reported in fruits of the Cerrado native plants such as *Eugenia lutescens* Cambess, *Campomanesia xanthocarpa* (O. Berg) and *Brosimum gaudichaudii* Trécul (Moreira et al. 2015); *Byrsonima crassifolia* Steud and *Eugenia dysenterica* DC (Sperandio et al. 2015) and also in fruits of seven more native species of the Cerrado: *Ouratea hexasperma* Baill, *B. gaudichaudii* Trécul, *Passiflora nitida* Kunth, *Myrcia tomentosa* DC, *Byrsonima coccolobifolia* Kunt, *Guapira graciliflora* (Mart. Ex Schmidt) and *C. brasiliense* Cambess (Coelho et al. 2020). Some of these species have the potential for biological control of post-harvest pathogens, such as *Penicillium digitatum in vitro* and *in vivo* tests (Sperandio et al. 2015), emphasizing the importance of knowledge about yeast diversity in the Cerrado native fruits and its biotechnological application.

Yeasts have a high biochemical and physiological versatility, which make them important sources of biomolecule prospecting, similar to enzymes that are commonly used in industrial applications (Carvalho et al. 2013). Currently, interest in the production of enzymes from microbial sources has increased due to the wide application potential, ranging from the production of bioenergy and biofuels to its application in food, textile and papermaking industries (Romo-Sánchez et al. 2010). However, it is still necessary to search for native yeast species not listed as good producers of active biomolecules. It is important to highlight the need to isolate and characterize yeasts from different habitats, aiming at describing the still unknown diversity, and to verify the biotechnological potential that these microorganisms may present (Romo-Sánchez et al. 2010; Carvalho et al. 2013).

Understanding the importance of the Cerrado bioeconomy, its native plants, and the scarcity of research on yeast diversity in native fruits of this Biome, this study aimed to: a) describe the occurrence, density, and diversity of culturable yeasts in fruits of the Cerrado native plants; and b) evaluate the potential of isolated strains for hydrolytic enzyme production.

Materials and Methods

1. Area of study and sampling of fruits

Samples were collected in the Northwest region of the state of Minas Gerais, in the municipality of Arinos, Brazil (Table 1). Fruits of 13 Cerrado native species were collected, as follows: *Anacardium humile* Mart., *Annona crassiflora* Mart., *Butia capitata* Mart., *Caryocar brasiliense* Cambess, *Eugenia dysenterica* DC., *Hancornia speciosa* Gomes, *Hymenaea stigonocarpa* Mart. Ex Hayne, *Mauritia flexuosa* Lf., *Passiflora cincinnata* Mast., *Psidium cattleyanum* Sabine, *Solanum lycocarpum* A.St-Hil, *Syagrus oleracea* Becc and *Talisia esculenta* Radlk (Figure S1). Samples of healthy fruits, ripe, without perforations and smashes, were collected, stored at 4ºC, and processed in less than 48 hours after collection.

2. Isolation and molecular identification

For the isolation of total yeasts (epiphytic + endophytic), samples of fruits from 13 species of plants were collected, being three different trees for each plant species and three different samples for each tree of the same plant species. Fruits were superficially washed with distilled running water to remove dust and dried naturally at room temperature. Aliquots of 10 g composed of pulp and peel of each fruit sample, in triplicate, macerated in 100 ml of peptone water (0.1%), and then homogenized under agitation at 150 rpm for 30 minutes, and diluted to 10^{-3}. Aliquots of 100µL were seeded in YM agar (0.3% yeast extract; 0.3% malt extract; 0.5% peptone; 10% glucose; 2% agar; 100mg. ml^{-1} chloramphenicol) (Kurtzman & Fell, 1998). The plates were incubated at 28 ºC for 5-7 days. After growth, colony-forming units (CFU) were counted, and isolation in pure cultures was performed from each colony's morphological characteristics. The pure cultures were cryopreserved using YM broth with 25% glycerol in a freezer at -80 ºC.

DNA was extracted according to modified Kurtzman & Fell protocol (1998). The isolates were grown in YM broth for 48 hours at 28 ºC under the agitation of 150 rpm. Cell lysis was performed using 0.1 g of glass beads and 200 µL of extraction buffer and agitated for 1 minute. For protein precipitation, 200 µL of phenol, chloroform, and isoamyl alcohol (25:24:1) was used, and subsequently, the DNA was precipitated using isopropyl alcohol (1 hour at -20ºC). The DNA was resuspended in 30µL of Milli-Q water and stored at -20 ºC.

The DNA amplification was performed according to the Kurtzman & Robnett protocol (1998) using domain D1/D2 of the major ribosomal

Table 1. Cerrado native species host plants collected in the municipality of Arinos, Minas Gerais, Brazil.

Botanical Family	Host species	Popular name	Geographic Coordinates	Date of collection
Anacardiaceae	*Anacardium humile* Mart.	Caju-do-Cerrado	15° 55' 01" S e 46° 6' 20" W	08/08/2014
Annonaceae	*Annona crassiflora* Mart.	Araticum	15° 55' 01" S e 46° 6' 20" W	03/14/2014
Apocynaceae	*Hancornia speciosa* Gomes	Mangaba	15° 55' 01" S e 46° 6' 20" W	03/14/2014
Arecaceae	*Butia capitata* Mart.	Coquinho-azedo	15° 51' 20" S e 45° 43' 52" W	03/16/2014
Arecaceae	*Mauritia flexuosa* Lf.	Buriti	15° 51' 20" S e 45° 43' 52" W	08/16/2014
Arecaceae	*Syagrus oleracea* Becc	Coco-guariroba	16° 1' 12" S e 45° 58' 39" W	03/30/2014
Caryocaraceae	*Caryocar brasiliense* Cambess	Pequi	15° 55' 01" S e 46° 6' 20" W	03/15/2014
Fabaceae	*Hymenaea stigonocarpa* Mart. Ex Hayne	Jatobá-do-Cerrado	15° 51' 20" S e 45° 43' 52" W	08/14/2014
Myrtaceae	*Eugenia dysenterica* DC.	Cagaita	15° 55' 01" S e 46° 6' 20" W	10/12/2014
Myrtaceae	*Psidium cattleyanum* Sabine	Araçá	15° 55' 01" S e 46° 6' 20" W	03/28/2014
Passifloraceae	*Passiflora cincinnata* Mast.	Maracujá-do-Cerrado	16° 1' 12" S e 45° 58' 39" W	05/19/2014
Sapindaceae	*Talisia esculenta* Radlk	Pitomba	15° 51' 20" S e 45° 43' 52" W	03/16/2014
Solanaceae	*Solanum lycocarpum* A.St-Hil	Lobeira	15° 51' 20" S e 45° 43' 52" W	06/09/2014

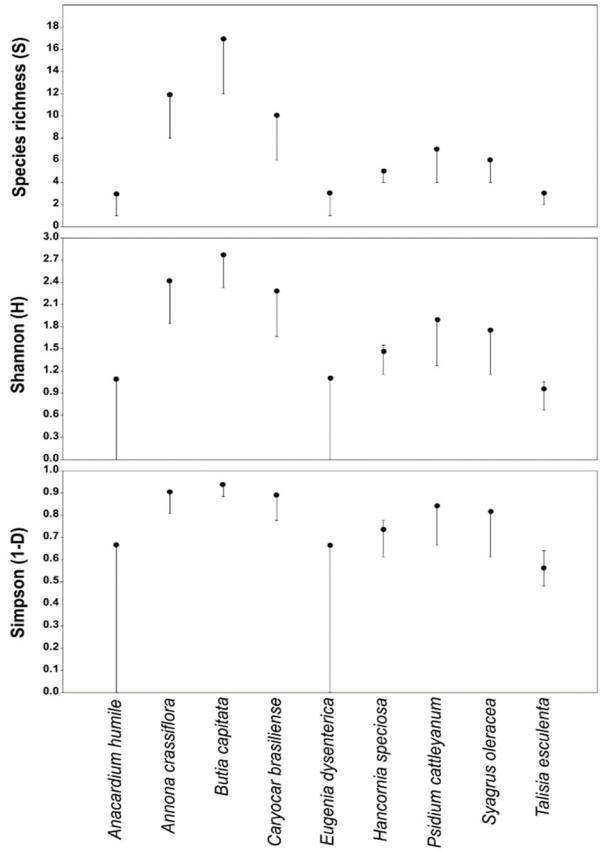


Figure 1. Diversity indexes of yeast communities present in fruits of the Cerrado native plants from the Northwest of Minas Gerais, Arinos, Brazil.

rDNA subunit (LSU) 26S, with the pair of primers: NL1 (5'-GCA TAT CAA TAA GCG GAG GAA AAG–3') and NL4 (5'-GGT CCG TGT TTC AAG ACG G -3') (O'donnel et al. 1993). The PCR reaction was performed with a final volume of 25µl, containing 20 pmol of each primer,1.5 mM $MgCl_2$, and 0.2 mM dNTPs. The thermocycling program consisted of initial denaturation at 94ºC for 3 minutes, followed by 33 denaturation cycles from 94 ºC to 1 minute, annealing at 56 ºC for 30 seconds, and extension at 72 ºC for 1 minute, and a final extension at 72 ºC for 6 minutes.

The amplicons were purified with the enzyme *ExoSAP-IT*® and sent for sequencing at the Catholic University of Brasília (UCB) using the ABI 3130xl Applied Biosystems sequencer, using the Sanger method (Sanger et al. 1997). The formation of their peaks ascertained the quality of the sequences. These sequences were prepared by removing initial and final noises with the Bio Edit Sequence Alignment Editor version 7.5. After that, they were submitted to the Database of the National Center for Biotechnology Information (NCBI (http://www.ncbi.nlm.nih.gov/), using the program *BLASTn*. The parameters of choice were lower e-value, greater coverage value, and greater identity. The alignment and phylogenetic analyses were made using the *MEGA 6 software*® using the Maximum-likelihood Estimation Method Maxim Verisiillability method (Tamura et al. 2013).

The diversity indices (Species richness S, Simpson 1-D, Shannon H) were calculated based on an abundance matrix (isolates *versus* host plant) using the *Past program* (version 3.13).

3. Enzymatic production

The enzymatic isolates characterization was performed as described in Souza (2008) and Landell (2009) with some modifications. The isolates were cultured in YM broth at 28 °C until reaching the cell density of 10^8 cells/mL. The evaluations were carried out using the "cup plate" methodology, where 100 µl of the yeast solution were inoculated in a perforation (cup) performed with a Pasteur pipette in triplicate at three equidistant points with a diameter of 6 mm. Culture media containing a specific substrate for each enzyme were used. Amylase production was evaluated in Agar-starch (Agar, 18 $g.L^{-1}$; starch, 10 $g.L^{-1}$), was cellulases were evaluated in Agar-CMC (Agar, 18 $g.L^{-1}$, carboxymethylcellulose, 10 $g.L^{-1}$). The Agar-pectin (Agar, 18 $g.L^{-1}$, pectin, 10 $g.L^{-1}$) was used to detect pectinases and Agar-gelatin-milk (Agar, 18 $g.L^{-1}$, 10% gelatin solution, skim milk 10%) for proteases. After a 24-hour incubation period, plates were washed with 0.1 N iodine solution for amylase analysis, Congo red 0.1% for cellulase analysis and 5 N hydrochloric acid for pectinase analysis. No revealing substance was required for protease tests. The formation of degradation halos detected the enzymes and production was expressed by forming the halos (mm).

Results

1. Yeast density and diversity

A total of 82 yeast isolates were recovered from fruits from nine of the 13 hostesses analyzed in this study. Yeast growth was not detected

in the fruits of four plant species, including *S. lycocarpum* (Lobeira), *H. stigonocarpa* (Jatobá-do-Cerrado), *M. flexuosa* (Buriti) and *P. cincinnata* (Maracujá-do-Cerrado). The host *B. capitata* (Coquinho-azedo) presented the highest number of isolates (21), while the fruits of *S. oleracea* (Coco-guariroba) presented the highest population density of yeasts (7.2 x 10^4 CFU .g^{-1} fruit). The fruits of *T. esculenta* (Pitomba), *C. brasiliense* (Pequi) and *E. dysenterica* (Cagaita) presented population densities lower than 1.0 x 10 CFU g^{-1}. The hostesses *A. humile* (Cajuzinho-do-Cerrado) and *E. dysenterica* (Cagaita) presented the smallest number of isolates (three isolates) (Table 2).

The highest richness of yeast species (S) was found in the fruits *of B. capitata,* followed by *A. crassiflora* and *C. brasilienses*. The fruits with the lowest species richness were *A. humile, E. dysenterica,* and *T. esculenta.* The diversity of yeasts in the fruits of plant species, represented by the Shannon (H) and Simpson (1-D) indexes, varied widely from plant to plant (Figure 1). The Shannon and Simpson indexes of *B. capitata* were 2.8 and 1.0, respectively, thus having the highest species diversity values compared to the other analyzed species. *A. crassiflora* occupied the second place with Shannon index of 2.4 and Simpson of 0.9, followed by *C. brasiliense* with Shannon of 2.3 and Simpson of 0.89. *T. esculenta* presented the lowest values in the Shannon and Simpson indexes.

Among the isolates, 26 yeast species were identified in fruit samples from nine plant species where there was colony growth (Table 3). The phylum Ascomycota was predominant, representing 80% of the isolates distributed in 10 genus: *Meyerozyma, Candida, Debaryomyces, Wickerhamomyces, Hanseniaspora, Pichia, Kurtzmaniella, Yarrowia, Eremothecium*, and *Lodderomyces*. Phylum Basidiomycota corresponds to 20% of the isolates, divided into four genus: *Rhynchogastrema, Papiliotrema, Pseudozyma*, and *Rhodotorula.*

The species composition of the culturable yeast communities varied among the different fruits (Figure 2). The species *Pichia terricola* showed higher relative abundance in the fruits of *H. speciosa.* In the fruits *B. capitata* and *P. cattleyanum*, the species *Papiliotrema flavescens* and P. *terricola* showed higher relative abundance.

The genera *Candida* and *Meyerozyma* were the most frequent, present in 89% of the fruits analyzed here. *M. caribbica* was the species with the highest occurrence, present in five different fruits, and the following plant species: *B. capitata* (Coquinho-azedo), *A. crassiflora* (Araticum), *H. speciosa* (Mangaba), *E. dysenterica* (Cagaita) and *A. humile* (Caju-Cerrado). The species *M. guilliermondii, Debaryomyces nepalensis, Hanseniaspora meyeri* and *Pichia terricola* were isolated in 44.4% of the fruits analyzed here. The species *D. fabryi* was less frequent here, exclusively in *B. capitata* fruits.

2. Enzymatic production

Of the 82 isolates, 43 (52,43%) isolates produced at least one of the enzymes sought in this study, and 12 isolates produced amylases, 21 isolates produced cellulases, 25 isolates produced proteases, and 18 isolates produced pectinase. The isolates with higher enzymatic production were recovered from the fruits of *B. capitata, A. crassiflora* and *S. oleracea* (Table 4). Of the 82 isolates, only 39 (47,56%) did not show the care of the enzymes investigated here, being they of the following species *Candida easanensis, Debaryomyces fabryi, D. nepalensis, Hanseniaspora meyeri, Meyerozyma guilliermondii, Pichia terricola, Pseudozyma aphidis, Wickerhamomyces anomalus* and *W. rabaulensis.*

Among the enzymes evaluated, the most produced were proteases being present in 52.08% of the isolates producing the enzymes researched; followed by cellulases, found in 41.66%; pectinases, found in 27.08% of the isolates; and finally, amylases found in 25% of the isolates.

Species of the genus *Candida* are among the best enzymatic producers, with four different species, *C. suratensis, C. oleophila, C. natalensis* and *C. intermedia*; followed by the genus *Hanseniaspora*, with the species *H. opuntiae*, *H. meyeri*, and *H. uvarum*; and finally, the genus *Debaryomyces* and *Meyerozyma*, both with two species. The others genera presented only one species capable of producing one or more of the enzymes tested in this study. Four yeast species produced the four enzymes sought, as *P. flavescens, H. meyeri, M. guilliermondii* and *Rhodotorula mucilaginosa* (Table 4). All these yeast species mentioned were isolated in more than three host species, evidencing that these species may be frequent in several Cerrado fruits.

Table 2. Yeast density per gram of fruit (CFU/g. fruit $^{-1)}$ and number of isolates in fruits of Cerrado native host plants, collected in the municipality of Arinos, Minas Gerais, Brazil.

Botanical Family	Host species	Popular name	Yeast density (CFU/g. $fruit^{-1}$)	Number of yeast isolates
Anacardiaceae	*Anacardium humile* Mart.	Cajuzinho-do-Cerrado	2.2 X 10^3	3
Annonaceae	*Annona crassiflora* Mart.	Araticum	4.4 X 10^2	15
Apocynaceae	*Hancornia speciosa* Gomes	Mangaba	5.8 X10^2	7
Arecaceae	*Butia capitata* Mart.	Coquinho-azedo	5.8 X 10^3	22
Arecaceae	*Mauritia flexuosa* Lf.	Buriti	N/C*	0
Arecaceae	*Syagrus oleracea* Becc	Coco-guariroba	7.2 X 10^4	7
Caryocaraceae	*Caryocar brasiliense* Cambess	Pequi	< 1.0 X 10	11
Fabaceae	*Hymenaea stigonocarpa* Mart. Ex Hayne	Jatobá-do-Cerrado	N/C*	0
Myrtaceae	*Psidium cattleyanum* Sabine	Araçá	2.4 X 10^2	9
Myrtaceae	*Eugenia dysenterica* DC.	Cagaita	< 1.0 X 10	3
Passifloraceae	*Passiflora cincinnata* Mast.	Maracujá-do-Cerrado	N/C	0
Sapindaceae	*Talisia esculenta* Radlk.	Pitomba	< 1.0 X 10	5
Solanaceae	*Solanum lycocarpum* A.St-Hil	Lobeira	N/C*	0
Total:				**82**

*N/C- There was no growth of yeast colonies.

Table 3. Inventory of yeast species in fruits of native plant species of the Northwest Cerrado, Arinos, Minas Gerais, Brazil: host species, isolate ID, yeast species, and GenBank match.

BOTANIC FAMILY	HOST SPECIES	ISOLATED ID	SPECIES	GENBANK MATCH	ID (%)
Anacardiaceae	*Anacardium humile*	CAJ3	*Debaryomyces nepalensis*	JX068681	100
		CAJ2	*Meyerozyma caribbica*	KP797883.1	99
		CAJ4	*Rhynchogastrema complexa*	GU321090.2	99
Annonaceae	*Annona crassiflora*	ARA5	*Candida easanensis*	AY634571.1	99
		ARA26	*Debaryomyces fabryi*	KP263777.1	99
		ARA12	*Debaryomyces fabryi*	KP263777.1	99
		ARA21	*Debaryomyces nepalensis*	JX068681	100
		ARA11	*Hanseniaspora meyeri*	FM200038	99
		ARA16	*Hanseniaspora meyeri*	FM200038	99
		ARA28	*Hanseniaspora opuntiae*	EU386744.1	99
		ARA13	*Lodderomyces sp.*	KF830177.1	95
		ARA22	*Meyerozyma caribbica*	KP797883.1	99
		ARA6	*Meyerozyma guilliermondii*	KM885980	99
		ARA18	*Meyerozyma guilliermondii*	KM885980	99
		ARA3	*Pichia sp.*	AB126678.1	99
		ARA25	*Pseudozyma aphidis*	AB617892.1	98
		ARA23	*Rhodotorula mucilaginosa*	KP760069.1	100
		ARA31	*Rhodotorula mucilaginosa*	KP760069.1	100
		ARA9	*Wickerhamomyces anomalus*	KM978209.1	99
Apocynaceae	*Hancornia speciosa*	MAN12	*Hanseniaspora meyeri*	FM200038	99
		MAN2	*Meyerozyma caribbica*	KP797883.1	99
		MA11	*Pichia terricola*	KJ506735.1	100
		MAN9	*Pichia terricola*	KJ506735.1	100
		MAN1	*Pichia terricola*	KJ506735.1	100
		MAN10	*Rhynchogastrema complexa*	GU321090.2	99
		MAN3	*Wickerhamomyces rabaulensis*	AB858464	100
Arecaceae	*Butia capitata*	COQ2	*Candida easanensis*	AY634571.1	99
		COQ37	*Candida suratensis*	AB500863.1	100
		COQ24	*Debaryomyces nepalensis*	JX068681	100
		COQ18	*Debaryomyces nepalensis*	JX068681	100
		COQ64	*Debaryomyces fabryi*	KP263777.1	99
		COQ11	*Eremothecium sinecaudum*	U43391.1	99
		COQ13	*Hanseniaspora uvarum*	KM589490	100
		COQ55	*Kurtzmaniella natalensis*	KJ794716.1	100
		COQ29	*Lodderomyces sp.*	KF830177.1	95
		COQ3	*Lodderomyces sp.*	KF830177.1	95
		COQ66	*Meyerozyma guilliermondii*	KM885980	99
		COQ35	*Meyerozyma caribbica*	KP797883.1	99
		COQ41	*Papiliotrema flavescens*	LK023746.1	100
		COQ42	*Papiliotrema flavescens*	LK023746.1	100
		COQ40	*Pichia myanmarensis*	AB126678.1	99
		COQ61	*Pichia myanmarensis*	AB126678.1	99
		COQ46	*Pichia terricola*	KJ506735.1	100
		COQ63	*Pichia terricola*	KJ506735.1	100
		COQ39	*Rhynchogastrema complexa*	GU321090.2	99
		COQ59	*Rhodotorula diobovata*	KC442275.1	99
		COQ52	*Yarrowia lipolytica*	KF830179.1	100
Arecaceae	*Syagrus oleracea*	GUA16	*Candida easanensis*	AY634571.1	99
		GUA8	*Hanseniaspora meyeri*	FM200038	99
		GUA5	*Hanseniaspora opuntiae*	EU386744.1	99
		GUA2	*Meyerozyma guilliermondii*	KM885980	99
		GUA3	*Papiliotrema flavescens*	LK023746.1	100
		GUA18	*Rhodotorula mucilaginosa*	KP760069.1	100
		GUA10	*Rhodotorula mucilaginosa*	KP760069.1	100

continue...

continuation....

Caryocaraceae	*Caryocar brasiliense*	PEQ16	*Debaryomyces nepalensis*	JX06868.1	100
		PEQ2	*Eremothecium sinecaudum*	U43391.1	99
		PEQ12	*Hanseniaspora occidentalis*	JX103176.1	100
		PEQ9	*Hanseniaspora opuntiae*	EU386744.1	99
		PEQ14	*Hanseniaspora uvarum*	KM589490	100
		PEQ18	*Lodderomyces sp.*	KF830177.1	95
		PEQ3	*Meyerozyma guilliermondii*	KM885980	99
		PEQ7	*Meyerozyma guilliermondii*	KM885980	99
		PEQ1	*Pichia terricola*	KJ506735.1	100
		PEQ8	*Rhynchogastrema complexa*	GU321090.2	99
		PEQ5	*Yarrowia lipolytica*	KF830179.1	100
Myrtaceae	*Eugenia dysenterica*	CAG2	*Candida suratensis*	AB500863.1	100
		CAG1	*Meyerozyma caribbica*	KP797883.1	99
		CAG4	*Rhynchogastrema complexa*	GU321090.2	99
Myrtaceae	*Psidium cattleyanum*	ARAA12	*Candida natalensis*	KJ794716.1	100
		ARAA16	*Hanseniaspora meyeri*	FM200038	99
		ARAA2	*Papiliotrema flavescens*	LK023746.1	100
		ARAA3	*Papiliotrema flavescens*	LK023746.1	100
		ARAA15	*Pichia myanmarensis*	AB126678.1	99
		ARAA4	*Pichia terricola*	KJ506735.1	100
		ARAA5	*Pichia terricola*	KJ506735.1	100
		ARAA17	*Rhodotorula diobovata*	KC442275.1	99
		ARAA9	*Yarrowia lipolytica*	KF830179.1	100
Sapindaceae	*Talisia esculenta*	PIT5	*Candida intermedia*	KF830176.1	99
		PIT1	*Eremothecium sinecaudum*	U43391.1	99
		PIT3	*Lodderomyces sp.*	KF830177.1	95
		PIT2	*Lodderomyces sp.*	KF830177.1	95
		PIT4	*Lodderomyces sp.*	KF830177.1	95

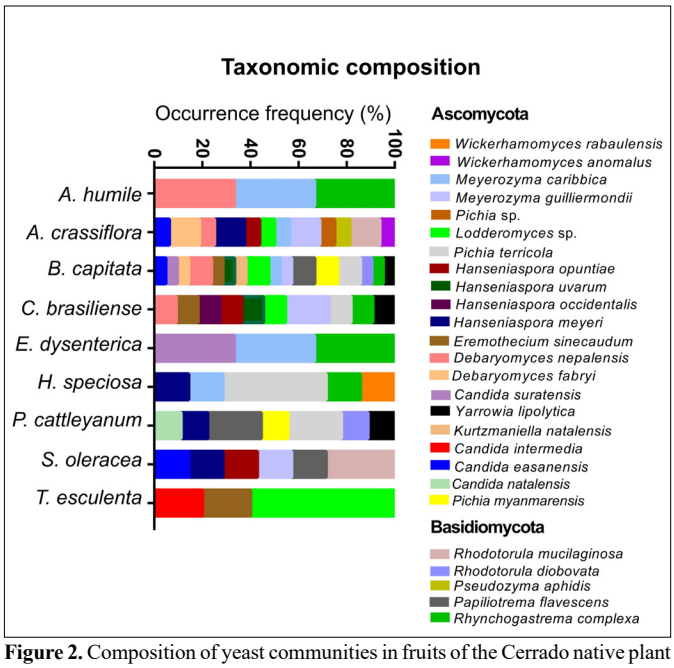


Figure 2. Composition of yeast communities in fruits of the Cerrado native plant species from the Northwest Minas Gerais, Arinos, Brazil.

Discussion

1. Yeasts in Cerrado fruits

The culturable yeast communities diverged among the fruits of the Cerrado native plant species evaluated in this study, regarding cell density and species diversity. The first variable factor among the fruits studied was the density of yeast cells per gram of fruit. The density of microbial cells in the plant may be influenced by abiotic and biotic factors (Hoffman et al. 2008; U'ren et al. 2012), such as seasonality, fruit physiology, host plant ecology, substrate type, fruit morphology, interactions between species, production of 'killer toxins' and competition for substrate (Carvalho et al. 2012; Kusari, et al. 2012; Glushakova & Chernov, 2010). The degree of fruit ripeness can also influence the density, since the more mature the fruit is, the greater the population density of microorganisms that colonize them (Glushakova & Kachalkin 2017). Considering that we use only fully ripe fruits, we hypothesized that the variation in population density among these studied fruits is more related to the differences in the characteristics intrinsic to each fruit species. Variations in nutritional composition (type and quality of available nutrients) and other physical and chemical characteristics have already been reported for the ripe fruits that we studied here (Silva et al. 2008; Rocha 2011; Fujita 2012).

A high population density of yeasts does not always reflect a greater richness of species (Isaeva et al. 2010). We observed these differences in fruits the *A. humile*, which presented three yeast species and 2.2 x 10^3 CFU g^{-1}, and fruits of *C. brasiliense*, which presented 11 yeast species and < 1.0 x 10 CFU g^{-1}. The diversity of yeast communities is also influenced by biotic and abiotic factors (Hoffman et al. 2008; U'ren et al. 2012; Glushakova & Chernov, 2010; Jindamorakot, 2004). Another factor that could interfere in diversity is the mutualistic relationship between microorganisms and plants. The characteristics of the type of colonized tissue can act by selecting the species that would colonize there (Ren et al. 2016; Dhayanithy et al. 2019; Ling et al. 2020). Therefore, we believe that the nutritional characteristics of fruits (quality and availability of nutrients) may be the main factor influencing the richness and abundance of culturable fruit yeast population.

Table 4. Results of amylase, cellulase, protease, and pectinase production tests by yeast isolates of native fruits from the Northwest Cerrado of Minas Gerais, Arinos, Brazil.

SPECIES	PHYLUM	ISOLATE ID	AMYLASE	CELLULASE	PROTEASE	PECTINASE
Candida intermedia	Ascomycota	PIT5	-	-	+	-
Candida suratensis	Ascomycota	COQ37	-	-	+	+
Candida suratensis	Ascomycota	CAG2	-	-	++	-
Debaryomyces fabryi	Ascomycota	ARA26	-	-	+	+
Debaryomyces fabryi	Ascomycota	ARA12	-	-	-	+
Debaryomyces nepalensis	Ascomycota	ARA21	+	-	-	+
Debaryomyces nepalensis	Ascomycota	COQ24	+	+	+	-
Debaryomyces nepalensis	Ascomycota	COQ18	-	-	++	-
Eremothecium sinecaudum	Ascomycota	COQ11	++	++	++	-
Hanseniaspora meyeri	Ascomycota	ARA16	-	+	-	+
Hanseniaspora meyeri	Ascomycota	ARAA16	+	+	-	+
Hanseniaspora opuntiae	Ascomycota	GUA5	++	+	-	-
Hanseniaspora opuntiae	Ascomycota	ARA28	+	+	-	-
Hanseniaspora uvarum	Ascomycota	COQ13	-	-	+	-
Kurtzmaniella natalensis	Ascomycota	COQ55	-	+	-	-
Lodderomyces sp.	Ascomycota	ARA13	-	+	-	-
Lodderomyces sp.	Ascomycota	PIT4	++	-	-	-
Meyerozyma caribbica	Ascomycota	ARA22	-	+	-	-
Meyerozyma caribbica	Ascomycota	CAG1	-	+	+	-
Meyerozyma guilliermondii	Ascomycota	GUA2	-	+	+	+
Meyerozyma guilliermondii	Ascomycota	ARA6	-	+	-	-
Meyerozyma guilliermondii	Ascomycota	COQ66	-	-	-	++
Pichia myanmarensis	Ascomycota	COQ40	-	-	+	-
Pichia terricola	Ascomycota	COQ63	-	+	+	-
Pichia terricola	Ascomycota	MA11	-	-	++	++
Pichia terricola	Ascomycota	MAN9	-	+	+	+
Pichia terricola	Ascomycota	MAN1	-	+	+	+
Pichia sp.	Ascomycota	ARA3	-	+	-	-
Pichia sp.	Ascomycota	ARAA15	+	-	-	-
Yarrowia lipolytica	Ascomycota	PEQ5	++	-	-	-
Yarrowia lipolytica	Ascomycota	ARAA9	-	-	+	+
Papiliotrema flavescens	Basidiomycota	ARAA2	+	-	-	-
Papiliotrema flavescens	Basidiomycota	ARAA3	++	+	-	-
Papiliotrema flavescens	Basidiomycota	GUA3	-	-	+	+
Rhynchogastrema complexa	Basidiomycota	CAJ4	-	-	+	-
Rhynchogastrema complexa	Basidiomycota	CAG4	-	-	++	+
Rhynchogastrema complexa	Basidiomycota	MAN10	-	+	-	-
Rhodotorula diobovata	Basidiomycota	ARAA17	-	-	+	+
Rhodotorula diobovata	Basidiomycota	COQ59	-	-	+	+
Rhodotorula mucilaginosa	Basidiomycota	GUA18	-	++	+	+
Rhodotorula mucilaginosa	Basidiomycota	GUA10	++	+	++	++
Rhodotorula mucilaginosa	Basidiomycota	ARA31	-	-	+	-
Rhodotorula mucilaginosa	Basidiomycota	ARA23	-	-	+	-

(-) absence, (+) halo up to 19 mm and (++) halo ≥ 20 mm.

A total of 82 isolates of yeasts were recovered from the fruits, with a predominance of Ascomycota yeasts. Our results are in agreement with the literature because fruits have a higher predominance of the phylum Ascomycota because it is a habitat rich in simple carbohydrates (Trindade et al. 2008; Negri et al. 2019; Ren et al. 2019) easily assimilated as a carbon source by yeasts (Carvalho et al. 2006). Also, it is already recognized that ascomycetous yeasts tend to predominate within plant tissues (Sperangio et al. 2015), while basidiomycetes are reported in the phylloplane, as they have adaptations to survive this environment, such as the ability to metabolize more carbohydrate sources complexes from the plant cell wall and produce pigments used for protection against ultraviolet rays (Li et al. 2020; Coelho et al. 2020).

Twenty-four yeast species were found, many of them present in more than one fruit species (Table 2). The genus *Candida* (Ascomycota) was the most frequent with 11 isolates. A higher frequency of the genus *Candida* has been observed in fruits of the Cerrado (Coelho et al. 2020). Studies to identify fungi in the Cerrado native fruits using a methodology similar to that used in this study have already been carried out, and many of the yeast species described here have not been reported in these fruits or other fruits (Sperandio et al. 2015; Coelho et al. 2020). Our results corroborate the findings of Sperandio (2015), who described the fruit and foliar yeast communities of *Byrsonima crassifolia* (Murici) and *E. dysenterica* (Cagaita), identifying the species *M. guilliermondii* and *R. mucilaginosa* in common among the those fruits studied. Meanwhile,

for *E. dysenterica* we have also identified the species *C. suratensis* and *Rhynchogastrema complexa*, showing new reports of yeast species colonizing these fruits.

In four plant species analyzed in this study, yeast growth was not detected in fruits. The absence of endophytic colonization yeasts in the fruits of *Passiflora cincinnata* can be explained by the presence of antifungal proteins in the fruits' pulp of the genus *Passiflora* (Jagessar et al. 2017; He et al. 2020). The antifungal activity of this genus seems to be restricted to pulp and seeds since Coelho et al. (2020) reported the presence of 4 yeast genera colonizing the fruit surface of *P. nitida* and also failed to obtain endophytic isolates. Silva (2017) reported the occurrence of yeasts colonizing the phylloplane of *P. incarnata*. The reasons for the absence of growth in the species *Solanum lycocarpum, Hymenaea stigonocarpo*, and *Mauritia flexuosa* do not seem to be linked to the substrate offered yeasts, since the fruits of *S. lycocarpum* present a large amount of carbohydrate and those of *M. flexuosa* large amount of lipid (Negri et al. 2016). Many studies have demonstrated the antimicrobial potential of *H. stigonocarpa* (Barbosa et al. 2015; Dimech et al. 2013; Martines et al. 2015), and *M. flexuosa* (Lima et al. 2006; Batista et al. 2012). These reports may explain the absence of yeasts in these fruits and present information that justifies investigating the phytomedical potential of these plants' products.

The absence of yeasts in fruits of these four plant species may suggest and/or reinforce the hypothesis that they are important sources of biological resources with potential for the production of molecules with antimicrobial action, mainly antifungal. The biotechnological potential of these Cerrado native plants aiming at the development of products for the control of pathogenic fungi deserves to be investigated in future studies. The fruit extract of *S. lycocarpum* (Lobeira) has already shown efficacy against harmful organisms such as the pathogen *Leishmania infantum* (Clementino et al. 2018) and the parasites *Haemonchus contortus* (Oliveira, 2013) and *cytostostomines* (Cyathostominae) (Souza, 2011). In contrast, the leaf extract of *M. flexuosa* demonstrated anti bactericidal activity against the pathogen *Pseudomonas aeruginosa* (Koolen et al. 2013).

2. Production of enzymes by yeasts from the Cerrado native fruits

Of the 82 yeast isolates recovered in this study, 48 (60% of the total) produced one or more of the enzymes studied (cellulase, protease, amylase, and pectinase). A wide variety of molecules and enzymes synthesized by different fungi species have been described (Li et al. 2016). In general, it can be said that fungi colonize environments with low nutrient availability, and as a result, they can present a wide variety of enzyme profiles, such as pectinases, amylases, cellulases, lipases, and protease (Mendes, 2010).

The production of hydrolytic enzymes has been reported as a common trait in plant-associated yeasts. Results similar to those obtained in this study were observed in yeast community (endophytic and epiphytes) isolated from bromeliad, where 40% to 60% presented amylolytic, cellulolytic, and proteolytic potential, stand out as producers of the exoenzymes species of *Candida, Debaryomyces, Metschnikowia, Pichia, Zygosaccharomyces, Cryptococcus, Fellomyces, Kockovaella, Rhodotorula, Sporobolomyces, Tremella, Aureobasidium, Itersonilia* and *Tilletiopsis* (Landell et al. 2006). Among the yeast species isolated in this study, yeasts from the genera *Candida*, *Debaryomyces*, *Hanseniaspora*, *Kloeckera*, *Lodderomyces*, *Pichia*, and *Rhodotorula*, are known for the diversity of synthesized enzymes and are used for the production of enzymes of industrial interest and in fermentative processes (Pretorius, 2000; Buzzini et al. 2002; Coutinho et al. 2013; Kot et al. 2016).

Among the yeast species evaluated, five produced the four enzymes. Few studies report the variety of enzymes produced by the yeasts *P. flavescens, Hanseniaspora meyeri, M. guilliermondii*, and *R. mucilaginosa;* however, these species of fungi are found in the soil, in rocks, in tree trunks, and because they colonize the most diverse environments, they are capable of synthesizing a wide variety of enzymes (Wirth, 2011; Andrade et al. 2012). Despite the need for more time for growth, the genus *Hanseniaspora* can produce proteases and glycolytic enzymes in larger quantities (Fleet, 2008; Comitini et al. 2011). Strains of species *M. guilliermondii* have been considered a great candidate for the biotechnological production of enzymes (Atzmüller et al. 2020).

The predominance of enzymatic groups varied among yeast species. Proteolytic enzymes were found in 25 isolates, thus representing the predominant enzymatic group. Several factors interfere in the enzymatic production of proteases, such as temperature, pH, the concentration of the substrate used, and the metabolism linked to the cell division process (Neves, 2006; Molnárová et al. 2014). Cellulolytic enzymes were found in 21 isolates, and it is known that cellulase production is among wild yeasts (Buzzini et al. 2002; Mendes et al. 2012). The production of pectinases occupied the third place in the number of isolated producers, with 18 isolates, and the degree of maturation of the fruits may have interfered in this result since pectin is a polysaccharide that is part of the cell wall that is depolymerizing with the ripening of the fruits (Trindade 2002; Paiva, 2009). Amylases were the least produced enzymes, which may be related to low starch use as a carbon source (Alberto et al. 2016). Another justification for the low production of amylases among the isolates in this study is that, according to Onofre (2015), these enzymes are produced mainly by saprophytic basidiomycetes filamentous fungi.

The low hydrolytic activities of fungi isolated from tropical regions can be observed due to the difficulties of visualization of these enzymes' production in a solid medium since fungi require a longer period to develop (Orlandelli et al. 2015; Dantas et al. 2017). Although some authors suggest a longer incubation time for evaluating hydrolytic activity in fungi, Marta et al. (2015) obtained positive results for fungal amylase production in a short incubation time (five days), similar to that used in this study. Another important point to be raised about the low enzyme production is that the diffusion of the enzyme and, consequently, the diameter of the hydrolysis halo are influenced by the molecular mass that the enzyme has, which can hinder or even prevent its diffusion in agar (Alberto et al. 2016). Thus, the enzymatic activity index can be considered low or non-existent, even if there is large enzymatic production by the microorganism.

To our knowledge, this study contributes to numerous unpublished findings. There were no reports yet of yeast associated with fruits such as, *A. crassiflora* (Araticum), *S. oleracea* (Coco-guariroba), *B. capitata* (Coquinho-azedo), *H. speciosa* (Mangaba), *T. esculenta* (Pitomba), *S. lycocarpum* (Lobeira), *H. stigonocarpa* (Jatobá-do-Cerrado), and *P. cincinnata* (Maracujá-do-Cerrado), the results of this study is unprecedented both in the analysis of their occurrence colonizing plant organs of the Cerrado biome, the identification of yeasts and their enzymatic potential.

Supplementary Material

The following online material is available for this article:

Figure S1 - *Fruits harvested for analysis: Passiflora cincinnata* (A), *Eugenia dysenterica* (B), *Mauritia flexuosa* (C), *Hymenaea stigonocarpa* (D), *Solanum lycocarpum* (E), *Caryocar brasiliense* (F), *Annona crassiflora* (G), *Psidium cattleyanum* (H), *Butia capitata* (I), *Syagrus oleracea* (J), *Hancornia speciosa* (K), *Talisia esculenta* (L) e *Anacardium humile* (M).

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Author Contributions

Helson Mario Martins do Vale: substantial contribution to the conception and design of the study; contribution to data analysis and interpretation; contribution to the preparation of the manuscript; contribution to critical review, adding intellectual content.

Jefferson Brendon Almeida dos Reis: contribution to data analysis and interpretation; contribution to the preparation of the manuscript; contribution to critical review, adding intellectual content.

Marcos de Oliveira: substantial contribution to the conception and design of the study; contribution to data collection; contribution to data analysis and interpretation; contribution to critical review, adding intellectual content.

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Catharine Abreu Bomfim: contribution to data analysis and interpretation; contribution to the preparation of the manuscript; contribution to critical review, 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

Effects of the presence of litter on the composition of stream tadpoles' assemblages in an Atlantic Forest remnant of southeastern Brazil

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Abstract: Many tropical anurans use forest streams to deposit their eggs, but resource use and selection by tadpoles in tropical forests are poorly known. In the present research, we hypothesized that leaf litter and water depth affect tadpole assemblages due to adult habitat selection for oviposition and/or microhabitat selection by tadpoles. Fieldwork was carried out in the Estação Biológica de Boracéia, an Atlantic Rainforest reserve in São Paulo state, southeastern Brazil. We sampled tadpoles during a year using 40 double-entry funnel-traps distributed along four streams in the forest. Only leaf litter effects are species dependent. We discussed that habitat structure significance depends on the morphological and ecological adaptation to forage and avoid competition within the tadpole community.
Keywords: *Amphibians;* Aplastodiscus leucopygius; Bokermannohyla hylax; *microhabitat selection;* Scinax obtriangulatus, Phasmahyla cochranae; *southeastern Brazil; tadpoles.*

Efeitos da presença de serapilheira na composição de assembleias de girinos de riacho em um remanescente de Mata Atlântica do sudeste do Brasil

Resumo: Uma variedade de espécies de anuros tropicais usa riachos da floresta para depositar seus ovos, mas o uso e a seleção de recursos por girinos em florestas tropicais são pouco conhecidos. Na presente pesquisa, nossa hipótese era a de que a presença de serapilheira e a profundidade das poça dos riachos influenciam a presença de girinos devido à seleção de habitats de ovipostura pelos adultos e/ou seleção de micro-habitats pelos girinos. O trabalho de campo foi realizado na Estação Biológica de Boracéia, uma reserva de Mata Atlântica no estado de São Paulo, sudeste do Brasil. Amostramos girinos durante um ano usando 40 armadilhas-de-funil de dupla entrada distribuídas ao longo de quatro riachos na floresta. Apenas os efeitos da presença de serapilheira foram significativos Nós discutimos as relações entre a estrutura do habitat e características morfológicas, ecológicas e adaptações para procura de alimento e para evitar competição no interior da comunidade de girinos.
Palavras-chave: *Anfíbios;* Aplastodiscus leucopygius; Bokermannohyla hylax; *girinos;* Phasmahyla cochranae; Scinax obtriangulatus; *seleção de micro-habitat; sudeste do Brasil.*

Introduction

Anuran amphibians exhibit a combination of particular reproductive strategies that includes selective breeding sites, clutch characteristics, rate and duration of larval development, and eventually parental care (Haddad & Prado 2005), linked to their spatial distribution and reproductive success (Haddad & Sawaya 2000, Wells 2007). Tadpoles are generally found in water bodies suitable for their development and success that are selected by their parents (Wells 2007). In these water bodies it is expected that local factors related to habitat structure and resource quality explain tadpole richness, diversity and development (Savage 1952, Stoler & Relyea 2013b, Almeida et al. 2015).

Generally, habitat use discerns among tadpoles of different species (Kopp & Eterovick 2006), as variation in morphology, physiology, and phenology impose restrictions on the way tadpoles explore the microhabitats (Fatorelli & Rocha 2009). When sharing the same site, tadpole assemblages are organized to avoid competition while keeping safe from predators (Heyer 1976). Most tadpoles are filter-feeders, which can impose high levels of competition to species sharing the same pond (Fatorelli & Rocha 2009), unless there is a partitioning of resources in terms of space, time, or food (Heyer 1976). For instance, tadpoles can differ in the foraging mode using the water surface, mid-water, or water bottom (Heyer 1973, 1976).

Resource quality also affects tadpole morphology and development, as larvae scratch the substrate and ingest nutrients directly by litter consumption or grazing microbial communities (Savage 1952, Stoler & Relyea 2013b). Leaf litter inputs are dominant energy and nutrient resources for tadpoles and yet can reduce their predation rate, acting as a refuge (Stoler & Relyea 2013a). Further, vegetation composition affects litter quality, which induces phenotypic and morphological changes on the consumers, potentially altering their fitness (Stoler & Relyea 2013b).

Many abiotic and biotic factors can influence the structure of tropical tadpole assemblages (Borges Júnior & Rocha 2013, Marques et al. 2019). A variety of tropical anurans use forest streams to deposit their eggs, and there are few reports on how changes in microhabitat influence tadpoles (Kopp & Eterovick 2006, Kopp et al. 2006, Caldas et al. 2019). In the Atlantic Rainforest, the composition of stream tadpoles' assemblages is influenced by abiotic and biotic factors (Eterovick & Barata 2006, Kopp & Eterovick 2006, Bertoluci et al. 2013, Jordani et al. 2017), making species more prone to resource partitioning (Melo et al. 2018). Atlantic rainforest streams are often composed of interconnected shallow puddles with rocky bottom, whose depth and presence of litter vary greatly. These are the main habitats to stream tadpoles, so it is expected physical characteristics of puddles influence tadpole occurrence. In the present study, we hypothesized that water depth and/or the presence of leaf litter affect the species composition of tadpoles' assemblages in Atlantic rainforest streams.

Material and Methods

1. Study site and data collection

Fieldwork was carried out in the Estação Biológica de Boracéia (EBB), an Atlantic Rainforest reserve with 16,450 ha located at 900 m a.s.l. in one of the wettest regions of São Paulo state, southeastern Brazil (Setzer 1946) (Figure 1). Rainfall was irregularly distributed during the study period, with total precipitation of 1,747.3 mm and rainy season extending from September to March (Bertoluci et al. 2013). The area is covered by Dense Ombrophylous Forest, with an understory relatively opened but denser along streams (Bertoluci & Rodrigues 2002).

We selected four streams to obtain data on the association of microhabitat variables and the species composition of tadpole assemblage (sites R1 to R4 in Bertoluci & Rodrigues 2002; Figure 1). R1 corresponds to a small stream (60 m long, 1.3 m wide, 22 cm maximum depth) located in the primary forest and containing interconnected rocky or muddy puddles with organic matter in decomposition, mainly dead leaves and sticks. R2 is a small stream (50 m, 1.8 m, 27 cm) in the forest edge. R3 is a small stream (96 m, 2 m, 32 cm) in the primary forest with interconnected puddles with a rocky, sandy bottom and dead leaves. R4 is a small stream (91 m, 2.4 m, 30 cm) inside the forest; its bed is mainly rocky, but some puddles have sand and dead leaves (Table 1).

Tadpole sampling were carried out with 40 double-entry funnel-traps constructed with two 2-L plastic bottles, which result in approximately 1.5-L traps; traps were entirely submerged at the bottom of the stream puddles (Figure 2). We estimated the relative abundances of tadpoles in 40 traps distributed along the selected streams (10 traps in each stream). Sampling was carried out monthly with traps kept active during 72 hours per month from September 1993 to September 1994. The species abundance was calculated by summing the total of all individuals collected through the year. The microhabitat of each plot was characterized based on two variables: water depth (measured with a ruler in the deepest point of each stream puddle, where the trap was positioned; depth did not vary significantly along the year) and presence or absence of leaf litter (0 or 1). We built a matrix crossing the tadpole species and their microhabitat features to conduct an ordination or gradient analysis.

2. Data analysis

In order to evaluate the effects of microhabitat variables on the tadpole composition, we used PerMANOVA (bray-curtis method), with presence/absence of litter as fixed factor and stream depth as covariate. Considering that our sampling observations are not independent (pseudo-replication) we used the stream ID (R1, R2, R3, and R4) to restrict the permutations in PerMANOVA, using the argument "strata" in the function "adonis" in R. We plotted the variables and species using NDMS. This analysis was performed using R 3.6.3 version. Significance level adopted in the study was 0.05.

Results

Four anuran tadpole species known to inhabit streams were captured in our study in EBB: *Aplastodiscus leucopygius* (N = 146), *Bokermannohyla hylax* (139), *Scinax obtriangulatus* (89) (Hylidae), and *Phasmahyla cochranae* (2) (Phyllomedusidae) (Figure 3). The analysis of microhabitat use and selection was performed with only 38 out of the 40 initial traps because two traps were empty. The number of tadpoles per trap varied from 0 to 79, and the abundance distributions for all species was very skewed (Table 2). Tadpoles of different species shared the same trap in 37% (Figure 4), mostly with *B. hylax* and *A. leucopygius*. These two species were captured together in 32% of the samplings. On the other hand, only two tadpoles of *S. obtriangulatus* were observed sharing the same trap with tadpoles of *B. hylax*. One tadpole of *S. obtriangulatus* was observed with 26 tadpoles of *B. hylax,*

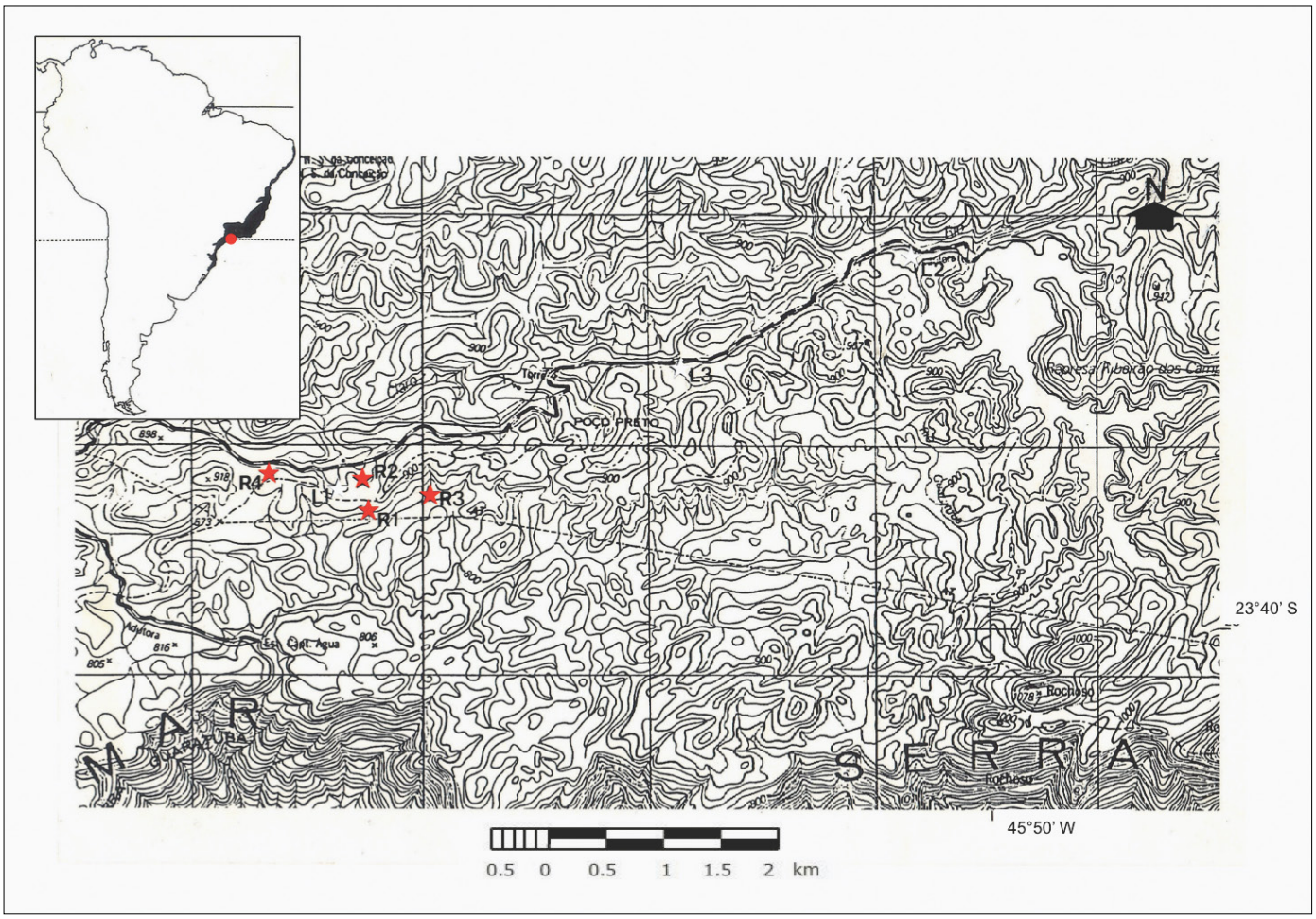


Figure 1. Location of the study site in the Atlantic rainforest (red circle) and of streams R1 to R4 in the study site (red stars).

Table 1. Characteristics of the four streams used for the study of tadpoles in a remnant of the in Atlantic Forest at the Estação Biológica de Boracéia, São Paulo state, southeastern Brazil.

Stream	R1	R2	R3	R4
Length (m)	60	50	96	91
Width (m)	1.3	1.8	2	2.4
Depth (cm)	22	27	32	30
Bed	rocky/muddy	sandy/rocky	rocky/sandy	rocky/sandy
Location	Primary forest	Forest edge	Inside the forest	Inside the forest

and in another occasion one tadpole was captured with two tadpoles of *B. hylax*. *Phasmahyla cochranae* tadpoles was observed sharing the same trap with one tadpole of *B. hylax*, and on another occasion, it was found in the same trap with one tadpole of *A. leucopygius* (Figure 4).

Using PerMANOVA we detected effect of presence/absence leaf litter on the composition of tadpole community ($F_{3,37}$ = 9.3238, p = 0.030) but not of the stream depth ($F_{3,37}$ = 1.4364, p = 0.677) (Figure 5).

Discussion

The tadpole assemblages studied in EBB showed partitioning organization with habitat structure discerning among tadpole species. These findings corroborate other studies in the Atlantic rainforest, like those of Jordani et al. (2017), which shows that habitat type (lentic or lotic) influences the structure of the assemblages, and of Kopp & Eterovick (2006), which demonstrates that patterns of species distributions are due to environmental and stochastic factors rather than by predation. According to Kopp et al. (2006), the choice of shallow or deep areas in the water column can be a strategy to avoid predation or interspecific competition. In the present study, we did not find a correlation with puddle depth, but species were associated with the presence of litter. An early description of *S. obtriangulatus* in Boracéia witnessed tadpoles of this species using the bottom of the puddle in a small stream in the forest (Heyer et al. 1990). Due to their anteroventral mouth tadpoles of *P. cochranae* forage swimming in the water surface and sometimes float motionless at mid-water (Leão-Pires

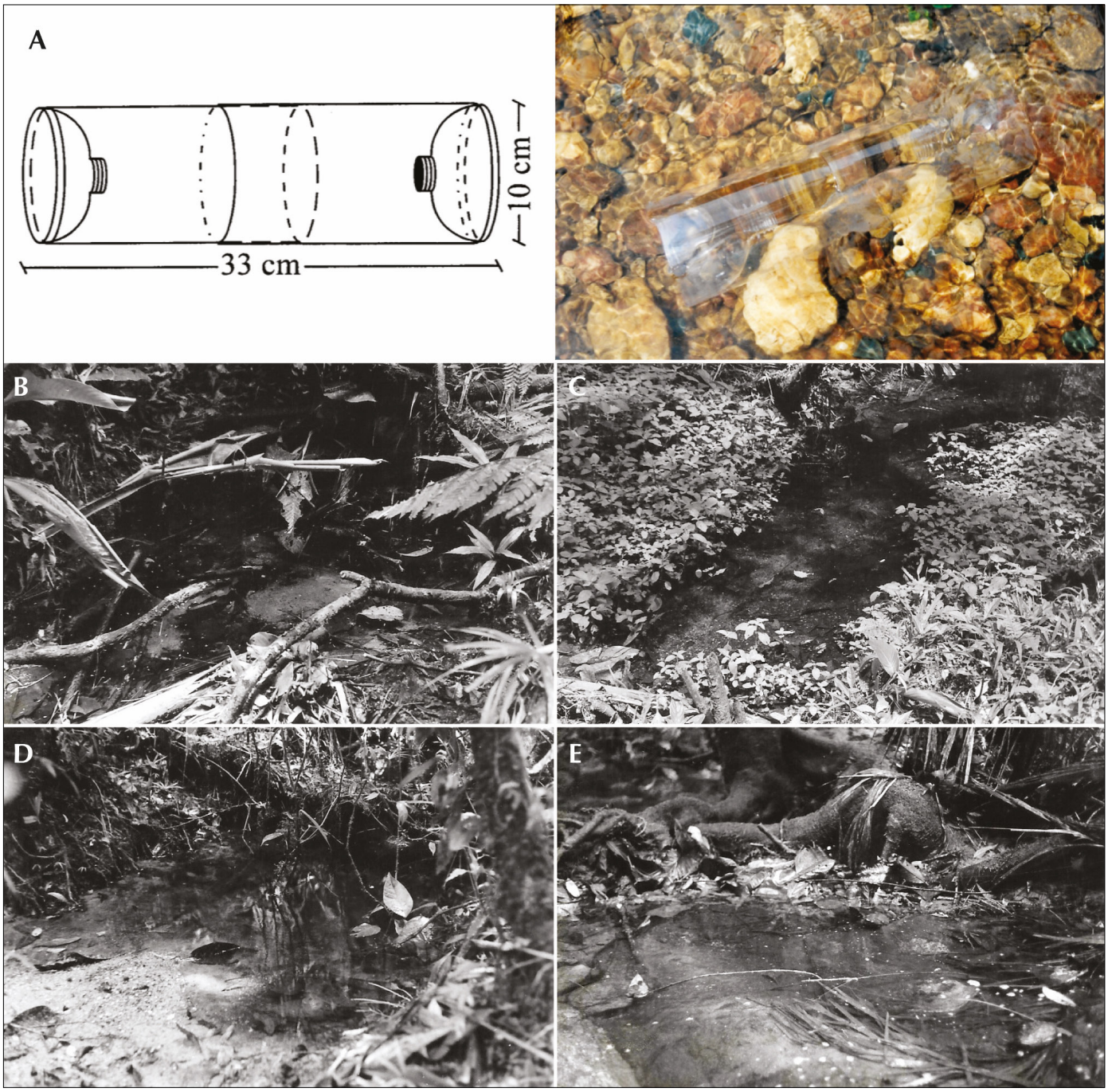


Figure 2. (A) Double-entry funnel-trap used in tadpole sampling (this photo was not taken at the study site). (B-E) Puddles in the streams R1 to R4, all of them containing leaf litter in the bottom.

et al. 2017). Puddle depth did not influence the occurrence of *Phasmahyla nordestinus* tadpoles, suggesting a strategy to avoid competition or a response to unpredictable temporary aquatics habitats, limiting the degree of specialization for resources in the Brazilian semi-arid, an environment subjected to water scarcity and irregularities (Caldas et al. 2019). *Phasmahyla cochranae* tadpoles present schooling and aggregation behavior associated with daylight (Leão-Pires et al. 2017). In the present study, only two tadpoles of *P. cochranae* were captured and on different occasions, which is easily explained by the fact that the traps were set at the bottom of the stream, reducing the probability of capturing non-benthic tadpoles. Apart from daylight, tadpole aggregation behavior is linked to water transparency, temperature, and other characteristics not investigated in the present study (Branch 1983, Spieler 2003). However, it is known that tadpoles of *P. cochranae* and *S. obtriangulatus* are more active during the day (Carvalho-e-Silva 1986, Leão-Pires et al. 2017). Behavior shift can also be a strategy to avoid overlapping and interspecific competition as well to assure protection against predators (Carlson & Langkilde 2013).

Diel activity behavior can be a sign of tadpole assemblage organization and partitioning (Heyer 1976). *Bokermannohyla hylax* and *A. leucopygius* tadpoles are also more active at night presumably to avoid predators

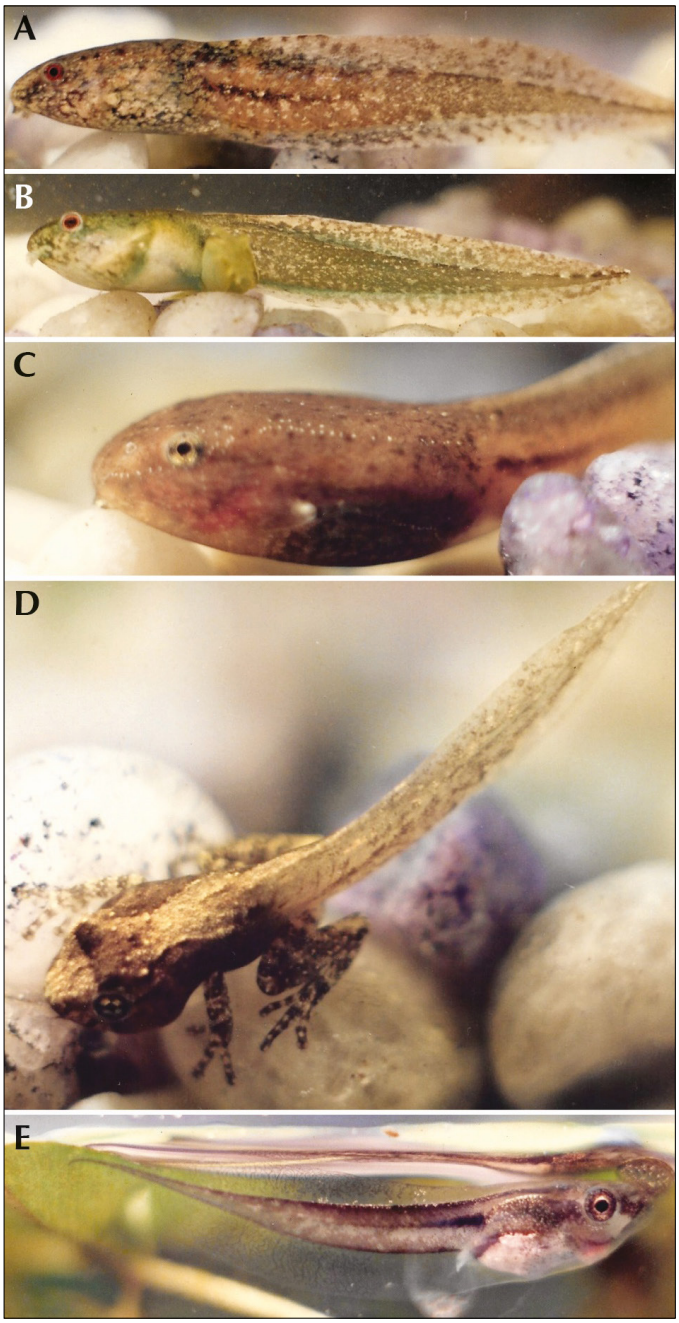


Figure 3. Tadpoles collected in this study. (A-B) *Aplastodiscus leucopygius* (cryptic form and tadpole changing to the green coloration of adults; note the red eyes), (C) *Bokermannohyla hylax* (note the unpigmented spiracle), (D) *Scinax obtriangulatus* (advanced stage of metamorphosis), (E) *Phasmahyla cochranae* (note the anterodorsal funnel-shaped oral disc).

(Bertoluci 2002, Gomes and Peixoto 2002). These two species show specialized reproductive modes associated with forest streams (Haddad & Prado 2005, Gomes & Peixoto 2002). Together they were the most abundant tadpoles in our sampling and often shared the same trap. The dark chocolate-brown coloration of *B. hylax* tadpoles shows an advantage when seeking cover among the leaf litter, rocks, and mud in the streambed (Bertoluci et al. 2003). This could likewise represent an advantage for *A. leucopygius* with a cryptic coloration that hides under litter and rocks (Gomes & Peixoto 2002), except in the advanced stages of metamorphosis, when tadpoles turn to green (Figure 3A-B).

Differences in the habitat structure used by tadpoles is perhaps a combination between oviposition site selection by adults and microhabitat selection by tadpoles, owing to evidences that each life-history stage evolves independently (Sherratt et al. 2017). Habitat structure, such as leaf litter cover and depth, humidity, vegetation, and canopy cover, offer insights into amphibian richness and abundance (Jongsma et al. 2014, Marques et al. 2019). Generally, oviposition sites will be near habitats suitable for mating by the adults, yet adult anuran and tadpoles may use distinct spatial resources during their complex life cycle (Haddad & Sawaya 2000, Rudolf & Rödel 2005, Wells 2007). *Aplastodiscus leucopygius* has a long breeding season, benefiting from the rain for reproduction (Bertoluci & Rodrigues 2002). This species shows a complex courtship with males guiding females to subterranean nests previously constructed by them (Haddad & Sawaya 2000). Tadpoles then scape from the nests chambers when it floods by the rise in the pond's water level caused by heavy rains and reach the water bodies in either streams or temporary ponds (Haddad & Prado 2005). This adaptation suggests some tolerance and flexibility of tadpoles to cope with external unpredictable factors influenced by hydrological cycles, water depth, or litter availability. In any case, high specializations to habitat structure represent disadvantageous to the species survivorship in unpredictable environments (Ultsch et al. 1999).

Tadpoles of different species show different habitat exploration strategies associated with their physiology, morphology, and phenology (Zimmerman & Simberloff 1996). A combination of evolutionary processes is involved either in the choice of oviposition sites by adults or in the resource use by tadpoles, being survival their end goal. Yet anuran mortality is highest during the larvae stage (Heyer 1973). Anurans in the Atlantic Rainforest are known for their specialized reproductive modes (Haddad & Prado 2005). The four species studied here showed various adaptations to their microhabitats, represented by distinct evolutionary processes that guarantee their safe development. In other words, each species has its own evolutionary strategy to ensure larval phase and adult recruitment success, a combination of adult selection for breeding and oviposition sites and tadpole strategies to forage, hide, and escape from predators and avoid competitors. Habitat use will then depend on the resources available when larvae emerge from eggs, as they have limited locomotor ability at this stage (Heyer 1976).

Tadpoles play essential roles in tropical streams not only as prey but also producing substantial amounts of egested particles (still understudied) that are critical nutrient sources in streams (Ramamonjisoa & Natuhara 2018, Iwai et al. 2009), and so they act as abiotic and biotic elements of aquatic communities (Stoler et al. 2016). Additional comparison between lentic and lotic habitats could show distinct outcomes as consumers may have different responses to litter in ponds and wetlands that retain litter for extended periods compared to streams (Melo et al. 2017, Stoler et al. 2016, Stoler & Relyea 2016).

We concluded that presence/absence of leaf litter has an effect on the composition of stream tadpoles' assemblages. Anyhow, the presence of vegetation can be an important variable influencing tadpole richness of both ponds and streams (Kopp et al. 2006). Vegetation type and presence were not investigated in the present study, but their influence could be an important component in the species composition (Kopp & Eterovick 2006, Melo et al. 2018). Future studies are recommended to comprehend each species' response to different types of resources, such as vegetation, water rate, streambed, daylight, and in lentic habitats, considering the species morphology and phylogeny.

Table 2. Captures of tadpoles of four anuran species in 38 traps in Atlantic Forest streams at the Estação Biológica de Boracéia, southeastern Brazil. Values are discriminated for sampling unities with (n = 27) and without (n = 11) litter. Values are presented as: (total number collected; number of plots where the species occurred) and mean ± standard deviation.

Plots	*Scinax obtriangulatus*	*Bokermannohyla hylax*	*Aplastodiscus leucopygius*	*Phasmahyla cochranae*
With litter	(84; 3) 3.1 ± 15.19	(114; 19) 4.2 ± 6.00	(136; 18) 5.0 ± 6.6	(1; 1) 0.0 ± 0.19
Without litter	(5; 2) 0.5 ± 1.21	(25; 10) 2.3 ± 1.62	(10; 5) 0.9 ± 1.2	(1; 1) 0.1 ± 0.30
Total	**(89; 5)**	**(139; 29)**	**(146; 23)**	**(2; 2)**

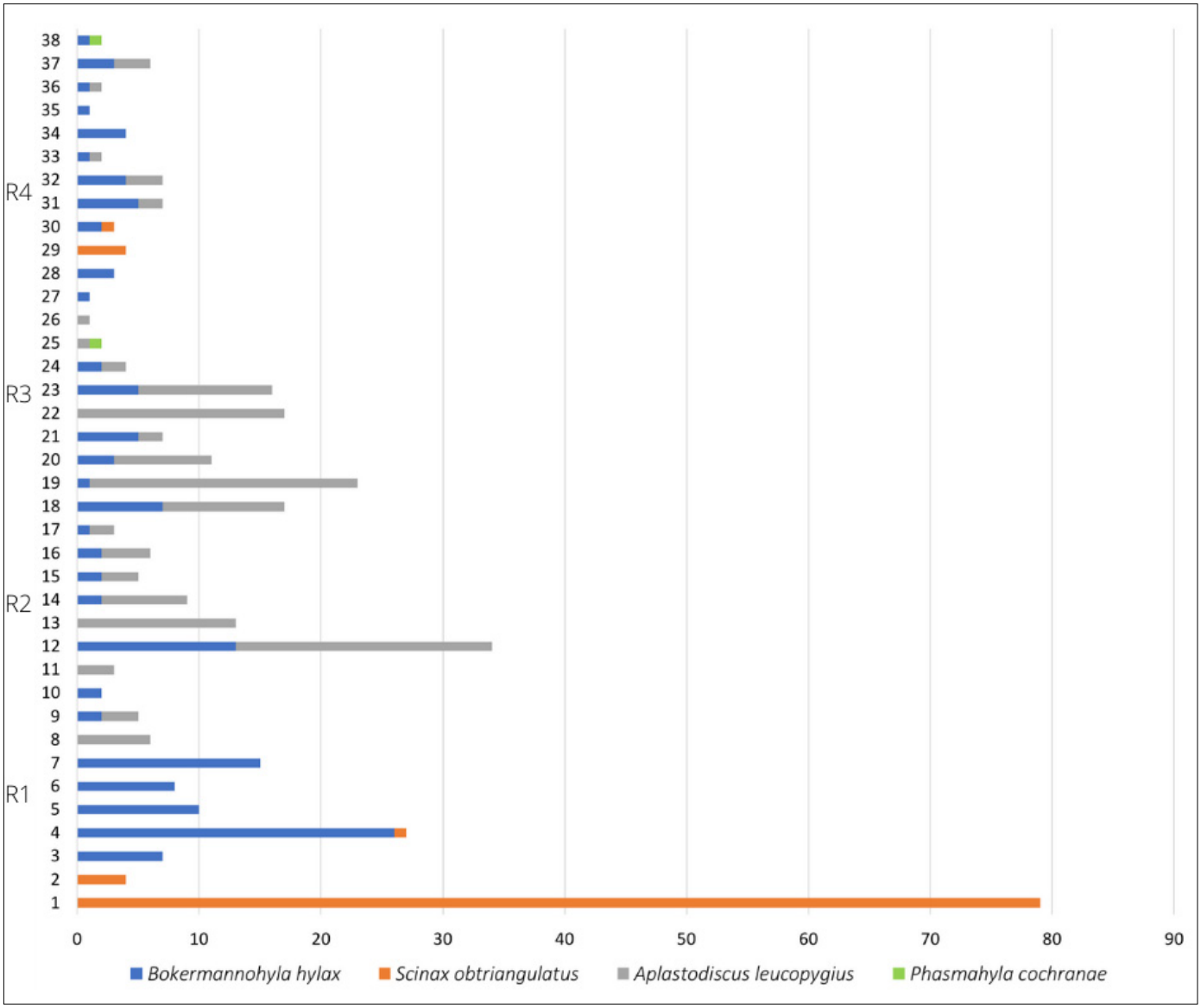


Figure 4. Tadpole abundances of four anuran species in 38 traps distributed in four streams of an Atlantic rainforest remnant of southeastern Brazil.

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Author Contributions

Jaime Bertoluci: Substantial contribution in the concept and design of the study, Providing resources, Data collection, Contribution to data

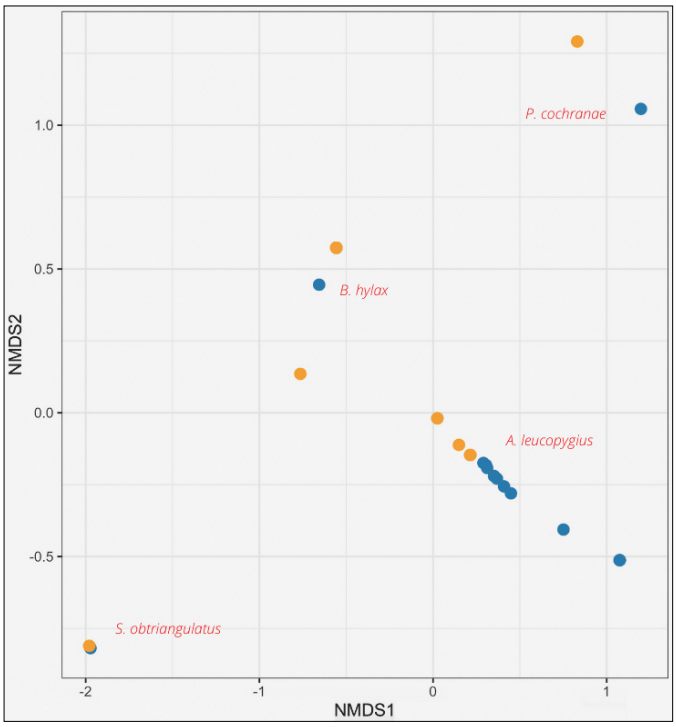


Figure 5. Biplot showing the systematic change of tadpole community composition (relative abundance) with change in water depth and presence of leaf litter in the streams studied at Estação Biológica de Boracéia, southeastern Brazil. Blue and orange circles represent observations with and without leaf litter, respectively.

analysis and interpretation, Contribution to manuscript preparation, Contribution to critical revision, adding intellectual content

Shirley Famelli: Contribution to data analysis and interpretation, Contribution to manuscript preparation, Contribution to critical revision, adding intellectual content

Pedro L. B. Rocha: Contribution to data analysis and interpretation, Contribution to manuscript preparation, Contribution to critical revision, adding intellectual content

Miguel T. Rodrigues: Substantial contribution in the concept and design of the study, Providing resources, Contribution to manuscript preparation, Contribution to critical revision, adding intellectual content.

Conflicts of Interest

We have no conflicts of interest.

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Drifting in a free-flowing river: Distribution of fish eggs and larvae in a small tributary of a Neotropical reservoir

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Abstract: We investigated spatial and temporal variations in the distribution of fish eggs and larvae in the Guareí River, a free-flowing tributary located in the upper section of the Jurumirim Reservoir, Paranapanema River, Brazil. Fish eggs and larvae were sampled ~ fortnightly from November 2017 to March 2018 (Cycle 1), and from November 2018 to March 2019 (Cycle 2), at three sites distributed along the entire course of the Guareí River. We collected 859 fish eggs and 1,340 larvae, comprising 19 taxa. We found reproductive activity of several fish species in the Guareí River, including long-distance migrants. However, there was no spatial differences in the assemblage structure and densities of fish eggs and larvae along the channel of Guareí River. We recorded temporal differences in larvae density only in Cycle 2. The consistent capture of fish eggs and larvae in two reproductive cycles is strong evidence that this river is a spawning site for a variety of fish species. Thus, we recommend maintaining its natural flow regime.
Keywords: *Fish reproduction; Ichthyoplankton; Jurumirim Reservoir; Migratory fish; Prochilodus lineatus.*

À deriva em um rio de fluxo livre: Distribuição de ovos e larvas de peixes em um pequeno afluente de um reservatório Neotropical

Resumo: Investigamos as variações espaciais e temporais na distribuição de ovos e larvas de peixes no rio Guareí, um afluente de fluxo livre localizado na parte superior do Reservatório de Jurumirim, bacia do rio Paranapanema, Brasil. Ovos e larvas de peixes foram amostrados ~ quinzenalmente de novembro de 2017 a março de 2018 (Ciclo 1), e de novembro de 2018 a março de 2019 (Ciclo 2), em três locais distribuídos ao longo de todo o curso do rio Guareí. Foram coletados 859 ovos de peixes e 1.340 larvas, compreendendo 19 táxons. Nós encontramos atividade reprodutiva de várias espécies no rio Guareí, incluindo espécies migradoras de longa distância. Contudo, não houve diferenças espaciais na estrutura das assembleias e nas densidades de ovos e larvas e ao longo do canal do rio Guareí. Diferenças temporais foram significativas apenas para densidade de larvas no Ciclo 2. A captura consistente de ovos e larvas de peixes em dois ciclos reprodutivos é uma forte evidência de que este rio é um local para a reprodução de várias espécies de peixes. Assim, recomendamos a manutenção do seu regime de fluxo natural.
Palavras-chave: *Reprodução de peixes; Ictioplâncton; Reservatório de Jurumirim; Peixes migratórios; Prochilodus lineatus.*

Introduction

The distribution of fish eggs and larvae in freshwater ecosystems reflects the reproductive success of species. Young forms are found in most aquatic environments, such as lakes (*e.g.*, Daga et al. 2009, Tondato et al. 2010), rivers (*e.g.,* Reynalte-Tataje et al. 2011, Zacardi et al. 2017), estuaries (*e.g.,* Sarpedonti et al. 2008, Marcolin et al. 2010) and others. In rivers, numerous species spawn in the channel, where larvae drift with the flow toward nursery areas located downstream. Depending on the species [*e.g.*, *Salminus brasiliensis* (Cuvier, 1816)], the larvae may be carried toward downstream reaches for dozens of kilometers (Rosa et al. 2020). In this sense, spatial and temporal assessments of ichthyoplankton distribution are important to understand reproductive and recruitment dynamics in an ecosystem (*e.g.*, Castro et al. 2002, Henry & Suiberto 2014, Rosa et al. 2020). This information plays an important role to guide conservation strategies (Nakatani et al. 2001, Bialetzki et al. 2016), especially in rivers subject to human impacts (*e.g.*, river regulation, fragmentation, habitat loss, pollution, deforestation).

Accessing spatial and temporal dynamics of fish eggs and larvae in small and medium-sized rivers has become increasingly necessary in tropical regions (*e.g.*, Reynalte-Tataje et al. 2020), where hydropower expansion has affected the functioning of many lotic systems (Ferreira et al. 2016, Winemiller et al. 2016). Dams cause hydrological changes with direct and indirect negative effects on the aquatic biota (Agostinho et al. 2008, Couto & Olden, 2018). Moreover, other activities (*e.g.*, agriculture and mining) have caused additional disturbances to small systems, with significant effects on fish biodiversity (Pelicice et al. 2017; Azevedo-Santos et al. 2019, 2021). Small to large sized tributaries deserve special attention, since they may act as biodiversity hotspots in riverine networks (Vitorino Júnior et al. 2016, Silva et al. 2019), especially in areas affected by dams (Marques et al. 2018, Sanches et al. 2020). However, many small tributaries remain uninvestigated, including those that flow into reservoirs, impeding the assessment of their significance in providing critical habitats for fish recruitment.

The Guareí River is a free-flowing tributary located in the Upper Paranapanema River (Fulan et al. 2012), Upper Paraná River, Brazil. This river flows to the Jurumirim Reservoir (Azevedo-Santos et al. 2020), the first impoundment in a "cascade of reservoirs along the Paranapanema River" (Pelicice et al. 2018: p.1-12). These aspects make the Guareí River an interesting case, with potential to act as spawning site and nursery ground for the regional fish fauna. In this study, we investigated spatial and temporal variations in the distribution of fish eggs and larvae in the Guareí River. In particular, we investigated the hypothesis that the Guareí River is a breeding site for several fish species, including long-distance migratory fish (*sensu* Agostinho et al. 2003), considering that it is a free-flowing river that preserves environmental heterogeneity and habitat diversity. Moreover, adult individuals of several species have been observed in this river (Azevedo-Santos et al. 2020), many of which have been reported in Jurumirim Reservoir (see also Kurchevski & Carvalho 2014). Therefore, we investigated three predictions: (i) the presence of eggs and larvae in the Guareí River, including migratory fishes; (ii) spatial gradients in the distribution of early forms, with more eggs in the upper course of the channel, and the predominance of larvae in lower reaches, as observed in large rivers (*e.g.*, Baumgartner et al. 2004); (iii) temporal variations in the density of fish eggs and larvae, considering that reproduction is a seasonal event (*e.g.*, Reynalte-Tataje et al. 2011).

Material and Methods

1. *Study area*

The Guareí River (*ca.* 90 kilometers; Leite et al. 2012) is a small tributary flowing into the Jurumirim Reservoir, Upper Paranapanema River (Henry et al. 2016). Lateral lakes and pools are found along its course, especially in the middle reach (V.M. Azevedo-Santos & R. Henry, personal observation). These lentic environments are connected with the main channel during the wet season. Despite the current hydroelectric expansion in Brazil, which has boosted the construction of small-sized dams (*cf.*, Ferreira et al. 2016), the Guareí River still preserves its original lotic condition (*i.e.*, no dams). Currently, the most notable human impacts in this river are the absence of riparian forests in some stretches (Azevedo-Santos et al. 2020) and water pollution (*e.g.*, solid wastes).

The three sampling sites cover the entire course of the Guareí River (Fig. 1). Site 1 (S1: ~5 m wide and ~ 629 m asl) is located in the upper course (23°21'56.83"S, 48°10'54.47"W), within the urban perimeter of the municipality of Guareí, São Paulo, Brazil. Site 2 (S2: ~13 m wide and ~ 593 m asl) is located in the middle course (23°27'54.27"S, 48°25'18.95"W), close to the Mineiros bridge, in the municipality of Angatuba, São Paulo. Site 3 S3: ~20 m wide and ~ 579 m asl) is located in the lower course (23°27'51.44"S, 48°34'40.34"W), near Aterradinho village, also in the municipality of Angatuba, São Paulo. Site 3 is located about 5 km (straight line) upstream from the confluence of the Guareí River with the Jurumirim Reservoir.

2. *Sampling and laboratory analysis*

Fish eggs and larvae were sampled about fortnightly (Table S1) from November 2017 to March 2018 (Cycle 1), and from November 2018 to March 2019 (Cycle 2). The sampling period was chosen based on Henry & Suiberto (2014), who indicated a high fish reproductive activity during these months. Collections occurred under license provided by Brazilian Institute of the Environment and Renewable Natural Resources (SISBIO 57047).

Sampling took place at night, as previous studies have shown higher densities of fish eggs and larvae during this period (*e.g.*, Garcia et al. 2018). We used an ichthyoplankton net (50 cm diameter and 300 µm mesh) equipped with a flowmeter ("General Oceanics" model 2030BR). The net was positioned near the water surface (~10 cm depth), at the center of the Guareí River channel for 10 minutes (passive collection). We repeated this procedure three times at each sampling event, totaling thirty minutes of water filtered at each site and collection date. The material collected was euthanized with eugenol (procedure frequently used for adult fishes; see Vicentin et al. 2019) and fixed in formalin with $CaCO_3$ as recommended in Nakatani et al. (2001).

In the laboratory, fish eggs and larvae were washed and separated from other materials (*e.g.*, leaves and debris) using a 50 µm sieve. The resulting sample was screened under a stereomicroscope to separate and count fish eggs and larvae. Fish larvae were determined to the lowest taxonomic level (including species) based on Nakatani et al. (2001). When necessary, a specialist confirmed the identification (see Acknowledgments section). In addition, the fish larvae were classified according to each development stage and degree of notochord flexion, following Ahlstrom & Ball (1954) and adapted by Nakatani et al. (2001; p. 33): "yolk-sac larvae", "pre-flexion", "flexion" or "post-flexion".

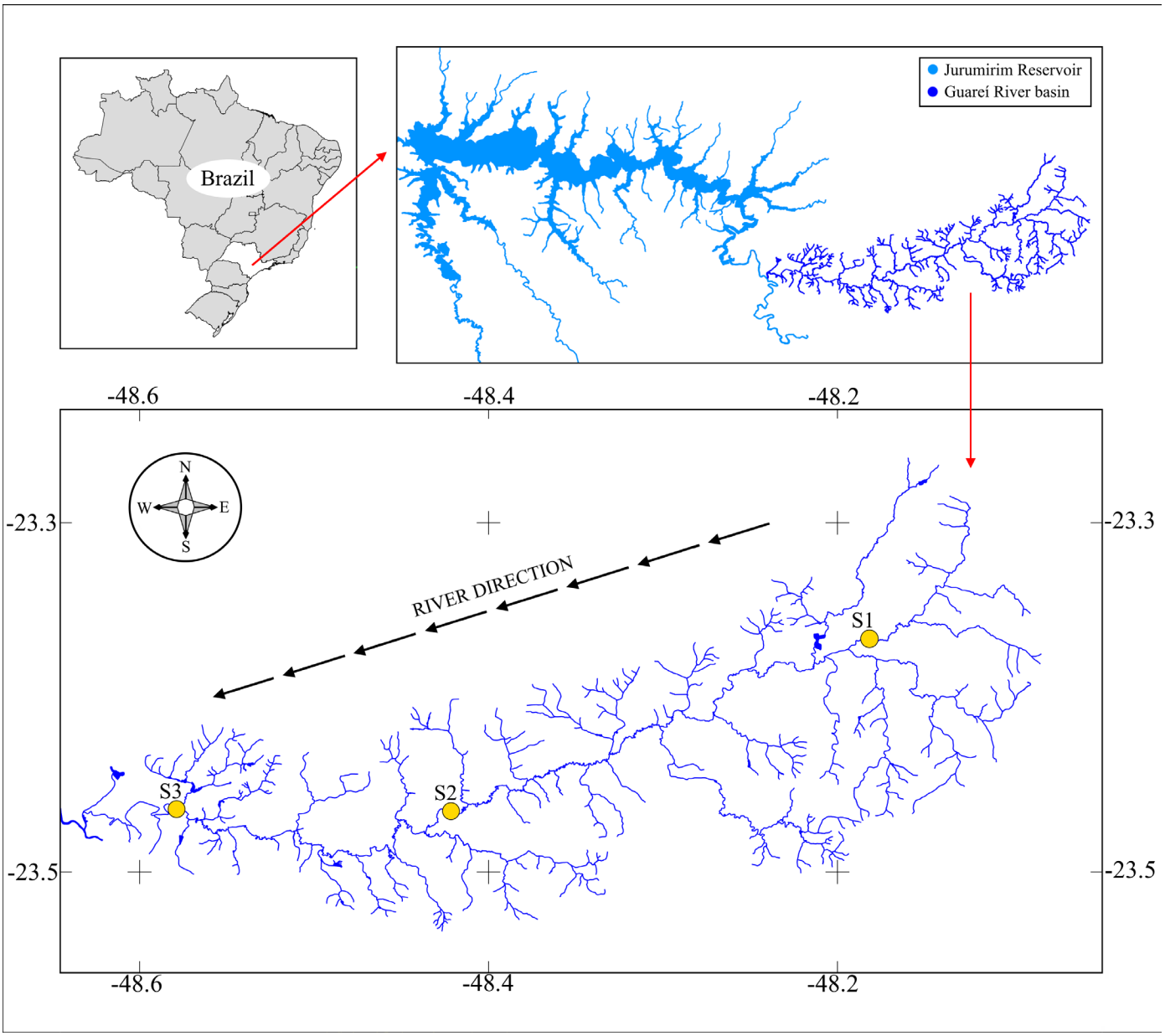


Figure 1. Location of the three sampling sites (in yellow) along the Guareí River, Paranapanema River basin (upper Paraná River system), São Paulo (modified from Azevedo-Santos *et al*., 2020).

The volume of water filtered by the planktonic net was calculated based on Nakatani *et al*. (2001). Fish eggs and larval densities (number/10m³) were calculated based on Tanaka (1973) *apud* Nakatani *et al*. (2001), considering adaptations made by these last authors.

3. *Data analysis*

We ran a Non-Metric Multidimensional Scaling analysis (NMDS) (Clarke & Warwick, 2001) to investigate assemblage structure patterns among sites (S1, S2, and S3). For this analysis, fish larvae were grouped at the family level, as many individuals were not identified at the species or genus levels. Density data were log (x + 1) transformed, and the analysis employed Bray-Curtis similarity (Clarke & Warwick, 2001) with the insertion of Dummy (0.01). Subsequently, a PERMANOVA was applied to test for differences in assemblage structure ($p < 0.05$) among sites. The NMDS and PERMANOVA were run in PRIMER 6.0.

Significant differences ($p < 0.05$) in egg and larval densities were investigated with non-parametric Anova (Kruskal-Wallis, H), considering sites (S1, S2 and S3) and sampling events (*e.g.*, Jan A, Jan B, so on) as factors. This same analysis was used to test differences between larval development stages in each sampling site. Data in each cycle were investigated separately. The Dunn test (Dunn, 1964) indicated differences among groups. Both tests, H and Dunn, were run in the FSA package (Ogle et al. 2019), R environment (R Development Core Team, 2018).

Results

We collected 859 fish eggs and 1,340 larvae in the Guareí River: 567 eggs and 307 larvae in Cycle 1, and 292 eggs and 1,033 larvae in Cycle 2. Captured larvae were identified up to the maximum level of class (total of one), orders (two), families (seven), genera (two), or species

(seven). A total of 19 taxa was recorded (Table 1; see also Table S2): 15 in Cycle 1, and 15 in Cycle 2. Seven taxa were identified at the specific epithet level. Among them is *Prochilodus lineatus* (Valenciennes, 1837) [Prochilodontidae], a long-distance migratory fish, but these larvae were recorded only in two sites during Cycle 2 (Table 1).

Assemblage structure of larvae was similar among sampling sites in both cycles (Fig. 2a-b). Within each cycle, no significant differences in assemblage structure between sampling sites were observed (Permanova, p = 0.24 and p= 0.11).

In Cycle 1, egg density ranged between 3.3 and 12.5 eggs/10m^3, and larval density ranged between 8.7 and 14.9 larvae/10m^3 among sampling sites (Fig. 3a-b). In Cycle 2, egg density ranged between 1.8 and 7.4 eggs/10m^3, and larval density ranged between 18.0 and 46.7 larvae/10m^3 among sampling sites (Fig. 3c-d). There were no significant spatial differences in the density of fish eggs (Kruskall-Wallis, Cycle 1: p = 0.72; Cycle 2: p = 0.72) and larvae (Kruskall-Wallis, Cycle 1: p = 0.97; Cycle 2: p = 0.78) among sites in both cycles.

Temporally, egg density ranged between 0 and 36.4 eggs/10m^3, and larvae between 0.5 and 42.1 larvae/10m^3 in Cycle 1 (Fig. 4a-b). On the other hand, egg density ranged between 0 and 17.9 eggs/10m^3, and larvae between 1.1 and 158.0 larvae/10m^3 in Cycle 2 (Fig. 4c-d). Statistical differences were found only for fish larvae in Cycle 2 (Table S3).

Table 1. Taxa and their respective average densities (fish larvae/10m^3) at each site during each sample cycle (classification of taxa in Table S2). Larvae identified up to the level of class[1], order[2], family[3], genus[4], and species[5].

Taxon	Cycle 1			Cycle 2		
	S1	S2	S3	S1	S2	S3
Actinopterygii[1]	3.4642	0.3287	1.9238	0.8437	0	0
Anostomidae[3]	0	0.1018	0.1130	0	1.0089	3.9260
Apareiodon affinis (Steindachner, 1879)[5]	0	1.3641	1.6488	0	0	1.0414
Astyanax spp.[4]	0.7436	0	0.1141	0	0.6668	0
Bryconamericus aff. *iheringii* (Boulenger, 1887)[5]	3.7678	0.2609	0.1959	0.6946	0.1830	0
Bryconamericus spp.[4]	1.1463	2.5315	1.2926	3.3124	2.1812	12.0052
Callichthyidae[3]	0	0	0	0.0194	0	0
Characidae[3]	5.4966	2.2468	1.0301	10.7488	29.3673	3.6576
Characiformes[2]	0.0279	1.6250	1.0529	0	0.5408	0.2719
Curimatidae[3]	0	0	0	1.6467	6.8202	0
Heptapteridae[3]	0.2549	0.3304	0.1223	0.7615	4.0958	0
Hoplias malabaricus (Bloch 1794)[5]	0	0.0407	0	0	0	0
Hoplosternum littorale (Hancock 1828)[5]	0.0208	0.0121	0	0	0	0
Parodontidae[3]	0	0	0.0235	0	0	0
Pimelodidae[3]	0	0.0339	0.0222	0	0	0
Prochilodus lineatus (Valenciennes, 1837)[5]	0	0	0	0	0.0609	0.0057
Schizodon nasutus Kner, 1858[5]	0	4.5731	1.1937	0	1.7162	3.4945
Serrasalmus maculatus Kner, 1858[5]	0	0	0	0	0.0852	0.3362
Siluriformes[2]	0	0	0.0128	0	0	0.0029

We recorded four different developmental stages for fish larvae (Fig. 5). In Cycle 1, the yolk-sac larvae stage was predominated (Fig. 5b; Table S4).

Discussion

Our results support the hypothesis that the Guareí River is a reproductive area for rheophilic and migratory fishes. We expect the same pattern in other small rivers flowing to hydroelectric reservoirs in Brazil. In general, the role of small tributaries in areas affected by impoundments — like the Guareí River — as spawning areas for fishes are often overlooked. In fact, studies usually focus on medium or large-sized rivers (e.g., Silva et al. 2019). Therefore, we fill an important knowledge gap concerning the distribution of fish eggs and larvae in these small watercourses.

We recorded larvae of the migratory fish *Prochilodus lineatus*, although in low density. This species is able to migrate hundreds of kilometers to spawn (Agostinho et al. 1993, Agostinho et al. 2003), but dams block migration routes and affect spawning dynamics — and populations usually decline in the impoundment and adjacent areas. The presence of preserved tributaries (*i.e.*, free-from-dams) can sustain populations (*e.g.*, Agostinho et al. 2003, Lopes et al. 2019), and the Guareí River seems to offer conditions for spawning. Our sampling also detected the presence of *Schizodon nasutus* Kner, 1858, a medium-sized rheophilic fish (maximum ~ 30 cm) (Nobile et al. 2015), that migrates small distances to spawn (Carvalho et al. 1998). Other species found were *Apareiodon affinis* (Steindachner, 1879), *Bryconamericus* aff. *iheringii* (Boulenger, 1887), *Hoplias malabaricus* (Bloch, 1794), *Hoplosternum littorale* (Hancock, 1828), and *Serrasalmus maculatus* Kner, 1858, non-migratory fishes (*sensu* Vazzoler 1996) with populations in the Jurumirim Reservoir (Kurchevski & Carvalho 2014). The reproduction of these species — which include several with commercial importance (see Novaes

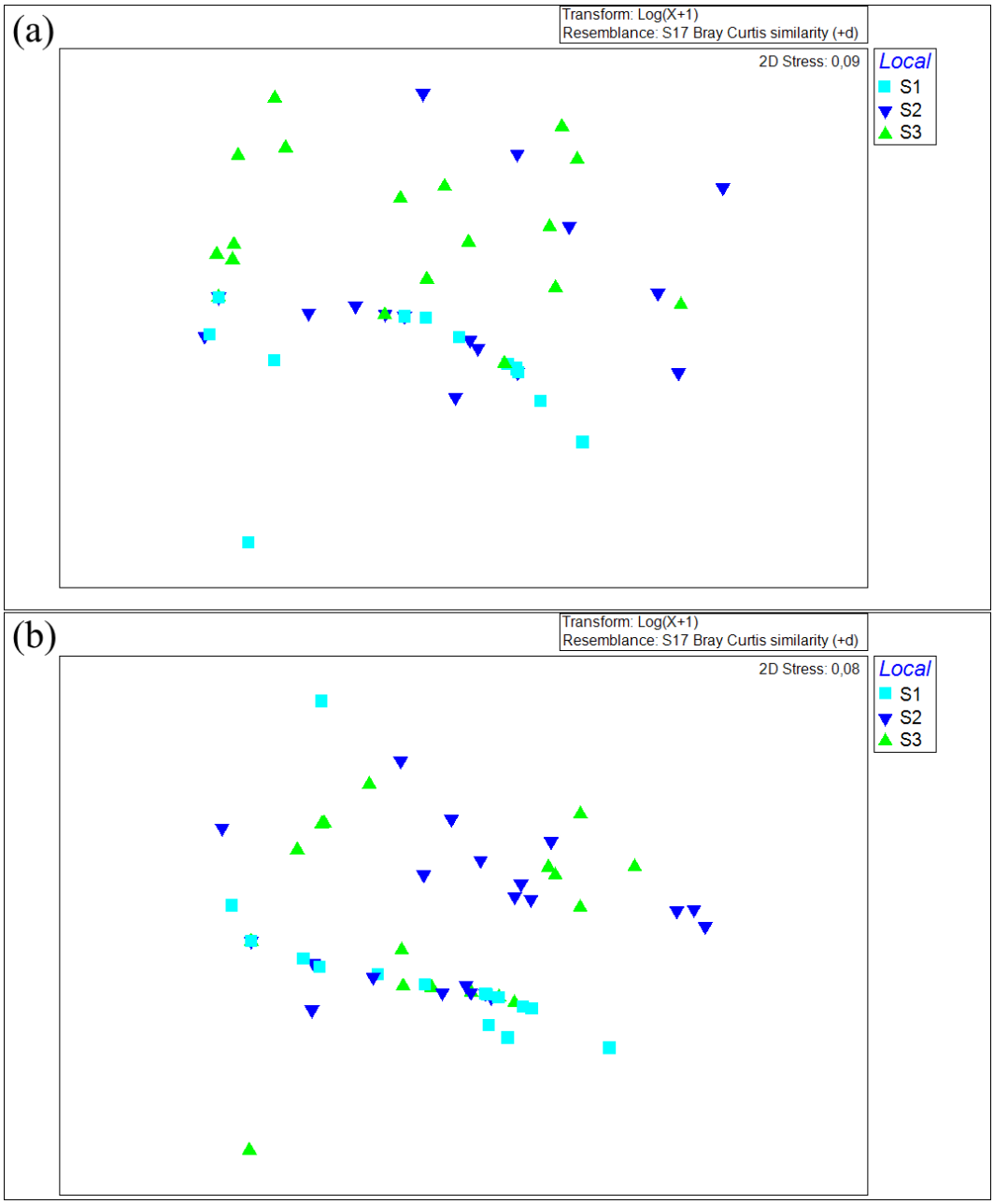


Figure 2. NMDS depicting spatial variation in fish larvae structure (Family level) in sampled sites along the Guareí River, Paranapanema River basin (upper Paraná River system), São Paulo, Brazil, in the: (a) Cycle 1; (b) Cycle 2.

& Carvalho 2009) — is indication that the Guareí River serves as a spawning ground for fishes with different reproductive strategies.

The fish larval structure was similar among sampling sites. However, it should be noted that the analyses were carried out mostly at the family level, since the identification of species is difficult (see Bialetzki et al. 2016, for a broader discussion on this issue). This aspect may have precluded the observation of differences in structure among sites. For example, representatives of Characidae may be widely distributed along the river, but with different species occupying the gradient headwater-mouth (Azevedo-Santos et al. 2020).

Contrary to our prediction, we observed no spatial gradient in the distribution of fish eggs and larvae along the Guareí River. The predominance of non-migratory fish in this river (Azevedo-Santos et al. 2020) may explain this pattern. Non-migratory fish release eggs in different localities along the river (Baumgartner et al. 2004), probably in the confluence with streams; they do not need to reach upper stretches to spawn, which is a common behavior among migratory fishes (Agostinho et al. 2003, Baumgartner et al. 2004). Our results show that in small rivers like the Guareí River (with few migratory species), different reaches may provide adequate conditions for spawning.

Contrary to our prediction, no significant temporal differences were found during Cycle 1, as reproduction occurred in all sampling months. Significant differences between peaks were found only for fish larvae in November A and December A during Cycle 2, reflecting the increased reproductive activity in these occasions. Our results suggest that small rivers like the Guareí do not present a clear temporal pattern

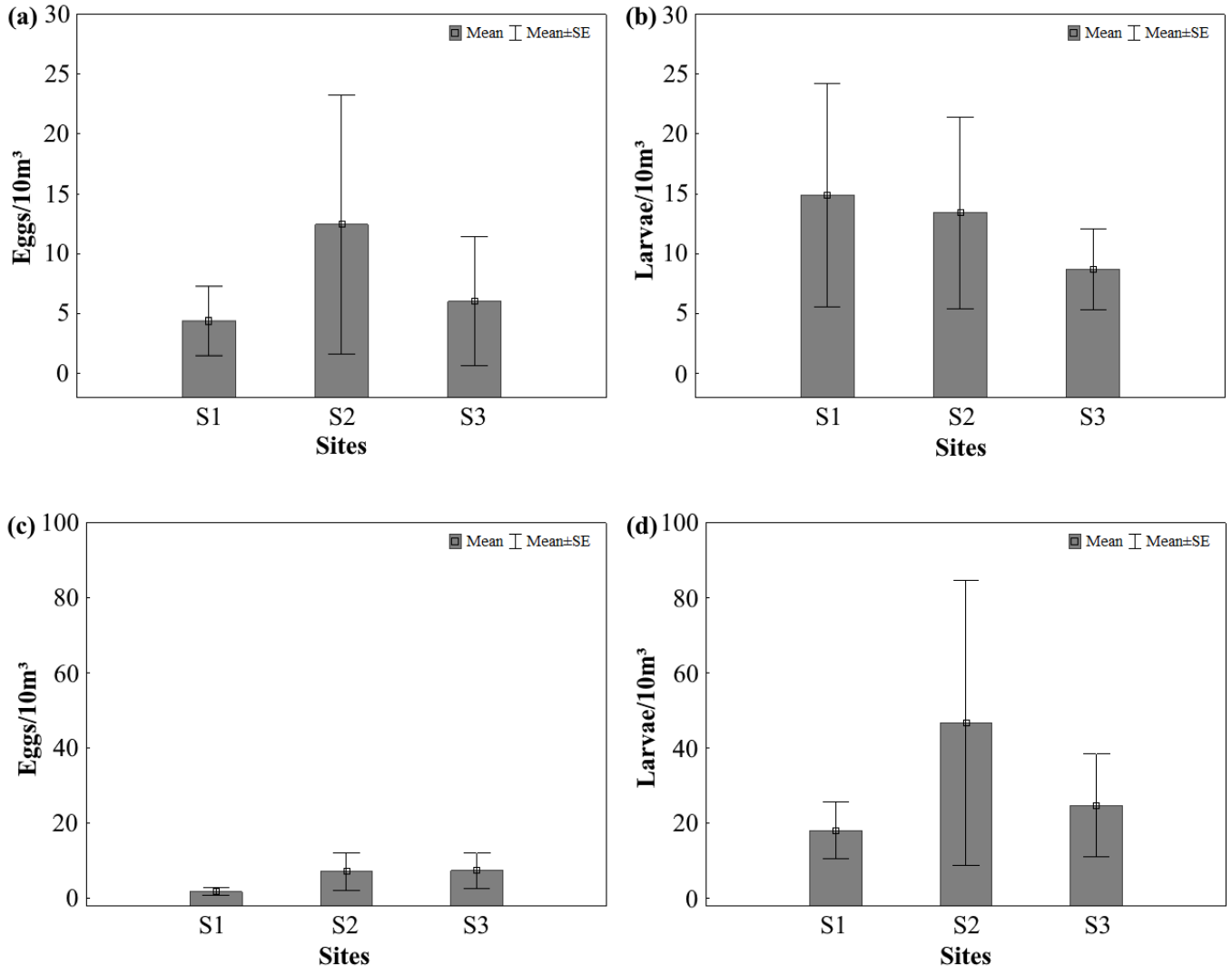


Figure 3. Average density and standard deviation of the ichthyoplankton collected at each site along the Guareí River: (a) eggs and (b) larvae, Cycle 1; and (c) eggs and (d) larvae, Cycle 2.

of reproduction peaks. Other possible explanation is that sampling occurred only in six months, when most species in the region reproduce (Henry & Suiberto 2014). Therefore, the detection of fine scale patterns and spawning peaks would require a different sampling design (*i.e.*, considering samplings in all months of the year).

At each site, the larval development stage was variable. In general, after hatching, the fish larvae develop during the drifting process in the river (Baumgartner et al. 2004). Then, results indicate that the river channel is an area of dispersion and growth. Considering the two cycles, fish larvae in more advanced development stages (*i.e.*, flexion and post-flexion) had lower densities when compared to the other stages (*e.g.*, yolk-sac larvae). As we used passive collection, we believe that larvae in flexion and post-flexion stages show some type of mobility (se also Sanches et al. 2020), impeding them to drift with the river flux up to the ichthyoplankton net. Another possibility is that fish larvae in these more advanced stages are able to remain in areas less affected by the current (*i.e.*, backwaters, including those close to vegetation), or in lateral lakes and ponds, which offer favorable conditions for feeding and survival.

A number of studies (*e.g.*, Nunes et al. 2015, Silva et al. 2015, Marques et al. 2018, Silva et al. 2019, Sanches et al. 2020) have shown or suggested the importance of tributaries for the maintenance of fish diversity in impounded areas. Therefore, the data presented here indicate that the Guareí River is important to the maintenance of fish assemblages in the Jurumirim Reservoir, given the connectivity between the two areas (*i.e.*, free-flowing river and dam). First, it is possible that migratory species (short or long distance) found in the Guareí River, and that also occur in the Jurumirim Reservoir (*e.g.*, *S. nasutus*, *P. lineatus*; Kurchevski & Carvalho 2014), are using this tributary as a route to complete their reproduction; since this affluent has important characteristics that many species require for spawning (*e.g.*, rapids, free-flow). Secondly, is possible that larvae of migratory or sedentary species that reproduce in the Guareí River may reach the Jurumirim Reservoir through drift; and in viable development stages for feeding and displacement. For example, Rosa et al. (2020) estimated that fish larvae can drift long distances until they reach growth areas. In the case of the Guareí River, larvae of *P. lineatus* (especially in stages more susceptible to drift, *e.g.*, pre-flexion) may reach the Jurumirim Reservoir

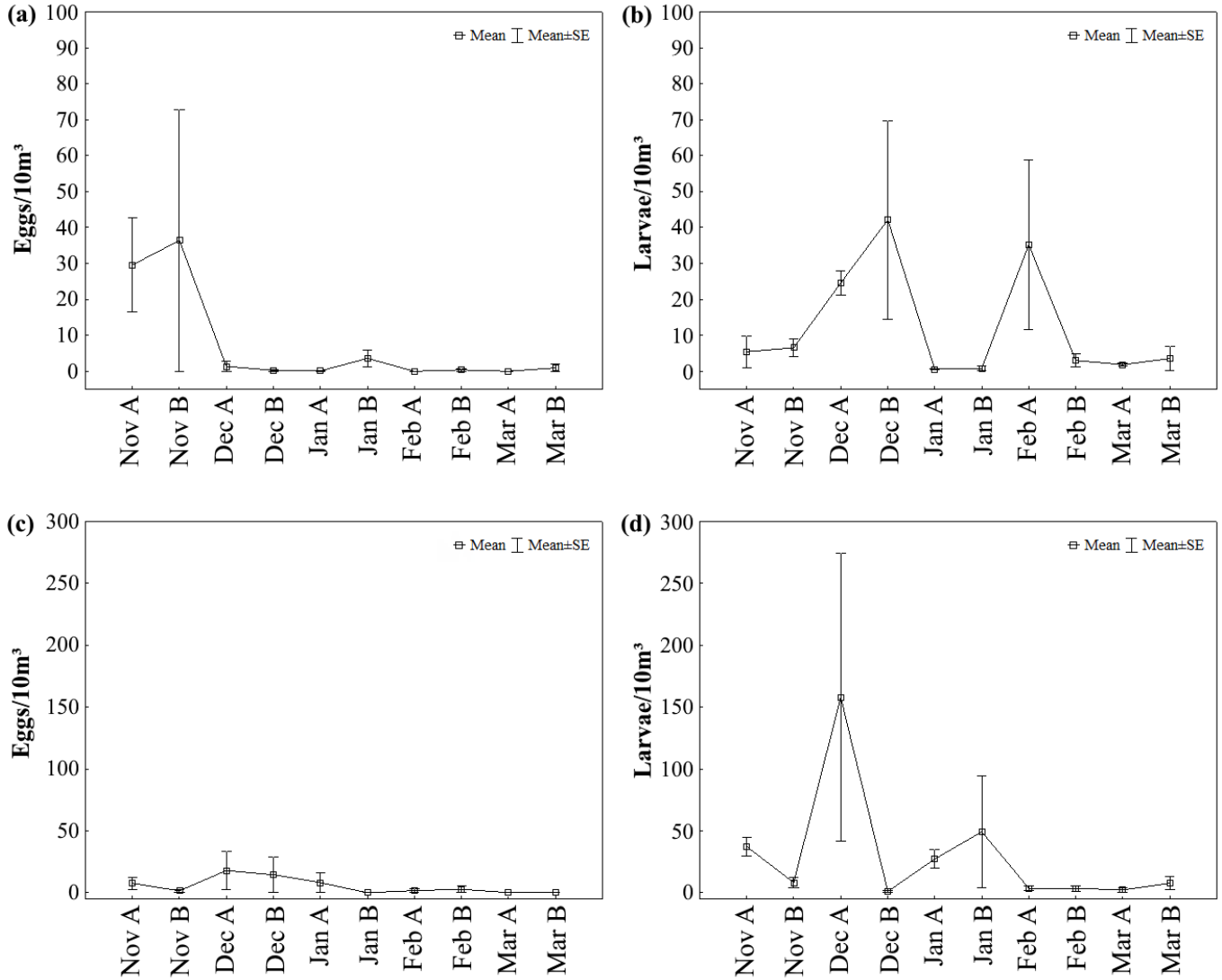


Figure 4. Average density of the ichthyoplankton collected at each sampling occasion in all sites along the Guareí River: (a) eggs and (b) larvae, Cycle 1; and (c) eggs and (d) larvae, Cycle 2.

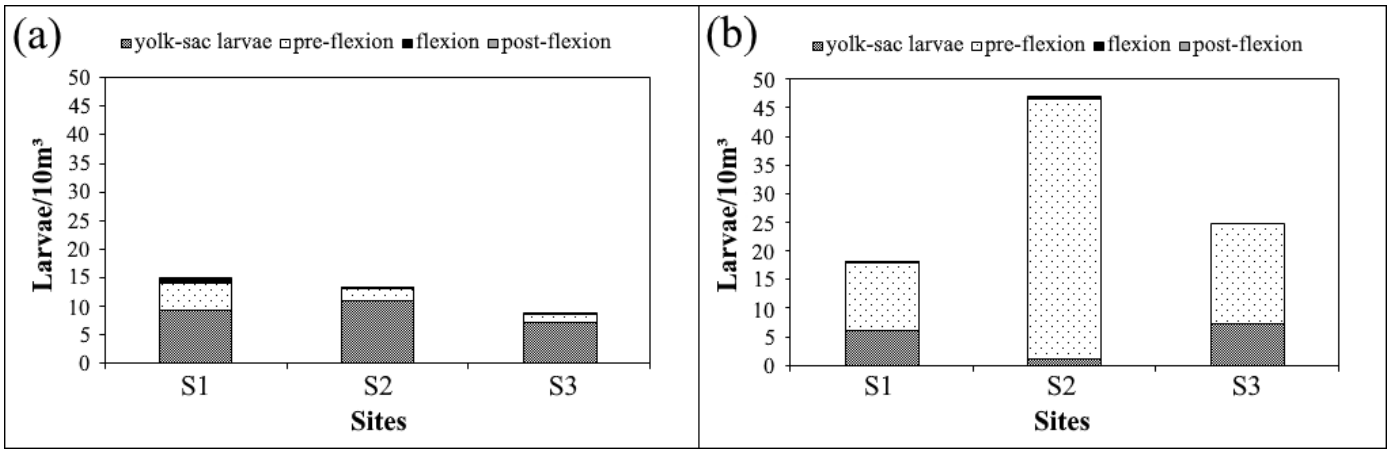


Figure 5. Average density of each larvae stages collected in (a) Cycle 1 and (b) Cycle 2 in each site of the Guareí River.

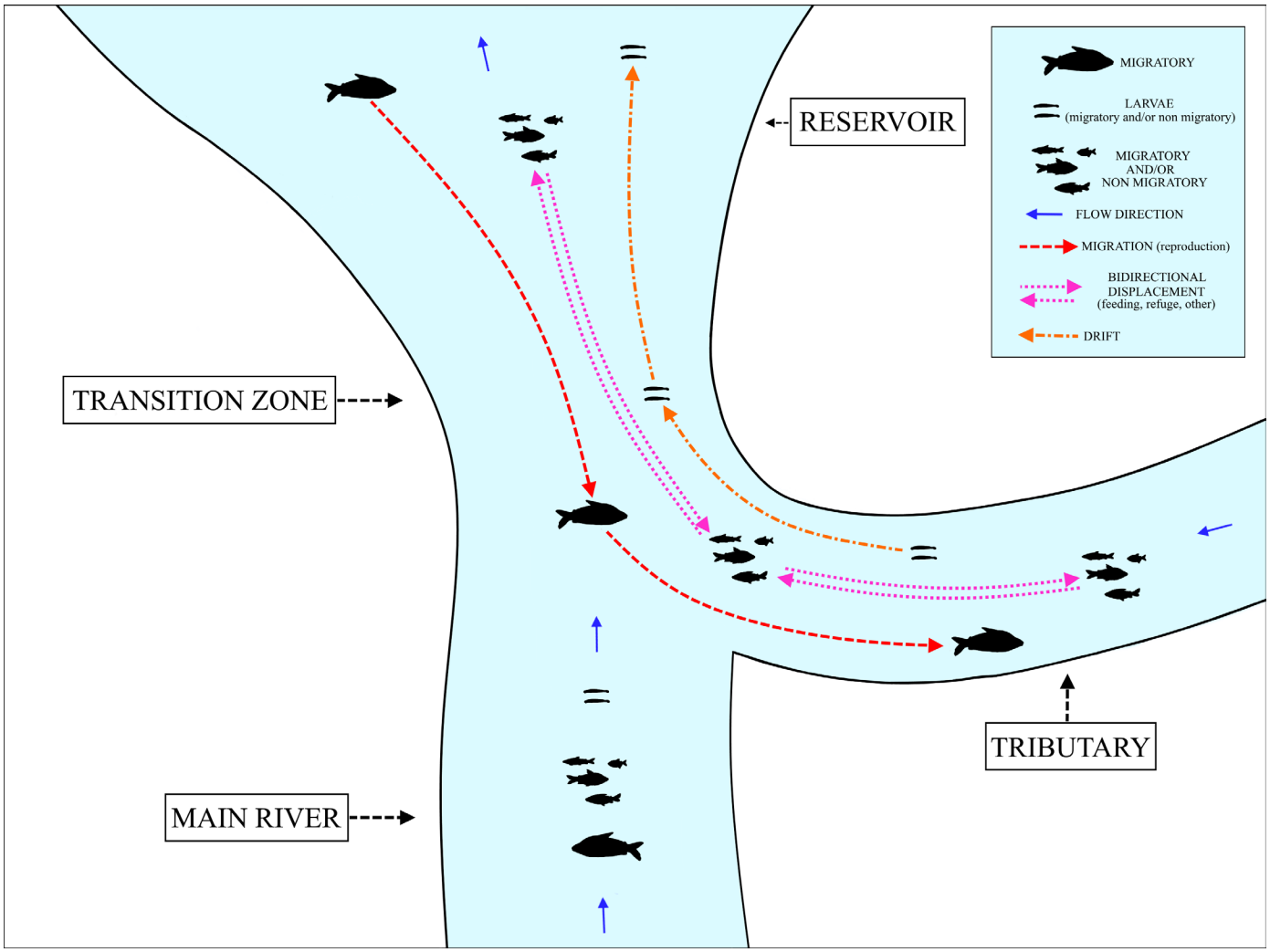


Figure 6. Conceptual model showing how the Guareí River may serve as a "biodiversity source" for the Jurumirim Reservoir, São Paulo, Brazil.

and, once in it, individuals will be able to find growth areas with food such as zooplankton, a resource present in dammed environments and freshwater areas adjacent to them (*e.g.*, Arcifa 1984, Nogueira 2001, Casanova & Henry 2004, Coelho & Henry 2021). This second explanation is reinforced by the data of Henry & Suiberto (2014), who showed the presence of *P. maculatus* larvae and other species at the confluence of the Guareí River with the Jurumirim Reservoir. Third, species may reproduce in the Guareí River, grow in this tributary, and then move to the Jurumirim Reservoir in short (seasonal) or long term (years) for different reasons, especially in search of food, space, or refuge (*e.g.*, macrophytes) (Fig. 6). In other words, we believe that the Guareí River may serve as a "biodiversity source" to the Jurumirim Reservoir. Thus, due to its importance for the reproduction of several fish species — and because it is a lotic tributary of a reservoir —, we emphasize the need to maintain its natural flow regime.

Conclusion

Our results confirmed the hypothesis that the Guareí River is a spawning area for several species, including long-distance migratory fish. However, we detected no spatial differences in assemblage structure or in the densities of fish eggs and larvae along the Guareí River. In addition, we recorded temporal differences in densities of fish larvae only in Cycle 2. As an important watercourse for fish reproduction, we recommend maintaining natural flow regime.

Supplementary Material

The following online material is available for this article

Table S1 - Detailed information about the months, their acronyms, and dates of collections at the three sample sites along the Guareí River, São Paulo, Brazil.

Table S2 - Classification (*sensu* Fricke *et al.*, 2018a, Fricke *et al.*, 2018b) of each taxon captured in the Guareí River, São Paulo, Brazil.

Table S3 - Significant results of Dunn's test for larvae collected in the Cycle 2 in the Guareí River, São Paulo, Brazil.

Table S4 - Results of the statistical analysis of the larval stages.

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Author Contributions

Valter M. Azevedo-Santos: performed the collection and identified taxa, performed data analysis, interpretation of data, wrote the first version, led the reviews and writing.

Vanessa S. Daga: performed data analysis, interpretation of data, and collaborated with writing.

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Conflicts of Interest

None.

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Article

A compilation of host plants and their gall-inducing insects for the Caatinga Biome

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Abstract: Caatinga is a seasonally dry tropical forest, one of the richest in plant species. Unfortunately, many groups of herbivorous insects associated with these plants are poorly known. This study aimed to investigate the diversity of gall-inducing insects (GII) and host plants (HP) in the Caatinga. For this, we compiled the information available in the literature of inventories on GII and their HP communities, and the described gall midge species. We found 100 species, 72 genera, and 32 families of HP hosting a total of 156 morphospecies of GII and 12 species of described cecidomyiids. Plant species with only one GII species represented 74% of hosts, but in super HP (i.e., HP with a high number of GII), despite the small number of HP species, there were many GII species. Fabaceae was also the most specious family, with 30% of HP species and 40% of GII. Furthermore, our results showed a low number of species of HP and GII for the Brazilian Caatinga, that we discussed this pattern with the following arguments, first, it is likely that the number of galling insect inventories for the Caatinga is under-sampled, second the Caatinga has a relatively smaller number of plant species when compared to other biomes, and finally, we argue that the Caatinga is a seasonally dry tropical forest where the deciduousness represents a relevant factor in the colonization and performance rates of GII.
Keywords: *Galls; Insect gall; Insect herbivores; Seasonally Dry Tropical Forest.*

Uma compilação de plantas hospedeiras e seus insetos galhadores para o bioma Caatinga

Resumo: A Caatinga é uma floresta tropical sazonalmente seca, uma das mais ricas em espécies vegetais. Infelizmente, muitos grupos de insetos herbívoros associados a essas plantas são pouco conhecidos. Este estudo teve como objetivo investigar a diversidade de insetos galhadores (IG) e plantas hospedeiras (PH) na Caatinga. Para isso, nós compilamos as informações disponíveis na literatura de inventários sobre a comunidade de IG e suas PH, e as espécies descritas de cecidomiídeos. Nós encontramos 100 espécies, 72 gêneros e 32 famílias de PH abrigando um total de 156 morfoespécies de IG e 12 espécies descritas de cecidomiídeos. Espécies de plantas com apenas uma espécie de IG representaram 74% das hospedeiras, mas para as super PH (ou seja, PH com alto número de IG), apesar do pequeno número de espécies de PH, havia muitas espécies de IG. Fabaceae foi a família mais rica, com 30% das espécies de PH e 40% dos IG. Além disso, nossos resultados mostraram um baixo número de espécies de PH e IG para a Caatinga brasileira, e discutimos esse padrão com os seguintes argumentos, primeiro, é provável que o número de inventários de insetos galhadores para a Caatinga seja subamostrado, segundo a Caatinga possui um número relativamente menor de espécies vegetais quando comparada a outros biomas e, por fim, argumentamos que a Caatinga é uma floresta tropical sazonalmente seca onde a deciduidade representa um fator relevante para as taxas de colonização e desempenho dos IG.
Palavras-chave: *Galhas; Galha de inseto; Insetos herbívoros; Floresta Tropical Sazonalmente Seca.*

Introduction

The Neotropical Seasonally Dry Forests are found from Northwestern Mexico to Northern Argentina and Southwestern Brazil in separate areas of varying sizes (Linares-Palomino et al., 2011). The Caatinga phytogeographic domain is a seasonally dry tropical forest (SDTF) (Pennington et al. 2009) endemic to Brazil. It represents one of the largest semiarid regions in South America, occurring over approximately 800,000 km^2 in Northeastern Brazil (Silva et al. 2017). Caatinga has an extended dry period in which rainfall is scarce (Silva et al. 2017), and as a result, most of the vegetation is deciduous (Prado 2003). The seasonality and rainfall distribution, associated with elevated temperatures and highly variable edaphic conditions, drive a diverse spectrum of Caatinga phytogeographic formations (Sampaio 1995; Moro et al. 2015). At least 13 different physiognomies span a broad range of woody plant densities, and this is collectively referred to as the Caatingas (Prado 2003). Their flora is considered the most diverse for SDTFs on Earth (Silva et al. 2019), harboring 4,891 species, 1,232 genera, 176 families of flowering plants, and 298 endemic species (Flora 2020) of 31 endemic genera (Queiroz et al. 2017). Fabaceae is the most species-rich family, with 490 species among 112 genera (Fernandes et al. 2020).

Many groups of herbivorous insects occur in the Caatinga, and among them are the leaf chewing (e.g., Coleoptera, Orthoptera, Lepidoptera, and Phasmatodea;), sap-sucking (mostly Hemiptera), wood-boring, and gall-inducing insects (Santos et al. 2011; Leal et al. 2018; Costa and Araújo 2019). Among these groups of herbivores, gall-inducing insects are noteworthy for being the herbivorous insect guild with a higher specificity for their host plants (Joy and Crespi 2007; Carneiro et al. 2009; Grandez-Rios et al. 2015). In the Neotropical region, gall inducers are poorly known taxonomically, and most of the species are new to science (Gagné and Jaschhof 2021), especially in the SDTF. Studies about gall-inducing insects in the Caatinga are recent, and the first studies were carried out about ten years ago (see Santos et al. 2011). In a recent review of the state of the art of gall-inducing insect studies in Brazil, Caatinga is identified as one of the least studied and most promising ecosystems (Araújo et al. 2019). In this context, there are still many gaps in the knowledge of patterns of galling insect diversity in the Brazilian Caatinga.

In the present study, we investigated the diversity patterns of host plants and galling insect species in the Brazilian Caatinga. No previous study has been published toward understanding general patterns in host plant richness and galling insect species throughout this ecosystem. In this context, the present work aimed to: a) compile the information available in the literature about inventories of insect galls and their host plants communities in the Caatinga; b) quantitatively and qualitatively analyze the richness of host plants and galling insect species; c) estimate the number of threatened species of host plants and galling insects; d) estimate the potential number of galling insects species for Caatinga; and e) describe the number of galling species per host plant, where each host plant had been classified in, single-hosts plants with only one gall species, multi-hosts those plants with two or more galls per plant and, super-hosts plants that hosted numerous galling insect species.

Material and Methods

1. Data collection for host plant and galling morphotypes

We conducted a comprehensive literature search for data about galling insects and their host plants in the Brazilian Caatinga. We searched potential studies through online academic databases, such as Google Scholar, JStor, ISI Web of Knowledge, Scielo, and Scopus. To search the online databases, we used the following terms which were combined in different ways: "galling insect," "insect gall," "inventories," "richness," "Brazil," "Brazilian," "seasonally dry tropical forest," and "Caatinga." Searches were conducted only in Portuguese and English. Our data compilation was focused on community studies, such as checklists and inventories of host plants and gall-inducing insects; therefore, we discarded paper that contained case studies involving botany, ecology, and zoology. Our data set results from the compilation of gall-inducing insects and their host plants recorded in different localities in the Brazilian Caatinga. From our searches, the data were obtained from nine papers from 2011 to 2019: Santos et al. (2011), Carvalho-Fernandes et al. (2012), Luz et al. (2012), Costa et al. (2014a), Costa et al. (2014b), Nogueira et al. (2016), Alcântara et al. (2017), Brito et al. (2018), and Costa and Araújo (2019).

We checked the name spelling and authorship, as well as the update of the host plant species according to Flora do Brasil 2020 (http://floradobrasil.jbrj.gov.br) (Flora do Brazil 2020). For this analysis, we used host plant species with valid, specific names according to Flora 2020 (156 records). For plant family classification, we used the APG IV (Chase et al. 2016). Then, we discarded all records with taxonomic uncertainty in the following situations: a) plants not identified at any taxonomic level (species, genus, or family; 32 records, 12%); b) plants that were identified only at the family level, or without genus identification, or in which the host plant was only referred to as "sp." (35 records, 13%); c) plants identified at the family and genus level followed by "sp." (41 records, 15%); and d) plants identified as *conferatum* (cf.), in this case, species were not confirmed to specific species (6 records, 2%). These data were discarded for the main analyses, and they were used later only to see the additive effects of the number of genera and families in the diversity of host plants (details in the Supplementary Material). Once the identity of the plant was confirmed, we obtained the following variables: the number of records (the number of studies that reported plant species), and the number of plant species by genus and family.

For gall-inducing insects, the taxon was not included because most studies do not provide their identification. Instead, they use gall morphology as a phenotypic trait to separate gall morphospecies. Then, for each study, we recorded the number of galling insects morphotypes by plant species. From there, we had a general list of plant species and the number of galling insect species found for each of the nine studies evaluated. We observed a lack of standardization in the description of gall morphotypes (Isaías et al. 2013), which led us to adopt some procedures to reduce the redundancy of their number. Most of the plant species (74 ssp., 74%) had only one record, so for them, we had no problems, because only a single author described the morphotypes. However, 26% (26 ssp.) of the plant species had from two to seven gall-inducing insect records for the same plant. In this situation, we use the following approach: a) when two or more authors reported equal numbers of gall morphotypes for the same species of plant, we arbitrarily selected one record and deleted the other records; and b) when two or more authors reported different numbers of gall morphotypes for the same plant species, we selected the plant record with the highest number of gall-inducing insect species. We used this criterion because plants with more reported galling insect species are expected to be more representative of the galling insect community. Although we understand

the limitations of this choice, we believe it is the best method to use, since there is little data available on galling species to directly estimate the number of galling insects by host plant species.

2. *Subset of data with only host plant species of Caatinga*

Our pre-analysis showed that the host plant community had many typical Cerrado species, which are not normally found in the Caatinga. This was because some studies were done in ecotone areas between Caatinga and Cerrado, and because of the presence of some phytophysiognomies in the Cerrado that occur within the Caatinga domain. Because of this, we wanted to know the additive effects that the plants of the Cerrado have on the diversity and data set of plants and galling insects of the Caatinga. We excluded plant species that occur in the Cerrado with no distribution in Caatinga. Thus, a subset of data with only host plants with distribution in the Caatinga was obtained from Fernandes et al. (2020). These authors published the most recent, comprehensive, and taxonomically verified checklist of the flowering plant species occurring in the Caatinga of Northeast Brazil, with 3,347 species, 962 genera, and 153 families.

3. *Data collection for Cecidomyiidae species*

After obtaining the host plant list, we manually added the described galling insect species associated with those host plant species. We searched for the new species of gall inducers in the same online academic databases used to produce the host plant list, changing only the terms which were combined among the following words (in Portuguese and English): "Cecidomyiidae," "gall," "new species," "Brazil," and "Caatinga" combined with the names of host plant species. The most important insect families referred to as gall inducer in the nine inventories in the Caatinga was Cecidomyiidae (Diptera), the richest gall inducer in the world (Gagné and Jaschhof 2021). Because of this, we also searched for cecidomyiids species in two sources: a) in the fifth edition of "A Catalogue of the Cecidomyiidae of the World" (Gagné and Jaschhof 2021); and b) in the Museu Nacional of Universidade Federal do Rio de Janeiro (MNRJ) and Museu de Zoologia of Universidade de São Paulo (MZUSP) databases, where the new species of cecidomyiid are deposited in Brazil. We discarded all records of gall inducers without identification to the species level (144 records). Once the gall inducers associated with the host plant species was confirmed, we obtained the following variables: the number of records (the number of studies that reported gall inducers associated with host plants), the number of gall inducers by host plant species, genus, and family, and the most frequent gall inducers species associated with the host plant species, genus, and family.

4. *Statistical analysis*

We made some descriptive statistical analyses for an overview of the data. First, we provide a rarefaction curve for species, genera, and families of gall-inducing insects number in relation to the number of studies. We also graphically represent the distribution of the number of gall-inducing insects' species by host plant species in relation the total number of host plant species and the estimated of the total number of galling insect species in the Caatinga. And finally, we ranked plots of the number of host plant records, host plant species galling insect species for 32 host plant families in the Caatinga.

Results

1. *Host plants and their galling insects*

Overall, we found 254 records (153 records to valid species) among 100 species, 72 genera, and 32 families of host plants in the nine studies compiled for the Brazilian Caatinga (Table S1, Table S2). When we compared our results with the taxa of species of plants of the Caatinga (*sensu* Flora do Brasil 2020), we registered that only 2% of the species (4,891 spp. total), 6% of the genera (1,232 genera total), and 18% of the families (176 families total) of all plants of the Caatinga host galling insects. The asymptote showed that families tend to stabilize with an increase in the number of studies. However, for species and genera, a greater increment of 160 studies is expected to stabilize the curve (Figure 1).

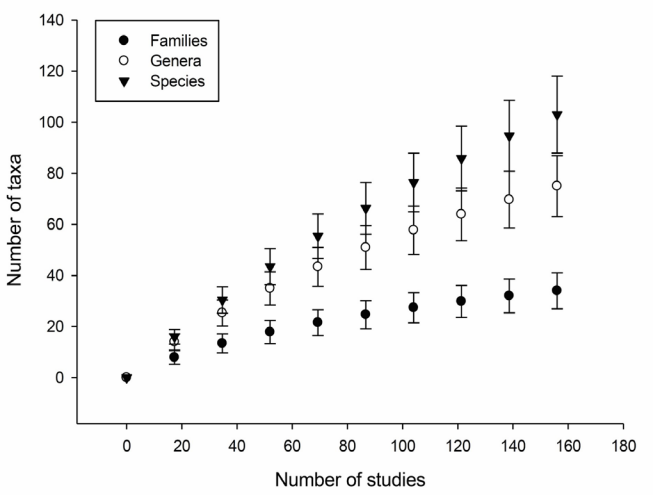


Figure 1. Rarefaction curves for species, genera, and families of host plants of galling insects by study number in the Caatinga. Bars dotted indicate 95% confidence intervals.

Additionally, we found two species that are vulnerable to extinction (VU) according to the Red List of Brazilian Flora, and they were: *Apuleia leiocarpa* (Vogel) J.F.Macbr. (Fabaceae; two gall morphotypes) and *Manilkara dardanoi* Ducke (Sapotaceae; one gall morphotype). Behind the species of host plants, three species are in the near-threatened (NT) category (*Bowdichia virgilioides* Kunth [Fabaceae], *Handroanthus impetiginosus* [Mart. ex DC.] Mattos [Bignoniaceae], and *Handroanthus impetiginosus* [Mart. ex DC.] Mattos [Bignoniaceae]), each with one galling morphotype.

In relation to galling insects, we found a total of 156 morphospecies of insect galls associated with 100 host plants in the Caatinga (Table S1). This equates to a ratio of 1.56. Twelve species of described cecidomyiids were associated with 10 host plant species from eight families that occur in the Caatinga (Table S3). Three species were of the family Fabaceae (*Andira humilis* Mart. ex Benth., *Bauhinia brevipes* Vogel and *Mimosa tenuiflora* [Willd.] Poir.) and one was of each family: Annonaceae (*Duguetia furfuracea* [A.St.-Hil.] Saff.), Calophyllaceae (*Calophyllum brasiliense* Cambess.), Caryocaraceae (*Caryocar brasiliense* Cambess.), Combretaceae (*Combretum leprosum* Mart.), Malpighiaceae (*Byrsonima intermedia* A.Juss.), Malvaceae (*Waltheria indica* L.), and Sapotaceae

(*Pouteria torta* [Mart.] Radlk.) (see the association in the Table S3). This represents only 7% of the morphotypes estimated on 10% of the host plants reported in Caatinga.

The single hosts, plants with only one gall species, were the most common hosts, comprising 74% (74 spp.) of all host plants. Multi-hosts, those plants with two or more galls per plant, represented 26% (26 spp.) of all hosts (Figure 2a). In addition, some plant species, called super-hosts, hosted numerous galling insect species. In this study, we considered those plants within our data sets with the highest number of galling insects. For example, two species were 2% of all plant species, and they were: *Copaifera langsdorffii* Desf. (nine spp.), and *Croton jacobinensis* Baill. (eight spp.; Table S1). Despite few species, these plant species had a large number of gall morphotypes, with about 11% of all gall species (17 spp.; Figure 2b).

The four most frequently recorded species represented about 13.1% of the total records: *Copaifera langsdorffii* Desf. (Fabaceae), *Bauhinia brevipes* Vogel (Fabaceae), *Bauhinia pulchella* Benth. (Fabaceae), and *Combretum leprosum* Mart. (Combretaceae) (Table 1, Table S4). Of the 100 species, 66 spp. (ca. 43.1%) were registered only once, 23 spp. (ca. 30.1%) were registered twice, and seven species (ca. 17.3%) were registered three times (Table S1). It is no accident that five species of inducers identified for the Caatinga were found in Fabaceae, two in *Bauhinia brevipes* and *Mimosa tenuiflora*, and one in *Andira humilis*.

Bauhinia was the plant genus that stood out because of the large number of records (N = 14, 9.2%). When the number of species per genera was considered, it showed that the most specious genera are *Croton* (N = 6 spp., 6%), *Bauhinia* (N = 5 spp., 5%), and *Eugenia* (N = 4 spp., 4%; Table 1, Table S4). In addition, another three genera (*Bauhinia*, *Croton*, and *Copaifera*) together had around 25% (39 spp.) of the total number of registered gall-inducing insect species, and 69 other genera, about 75% (117 galls ssp.; Table 1, Table S3).

Fabaceae was the plant family with the most records (N = 59, 38.6%) (Figure 3a). When the number of host plant species and galling species per family was considered, it showed that Fabaceae was also the most specious family. It corresponded to one third the number of species

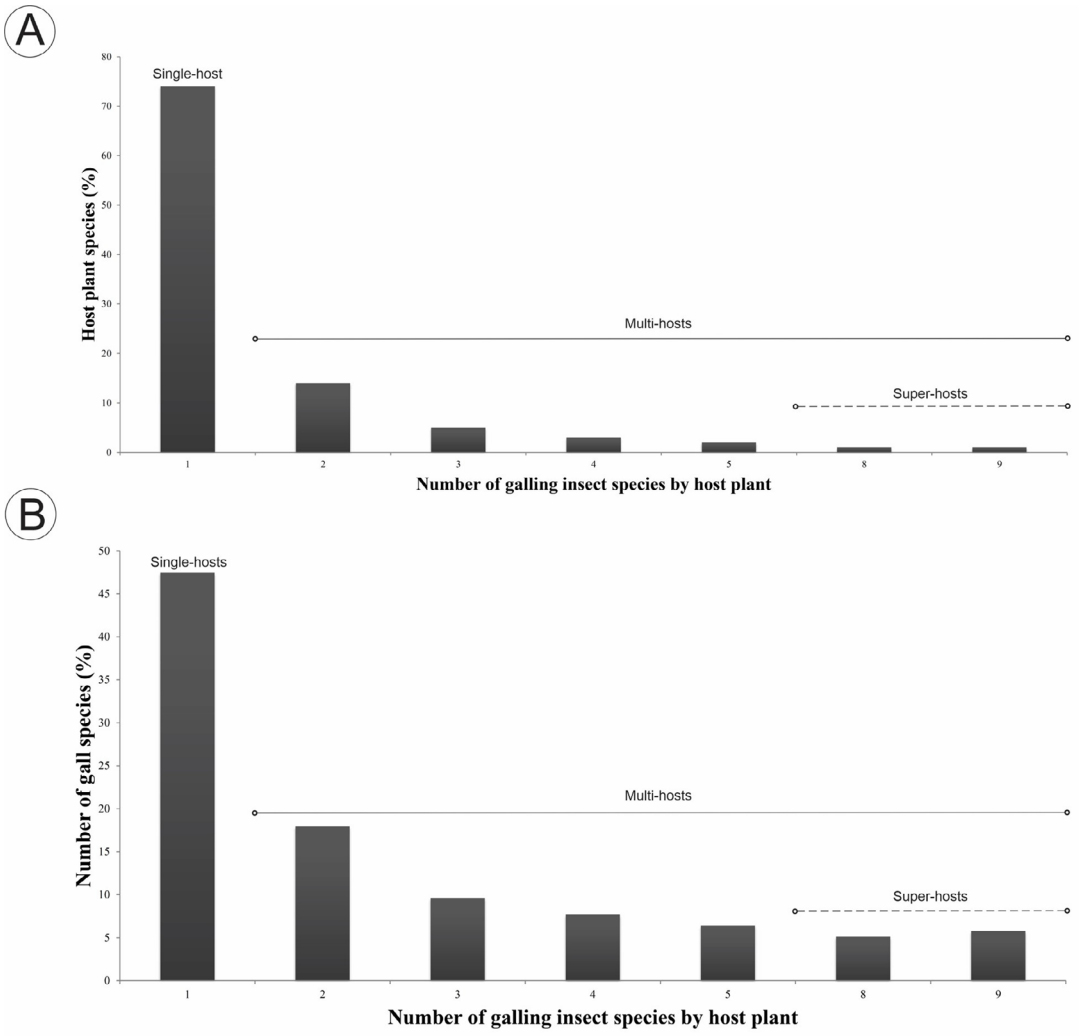


Figure 2. Distribution of the number of galling insect species by host plant species in relation the total number of host plant species (A) and the estimated of the total number of galling insect species (B) in the Caatinga. We highlight in this figure the single-hosts, plant species with only one insect species; the multi-hosts, plant species with two or more gall species; and the super-hosts, plant species with eight or more galls. The implications for single-, multi- and super-host were put into the results and discussed posteriorly.

Table 1. Genera with more host plant species and more galling insect species in the Caatinga and the ratio of the estimated number of gall species by host plants. The complete list of all 72 genera was placed as supplementary data (Supplementary Table 3).

Host genera	Host plant richness (%)	Number of galling species (%)	Number of galling species/host plant species
Croton	6 (6%)	14 (9.0%)	2.3
Bauhinia	5 (5%)	16 (10.3%)	3.2
Eugenia	4 (4%)		1.8
Copaifera		9 (5.8%)	9.0
Subtotal	16 (16%)	46 (29,5%)	
Others (68)	84 (84%)	110 (70.5%)	
Total	100 (100%)	156 (100%)	

found (N = 30 spp., 30%) (Figure 3b) and approximately 40% of the number of galls morphospecies quantified (61 galls ssp.; Figure 3c).

We compiled 12 cecidomyid gall midge species associated with the plants that occurred in the Caatinga: *Anisodiplosis waltheriae* Maia, *Asphondylia byrsonimae* Maia & Couri, *Asphondylia microcapillata* Maia, *Schizomyia macrocapillata* Maia, *Bruggmanniella duguetiae* Urso-Guimarães & Amorim, *Contarinia gemmae* Maia, *Houardodiplosis rochae* Tavares, *Lopesia andirae* Garcia, Lima, Calado & Urso-Guimarães, *Lopesia mimosae* Maia, *Lopesia pernambucensis* Maia, *Prodiplosis floricola* (Felt), and *Youngomyia matogrossensis* Proença & Maia. Nevertheless, only four cecidomyid species are recorded in this biome: *Houardodiplosis rochae* Tavares, *Lopesia mimosae* Maia, *Lopesia pernambucensis* Maia, and *Schizomyia macropillata* Maia.

2. *Only Caatinga*

We then removed the Cerrado species from the data set and analyzed only the species that occur in the Caatinga, according to Fernandes et al. (2020). We found that Cerrado plants contributed with 22% to the diversity of host plants and 19% to the richness of galling insects. The results showed that the plant richness fell to 78 spp. (2% of Caatinga flora), 58 genera (6%), and 25 families of host plants (16%), and 127 gall morphospecies. Of these species, 10 host plants spp. (*Annona leptopetala* [R.E.Fr.] H.Rainer [Annonaceae], *Calliandra macrocalyx* Harms [Fabaceae], *Cnidoscolus quercifolius* Pohl [Euphorbiaceae], *Croton adamantinus* Müll.Arg. [Euphorbiaceae], *Croton blanchetianus* Baill. [Euphorbiaceae], *Croton jacobinensis* Baill. [Euphorbiaceae], *Manihot dichotoma* Ule [Euphorbiaceae], *Mimosa pseudosepiaria* Harms [Fabaceae], *Neocalyptrocalyx longifolium* [Mart.] Cornejo & Iltis [Capparaceae], and *Varronia leucocephala* [Moric.] J.S.Mill. [Boraginaceae]) and another 20 galling insect spp. were endemic to the Caatinga.

Discussion

In our results, we found a low number of species of host plants (100 spp.) and gall-inducing insects (156 spp.). When we compared this result with other biomes, the difference was clearer. In a recent study, Cintra et al. (2020) compiled information from several localities in the Cerrado using community studies about plant-galling insect species and their host plants. They found 505 host plant species and 996 gall-inducing insect species. We propose three arguments to explain this pattern. First, it is likely that the number of galling insect inventories for the Caatinga is under-sampled, as indicated by the rarefaction curve. The number of inventories in the Caatinga is low compared to more studied biomes, such as the Cerrado and Atlantic Forest (Araújo et al. 2019). For example, for the Cerrado, there are more than 32 inventories (Cintra et al. 2020) against just nine for the Caatinga. This low number of inventories in the Caatinga can generate a shortlist of the number of species of host plants. However, when we compare the average number of galls morphotypes found in the inventories, the results showed that the richness of galling insects in the Caatinga is smaller than in other biomes. In this study, on average number of galls/inventories for the Caatinga was 41 (N = 9 inventories), while for the Cerrado was 49 (N = 32 inventories) (Cintra et al. 2020; see also Araújo et al., 2019).

Our second argument is that the Caatinga has a relatively smaller number of plant species compared to the Cerrado, for instance. The Caatinga flora has 4,891 valid spp., 1,232 genera, and 176 families of flowering plants. Meanwhile, the Cerrado flora has 12,420 valid spp., 1,662 genera, and 187 families (Flora do Brazil 2020). In absolute numbers, this difference is remarkable because the Cerrado has 2.5 times more species than the Caatinga. Therefore, with less potential host species for radiation and galling insect diversification, the Caatinga accumulates few species of host plants and, consequently, few galling insect species.

A third argument is that the Caatinga is a seasonally dry tropical forest, in other words, a semiarid environment, with low rainfall, often irregular rains and with marked seasonality (Marengo et al. 2017). During the dry season in the Caatinga, many species lose their leaves, constituting a strongly deciduous vegetation (Queiroz et al. 2017). Insects induce galls preferentially on the leaves (e.g., about 60%, see Maia et al. 2014), compared to other organs of the host plant. Consequently, there is a drastic reduction in the quantity and quality of resources available to galling insects, e.g., meristematic tissues. This may be the main limiting factor for limited adaptative radiation from galling insects in the Caatinga. Andrade et al. (2020) monitored herb communities for three weeks in the Caatinga to determine if rainfall reduction decreases insect herbivory. They found no leaf damaged by galling insects, even in the driest plots. According to Mendonça (2001), the deciduousness is a relevant factor in the colonization and performance rates of galling insects and can determine the patterns of diversity and distribution of this species.

Besides, the Caatinga is a xeric environment with high hygrothermal stress Fernandes and Price (1988, 1991) argue that the richness of gall-inducing insects is higher in hygrothermal stressed habitats (hygrothermal stress hypothesis). Then, according to this hypothesis, we expected to find in Caatinga a high richness of host plants and gall-

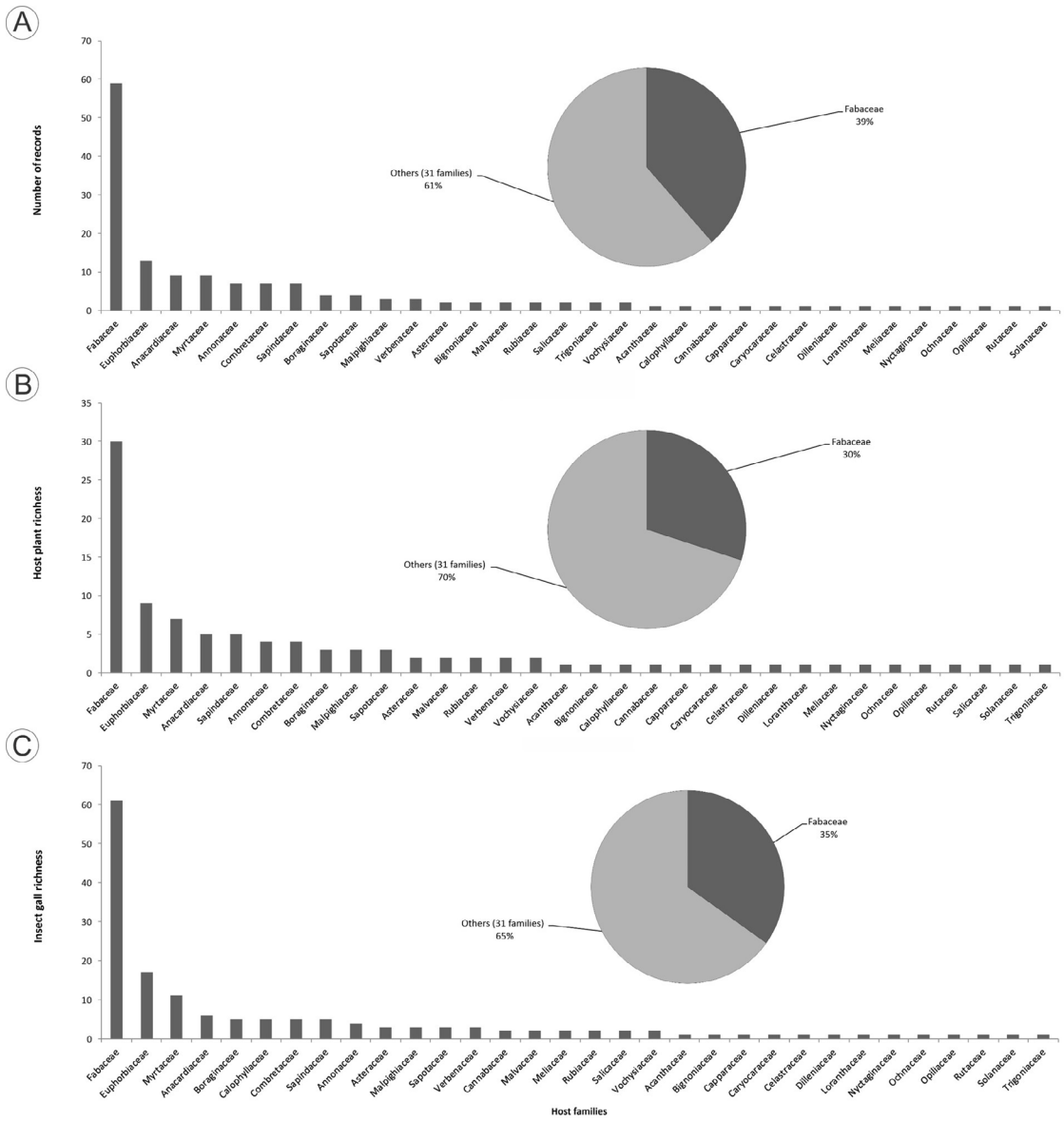


Figure 3. Rank plots of the number of host plant records (A), host plant species (B) and galling insect species (C) for 32 host plant families in the Caatinga. In the right corner of each figure, we show the proportion of Fabaceae, the family with the highest numbers of records, host plant and insect galls in relation to others 31 families.

inducing insect, but these predictions were not confirmed in this study nor in a study by Andrade et al. (2020) that expected more leaf damage by endogenous insects (leaf-mining and galling insects) in drier areas (with high hygrothermal stress) in the Caatinga. We argue that herbivory patterns by galling insects in the Caatinga are mainly ruled from bottom to top, being the aridity a strong factor that reduces plant resources to endophytic herbivores. For instance, during the transition between climatic seasons in the Caatinga, many plants still feature incomplete leaf replacement or deciduous characteristics (Albuquerque et al. 2012). Although, other abiotic factors (soil quality and water stress) and biotic factors (plant age, plant density, and natural enemies) may also affect gall-inducing species richness at different scales (Fernandes and Price 1991; Lara and Fernandes 1996; Ribeiro et al. 1998).

Only four gall midge species have been recorded in the Caatinga. If we consider that there are about 260 species of Cecidomyiidae occurring in Brazil (V.C. Maia *personal communication*), we notice that the Caatinga fauna includes less than 2% of the Brazilian richness. However, the occurrence of the other eight gall midge species is possible, because they induce galls on host plants reported in the Caatinga. Furthermore, two other species could be added to this list: *Anadiplosis caetetensis* Tavares, 1920, and *Styraxdiplosis caetetensis* Tavares, 1918, as both were described from Caetité (Bahia), a municipality occupied by Caatinga and Atlantic Forest. If we consider only the gall inducers recorded in the areas of Caatinga, only four species will remain in the list: *Schizomyia macrocapillata* Maia, 2005, *Houardodiplosis rochae* Tavares, 1925, *Lopesia mimosae* Maia, 2009, and *Lopesia pernambucensis* Maia, 2009, which is only 3% of the gall-inducing insects. We estimated that 93% of the gall-inducing species recorded in the Caatinga inventories are still undescribed, so further studies to identify the most representative groups of gall inducers for this biome

are needed. For this, it is necessary to obtain all the stages of life for these gall-inducing insects.

In our study, Fabaceae were the most recurrent plant family with a total of 30 host plant species and 61 gall-inducing insect species. This is the most species-rich family detected in STDFs (Pennington et al. 2000; Meguro et al. 2007; Fernandes et al. 2020). Several Brazilian inventories in different biomes also point out the Fabaceae as one of the plant families with the highest number of insect galls (reviewed in Araújo et al. 2019). Additionally, host plant family size may be an important factor for the regional prediction of gall-inducing insect species richness (Araújo 2011), once gall-inducing insects generally exhibit opportunistic adaptive irradiation (Price 2005).

The *Copaifera langsdorffii,* is a tropical arboreal tree, with the richest fauna of gall inducers insects (with 23 morphotypes) (Costa et al. 2010). Because of this, *C. langsdorffii* is considered a super host species. In our study, we recorded nine galling species for *C. langsdorffii*. Super host species may be responsible for the differences in local and regional patterns of gall-inducing insect richness (Fernandes and Price 1988) and, as such, represent keystone species for galling insects (Araújo et al. 2013).

Conclusions

Our results showed a low number of species of host plants and gall-inducing insects for the Brazilian Caatinga, and we discussed this pattern with three arguments. Initially, it is probable that the numbers of galling insect inventories for the Caatinga were under-sampled. When we compared the average number of galls found in the inventories, the results showed that the richness of galls in the Caatinga is smaller than in other biomes, such as the Cerrado and Atlantic Forest (Araújo et al. 2019). Secondly, we argue that the Caatinga has a relatively smaller number of plant species, which means that, with less potential host species for radiation and galling insect diversification, the Caatinga accumulates few species of host plants and, consequently, galling insect species. Lastly, we argue that the Caatinga is a seasonally dry tropical forest (Marengo et al. 2017), and so during the dry season in the Caatinga, many species lose their leaves, showing a strongly deciduous vegetation (Queiroz et al. 2017). For this reason, according to Mendonça (2001), the deciduousness represents a relevant factor in the colonization and performance rates of galling insects and can determine the patterns of diversity and distribution of this species.

Supplementary Material

The following online material is available for this article:

Supplementary Material - Beyond: an analysis by genus and families of unidentified host plant species.

Table S1 - The complete list of all 100 host plant in the Caatinga Biome, with number of records (NR), proportion of number of records [NR(%)], number of galling insect species (NGI), and proportion of galling insect species [NGI (%)].

Table S2 - Study location and coordinates of inventories about gall-inducing insects and their host plants in Caatinga Biome.

Table S3 - The list of 12 known gall inducers associated with the host plant species of the Caatinga Biome, including additional information.

Table S4 - The complete list of all 72 host plant genera in the Caatinga Biome, with number of records (NR), proportion of number of records [NR(%)], number of host plant species (NHP), proportion of host plant species [NHP (%)], number of galling insect species (NGI), proportion of galling insect species [NGI (%)] and also the ratio of the number of gall species by host plants (NGI/NHP)

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Authors Contributions

Fernanda Cristina Franco Cintra: Substantial contribution in the concept and design of the study, contribution to data collection, contribution to data analysis and interpretation, contribution to manuscript preparation, adding intellectual content.

Valéria Cid Maia: Contribution to data collection, and data interpretation.

Maria Virginia Urso-Guimarães: Contribution to data collection, and data interpretation.

Walter S. de Araújo: Contribution to data interpretation adding intelectual content.

Marco Antônio Alves Carneiro: Contribution to data analysis.

Henrique Venâncio: Contribution to data collection, and data interpretation.

Wanessa R. Almeida: Contribution to data collection, contribution to data analysis and interpretation.

Jean Carlos Santos: Substantial contribution in the concept and design of the study contribution to data collection, contribution to data analysis and interpretation and contribution to critical revision.

Conflicts of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Point-of-View

Consequences of a new species and different stocks of Spiny Red Lobster in Brazil

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Abstract: The Spiny Red Lobster has an important commercial role in Brazil. However, a downward trend in the production of lobsters due to overfishing has been observed and there is also a devaluation of the product in the international market due to the instability in the size pattern of lobsters commercialized. Here in Brazil we detected two issues regarding the Spiny Red Lobster: (1) According to recent studies, there are genetic and morphological differences between Caribbean and Brazilian populations, which may be considered different species and; (2) Current legislation, such as seasonal closures, does not consider the multiple probable stocks of the species, which have direct implications in management and conservation. Thus, the recognition of the Spiny Red Lobster from Brazil as *Panulirus meripurpuratus* and investments on population and biological research are essential to improve its management considering regional stock differences.
Keywords: *Spiny lobster; genetic variability; fishing stocks; conservation measures.*

Consequências de uma nova espécie e diferentes estoques de Lagosta Vermelha no Brasil

Resumo: A lagosta vermelha tem um importante papel comercial no Brasil, porém, uma tendência de queda na produção de lagostas devido a sobrepesca tem sido observada e há também uma desvalorização do produto no mercado internacional devido à instabilidade no comprimento das lagostas comercializadas. Aqui no Brasil, detectamos dois problemas em relação à lagosta vermelha: (1) De acordo com estudos recentes, existem diferenças genéticas e morfológicas entre as populações caribenha e brasileira e; (2) Atualmente a legislação não considera os múltiplos estoques prováveis da espécie. Desta forma, os períodos de defeso sazonais não consideram os diferentes estoques, o que tem implicações diretas no manejo e na conservação. Logo, o reconhecimento da lagosta vermelha do Brasil como *Panulirus meripurpuratus* e investimentos em pesquisas biológicas e populacionais são fundamentais pra facilitar seu manejo considerando diferenças regionais nos seus estoques.
Palavras-chave: *Lagosta espinhosa; variabilidade genética; estoques pesqueiros; medidas de conservação.*

Introduction

The Palinuridae Family comprises 49 species, which have very distinct characteristics such as: coloring patterns, long antennas and the presence of numerous thorns on the carapace (Spanier & Lavalli 2006). In Brazil, the most commercially important lobsters are spiny lobsters, popularly known as "Red Lobster" and "Green Lobster", recognized respectively as *Panulirus argus* (Latreille 1804) and *Panulirus laevicauda* (Latreille 1817), with the former being more abundant (Dias Neto 2008).

In Brazil, lobster fishing has an important commercial role in a large part of the coastline and the product of this activity is predominantly intended for the foreign market (Aragão 2013). This commercialization is commonly carried out in three ways: frozen lobster tail, frozen whole lobster and live lobster, with frozen lobster tail as the most exported product (Silva & Fonteneles-Filho 2011). Lobster exports from Brazil in 2020 were approximately 2,668 tonnes (Brasil 2021). However, despite the absence of updated fisheries statistics data in Brazil, there is a downward tendency in production between 1990 and 2014 of the order of 38% caused by overfishing, making the production levels of this fishery unstable (CeDePesca 2014, Cavalcante et al. 2018). This instability in production, as well as in the size of the lobsters, may have caused a devaluation of the product between 2007 and 2018 of approximately 25% (Dias Neto 2010, Aragão 2013, FAO 2021).

In Brazil, the maturity size of the Spiny Red Lobster is 13 cm in tail length (Ivo & Pereira 1996), which led to the determination of the minimum

catch size for the species (IBAMA 2006). The periods of reproductive occurrence (spawning season) occurs from January to April and September to October (Soares & Cavalcante 1985). Until 2019 the closed season for Spiny Red Lobster was from December 1 to May 31 (IBAMA 2008). Currently, the closed season goes from November 1 to April 30 (MAPA 2019). It has not yet been possible to assess the impacts caused by this change, as the last closed season is temporarily suspended due to the Covid-19 pandemic (MAPA 2020). The present work aims to discuss the implications caused by the use of inappropriate nomenclature of the Brazilian red lobster species and the possible multiple stocks along the Brazilian coast concerning management measures of this resource in the country.

Which is the Spiny Red Lobster Species in Brazil?

In the late 1990s, a study using mitochondrial DNA sequencing of lobsters from the Caribbean and Brazil identified high rates of divergences among specimens from the two areas (Sarver et al. 1998). The study also suggested provisional recognition of two subspecies of spiny lobster, *P. argus westonii* representing populations of Brazil and *P. argus argus* representing populations of the Caribbean. Later, a study using sequences from the mitochondrial DNA control region of *P. argus* observed high divergence between Southwest Atlantic and Caribbean populations. (Diniz et al. 2004). However, no taxonomic conclusion was performed. According to the Management Plan for the sustainable use of lobsters in Brazil (Dias-Neto 2008), based on several studies (Ogawa et al. 1991, Silberman & Walsh 1994, Diniz et al. 2005), the lobster *P. argus* from the Brazilian coast and the Caribbean Sea should be considered as distinct ecological and genetic units.

Giraldes & Smyth (2016), describe *Panulirus argus* occurring in Brazil, as being *Panulirus meripurpuratus* sp. nov. Due to the biogeographical barrier of the western Atlantic, created by the mouth of the Amazon River channel, there was genetic separation of *P. argus* and *P. meripurpuratus* in different populations, with *P.argus* to the north of the Amazon River plume and *P. meripurpuratus* to the south. After the new taxonomic definition of *P. meripurpuratus*, several studies disregarded the new nomenclature (Bevilacqua 2017, Cintra et al. 2018, Cavalcante et al. 2018, Oliveira 2018, Aragão & Cintra 2019), including the "Evaluation of the Management Plan for a Sustainable Use of Lobsters in Brazil" (Dias-Neto 2017) and the recent seasonal closure legislation (MAPA 2019). This may be due to the lack of knowledge of the published work by Giraldes & Smyth (2016). However, some authors have already identified the species with the new taxonomic category (Lima & Andrade 2018, D'oliveira 2017, Ribeiro 2017, Santana et al. 2016). Based on the new taxonomic definition, from now on we will consider the Brazilian species *P. argus* as *P. meripurpuratus.*

Spiny Red Lobster Stock Units in Brazil

In Brazil, a study using PCR markers (RAPDs) suggested the existence of two populations of *P. meripurpuratus*, one distributed between Ceará and Pará and the other from Pernambuco to Bahia (Carreiro 2001). Also, due to the Brazilian coast extension and the influence of different marine currents, it is probable to have different stocks of spiny red lobsters in Brazil (Diniz et al. 2010). These analyses that suggested different stock units only considered lobsters from the North and Northeast, preventing a comparison with lobsters from the Southeast region. Reinforcing the hypothesis of multiple stocks, a study considered two different stocks in Brazil, the first from Pará to Bahia and the second from Southern Bahia to São Paulo (Tourinho 2013).

In order to manage an economically important fishery resource throughout its entire distribution, such as *P. meripurpuratus,* including all environmental and ecological particularities, it is necessary to investigate how stocks are structured. In addition, conducting biological studies in each stock, such as recruitment, reproduction, age and growth, and mortality is essential to characterize the necessary aspects for the assessment of these stocks (Pollock 1993, Fonteles-Filho 1994, Dias-Neto 2010).

Ecological Consequences

The non-recognition of *P. meripurpuratus* prevents the correct determination of the area of occurrence of both (*P. argus* and *P. meripurpuratus*), since this area is more restricted than previously established (see Giraldes & Smyth 2016), generating direct consequences in the stock assessments.

The existence of different stocks of spiny red lobster in Brazil and the absence of detailed studies on different stock units have led to the establishment of a minimum catch size and seasonal closure extrapolation to a large part of the cost, with a single rule being applied to places where biological and ecological parameters of the species may be different. The possible direct consequence for that is the inadequate management of *P. meripurpuratus*, since the management of this resource does not consider the specific biological characteristics of each fishing stock.

According to fishermen from southern Bahia and Espírito Santo, the closed season implemented in the region (which is based on estimated population parameters from Ceará stocks) does not match the actual spiny red lobster spawning season (Almeida 2019). The modification of the closed season ordinance between 2008 and 2019 (IBAMA 2008, MAPA 2019) changing this closing period is an indication that the closed period was not adequate for the whole area of occurrence, considering that there are no studies about spawning season for the different regions or stocks. In this way, it is difficult to state that the period of closure determined is suitable for all regions of the country. This possibly wrong closed season in some locations throughout the spiny red lobster distribution in Brazil has resulted in the capture of breeding females in a fundamental period to maintain stock balance.

Recommendations

To solve this issue of one of the most profitable fishing resources in Brazil, this brief review recommends:

- The adoption of the new nomenclature *P. meripurpuratus* for spiny red lobster populations found from south of Amazon River plume in Brazil, including the adoption of this name in future fisheries regulations, and recognizing that previous regulations that cite *P. argus* are, in fact, referring to *P. meripurpuratus*, an endemic species.

- The dissemination of the new nomenclature to all stakeholders involved in the economic use of the Brazilian spiny red lobster, thus facilitating its commercialization and appreciation in the foreign market.

- Investments on population and biological research for lobster species in Brazil, in order to support the development of improved

regulations on minimum catch sizes and seasonal closures that take into account regional stock differences.

- The assessment of the conservation status and extinction risk of *P. meripurpuratus* as a way to support, with better information, the development of strategies to promote the recovery and sustainable use of this species.

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Author Contributions

Luciano Pinto de Almeida: Concepted and designed the study. Contributed with data collection. Contributed with interpretation and manuscript preparation.

Jones Santander-Neto: Concepted and designed the study. Contributed with data collection. Contributed with interpretation and manuscript preparation. Contributed with critical revision.

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Mauricio Hostim-Silva: Contributed with interpretation and manuscript preparation. Contributed with critical revision.

Conflicts of Interest

The authors declare that have no conflicts of interest

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Article

Genetic structure and diversity in *Neochen jubata* (Aves: Anatidae) from the Araguaia River, GO, Brazil

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Abstract: The Orinoco Goose *(Neochen jubata)* is a few-known and endemic Anatidae to South America, inhabiting sandy beaches along medium and large rivers, with a well-developed riparian forest and in swamp savannas and large freshwater baths. Recent data indicate the presence of longitudinal migratory behavior, and despite them, there are no records on the genetic profile of this species. The Araguaia River region, in the municipality of Luiz Alves, Goiás, receives an undetermined number of ducks seasonally, and there is little information about the individuals who visit this place, constituting the ideal scenario for a study able to offer a genetic overview perspective of this species and to understand the relationship between these individuals better. For this, we genetically characterized 61 individuals sampled in three distinct years of collection using microsatellite molecular markers and mitochondrial DNA. Genetic diversity analyses revealed low levels of heterozygosity for all sampled groups. However, they are within the equilibrium proposed by Hardy-Weinberg (HWE), as inbreeding or drift are not acting in these groups. The parentage analysis supports it, showing a high number of unrelated individuals over the years. AMOVA showed a significant difference among groups. These results may reflect the structure of this migratory species in that region, with the paired differentiation test of individuals from 2013 and 2014 being more similar to each other than those from other years, indicating a possible genetic structure diagnosed by the years of capture. However, there is a high allelic sharing among the three sampled groups, suggesting that these individuals are a population that connects over time and that they have a philopatric relationship with the location. The results found in this study constitute an initial milestone for the genetic knowledge of the mallard duck that should be raised in many other genetic studies.
Keywords: *Microsatellite; mitochondrial DNA; Orinoco Goose; kinship; structure population..*

Estrutura populacional e diversidade genética de *Neochen jubata* (Aves: Anatidae) no rio Araguaia, GO, Brasil

Resumo: O ganso-do-orinoco *(Neochen jubata)* é um anatídeo endêmico da América do Sul, cujo habitat são praias arenosas ao longo de rios médios e grandes, com uma vegetação ripária bem desenvolvida e em savanas do pântano com extensos banhados de água doce. Dados recentes indicam a presença de comportamento migratório longitudinal e, apesar destes, não existem registros sobre o perfil genético dessa espécie. A região do rio Araguaia, no município de Luiz Alves, Goiás, recebe um número indeterminado de patos sazonalmente e há poucas informações sobre os indivíduos que visitam este local, constituindo o cenário ideal para um estudo capaz de oferecer uma perspectiva genética geral dessa espécie e também de entender melhor a relação de parentesco entre esses indivíduos. Para tal, caracterizamos geneticamente 60 indivíduos amostrados em três anos distintos de coleta, utilizando marcadores moleculares microssatélites e DNA mitocondrial. As análises de diversidade genética revelaram baixos níveis de heterozigosidade para todos os grupos amostrados. No entanto, eles estão dentro do Equilíbrio proposto por Hardy-

Weinberg (HWE), pois a consanguinidade ou a deriva não estão atuando nesses grupos, a análise de parentesco apoia este resultado indicando um alto número de indivíduos não relacionados ao longo dos anos. A AMOVA apresentou diferença significativa entre os grupos. Esses resultados podem refletir a estrutura dessa espécie migratória naquela região, com o teste de diferenciação pareada de indivíduos de 2013 e 2014 sendo mais semelhantes entre si do que os de outros anos, indicando uma possível estruturação genética diagnosticada pelos anos de captura. No entanto, há um alto compartilhamento alélico entre os três grupos amostrados sugerindo que esses indivíduos são uma população que se conecta ao longo do tempo e que têm uma relação filopátrica com o local. Os resultados aqui encontrados constituem um marco inicial para o conhecimento genético do ganso-do-orinoco que contribuirá para novos estudos sobre esta espécie considerada "quase ameaçada" pela IUCN.

Palavras-chave: *Microssatélite; DNA mitocondrial; ganso-do-orinoco; parentesco; estrutura populacional.*

Introduction

The Orinoco Goose (*Neochen jubata* (Spix 1825)) is one of the lesser-known species of waterfowl endemic to South America inhabiting sandy beaches, along rivers, savannas, and wetlands (Carboneras 1992, Sick 2001, Endo *et al*. 2014); in Brazil, it occupies the basis of the Amazon River (Luna *et al*. 2008, Endo *et al*. 2014) and Araguaia River (Pinheiro & Dornas 2009). It is estimated that Amazon's population is smaller and more fragmented than in the Araguaia River basin, which acts as a remnant stronghold of this species (Endo *et al*. 2014).

The existence of longitudinal migratory behavior in Orinoco Goose between southern Peru and northern Bolivia was recently described (Davenport *et al*. 2012), and there are reports of a seasonal occurrence of Orinoco Goose in the Juruá River, Amazon basis, suggesting that this population migrates to other regions during the rainy season due to restrictions imposed by the seasonal flood regime and that the dynamics of rivers determine the use of habitat in this species. (Endo *et al*. 2014). The district of Luiz Alves, Goiás, region of the Araguaia River, receives an indeterminate number of Orinoco Goose seasonally; however, little is known about these individuals who visit this area, whether they are the same population with related animals or only birds that converge annually to this region. According to BirdLife International, migratory is when "a substantial proportion of the global or regional population makes regular or seasonal cyclical movements beyond the breeding range, with predictable timing and destinations". An excellent comprehension of the migratory behavior of animals is essential to consider conservation strategies, and ecological and genetic studies from populations are necessary (Kirby *et al*. 2008).

In the IUCN, the Orinoco Goose is classified as "almost threatened," presenting a population decline rated as slow to moderate, mainly caused by anthropological activities such as hunting and habitat destruction (Endo *et al.* 2014; IUCN 2018). In the state of São Paulo, *Neochen jubata* is extinct in the wild, and the population in the Juruá River is also negatively impacted by agricultural and hydroelectric expansions due to seasonal flooding (Endo *et al*. 2014). These anthropic activities can generate great interference in the flow of the local biota because, during the flood season, most aquatic species seek refuge in the floodplains transformed into irrigated rice monocultures (Pinheiro & Dornas 2009). The increasing loss and fragmentation of natural habitats, especially in the last centuries, have contributed significantly to the decline and population isolation of wild species, causing even local extinctions, such as the Alagoas Curassow (*Mitu mitu*), Glaucous Macaw (*Anodorhynchus glaucus*) and the Brazilian Merganser (*Mergus octosetaceus*) (Leite-Pitman *et al.* 2002, Marini & Garcia 2005). Anthropic action has been responsible for the extinction of species and populations or causes a drastic decrease in their distribution and density, thus increasing their risk of extinction in the short and long term (Frankham *et al.* 2010). This decreased population can also lead to a decrease in genetic diversity, with the elimination of variants (alleles and haplotypes) of these populations. This fact could compromise the population's ability to respond to selective pressures, such as diseases and environmental changes, to guarantee their reproductive success (Frankham *et al.* 2010).

In recent decades, the evolution of molecular genetics has brought tools that make it possible to estimate genetic diversity in different species, identifying and quantifying differences between populations. Molecular markers that show variability that allows studying a biological issue have been widely used for population studies (Avise 1994). According to scientific databases, there are three studies aimed at the study of *N. jubata,* and these are focused on the description of their migratory habits and abundance estimates, with no records yet on the genetic profile of the species (Kriese 2004, Endo *et al*. 2014, Davenport *et al*. 2012). The only study carried out with *N. jubata* in Brazil was on the seasonal abundance of the population in the Juruá River, Amazonas (Endo *et al*. 2014). Thus, this work is a pioneer in investigating the distribution of genetic variability in individuals of *N. jubata*, so the objective of this study is to genetically characterize the individuals sampled in three different years using microsatellite DNA loci and mitochondrial DNA as molecular markers, therefore offering a genetic panorama that is still non-existent for *N. jubata* and better comprehension about the relationship among these individuals.

Material and Methods

1. Genetic sampling

A total of 60 blood samples from *N. jubata* were donated by Professor Karin Werther, Departamento de Patologia Veterinária – UNESP, FCAV, Jaboticabal (Table 1). The samples were harvested from free individuals living in the Araguaia River, Goiás State, Brazil, at two locals (13º30'00.0 "S 50º43'29.51" W [1] 13º17'49.0 "S 50º36'16.5" W [2] at) and (13º13'02.1 "S 50º34'37.8" W [3]) (Figure 1), was not specified the exact location of each individual, but the collection area in general. These animals were captured manually in September/October during the molting period from 2010 (samples 1-21), 2013 (samples 22-41), and 2014 (samples 42-60). All procedures for handling and capturing animals were approved by the Ethics Committee on the Use of Animals (C*omissão de Ética no Uso de Animais - CEUA*) of the Faculdade de Ciências Agrárias e Veterinárias, Câmpus de Jaboticabal – UNESP on June 8, 2011 at number 012273/11. Blood samples collected

by venous puncture were preserved in alcohol. Subsequently, the sexing of these individuals was performed by applying molecular methods.

Genomic DNA was extracted using a phenol-chloroform method protocol developed by the *Laboratório de Biodiversidade e Evolução Molecular* – UFMG (LBEM 2018) and currently stored in the *Laboratório de Biologia Evolutiva* (LaBE) – UNESP, FCAV, Câmpus de Jaboticabal.

2. *Mitochondrial DNA*

The control region of the mitochondrial DNA was amplified using the primer pairs forward: L78-GTTATTTGGTTATGCATATCGTG and reverse: H774-CCATATACGCCAACCGTCTC (Sorenson & Fleischer 1996, Sorenson *et al.* 1999). Polymerase chain reaction (PCR) reactions were patterned to a final volume of 25 µl containing 12.5 µl of Green Master Mix-Promega, 1 µl of the forward and reverse primers at 2 mM, 8.5 µl of deionized water and 2.0 µl of DNA with 100 ng. PCR conditions started with an initial denaturation cycle of 94°C for 7 minutes, followed by 45 cycles of 94°C for 20 seconds, 49°C for 20 seconds, 72°C for 1 minute, and 72°C for 7 minutes. The final check of the process was performed by 1% agarose gel electrophoresis to verify the presence of the expected bands. The amplified products of mitochondrial DNA were purified with Wizard® SV Gel and PCR Clean-Up System reagent set (Promega) following the manufacturer's instructions. Sequences and specimen voucher information, including collection year and sex identification, are archived in GenBank (accession numbers MT675220–MT675248).

3. *Microsatellite DNA*

Microsatellite DNA loci were amplified using five pairs of primers developed for other species of Anatidae (Table 2) with proven applicability to members of the Tadorninae subfamily (Maak *et al.* 2003, Paulus & Tiedemann 2003).

The PCRs were performed in a final volume of 25 µl containing 12.5 µl of Green Master Mix-Promega, 1 µl of the forward and reverse primers at 2 mM, 8.5 µl of deionized water and 2.0 µl of DNA with 100 ng. The reactions were amplified under the following conditions: one cycle at 94°C for 5 min, 88°C for 1 min; three cycles 94°C for 1 min, annealing temperature specific for each locus (Table 2) for 1 min; 72°C for 1 min; 38 cycles of 94°C for 1 min, annealing temperature -3°C for 1 min, 72°C for 1 min; and final extension at 72°C for 10 min. After confirming the amplification of the microsatellite loci, the PCR product was applied in 6% polyacrylamide gel, where staining with silver was performed to visualize the microsatellite alleles. Gels for the five loci were analyzed, and each allele was characterized by its size and position on the gel relative to the molecular weight marker of 50 bp (Jena Bioscience).

Table 1. List of individuals of *N. jubata* captured in the Araguaia River, GO, voucher number of the *Laboratório de Biologia Evolutiva* - LaBE and sex determined by molecular analyzes.

	Voucher Number – LaBE	
Years - Groups	**Male**	**Female**
2010 - Group A	1, 2, 4, 5, 6, 8, 9, 10, 12, 13, 16, 19, 20	3, 7, 11, 14, 15, 17, 18, 21
2013 - Group B	23, 26, 27, 28, 29, 30, 31, 32, 33, 34, 37, 40, 41	22, 24, 25, 35, 36, 38, 39
2014 - Group C	44, 45, 48, 49, 52, 56	42, 43, 46, 47, 50, 51, 53, 54, 55, 57, 58, 59, 60

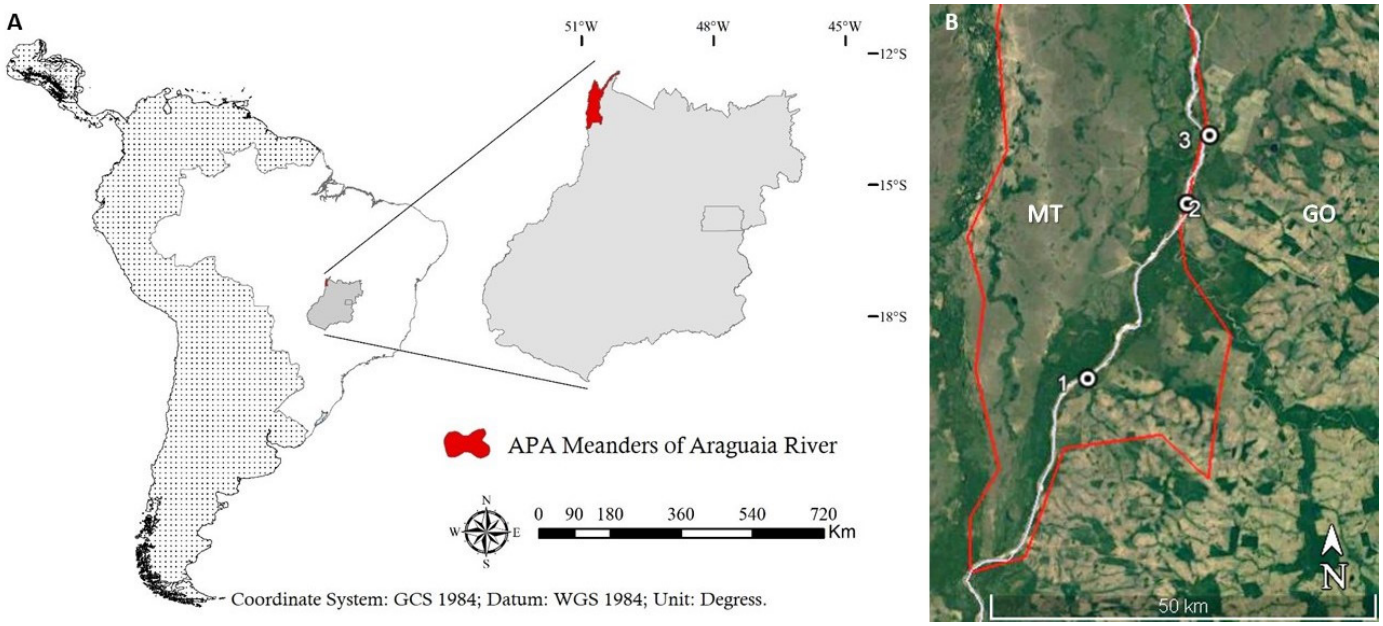


Figure 1. A) APA Meanders of Araguaia River location. Source:< https://portaldemapas.ibge.gov.br/> last access in 29/01/2018. B) Location map of the captures from individuals of *N. jubata* in 2010, 2013, and 2014, whose blood samples were used in this work. Source:< http://earth.google.com/> last access in 03/01/2021.

Table 2. Characteristics of the five pairs of microsatellite DNA primers used to amplify the genetic variability of *N. jubata* individuals from the Araguaia River, GO.

Locus	Primer Sequence	Annealing Temperature	Repeat Sequence
***Smo6**	F: GGGGTGGGAAAGAAGCAGTTTAG R: TCCTGGGACTTTGAAAGTGGCTC	65°C	(TG)18T4(TG) 2
***Smo8**	F: TGCCTTATAGGATGTCACTCTTC R: AAAATACTATGCTCGTTTCAAAA	54°C	(TG) 11
***Smo10**	F: TCCTAGCGACAGCAATTCTAATG R: CATTGTTCATTGTTTCTTCTTCA	50°C	(TG) 31
***Smo1**	F: CTTAAGGTATTGTGCTTTATA R: TGGTCCAAAGGGTGTTCTCAGAA	54°C	(GA) 17
****APH08**	F: AAA GCC CTG TGA AGC GAG CTA R: TGT GTG TGC ATC TGG GTG TGT	58°C	(CA) 12

*Paulus & Tiedemann 2003; **Maak et al. 2003

4. Genetic diversity

We amplified a total of 29 sequences with 650 bp each for the mtDNA control region gene, including samples 1-8 and 10 (Group A), 22-31 (Group B), and 42-51 (Group C). These samples were divided according to each collected the years 2010, 2013 and 2014, respectively and each specimen was genotyping (Table 1). The genetic diversity levels of the groups were estimated using ARLEQUIN software (Excoffier *et al*. 2005), considering indices of the total number of alleles (Na), observed heterozygosity (H_O) and expected heterozygosity (H_E). They were also tested for possible deviations, the Hardy-Weinberg equilibrium (HWE), and linkage equilibrium. Additionally, the same software estimated the degree of differentiation between the three sampled groups employing Wright's statistics by analyzing the percentages of F_{ST} (AMOVA) and calculated the pairwise F_{ST} indices to three groups sampled, and the test was run with 10000 permutations to evaluate the statistical significance of the calculated value ($\alpha = 0.05$). For the distribution of genetic diversity, the assurance of the best number of clusters for the genotypes sampled was calculated by STRUCTURE v.2.3.4 (Pritchard *et al*. 2000), where the models used were admixture and the frequencies of correlated alleles. Group numbers (k) were tested, fluctuation from one to seven with ten runs for each one, and the parameters placed were 50000 burn-in and 1000000 Markov Chain Monte Carlo (MCMC) replicates. Finally, the most likely number of groups was assessed with the statistic described by Evanno *et al*. (2005) and visualized in STRUCTURE HARVESTER v.0.6.92 (Earl & vonHoldt 2012).

5. Parentage analysis

The possible parentage among individuals was performed using the software CERVUS v.3.0.7 (Marshall *et al*. 1998), which realizes genetics analysis on population study doing inferences based on molecular markers such as microsatellites, generating through exclusion process locus-by-locus a likelihood score. This value corresponds to a similarity between parentages and offspring and is expressed more commonly as an LOD score.

The LOD score is obtained by the natural log (log to base e) of the overall likelihood ratio, returning positive and negative values. When the candidate's parent is more likely to be the birth parent, the LOD score value is positive; however, if the offspring are less likely to relate to their possible parentage, the LOD score sets a negative value. Lastly, an LOD score equal to zero indicates that the candidate parent has the same chances of being the birth parent as not being.

Results

1. Genetic diversity

We amplified a total of 29 sequences with 650 bp each for the mtDNA control region gene, including individuals 1-8 and 10 (group A), 22-31 (group B), and 42-51 (group C). As a result, we obtained only two haplotypes (Attached 1), and this analysis revealed low haplotype diversity (Hd) of 0.069 and only eight polymorphic sites (S). The genetic distance among the three sampled groups was 0.001. Therefore, no further analysis was performed to detect the partition of genetic variability.

For the five microsatellite loci, it performed on a total sample of 60 individuals of *N. jubata*, and all loci were polymorphic; the average number of alleles per locus was 5.4, ranging from 4 (Smo8) to 7 (APH08), resulting in 27 alleles for the individuals (Table 3).

According to the collection years, analysis of diversity patterns revealed exclusive alleles in the three sampled groups (Table 3). Each group was analyzed separately, and we observed H_O values ranging from 0.083 (B) to 0.192 (C), while H_E ranged from 0.514 (A) to 0.655 (C) (Table 4). The heterozygosity levels observed in the three groups were lower than the expected heterozygosity, but there were no deviations in the balance of HWE (Table 4). The test of linkage disequilibrium between pairs of loci has as a null hypothesis that the genotypic distribution in one locus is independent of the distribution in another. The three years sampled presented loci in this condition ($p = > 0.05$), with group A showing the highest number of loci in equilibrium, while group C had the lowest level.

2. Distribution of genetic diversity

The genetic structure used to investigate the individuals sampled in three different years resulted in three analysis groups. AMOVA was used to test the structure considering all groups as a single group, without hierarchical levels. For this grouping, the *p*-value ($p = 0.000$) was significant and showed a moderated value to F_{ST} (0.21) (Table 5), also evidencing that the highest percentage of the variation is within

Table 3. Frequency of the alleles identified in the five microsatellite loci for 60 individuals of *N. jubata* captured in the Araguaia River, GO in the years of 2010 (group A), 2013 (group B), and 2014 (group C). Exclusive alleles found indicated with an asterisk.

Loci		Years of sampling		
		2010 (A)	2013 (B)	2014 (C)
Smo1		N=16	N =17	N =16
Allele	1	0.250	0.588	0.406
	2	0.593	0.323	0.468
	3	0.093*	0.000	0.000
	4	0.062	0.058	0.093
	5	0.000	0.029	0.031
Smo6		N=20	N=19	N=18
Allele	1	0.225	0.210	0.111
	2	0.675	0.157	0.277
	3	0.000	0.631	0.611
	4	0.075*	0.000	0.000
	5	0.025*	0.000	0.000
Smo8		N=20	N=19	N=18
Allele	1	0.050	0.263	0.166
	2	0.000	0.000	0.277*
	3	0.150	0.631	0.444
	4	0.800	0.105	0.111
Smo10		N=20	N=19	N=20
Allele	1	0.250	0.105	0.166
	2	0.000	0.210*	0.000
	3	0.000	0.263*	0.000
	4	0.000	0.105	0.166
	5	0.650	0.157	0.000
	6	0.100	0.157	0.666
APH08		N=20	N=19	N=18
Allele	1	0.175	0.131	0.138
	2	0.000	0.473	0.138
	3	0.325	0.157	0.111
	4	0.250	0.105	0.277
	5	0.225	0.052	0.027
	6	0.000	0.078	0.250
	7	0.025	0.000	0.055

Table 4. Allelic diversity and Hardy-Weinberg Equilibrium calculated at five microsatellite loci for 60 individuals of *N. jubata* captured in Araguaia River, Go in the years 2010 (group A), 2013 (group B) and 2014 (group C).

			HWE			
Groups	**Loci**	**A**	**H_o**	**H_E**	***p*-value**	**s.d.**
2010 (A)	Smo1	4	0.111	0.547	0.000	0.000
	Smo6	4	0.190	0.483	0.000	0.000
	Smo8	3	0.000	0.329	0.000	0.000
	Smo10	3	0.000	0.441	0.000	0.000
	APHO08	5	0.619	0.770	0.000	0.000
	Overall	3.8	0.184	0.514		
2013 (B)	Smo1	4	0.166	0.544	0.000	0.000
	Smo6	3	0.000	0.528	0.000	0.000
	Smo8	4	0.000	0.579	0.000	0.000
	Smo10	6	0.000	0.841	0.000	0.000
	APHO08	6	0.250	0.728	0.000	0.000
	Overall	4.6	0.083	0.644		
2014 (C)	Smo1	4	0.210	0.603	0.000	0.000
	Smo6	3	0.000	0.553	0.000	0.000
	Smo8	4	0.000	0.717	0.000	0.000
	Smo10	4	0.000	0.575	0.000	0.000
	APHO08	7	0.700	0.825	0.000	0.000
	Overall	4.4	0.192	0.655		

Observed number of alleles (A), observed (H_o), and expected (H_E) heterozygosities.

Table 5. Analysis of molecular variance (AMOVA) using five microsatellite loci without hierarchical analysis, for 60 individuals of *N. jubata* captured in the Araguaia River, GO in the years 2010, 2013 and 2014.

Source of variation	d.f.	Variance components	Percentage of variation
Among groups	2	0.410	21.00
Within groups	119	1.549	79.00
Total	121	1.959	
Fixation Index		F_{ST}: 0.21	

Table 6. Pairwise F_{ST} for the three groups of *N. jubata* analyzed in the Araguaia River, GO in the years 2010 (group A), 2013 (group B) and 2014 (group C).

Groups of sampling	(A)	(B)	(C)
(A)	0.00000		
(B)	0.28292*	0.00000	
(C)	0.25148*	0.07234*	0.00000

*$p < 0.05$

the groups, with only a small part of the variation distributed between the groups. We estimated the pairwise differentiation indices with an exact comparison among the three groups (Table 6). According to the comparisons, those involving the pair of groups A and B tended to yield the highest values of differentiation index analyses, unlike the pairs of groups B and C that presented the lowest differentiation values.

Structure analysis realized by STRUCTURE was used to visualize the genetic similarity among individuals and test the structure among the three groups analyzed. The results produced using the method proposed by Evanno *et al*. (2005) revealed that the individuals sampled's genetic variation can be ideally distributed in two groups (K = 2) according to their similarity. Individuals from groups B and C showed similar proportions of colored segments representing the probability that they belong to the cluster with that color (Figure 2).

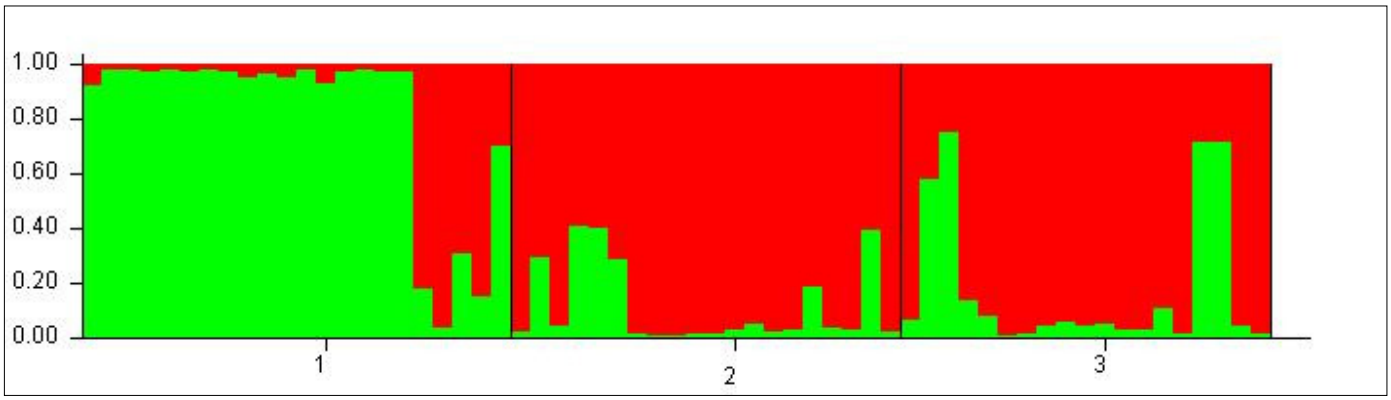


Figure 2. Graph of the Bayesian analysis with the distribution of *N. jubata* individuals captured at the Araguaia River, GO in the years 2010, 2013, and 2014. Each individual is represented by a vertical bar; each color per bar's length indicates the probability of membership in each genetic cluster.

3. Parentage analysis

We evaluated the sample genetically intended possible relationships among individuals of the groups over the years. Using CERVUS software to analyze five microsatellite loci, we compared the possible offspring with candidates' mothers and fathers. Our results show loci Smo8 and Smo10 with the highest frequency of null alleles (1.0000), and the lowest locus frequency found was APH08 (0.2462). In addition, it had a total of 13 possible kinships involving 22 individuals, in which four relationships were in strict confidence (95%) and nine relationships were in relaxed confidence (80%). Of these 13 relationships, 12 parents were individuals collected in the same year, only one pair of parents had their mother and father sampled in different years; that is, the software indicated that they were parents of the same individual, but the mother was sampled in one year and the father in another year. Furthermore, individual parentage analysis at relaxed confidence showed 3% and 4% of offspring assigned to mothers and fathers, respectively. These results could demonstrate that over the years, there was an exchange of alleles between the groups of *N. jubata*.

Discussion

Our results produced by the mitochondrial DNA gene's control region showed that the *N. jubata* groups from the Araguaia River showed very low diversity indexes and identified only two haplotypes. However, the five loci of microsatellite DNA demonstrated a moderate difference between the three groups and indicated a higher percentage of variation occurred in the same years of sampling. Although we had little mitochondrial data, this result can occur because SSR nuclear markers are higher polymorphic than mitochondrial DNA and can reveal more recent effects of reproductive isolation or low gene flow (Loxdale & Lushai 1998, Hartl & Clark 2010). Another possible explanation for these results is that low genetic variability is linked to the birds' physiological characteristics. With few exceptions, bird species often have high longevity (Holmes *et al*. 2001). As documented in other bird species, the long life cycle associated with less oxidative damage to mitochondrial DNA can result in a lesser accumulation of mutations (Barja 2004, Hickey 2008).

Due to different allelic compositions, the AMOVA showed a significant difference between the groups (F_{ST} 0.21). However, it is possible to see that the highest variation is within the groups, so the three groups share 79% of all the allelic variation detected here. These results may reflect the structure of this migratory species in that region, with the paired differentiation test of individuals 2013 and 2014 being more similar to each other than those of other years. However, it should be highlighted that the value considered moderate for AMOVA (F_{ST} 0.21) may include the geographical structure of the individuals, as although the groups in the analysis were drawn up by the years of capture, they also contain the distinct sampling locals. This indicates that this species can both present a genetic structure diagnosed by the years of capture, as well as a geographic structure, evidenced by the different locals sampled.

To assess whether differences in the temporal scale of sampling for the three groups could have influenced the observed genetic structure, we focused particular attention on STRUCTURE analysis. This result showed that the B and C groups are more genetically similar to each other, confirming the pairwise analysis data.

The biology of the Anatidae family could explain the existence of these two genetic groups in this population, one formed by the individuals captured in 2010 (A) and the other formed by the individuals captured in the years 2013 (B) and 2014 (C), once to the sexual maturation of the individuals occurring after the first or the second year of life and the formation of peers that is also slow to establish and tends to last for several years (Johnsgard 2010). Therefore, any allelic diversity introduced between groups will take at least three years to reflect the population's genetic pool. Another possible cause is the absence of samples in the intervening years between "2010" and "2013" since individuals' analysis in those years could gradually detect this homogenization.

Our results showed a different genetic pattern from that observed for other species of migratory birds *Somateria mollissima* (Linnaeus, 1758) (Aves: Anatidae) studied in northern Europe. Mitochondrial DNA showed differences between colonies as a product of the oldest history of colonization of these species in the region related to the Pleistocene refuge event and little divergence between colonies when studied by microsatellite DNA loci, probably influenced by the philopatric of females (Tiedemann *et al*. 2004). When comparing these data with ours by *N. jubata* presented here, we could infer that due to the absence of difference for mitochondrial DNA, our sampled groups could represent a single population that migrates to this region seasonally, in addition to having a high rate of gene flow that prevents diversification among individuals. Although it is not possible to affirm, it may be that *N. jubata* is philopatric by males, so that the difference verified over the

years sampled by the nuclear marker is the product of the dispersion incorporated to distinct locals of permanence promoted by the other sex capable of preventing moderately population structuring, since most of the variation is within the sampled groups.

The kinship tests demonstrated a high number of unrelated individuals over the years, agreeing with HWE results and reinforcing that there is no deviation in the sampled groups. Nevertheless, the presence of closely related individuals in all years, even though to a lesser extent reinforces, as stated above, the hypothesis that the three groups A, B and C form a single population that connects over time that returns to the Araguaia River seasonally. These findings are in accord with the premise that groups of *N. jubata* formerly considered independent are the same population occupying different reproduction areas (Endo *et al*. 2014, IUCN 2018).

The recurrence of Orinoco Goose in the Araguaia River, coinciding with its reproduction, in the dry season may also indicate some degree of philopatric individuals who tend to return to their area of origin to mate (Greenwood 1980), agreeing with our genetic data. Familiarity with a specific local brings several advantages for an animal, such as predator evasion, higher resource efficiency, reduced hostility, and possible cooperation with related individuals (McKinnon *et al*. 2006, Sonsthagen *et al*. 2009)

It is the first molecular study on the populations of *N. jubata*, and many questions still exist to be answered, but this study may already aid in the conservation policies of this species.

Supplementary Material

The following online material is available for this article:

Attached 1 - Polymorphic sites and two haplotypes for the control region of the mitochondrial DNA of *Neochen jubata*.

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Author Contributions

Maria Cecília Pereira: The author had a fundamental role in the development of this work, realized laboratory work to produce data for analysis and analyzed and interpreted the data on genetic diversity, in addition to contributing substantially to the writing and revision of the manuscript.

Thaís Coelho: The co-author analyzed and interpreted data related to kinship analysis and their relationship with genetic diversity data, in addition to contributing to the writing and revision of the manuscript.

Karin Werther: The co-author had a fundamental role in the data collection of this work, collecting biological material that was later processed and analyzed, in addition to contributing to the writing of the manuscript and its review.

Rafael Biccio Andreazzi: The co-author analyzed and interpreted data related to kinship analysis and their relationship with genetic diversity data, in addition to contributing to the writing of the manuscript.

Adriana Coletto Morales: The co-author and advisor had a fundamental role in the development of the intellectual and experimental design of this work, in addition to contributing to the writing of the manuscript, supervising the development and revising.

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

Historical review on the type locality of *Knodus victoriae* (Steindachner 1907) (Teleostei: Characidae) and *Loricaria parnahybae* Steindachner 1907 (Teleostei: Loricariidae)

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AGUIAR, R.G., GUIMARÃES, E.C., CARVALHO-COSTA, L.F., OTTONI, F.P. **Historical review on the type locality of *Knodus victoriae* (Steindachner 1907) (Teleostei: Characidae) and *Loricaria parnahybae* Steindachner 1907 (Teleostei: Loricariidae).** Biota Neotropica 21(4): e20211226. https://doi.org/10.1590/1676-0611-BN-2021-1226

Abstract: Based on the information and evidence on the zoological expedition led by the senior Austrian zoologist Franz Steindachner in 1903, the examination of original species descriptions using material collected in this expedition, the scientific literature on this expedition, examination of specimens of *Knodus victoriae*, and the consultation of State decrees modifying the name of localities and municipalities, we propose herein updated and accurate type localities for *Knodus victoriae* and *Loricaria parnahybae*. The accurate type locality for both species is at the mouth of a stream that flows into the Parnaiba River, Alto Parnaíba municipality in the State of Maranhão, upper Parnaiba River basin, northeastern Brazil. This update in the type locality aims to avoid doubts and confusion that hinder biogeographic and taxonomic studies.
Keywords: *Characiformes; Santa Filomena; Siluriformes; Taxonomy; Vienna Imperial Academy of Sciences.*

Revisão histórica sobre a localidade tipo de *Knodus victoriae* (Steindachner 1907) (Teleostei: Characidae) e *Loricaria parnahybae* Steindachner 1907 (Teleostei: Loricariidae)

Resumo: Com base em informações e evidências da expedição zoológica liderada pelo zoólogo sênior austríaco Franz Steindachner em 1903, exame das descrições originais das espécies que utilizaram material coletado nessa expedição, literatura científica sobre essa expedição, exame de exemplares de *Knodus victoriae*, e consulta a decretos estaduais que modificaram o nome de localidades e municípios, nós propomos a atualização com acurácia das localidades tipos de *Knodus victoriae* e *Loricaria parnahybae*. A localidade tipo acurada para ambas as espécies é na foz de um riacho que desagua no rio Parnaíba, no município de Alto Parnaíba no Estado do Maranhão, bacia do alto rio Parnaíba, nordeste do Brasil. Esta atualização na localidade tipo visa evitar dúvidas e confusões que podem atrapalhar estudos biogeográficos e taxonômicos.
Palavras-chave: *Academia Imperial de Ciências de Viena; Characiformes; Santa Filomena; Siluriformes; Taxonomia.*

Introduction

In 1903, the Vienna Imperial Academy of Sciences organized an important expedition to Brazil, led by the Austrian zoologist Franz Steindachner (1834–1919) (Vanzolini 1992, Böhme 1996), aiming to explore a vast area in the northeast and northern regions of the country (Mello-Leitão 1941, Böhme 1996). On January 2nd, 1903, they left Genoa (Italy) and arrived at the port of Recife (State of Pernambuco), northeastern Brazil, on February 16th of the same year, where the expedition started (Vanzolini 1992, Böhme 1996). Steindachner and his team traveled for about eight months through different localities (Vanzolini 1992, Böhme 1996). On June 11th, 1903, the expedition arrived at Santa Filomena (State of Piauí) (Vanzolini 1992), in the upper Parnaiba River, at the border between the States of Piauí and Maranhão. Soon after the arrival, Steindachner received fishes from the Parnaiba River, and from a neighboring tributary of Parnaíba, the Medonho River (Böhme 1996), whose mouth is located near the ancient village of Vitória do Alto Parnaíba, currently Alto Parnaíba municipality (State of Maranhão) according to the State of Maranhão decree-law number 820 (IBGE 2017). They left Santa Filomena and its surrounding areas on July 20-21th, 1903 after spending about 20 days collecting and receiving fish specimens from this region and vicinities (Steindachner 1907a, b, c, Vanzolini 1992, Böhme 1996). The Alto Parnaíba municipality (State of Maranhão) is about 2 km away in a straight line from Santa Filomena municipality (State of Piauí), both located at the border between the states on the banks of the Parnaiba River, which separates them (Figure 1).

The expedition resulted in the description of new fish species from the Parnaiba River basin (e.g., Steindachner 1906, Steindachner 1907a, b, c), such as: *Corydoras julii* Steindachner 1906, *Corydoras treitlii* Steindachner 1906, *Corydoras raimundi* Steindachner 1907 [*Aspidoras raimundi*], *Loricaria parnahybae* Steindachner 1907, *Prochilodus lacustris* Steindachner 1907, *Tetragonopterus sanctaefilomenae* Steindachner 1907 [*Moenkhausia sanctaefilomenae*], *Tetragonopterus victoriae* Steindachner 1907 [*Knodus victoriae*] and *Xenocara damasceni* Steindachner 1907 [*Ancistrus damasceni*]. Some of these species have confusing, inaccurate and outdated type localities, with municipality's names no longer corresponding to current names. Therefore, we aimed to provide an accurate and updated type locality for two species described by Steindachner — *Knodus victoriae* and *Loricaria parnahybae* — whose type material was collected during his 1903 expedition in Brazil, but remain with inaccurate and outdated type localities.

Methods

Information on the 1903 Steindachner's expedition and type localities, including their updated names, were based on the following literature: Steindachner (1906), Steindachner (1907a, b, c), Mello-

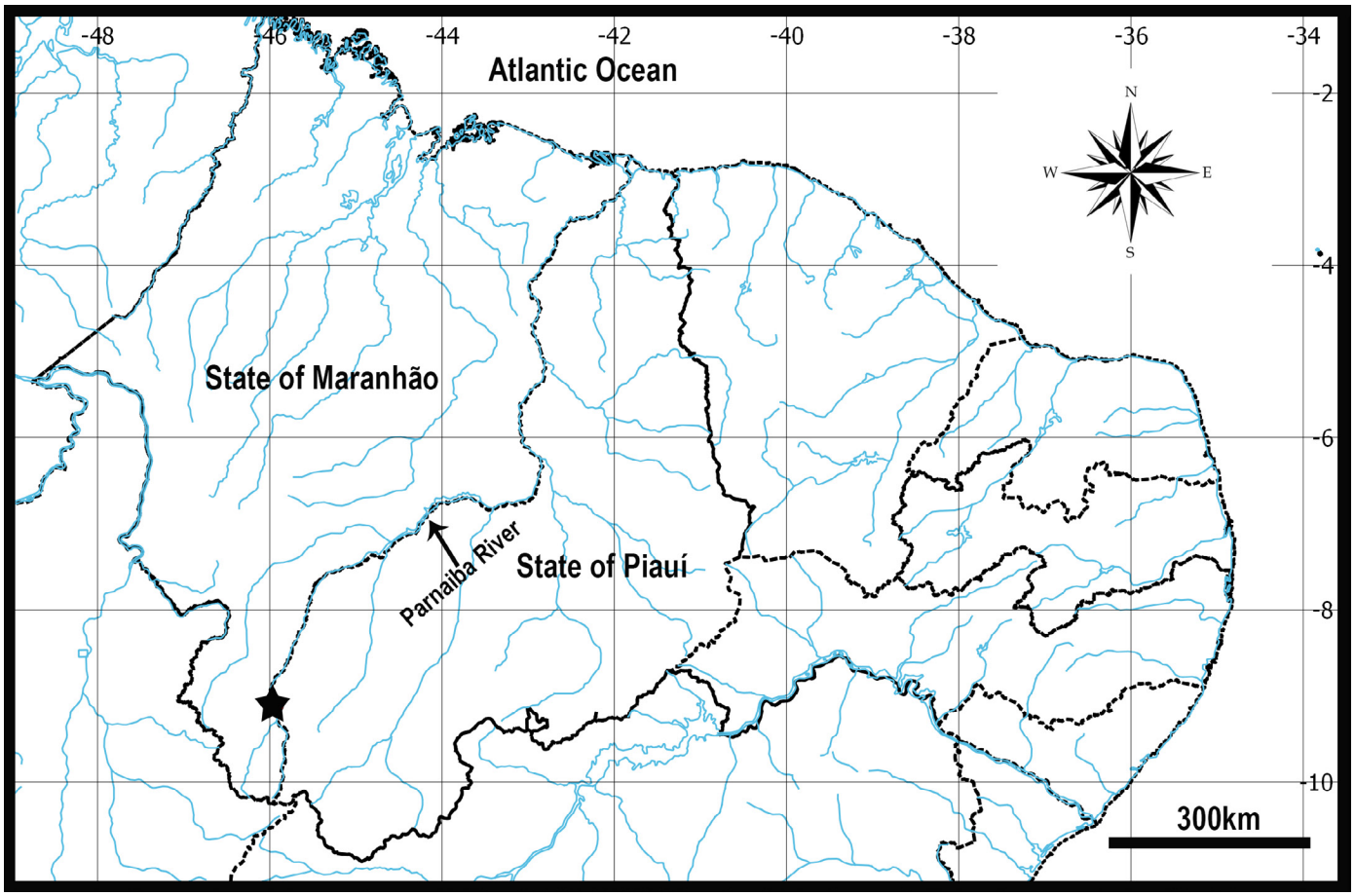


Figure 1. Map showing the updated and accurate type locality of *Knodus victoriae* and *Loricaria parnahybae*. Black star corresponds to the municipalities of Alto Parnaíba (State of Maranhão) and Santa Filomena (State of Piauí), about 2 km away, both located at the border between these states on the banks of the Parnaiba River.

Leitão (1941), Weitzman et al. (1964), Nijssen and Isbrücker (1976, 1980), Vanzolini (1992), Böhme (1996), Reis et al. (2003), Buckup et al. (2007), IBGE (2017), and Fricke et al. (2021). Vanzolini (1992) provided detailed information on the expedition itinerary, maps and diary, allowing us to have access to these information. In addition, ECG conducted a collection expedition in the Alto Parnaíba municipality (State of Maranhão), depositing specimens of *Knodus victoriae* collected at this locality in the Coleção Ictiológica do Centro de Ciências Agrárias e Ambientais of the Universidade Federal do Maranhão (CICCAA).

Results and Discussion

Original type localities of the two species are described in Steindachner (1907a, 1907b). Both species were described for the Parnaiba River basin, near the ancient village of Vitória do Alto Parnaíba[now Alto Parnaíba municipality (State of Maranhão)], according to the following excerpts from Steindachner (1907a, 1907b) translated from German to English:

a) *Tetragonopterus victoriae* Steindachner [F.] 1907a:83 [currently *Knodus victoriae*]

Original excerpt: "*Diese art, welche häufig in einem kleinen Bache nächst seiner Mündung in den Parnahyba bei dem Städtchen Victoria vorkommt...*" (Steindachner 1907a: 84).

Translated to English: *"This species, which is very common in a small stream near to its mouth in the Parnahyba river, near the town of Victoria ...."*

b) *Loricaria parnahybae* Steindachner [F.] 1907b:153

Original excerpt: "*...aus dem Rio Parnahyba an der Mündung eines Baches bei dem Stadtchen Victoria.*" (Steindachner 1907b:154)

Translated to English: *"...from the Rio Parnahyba at the mouth of a stream near the town of Victoria."*

For several years, some authors have been literally keeping these type localities according to their original description (e.g., Reis et al. 2003), either reporting them to the State of Maranhão or making simple or wrong interpretations (e.g., Eigenmann 1918, Buckup et al. 2007, Fricke et al. 2021, Scharpf & Kenneth 2021); however, none of them updated the name of the locality *"Victoria"*, currently Alto Parnaíba municipality (see Introduction). Interpretations keeping the original name of the localities may suggest that it is at some point at the mouth of the Parnaiba River. The location "*Städtchen Victoria* (*town of Victoria)"* [village of Vitória do Alto Parnaíba, currently Alto Parnaíba municipality in the State of Maranhão (IBGE 2017)], is actually located in the upper Parnaiba River basin section, and not in its lower portion (near the mouth).

Therefore, the most accurate type locality of both *Knodus victoriae* and *Loricaria parnahybae* is at the mouth of a stream that flows into the Parnaiba River, Alto Parnaíba municipality in the State of Maranhão, upper Parnaiba River basin, northeastern Brazil. This region encompasses bordering headwaters and river portions between the upper Parnaiba and São Francisco River basins. This updated type locality can change the biogeographic interpretations for these two species, and it may also be important for future DNA-based taxonomic or systematic studies in case specimens need to be collected.

Previous studies also corroborate our conclusions. For instance, Weitzman et al. (1964) and Nijssen and Isbrücker (1976) also concluded that the type locality of *Aspidoras raimundi*, originally addressed to the location "*….in dem Bächchen, welches bei Victoria in den Rio Parnahyba mündet*" (Steindachner 1907c:83) (translated to English: *"in the stream, which ends near Victoria in the Rio Parnahyba*"), currently corresponds to the mouth of a stream flowing to the Parnaiba River at Alto Parnaiba, State of Maranhão, Brazil. Nijssen and Isbrücker (1980) also reported a similar case with *Corydoras julii* and *Corydoras treitlii* that also had their type localities originally addressed to the same location in the *"Rio Parnahyba*" at "*Victoria*", but the type localities of both species were updated to: Brazil-Maranhão, creek into Rio Parnaiba near Alto Parnaíba (=Victoria) (09°08'S; 45°56'W). However, none of these authors explained in detail how they obtained their conclusions on the updated name of the locality.

Misinterpretations of type localities based on historical works are recurrent. Several species with old descriptions have inaccurate and/or confusing type localities (e.g., Steindachner 1907a, b, c, Lucena and Lucena 1990), which are often literally translated to English — changing the original context (e.g., the type locality of *Knodus victoriae*, Fricke et al. 2021). However, erroneous designation or wrong interpretations of type localities hinders biogeographical and taxonomic studies as accurate type localities are crucial for these type of studies (Ottoni et al. 2020). Therefore, several studies have been correcting and updating type localities more accurately to avoid taxonomic and biogeographic confusions (e.g., Lima and Géry 2001, Lucinda and Lucena 2012, Koerber 2016, Ottoni et al. 2020).

Therefore, considering: 1) that there is no municipality with the name "Victoria" in the lower Parnaiba River region; 2) the translation of the Steindachner's original descriptions; 3) specimens of *Knodus victoriae* collected by ECG (in 2021) in the Alto Parnaíba municipality (State of Maranhão) fit the original description of the species, and the features of its type material; and 4) the State decree modifying the name of localities and municipalities [the State of Maranhão decree-law number 820 (IBGE 2017)]; all of these evidences corroborate the updating of the type locality of *Knodus victoriae* and *Loricaria parnahybae* to the mouth of a stream that flows into the Parnaiba River, Alto Parnaíba municipality in the State of Maranhão, upper Parnaiba River basin, northeastern Brazil (Figure 1).

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Author Contributions

Rayane Gonçalves Aguiar: 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.

Erick Cristofore Guimarães: 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; collection expedition in the Alto Parnaíba municipality (State of Maranhão).

Luis Fernando Carvalho-Costa: 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; English language review.

Felipe Polivanov Ottoni: Concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Conflicts of Interest

There is no conflict of interest.

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The vascular flora of Porto Ferreira State Park: an ecotonal area in São Paulo State, southeastern Brazil

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Abstract: The Porto Ferreira State Park (PFSP) is located in the State of São Paulo southeastern Brazil, in an intriguing transitional area between the Atlantic Forest and *Cerrado* – both hotspots of biodiversity – represented mainly by the *cerradão* (CER), and the seasonal semideciduous forest (SSF), with its alluvial variation vegetation type (riparian forest – RP). Ecotonal areas play an important role in providing ecological and phytogeographic knowledge regarding the flora and vegetation of this region. Despite various studies on the PFSP, knowledge of this region remains fragmented. In this study, we aim to conduct an updated checklist of the PFSP vascular flora, including a compilation of all the studies conducted in this protected area, plus field work carried out by the authors from 2014 to 2017. In addition, given its ecotonal characteristics, we completed a floristic similarity analysis between the PFSP and other floristic surveys that examined the same vegetation types present in this study, to gain a better understanding of their phytogeographic relationships. Overall, 684 species, belonging to 387 genera and 107 families, were recorded. The SSF presented the richest vegetation type (478 species), followed by the CER (418) and the RP (231). The most diverse families were Fabaceae (64 species), Myrtaceae (41), Orchidaceae (39), Rubiaceae (37), Asteraceae (35), Bignoniaceae (26) and Malvaceae (20). Moreover, eight threatened species, at regional and national levels, were found. To date, 412 species have been added to the floristic list produced for the PFSP. The life forms with the highest number of species were trees (286 species), herbs (176) plus shrubs and subshrubs (123). Our research findings indicate floristic patterns with higher levels of similarity among species in geographical proximity, including those in ecotonal areas encompassing different vegetation types. These results rank the PFSP among some of the most species-rich conservation units with seasonal climates, and therefore is of great importance for plant conservation in the southeast of Brazil.
Keywords: *Atlantic Forest; Cerrado; floristic; protected area; seasonal semideciduous forest.*

Flora vascular do Parque Estadual de Porto Ferreira: uma área ecotonal no estado de São Paulo, sudeste do Brasil

Resumo: O Parque Estadual de Porto Ferreira (PEPF) está localizado no estado de São Paulo, sudeste do Brasil, em uma intrigante área de contato entre a Mata Atlântica e o Cerrado – ambos hotspots de biodiversidade –, representada principalmente pelo cerradão (CER), a floresta estacional semidecidual (FES) e pela variação dessa última, com influência aluvial (FESA). As áreas ecotonais desempenham um papel importante no conhecimento ecológico e fitogeográfico da flora e da vegetação. Mesmo com muitos estudos realizados no PEPF, as informações encontram-se dispersas. Dessa forma, produzimos um checklist atualizado da flora vascular, resultante da compilação de vouchers, estudos realizados no PEPF e de esforços de coleta realizados pelos autores entre os anos de 2014 e 2017. Além disso, para entender suas relações fitogeográficas, realizamos uma análise de similaridade florística entre o PEPF e outros levantamentos realizadas nas mesmas fitofisionomias da área estudada. Registramos 684 espécies pertencentes a 387 gêneros e 107 famílias. A FES foi a fitofisionomia mais rica (478 espécies), seguida pelo CER (418) e a FESA (231).

As famílias mais ricas foram Fabaceae (64 espécies), Myrtaceae (41), Orchidaceae (39), Rubiaceae (37), Asteraceae (35), Bignoniaceae (26) e Malvaceae (20). Oito espécies ameaçadas em âmbito regional e nacional foram encontradas. Desde a última lista florística produzida para o PEPF, 412 espécies foram adicionadas. As formas de vida com maiores números de espécies foram: árvores (286 espécies), ervas (176) e arbustos mais subarbustos (123). A análise de similaridade corroborou o padrão de que áreas mais próximas geograficamente são mais similares entre si, e esse padrão foi encontrado, também, para áreas ecotonais envolvendo diferentes fitofisionomias. Os resultados encontrados colocam o PEPF entre as unidades de conservação com maior número de espécies vegetais sob o domínio de clima sazonal, possuindo, portanto, grande importância para a conservação de espécies de plantas no Sudeste do Brasil.

Palavras-chave: *Mata Atlântica; Cerrado; florística; unidade de conservação; floresta estacional semidecidual.*

Introduction

Brazil is home to one of the richest plant diversities in the world, with more than 34,000 species of vascular plants (BFG, 2021). This great diversity is mainly due to Brazil's vast geographical area, its heterogeneous topography, as well as its climate, and biogeographical features (Fiaschi & Pirani, 2009). Traditionally, it has been divided into major landscapes and macroecological ecoregions (Ab'Sáber, 1970, 2003). Among the biogeographical units recognized in Brazil, the *Cerrado* and the Atlantic Forest are classified as biodiversity hotspots for global conservation, hosting an overwhelming number of endemic species threatened by anthropic actions (Myers et al., 2000; Mittermeier et al., 2004).

The biogeographic province, known as the *Cerrado,* mainly spans over central Brazil, with its southern limits reaching the northern part of the State of Paraná, the northern region of Argentina, and eastern Bolivia (Morrone, 2017; Velazco et al., 2018). It comprises a set of vegetation types, ranging from grasslands with herbaceous plants dominating the landscape (*campo limpo*), to savannas (*campo sujo* and *cerrado sensu stricto*) and forests (*e.g. cerradão* and gallery forests) (Coutinho, 2006; Batalha, 2011). The *Cerrado* is the second largest phytogeographical unit of Brazil, spanning 2 million km² or 23.9% of the national territory (IBGE, 2004). The main threats to the *Cerrado* vegetation are the expansion of intensive agriculture activity, and raising livestock (Ratter et al., 2006; Klink & Moreira, 2002). Nevertheless, the *Cerrado* is considered one of the world's richest savanna vegetation (Klink & Machado, 2005; Simon et al. 2009), containing more than 12,000 species of vascular plants (BFG, 2015; Flora do Brasil, 2020). In the State of São Paulo the *Cerrado* occurs mainly in the central region, but extends to eastern portions of the State as well, with enclaves in the Atlantic Forest matrix (Baitello et al., 2013).

The Atlantic Forest covers nearly 1.1 million km² (IBGE, 2004), distributed over a broad latitudinal, ranging from the State of Piauí to Rio Grande do Sul (SOS Mata Atlântica, 2016), and reaching inland to northern Argentina and eastern Paraguay (Spichiger et al., 2006; Fiaschi & Pirani, 2009). Brazil's Atlantic Forest hosts an overwhelming species richness of vascular plants (BFG 2015; *Flora do Brasil*, 2020), being one of the world's top five species-rich areas (Barthlott et al., 2005). Traditionally, the Atlantic Forest has been considered a single biogeographical unit with subdivisions (*e.g.* Morellato & Haddad, 2000). However, more than distinct vegetation types, singular biogeographical histories of the biota have been suggested for different parts of the Atlantic Forest (Vieira et al., 2015; Morrone 2014, 2017; Eisenlohr & Oliveira-Filho, 2015) justifying its division in three provinces (Morrone 2014, 2017). Among these biogeographical provinces, the inland and seasonal vegetation type is represented by the Paraná Forest province (Morrone, 2017; Zanotti et al., 2020), and it is the one most threatened by the reduction of the original area (Ribeiro et al., 2009). The floristic richness of the seasonal forest is considerably high (Souza et al., 2019a) and holds regional and typical species (Eisenlohr & Oliveira-Filho, 2015; Vieira et al., 2015; Morrone 2014, 2017).

In the State of São Paulo, the *Cerrado* and Atlantic Forest mix in a complex and transitional area, in scattered patches of each or at ecotones (Durigan et al., 2012). The *Cerrado* forest formation is very common there, with a great richness of tree species, mainly influenced by contact with Atlantic Forest taxa (Françoso et al., 2016). On the other hand, the innermost vegetation type of the Atlantic Forest is characterized by a well-marked dry season, and a characteristic composition, despite sharing several species with the rainy coastal forest and the *cerradão* (Eisenlohr & Oliveira-Filho, 2015). Ecotones represent a transition between ecological communities, with a mixture of the floristic and faunistic characteristics of two different and relatively homogenous ecological community types (Allen & Starr, 1982). Studies indicate that richness and abundance tend to peak at ecotonal areas (Kark & van Rensburg, 2006) and contribute to São Paulo's high level of plant richness, having one of Brazil's greatest numbers of species (BFG, 2015; Flora do Brasil, 2020).

Studies on the biodiversity of plant communities are considered fundamental, and one of the first steps toward the establishment of models for the preservation and conservation of ecosystems (Morellato & Leitão-Filho, 1992; Ferreira Júnior et al., 2008). Given these characteristics, the PFSP, floristically, has drawn great attention. From 1984 to present, 12 studies regarding its flora have been carried out, as well as aleatory collections deposited in herbaria. These studies include climbing plants (Vargas et al., 2018), ferns (Colli et al., 2003), non-arboreal plants (Oliveira, 2012; Osaco, 2012), trees (Bertoni, 1984; Bertoni & Martins, 1987; Bertoni et al., 2001; Sabino, 2013; Konopczyk, 2014) and vascular epiphytes (Marcusso et al., 2016). However, this data is fragmented, and remains to be systematically organized. The Management Plan (São Paulo, 2003) represents the last overall floristic list presented for this protected area.

Thus, we compiled the checklist of the vascular flora of the PFSP, based on fieldwork, studies conducted in the area, and herbarium collections, aiming to extend and systematize the scattered floristic information on the region. This data can support restoration and conservation projects in the central region of the State of São Paulo, given that several private lands of the region present a deficit in native vegetation and must be restored in accordance with the Native Vegetation Protection Law (Tavares et al., 2019).

Our work also provides a foundation on which to update the Management Plan of this important vegetation-protected area. In addition, we explored and discussed the floristic identity concerning the ecotonal condition of the PFSP, comparing our data with other floristic surveys carried out on the same vegetation types.

Material and Methods

The Porto Ferreira State Park (PFSP), known locally as "Mata do Procópio", is located in the municipality of Porto Ferreira, of the State of São Paulo, in the southeastern region of Brazil (Figure 1). The PFSP is one of more than 50 integral protected areas in São Paulo (*Instituto Florestal/Fundação Florestal*, 2008, Colli-Silva et al., 2016), founded in 1962, initially categorized as a State Reserve, and later (1987) becoming a State Park (São Paulo, 2003). Under the central geographical coordinates 21°51'S and 47°25'W, the park is bordered by the Mogi Guaçu river to the south, and by the SP-215 highway to the north, occupying an area of 611.55 hectares (São Paulo, 2003). The PFSP is part of the region of the Peripheral Depression of São Paulo (Depression of Mogi Guaçu) belonging to the Paraná Basin (Rossi et al., 2005).

According to Köeppen-Geiger classification, the climate of the region is classified as Cwa, dry winter mesothermal (Alvares et al., 2013). The annual mean temperature is 22ºC, and the annual mean precipitation is 1470 mm (INMET 2019).

The vegetation of the Mogi Guaçu basin is mainly composed of Atlantic Forest, with seasonal semideciduous forest (SSF) being the most common vegetation type (Bertoni 1984; Veloso & Góes Filho, 1982). However, PFSP is composed of different vegetation types, presenting the forested savanna in the north (CER, with altitudes between 605-575 m), and to the south, SSF (with altitudes between 575-535 m) (Rossi et al., 2005). Parallel to the Mogi Guaçu river, riparian forest is found (RP, with an average altitude of 530 m) (Bertoni & Martins, 1987; Konopczyk, 2014) (Figure 2). These vegetation types can be distinguished mainly by their structures, of which the CER presents a small average height and high density, while the SSF presents a greater average height and lower density (Vargas et al. 2018), and finally, the RP having the lowest density and diversity (Konopczyk, 2014). In addition, there are ecotonal areas among them (Sabino, 2013), as well as riverine variations (Konopczyk, 2014).

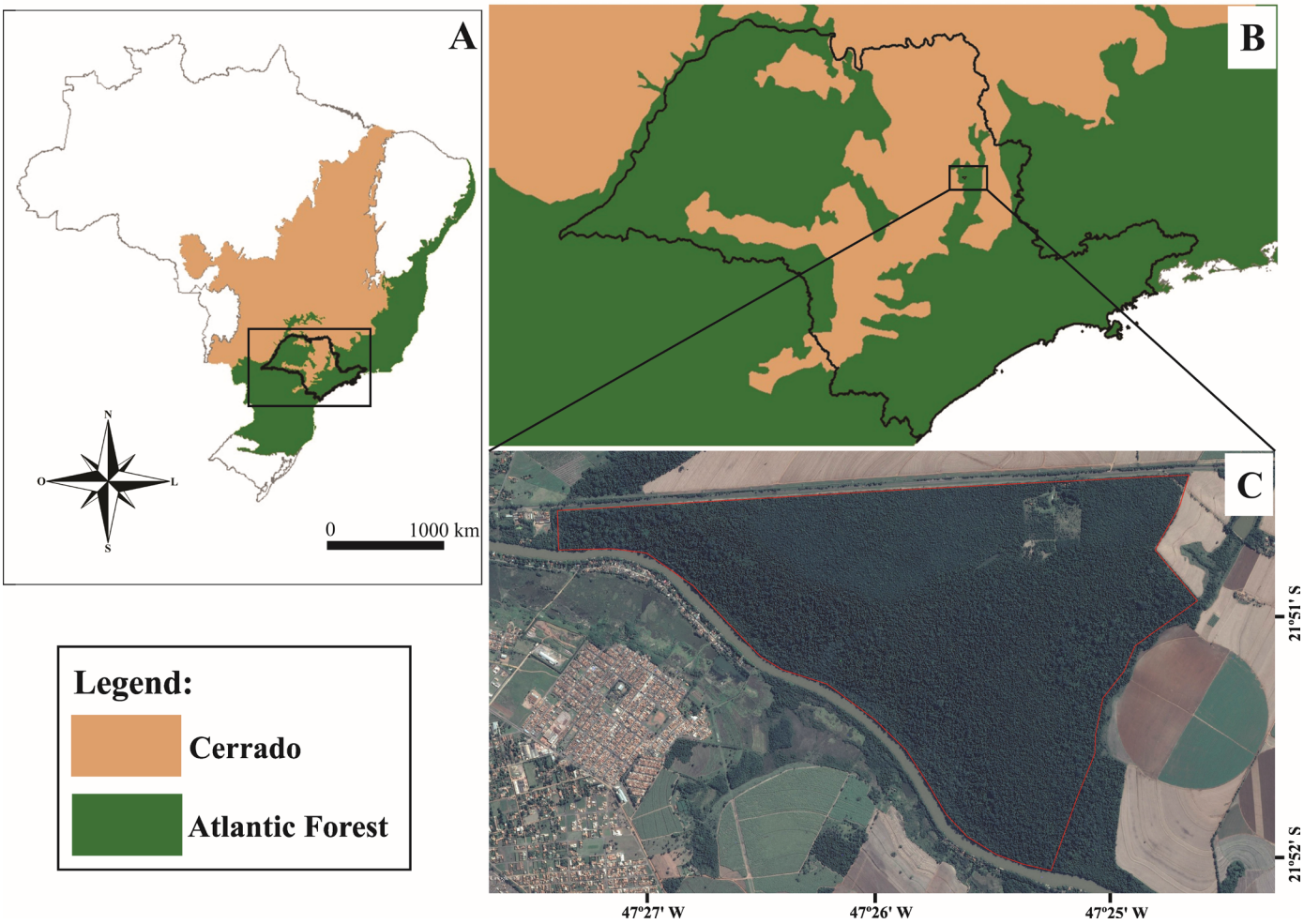


Figure 1. Location of Porto Ferreira State Park (PFSP), Porto Ferreira, São Paulo State. A. Atlantic Forest and the *Cerrado* in Brazil and the location of São Paulo State; B. Location of PFSP; C. PFSP satellite view, adapted from Google Earth.

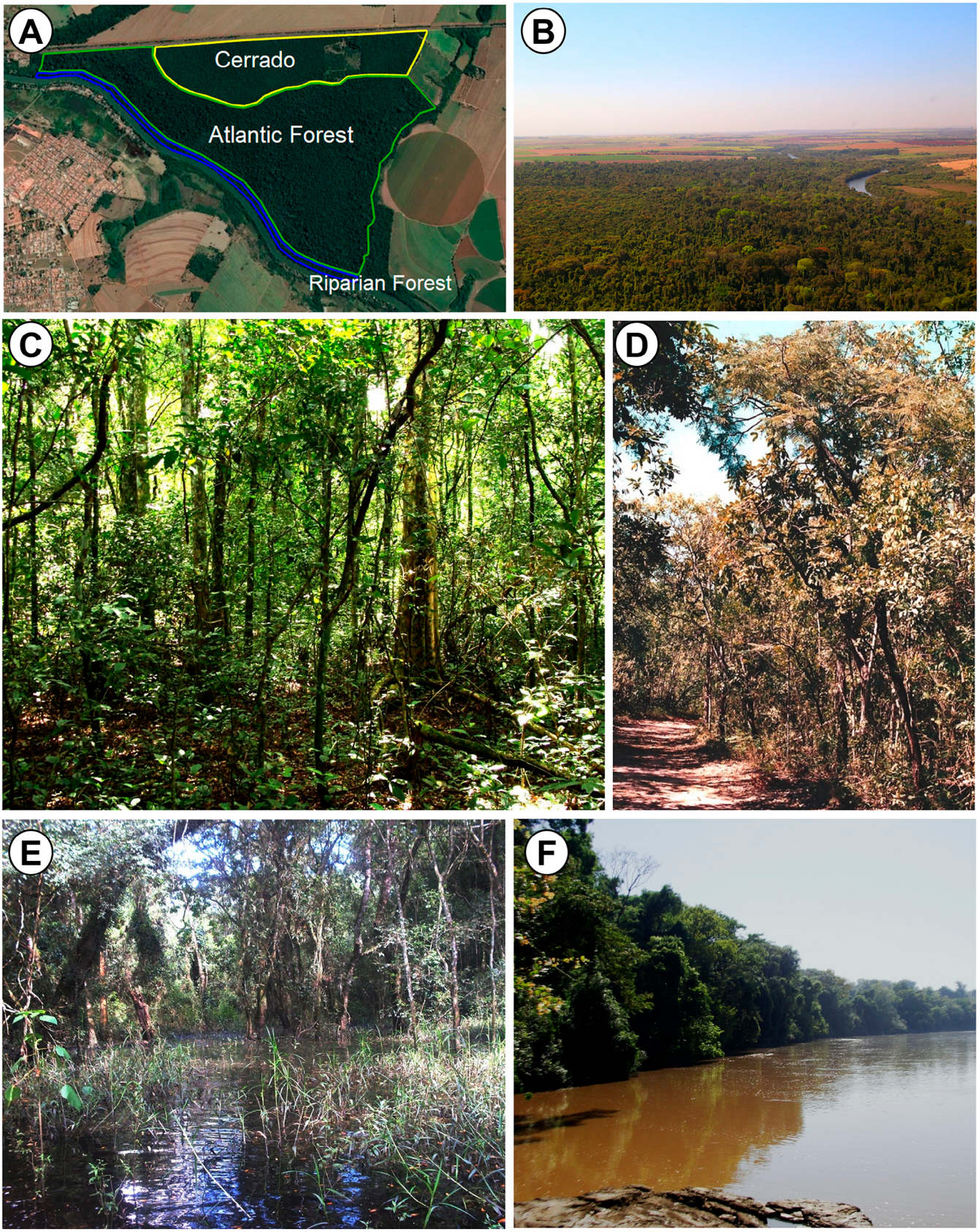


Figure 2. Vegetation types of Porto Ferreira State Park (PFSP), Porto Ferreira, São Paulo State. A: map indicating the vegetation types; B: aerial view of PFSP; C: seasonal semideciduous forest; D: cerradão; E: riparian forest; F: Mogi Guaçu river (A. Adapted from Google Earth; B. PFSP photo collection; C./F. Gabriel Mendes Marcusso; D. PFSP photo collection; E. Rafael Konopczyk).

The PFSP represents one of the few protected areas in São Paulo which comprises the contact between the *Cerrado* and Altantic Forest, becoming an important biotic pool of both, in a single and relatively small area. It also holds one of the largest and tallest populations of *Cariniana legalis* (Mart.) Kuntze and *Cariniana estrellensis* (Raddi) Kuntze (Lecythidaceae), with several individuals reaching up to 50 m. These trees are iconic elements of the PFSP.

The PFSP vascular flora checklist was created from the following: specimens collected by the authors from 2014 to 2017, using the walking research method (Filgueiras et al., 1994); the systematization of all other lists found in surveys carried out in PFSP (Bertoni, 1984; Bertoni & Martins, 1987; Bertoni et al., 2001; São Paulo, 2003; Colli et al., 2003; Oliveira, 2012; Osaco, 2012; Dickfeldt et al., 2013; Sabino, 2013; Konopczyk, 2014; Marcusso et al., 2016; Vargas et al., 2018); and the compilation of vouchers present in the Specieslink database (CRIA, 2019). We considered only native taxa identified at the taxonomic level of species and excluded those with dubious identification, at the genera-level and exotic species (cited in a separate table – Appendix 1). For angiosperms, the taxa classification followed the APG IV system (2016), and for ferns or lycophytes, the PPG I system (2016). The nomenclature and synonymizations were updated according to the *Flora do Brasil* (2020). When the data from *Flora do Brasil* (2020) were outdated or not available, we used the *Tropicos* (2019) database.

The life forms of the species were obtained through field observations, assessing the herbarium specimen labels information and, when this was not possible, we consulted the *Flora do Brasil* (2020) data. Shrubs and subshrubs were unified in a single category. To assess the number of exclusive and common species among the vegetation types in the study area, we built Venn diagrams for all the species together, and for each life form. The threatened species were classified according to The Red Book of Brazilian Flora (Martinelli & Moraes, 2013) and the list of threatened flora of São Paulo (SMA-SP, 2016).

The similarity in species composition was estimated by the Jaccard Index (Mueller-Dombois & Ellenberg, 1974), as well as this study and 14 others carried out in *Cerrado sensu lato*, SSF and RP vegetation types. Only vascular or phanerogamic floristic surveys were compared, which included studies performed in the South and Southeast regions of Brazil. Only native taxa identified at the taxonomic level of species were considered. Studies that sampled more than one vegetation type were subdivided into independent lists (*e.g.* Durigan et al., 1999), resulting in 22 lists (Table 1). We used a binary matrix with presence (1) and absence (0) to conduct an agglomerative hierarchical clustering analysis (Legendre & Legendre, 2012), by employing UPGMA (average linkage), and Jaccard dissimilarity in the vegan package (Oksanen et al. 2013) in R (R Core Team 2020).

Table 1. Studies of flora compared with this study.

CODE FOR THE STUDIES	STUDY SITE	VEGETATION TYPE	NSa / N	REFERENCE
A	Porto Ferreira - SP	Ssf	478 / 478	Present study
B	Porto Ferreira - SP	Cer	418 / 418	Present study
C	Porto Ferreira - SP	Rp	231 / 231	Present study
D	Piracicaba - SP	Ssf	269 / 289	Corrêa et al. 2018
E	Jundiaí, Itupeva, Cabreúva, Pirapora do Bom Jesus and Cajamar - SP	Ssf	835 / 976	Lombardi et al. 2012
F	Campinas - SP	Ssf	187 / 201	Guaratini et al. 2008
G	Descoberto - MG	Ssf	648 / 708	Forzza et al. 2014
H	São João Nepomuceno - MG	Ssf	174 / 204	Pifano et al. 2013
I	Caratinga - MG	Ssf	826 / 1048	Lombardi & Gonçalves 2000
J	Londrina - PR	Ssf	468 / 508	Rossetto & Vieira 2013
K	Avaré - SP	Rp+Ssf	90 / 93	Cielo-Filho et al. 2015
L	Avaré - SP	Cer	153 / 181	Cielo-Filho et al. 2015
M	Avaré - SP	Ec	33 / 33	Cielo-Filho et al. 2015
N	Santa Rita do Passa Quatro - SP	Cer	145 / 148	Batalha & Mantovani 2001
O	Santa Rita do Passa Quatro - SP	Css	336 / 339	Batalha & Mantovani 2001
P	Assis - SP	Cer	214 / 242	Durigan et al. 1999
Q	Assis - SP	Rp	120 / 134	Durigan et al. 1999
R	Assis - SP	Css	222 / 298	Durigan et al. 1999
S	Pirassununga - SP	Csl	339 / 358	Batalha et al. 1997
T	Pratânia - SP	Css	113 / 120	Carvalho et al. 2010
U	Bauru - SP	Csl	360 / 371	Cavassan & Weiser 2015
V	Botucatu - SP	Css	170 / 177	

Ssf: seasonal semideciduous forest; Rp: riparian forest; Cer: cerradão; Csl: cerrado *sensu lato*; Css: cerrado *sensu stricto*; Cc: campo cerrado; Ec: ecotone Ssf-Cer; NSa: number of taxons used in similarity analysis; N: total number of taxons.

Results

A total of 684 species distributed in 107 families and 387 genera were recorded (640 angiosperms and 44 ferns or lycophytes) (Table 2). The richest families were Fabaceae, with 64 species, followed by Myrtaceae (41), Orchidaceae (39), Rubiaceae (37), Asteraceae (35), Bignoniaceae (26), Malvaceae (20), Euphorbiaceae (19), Malpighiaceae and Sapindaceae (17 each) (Figure 3). These families account for 46% of the surveyed species, and 35 families (32.7%) had one single species. The richest genera were *Eugenia* (19 species), *Miconia* (14), *Myrcia* (11), *Solanum* (nine), *Peperomia* and *Serjania* (eight each). A separate list shows 152 excluded species and the reason for the exclusion (Appendix 1). The richest vegetation type was SSF, with 478 species, followed by the CER (418) and the RP (231).

From the registered species, 581 were listed in previous surveys, and 527 of them we found in herbaria vouchers. Added to the last floristic list prepared for the management plan, were 412 species, 70 of which were drawn from aleatory collections (not cited in previous surveys), and 33 from collections carried out by the authors of this study. Eight species recorded here are on the threatened list at the national level (Martinelli & Moraes, 2013) two of which - *Anemopaegma arvense* (Vell.) Stellfeld ex de Souza and *Cariniana legalis* (Mart.) Kuntze - are endangered, and six species [*Euterpe edulis* Mart., *Zeyheria tuberculosa* (Vell.) Bureau ex Verl., *Croton leptobotryus* Müll.Arg., *Cedrela fissilis* Vell., *Cattleya walkeriana* Gardner and *Isabelia virginalis* Barb.Rodr.] are listed as vulnerable. The list of threatened São Paulo State flora (SMA 2016) follows the same species and threat category as on the national list, except for *Cariniana legalis* (Mart.) Kuntze, classified as vulnerable.

Table 2. List of vascular flora species from Porto Ferreira State Park, municipality of Porto Ferreira, São Paulo State, southeastern Brazil.

Family/Species	Life form	Voucher	Source	Veg. type
ACANTHACEAE				
Justicia lythroides (Nees) V.A.W.Graham	Herb	HRCB, 52297	IV, XIII	cer, ssf
Mendoncia puberula Mart.	Climbing	HRCB, 52653; UEC, 173877	IV, IX, XIII	ssf
Ruellia brevifolia (Pohl) C.Ezcurra	Shrub	HRCB, 52389; MBML, 43930	IV, XIII	cer, ssf
Ruellia jussieuoides Schltdl. & Cham.	Shrub	HRCB, 52299	IV, XIII	cer, ssf
AMARANTHACEAE				
Alternanthera brasiliana (L.) Kuntze	Shrub	HRCB, 52458	IV, XIII	ssf
Chamissoa acuminata Mart.	Shrub	HRCB, 52323; HRCB, 68052	IV, IX, XIII	ssf
Pfaffia tuberosa (Spreng.) Hicken	Herb	HRCB, 54948; FUEL, 53509	IV, XIII	rp
AMARYLLIDACEAE				
Hippeastrum puniceum (Lam.) Kuntze	Herb	HRCB, 71787	XIII	rp
ANACARDIACEAE				
Astronium graveolens Jacq.	Tree		II, V, VI, VII, X	cer, ssf, rp
Astronium urundeuva (M. Allemão) Engl.	Tree		VI, X	cer, ssf
Lithraea molleoides (Vell.) Engl.	Tree	SPSF, 24691; UEC, 44048	III, XIII, X	cer
Schinus terebinthifolia Raddi	Tree		III, X	cer, ssf
Tapirira guianensis Aubl.	Tree	SPSF, 24702; UB, 147873	I, II, III, V, VI, VIII, X, XIII	cer, ssf, rp
Tapirira obtusa (Benth.) J.D.Mitch.	Tree		II, VI, X	cer, ssf, rp
ANEMIACEAE				
Anemia phyllitidis (L.) Sw.	Herb	BHCB, 141939	IV, XI, XIII	cer, ssf
Anemia tomentosa var. anthriscifolia (Schrad.) Mickel	Herb	BHCB, 153399	IV	cer, ssf
Anemia villosa Humb. & Bonpl. ex Willd.	Herb		XI	cer, ssf
ANNONACEAE				
Annona coriacea Mart.	Tree, Shrub	SPSF, 27349	III, X, XIII	cer
Annona crassiflora Mart.	Tree		III, X	cer
Annona dioica A.St.-Hil.	Shrub	UEC, 30475	III, X, XIII	cer
Annona sylvatica A.St.-Hil.	Tree		III, VI, X	cer
Duguetia furfuracea (A.St.-Hil.) Saff.	Tree		III, X	cer
Duguetia lanceolata A.St.-Hil.	Tree	HRCB, 62083	III, VI, X, XIII	cer, ssf, rp
Guatteria australis A.St.-Hil.	Tree	SPSF, 25925	III, X, XIII	cer, ssf, rp
Xylopia aromatica (Lam.) Mart.	Tree	MBM, 287171; SPSF, 27379	III, VI, X, XIII	cer
Xylopia brasiliensis Spreng.	Tree		III, V, VI, X	cer, ssf, rp
Xylopia sericea A.St.-Hil.	Tree		VI	cer

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Family/Species	Life form	Voucher	Source	Veg. type
APOCYNACEAE				
Aspidosperma cylindrocarpon Müll.Arg.	Tree		I, II, VII, X	ssf, rp
Aspidosperma polyneuron Müll.Arg.	Tree		II, X	ssf, rp
Aspidosperma ramiflorum Müll.Arg.	Tree	HRCB, 71805	I, X, XIII	ssf
Aspidosperma tomentosum Mart.	Tree		III, X	cer
Forsteronia australis Müll.Arg.	Climbing	HRCB, 67992	IX	cer
Forsteronia glabrescens Müll.Arg.	Climbing	HRCB, 52508	IV, XIII	cer, ssf
Forsteronia pubescens A.DC.	Climbing	HRCB, 67993	IX	cer, ssf
Gonolobus rostratus (Vahl) R.Br. ex Shult.	Climbing	HRCB, 52643	IV, XIII	cer
Mandevilla pohliana (Stadelm.) A.H.Gentry	Shrub	UEC, 37775	XIII	cer
Odontadenia lutea (Vell.) Markgr.	Shrub	HRCB, 68001	IX	cer
Oxypetalum appendiculatum Mart.	Climbing	HRCB, 67994	IX	cer
Prestonia coalita (Vell.) Woodson	Climbing	HRCB, 52381; HRCB, 67995	IV, IX, XIII	cer, ssf
Secondatia densiflora A.DC.	Climbing	HRCB, 67996	IX	cer, ssf
Temnadenia violacea (Vell.) Miers	Climbing	HRCB, 52464; HRCB, 71791	IV, IX, XIII	cer, ssf
AQUIFOLIACEAE				
Ilex cerasifolia Reissek	Tree	SPSF, 27381; MBM, 288153	III, X, XIII	cer
ARACEAE				
Philodendron propinquum Schott	Herb	HRCB, 62017	VIII, XIII	cer, ssf, rp
Thaumatophyllum bipinnatifidum (Schott ex Endl.) Sakur., Calazans & Mayo	Herb	HRCB, 62030	VIII, XIII	ssf
ARALIACEAE				
Dendropanax cuneatus (DC.) Decne. & Planch.	Tree	SPSF, 25481	I, V, VI, X, XIII	cer, ssf, rp
Didymopanax morototoni (Aubl.) Decne. & Planch.	Herb	HRCB, 71801	I, III, VI, X, XII, XIII	ssf
Didymopanax vinosus (Cham. & Schltdl.) Marchal	Tree	HRCB, 52466	IV, X, XIII	cer, ssf, rp
Hydrocotyle leucocephala Cham. & Schltdl.	Shrub	HRCB, 52290	IV, XIII	cer
ARECACEAE				
Acrocomia aculeata (Jacq.) Lodd. ex Mart.	Herb		III, VI, X	cer, rp
Allagoptera campestris (Mart.) Kuntze	Herb		III, X	cer
Euterpe edulis Mart.*	Herb		I, V, VI, X	cer, ssf, rp
Geonoma brevispatha Barb.Rodr.	Herb		III, X	cer, rp
Syagrus loefgrenii Glassman	Herb	SPSF, 20831	XIII	cer
Syagrus oleracea (Mart.) Becc.	Herb		I, X	ssf, rp
Syagrus romanzoffiana (Cham.) Glassman	Herb		I, II, III, VI, X	cer, ssf, rp
ARISTOLOCHIACEAE				
Aristolochia labiata Willd.	Climbing	HRCB, 52506; HRCB, 67998	IV, IX, XIII	cer, ssf
ASPARAGACEAE				
Herreria latifolia Woodson	Climbing	SPSF, 26298	XIII	cer, ssf
ASPLENIACEAE				
Asplenium auriculatum Sw.	Herb	UEC, 62342	XIII	ssf
Asplenium claussenii Hieron.	Herb	APO, 100	IV, XI	ssf, rp
Asplenium formosum Willd.	Herb	UEC, 62341	XI, XIII	ssf
Asplenium inaequilaterale Willd.	Herb		XI	ssf
Asplenium otites Link	Herb		XI	ssf

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Family/Species	Life form	Voucher	Source	Veg. type
ASTERACEAE				
Acanthospermum australe (Loefl.) Kuntze	Herb	HRCB, 52523	IV, XIII	cer, ssf
Baccharis dracunculifolia DC.	Shrub	HRCB, 59922	III, X, XIII	cer
Baccharis retusa DC.	Shrub	SPSF, 20788	XIII	cer
Bidens gardneri Baker	Herb	HRCB, 52402	IV, XIII	cer, ssf
Bidens segetum Mart. ex Colla	Climbing	HRCB, 52447	IV, IX, XIII	cer
Centratherum punctatum Cass.	Shrub	SPSF, 25939	XIII	cer
Chaptalia nutans (L.) Pol.	Herb	HRCB, 52662	IV, XIII	cer
Chromolaena laevigata (Lam.) R.M.King & H.Rob.	Shrub	HRCB, 52428	IV, XIII	cer, ssf
Chromolaena pedunculosa (Hook. & Arn.) R.M.King & H.Rob.	Shrub	HRCB, 52407	IV, XIII	cer, ssf
Chrysolaena obovata (Less.) Dematt.	Shrub	UEC, 25226	XIII	cer
Cyrtocymura scorpioides (Lam.) H.Rob.	Shrub	HRCB, 55870	IV, IX, XIII	ssf
Dasyphyllum brasiliense (Spreng.) Cabrera	Shrub	HRCB, 68000	IX	ssf
Elephantopus mollis Kunth	Herb	HRCB, 52314	IV, XIII	cer, ssf
Emilia fosbergii Nicolson	Herb	HRCB, 52524	IV, XIII	cer, ssf
Exostigma notobellidiastrum (Griseb.) G.Sancho	Herb	HRCB, 52646	IV, XIII	ssf
Melampodium divaricatum (Rich. ex Pers.) DC.	Shrub	HRCB, 52274; SP, 454549	XIII	ssf
Melampodium paniculatum Gardner	Shrub	HRCB, 52647	IV, XIII	ssf
Mikania cordifolia (L.f.) Willd.	Climbing	HRCB, 52453	IV, IX, XIII	cer
Mikania laevigata Sch.Bip. ex Baker	Climbing	HRCB, 53129	IV, IX, XIII	cer
Mikania triangularis Baker	Climbing	HRCB, 53122	IV, XIII	ssf
Moquiniastrum barrosoae (Cabrera) G. Sancho	Shrub	SPSF, 11351; HRCB, 55875	XIII	cer
Moquiniastrum paniculatum (Less.) G. Sancho	Shrub	UEC, 178504	IV, XIII	cer
Moquiniastrum polymorphum (Less.) G. Sancho	Tree		V	cer, ssf
Moquiniastrum pulchrum (Cabrera) G.Sancho	Shrub	UEC, 160575; SPSF, 20787	XIII	cer
Orthopappus angustifolius (Sw.) Gleason	Herb	HRCB, 52510	IV, XIII	cer, ssf
Piptocarpha macropoda (DC.) Baker	Tree	IPA, 89165; UEC, 44055	III, VI, X, XIII	cer, ssf
Piptocarpha rotundifolia (Less.) Baker	Tree	SPSF, 24695	III, X, XIII	cer
Porophyllum ruderale (Jacq.) Cass.	Herb	HRCB, 52480	IV, XIII	cer, ssf
Smallanthus connatus (Spreng.) H.Rob.	Herb	UEC, 181664	IV, XIII	ssf
Synedrella nodiflora (L.) Gaertn.	Shrub	HRCB, 52528	IV, XIII	cer, ssf
Trichogonia attenuata G.M.Barroso	Shrub	INPA, 172202; UEC, 45236	XIII	cer
Trichogoniopsis adenantha (DC.) R.M.King & H.Rob.	Shrub	HRCB, 52416	IV, XIII	cer, ssf
Vernonanthura divaricata (Spreng.) H.Rob.	Tree	SPSF, 25983; UEC, 166595	III, X, XIII	cer, ssf
Vernonanthura polyanthes (Sprengel) Vega & Dematteis	Shrub	SPSF, 25988; MBM, 276431	III, X, XIII	cer, ssf
Vernonia rubriramea Mart. ex DC.	Herb	HRCB, 52468; IAC, 55612	IV, XIII	cer, ssf
ATHYRIACEAE				
Diplazium cristatum (Desr.) Alston	Herb	UEC, 173868; HUEFS, 201975	IV, XI, XIII	ssf
BIGNONIACEAE				
Adenocalymma axillare (K.Schum.) L.G.Lohmann	Climbing	HUEFS, 179649	XIII	cer
Adenocalymma bracteatum (Cham.) DC.	Climbing	HRCB, 52384; HRCB, 52516	IV, IX, XIII	cer, ssf
Adenocalymma marginatum (Cham.) DC.	Climbing	HRCB, 52438	IV, IX, XIII	cer, ssf
Amphilophium crucigerum (L.) L.G.Lohmann	Climbing	HRCB, 68002	IX	cer, ssf
Amphilophium elongatum (Vahl) L.G.Lohmann	Climbing	HRCB, 52437; HRCB, 68003	IV, IX, XIII	cer, ssf

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Family/Species	Life form	Voucher	Source	Veg. type
Anemopaegma arvense (Vell.) Stellfeld ex de Souza *	Shrub	UEC, 544	XIII	cer
Anemopaegma chamberlaynii (Sims) Bureau & K.Schum.	Climbing	HRCB, 52521	IV, XIII	cer, ssf
Bignonia campanulata Cham.	Climbing	HRCB, 52382; HRCB, 68006	IV, IX, XIII	cer, ssf
Cuspidaria convoluta (Vell.) A.H.Gentry	Climbing	HRCB, 68007	IX	cer, ssf
Cuspidaria pulchella (Cham.) K.Schum.	Climbing	UEC, 602	XIII	cer
Cuspidaria pulchra (Cham.) L.G.Lohmann	Shrub	HRCB, 52475	IV, IX, XIII	cer, ssf
Dolichandra unguis-cati (L.) L.G.Lohmann	Climbing	HRCB, 68009	IX	ssf
Fridericia craterophora (DC.) L.G.Lohmann	Shrub	HRCB, 68005	IX	cer
Fridericia florida (DC.) L.G.Lohmann	Climbing	HRCB, 68004	IX	cer
Fridericia formosa (Bureau) L.G.Lohmann	Climbing	HRCB,52533; HRCB, 68010	IV, IX, XIII	cer, ssf
Fridericia platyphylla (Cham.) L.G.Lohmann	Shrub, Climbing	SPSF, 20825	III, X, XIII	cer
Fridericia speciosa Mart.	Shrub	HRCB, 68061	IX	cer, ssf
Handroanthus ochraceus (Cham.) Mattos	Tree		III, VI, X	cer, ssf
Handroanthus vellosoi (Toledo) Mattos	Tree		I, II, VI, X	cer, ssf, rp
Jacaranda caroba (Vell.) DC.	Shrub		III, X	cer, ssf
Lundia obliqua Sond.	Climbing	HRCB, 52519	IV, IX, XIII	cer, ssf
Pyrostegia venusta (Ker Gawl.) Miers	Climbing	HRCB, 68060	IV, IX, XIII	cer, ssf
Stizophyllum perforatum (Cham.) Miers	Climbing	HRCB, 68012; MBML, 43933	IV, IX, XIII	cer, ssf
Tanaecium selloi (Spreng.) L.G.Lohmann	Climbing	HRCB, 52497	IV, IX, XIII	cer, ssf
Zeyheria montana Mart.	Tree		III, X	cer, ssf
Zeyheria tuberculosa (Vell.) Bureau ex Verl.*	Tree		I, X	ssf
BIXACEAE				
Cochlospermum regium (Mart. ex Schrank) Pilg.	Shrub		III, X	cer
BLECHNACEAE				
Blechnum lanceola Sw.	Herb		XI	ssf, rp
BORAGINACEAE				
Cordia americana (L.) Gottschling & J.S.Mill.	Tree		I, X	ssf, rp
Cordia sellowiana Cham.	Tree	UEC, 44043	III, V, X, XIII	cer, ssf, rp
Cordia tarodae M.Stapf	Tree	UEC, 45624	XIII	ssf
Cordia trichotoma (Vell.) Arráb. ex Steud.	Tree		X	cer, ssf
Myriopus rubicundus (Salzm. ex DC.) Luebert	Climbing	HRCB, 68013	IX	cer
Varronia urticifolia (Cham.) J.S.Mill.	Shrub	HRCB, 68014	IX	cer
BROMELIACEAE				
Acanthostachys strobilacea (Schult. & Schult.f.) Klotzsch	Herb	HRCB, 62025	VIII, XIII	ssf, rp
Aechmea bromeliifolia (Rudge) Baker	Herb	HRCB, 53966	IV, VIII, XIII	cer, rp
Billbergia distachia (Vell.) Mez	Herb	HRCB, 64216	VIII, XIII	rp
Tillandsia loliacea Mart. ex Schult. & Schult.f.	Herb	HRCB, 62042	IV, VIII, XIII	cer, ssf, rp
Tillandsia pohliana Mez	Herb	HRCB, 55873	IV, VIII, XIII	cer, ssf
Tillandsia recurvata (L.) L.	Herb	HRCB, 53494	IV, VIII, XIII	cer, ssf, rp
Tillandsia tenuifolia L.	Herb	HRCB, 62029	VIII, XIII	ssf
Tillandsia tricholepis Baker	Herb	HRCB, 62381; MBML, 43977	IV, VIII, XIII	cer, ssf, rp
BURSERACEAE				
Protium heptaphyllum (Aubl.) Marchand	Tree	SPSF, 25408; UEC, 49396	I, II, III, V, VI, X, XIII	cer, ssf, rp

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Family/Species	Life form	Voucher	Source	Veg. type
CACTACEAE				
Epiphyllum phyllanthus (L.) Haw.	Herb	HRCB, 54943	IV, VIII, XIII	cer, ssf, rp
Lepismium warmingianum (K.Schum.) Barthlott	Herb	HRCB, 54942	IV, VIII, XIII	rp
Pereskia aculeata Mill.	Climbing	HRCB, 54944; FUEL, 53546	IV, IX, XIII	ssf
Rhipsalis baccifera (J.M.Muell.) Stearn	Herb	HRCB, 54010	IV, VIII, XIII	cer, ssf, rp
Rhipsalis cereuscula Haw.	Herb	HRCB, 62020	VIII	cer, ssf
Rhipsalis floccosa Salm-Dyck ex Pfeiff.	Herb	HRCB, 62558	VIII	rp
Rhipsalis teres (Vell.) Steud.	Herb	HRCB, 54009	IV, VIII, XIII	cer, ssf, rp
CALOPHYLLACEAE				
Calophyllum brasiliense Cambess.	Tree	HRCB, 71782	VI, VII, XIII	cer, ssf, rp
Kielmeyera variabilis Mart. & Zucc.	Shrub		III, X	cer
CANNABACEAE				
Celtis iguanaea (Jacq.) Sarg.	Shrub	HRCB, 55490; SPSF, 25994	III, IV, IX, X, XIII	cer, ssf
Trema micrantha (L.) Blume	Shrub	HRCB, 74507	I, X, XIII	ssf, rp
CANNACEAE				
Canna paniculata Ruiz & Pav.	Herb	HRCB, 52268	IV, XIII	ssf
CARICACEAE				
Jacaratia spinosa (Aubl.) A.DC.	Tree		X	ssf
CARYOCARACEAE				
Caryocar brasiliense Cambess.	Tree	UEC, 1285; HRCB, 74505	III, X, XIII	cer
CELASTRACEAE				
Monteverdia communis (Reissek) Biral	Tree, Shrub		II, X	ssf, rp
Monteverdia gonoclada (Mart.) Biral	Tree, Shrub	SPSF, 25970	XIII	ssf, rp
Semialarium paniculatum (Mart. ex Schult.) N.Hallé	Climbing	HRCB, 55492	IV, IX, XIII	ssf
CHRYSOBALANACEAE				
Hirtella hebeclada Moric. ex DC.	Tree		II, X	ssf, rp
CLETHRACEAE				
Clethra scabra Pers.	Tree	UEC, 44047	III, VI, X, XIII	cer, ssf, rp
CLUSIACEAE				
Garcinia gardneriana (Planch. & Triana) Zappi	Tree	SPSF, 25936; HRCB, 71785	X, XIII	ssf, rp
COMBRETACEAE				
Terminalia argentea Mart.	Tree, Shrub	SPSF, 17398; HRCB, 58786	III, VI, X, XIII	cer, ssf
Terminalia glabrescens Mart.	Tree	SPSF, 17396	I, II, III, V, VI, X, XIII	cer, ssf, rp
Terminalia triflora (Griseb.) Lillo	Tree, Shrub	MBM, 169207	XIII	rp
COMMELINACEAE				
Commelina obliqua Vahl	Herb	HRCB, 52456	XIII	cer
Dichorisandra hexandra (Aubl.) C.B.Clarke	Climbing	HRCB, 52280; CEN, 85755	IV, IX	ssf
Gibasis geniculata (Jacq.) Rohweder	Herb	HRCB, 52652; HURB, 3225	IV, XIII	ssf
Tradescantia zanonia (L.) Sw.	Herb	HRCB, 62046	IV, VIII, XIII	cer, ssf
Tripogandra diuretica (Mart.) Handlos	Herb	HRCB, 52279; UEC, 173873	IV, XIII	ssf
CONNARACEAE				
Connarus suberosus Planch.	Tree, Shrub	SPSF, 24704	III, X	cer
Rourea induta Planch.	Shrub	SPSF, 27336; HURB, 3592	XIII	cer
CONVOLVULACEAE				
Camonea umbellata (L.) A.R. Simões & Staples	Climbing	HRCB, 52517; CEN, 85754	XIII	cer, ssf
Distimake macrocalyx (Ruiz & Pav.) A.R. Simões & Staples	Climbing	HRCB, 52656; SPSF, 27346	IV, IX, XIII	cer, ssf
Ipomoea chondrosepala Hallier f.	Climbing	HRCB, 52518	IV, IX, XIII	cer, ssf
Ipomoea saopaulista O'Donell	Climbing	HRCB, 52504	IV, IX, XIII	cer, ssf

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Family/Species	Life form	Voucher	Source	Veg. type
CUCURBITACEAE				
Psiguria ternata (M.Roem.) C.Jeffrey	Climbing	HRCB, 68016	IX	cer
Wilbrandia hibiscoides Silva Manso	Climbing	UEC, 43383	XIII	ssf
CUNONIACEAE				
Lamanonia ternata Vell.	Tree	UEC, 75747	III, X, XIII	cer, ssf
CYATHEACEAE				
Cyathea delgadii Sternb.	Herb		XI	rp
CYPERACEAE				
Cyperus laxus Lam.	Herb	HRCB, 52433	IV, XIII	cer, ssf
Cyperus luzulae (L.) Retz.	Herb	HRCB, 54933	IV, XIII	rp
Cyperus simplex Kunth	Herb	HRCB, 52459	IV, XIII	cer
Rhynchospora exaltata Kunth	Herb	HRCB, 52423; UEC, 16576	IV, XIII	cer, ssf
Scleria gaertneri Raddi	Herb	HRCB, 52434	IV, XIII	cer, ssf
Scleria latifolia Sw.	Herb	HRCB, 71789	IX, XIII	ssf, rp
DILLENIACEAE				
Davilla elliptica A.St.-Hil.	Shrub, Climbing	HRCB, 52451	III, IV, IX, X, XIII	cer, ssf
Davilla rugosa Poir.	Climbing	HRCB, 52663	IV, IX, XIII	cer, ssf
Doliocarpus dentatus (Aubl.) Standl.	Shrub, Climbing	HRCB, 52500	IV, IX, XIII	cer, ssf
DIOSCOREACEAE				
Dioscorea dodecaneura Vell.	Climbing	JAL, 7736	IV, IX	cer, ssf
Dioscorea olfersiana Klotzsch ex Griseb.	Climbing	HRCB, 52395	IV, IX, XIII	cer, ssf
DRYOPTERIDACEAE				
Bolbitis serratifolia Schott	Herb		XI	ssf
Ctenitis eriocaulis (Fée) Alston	Herb	BHCB, 60861	XI, XIII	rp
Ctenitis submarginalis (Langsd. & Fisch.) Ching	Herb	JAL, 7772	IV, XI	cer, ssf
Lastreopsis effusa (Sw.) Tindale	Herb		XI	ssf
Polystichum platyphyllum (Willd.) C.Presl	Herb		XI	ssf
ELAEOCARPACEAE				
Sloanea hirsuta (Schott) Planch. ex Benth.	Tree	HRCB, 4966; UEC, 25465	XIII	ssf
ERYTHROXYLACEAE				
Erythroxylum buxus Peyr.	Shrub	UEC, 44051	XIII	rp
Erythroxylum cuneifolium (Mart.) O.E.Schulz	Shrub	FUEL, 39773	III, X, XIII	cer
Erythroxylum deciduum A.St.-Hil.	Tree, Shrub	BOTU, 20419	V, XIII	cer, ssf
Erythroxylum pelleterianum A.St.-Hil.	Shrub	TEPB, 25904	III, V, X, XIII	cer, ssf
Erythroxylum suberosum A.St.-Hil.	Tree, Shrub	SPSF, 25273	III, X, XIII	cer
Erythroxylum subracemosum Turcz.	Tree, Shrub		III, X	cer
Erythroxylum tortuosum Mart.	Tree, Shrub		III, X	cer
EUPHORBIACEAE				
Actinostemon concepcionis (Chodat & Hassl.) Hochr.	Shrub	HRCB, 62085; SPSF, 49093	III, V,VII, X, XIII	cer, ssf, rp
Actinostemon klotzschii (Didr.) Pax	Tree, Shrub	INPA, 78113	I, II, III, X, XIII	cer, rp
Alchornea glandulosa Poepp. & Endl.	Tree	SPSF,25976	III, VI, X, XIII	cer, ssf, rp
Aparisthmium cordatum (A.Juss.) Baill.	Tree		V	ssf
Cnidoscolus urens (L.) Arthur	Shrub	SPSF, 19516; SPSF, 20820	XIII	ssf
Croton floribundus Spreng.	Tree	HRCB, 74503	I, II, III, V, VI, X, XIII	cer, ssf, rp
Croton leptobotryus Müll.Arg. *	Shrub	HRCB, 71804	XIII	cer

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Family/Species	Life form	Voucher	Source	Veg. type
Croton lundianus (Didr.) Müll.Arg.	Shrub	HRCB, 52414	IV, XIII	cer, ssf
Croton salutaris Casar.	Tree		I, X	ssf, rp
Croton urucurana Baill.	Tree	HRCB, 62052	I, II, VII, X, XIII	rp
Dalechampia pentaphylla Lam.	Climbing	HRCB, 52431	IV, IX, XIII	cer, ssf
Dalechampia stipulacea Müll.Arg.	Climbing	HRCB, 52318	IV, IX, XIII	ssf
Dalechampia triphylla Lam.	Climbing	HRCB, 68019	IX	ssf
Euphorbia sciadophila Boiss.	Herb	HRCB, 52272	IV, XIII	ssf
Gymnanthes klotzschiana Müll.Arg.	Tree, Shrub	HRCB, 62050; SPSF, 49075	I, II, VII, X, XIII	ssf, rp
Mabea fistulifera Mart.	Tree, Shrub	IAC, 54530; SPSF, 20783	III, X, XIII	cer
Maprounea guianensis Aubl.	Tree	SPSF, 25905	III, V, VI, XIII	cer, ssf
Pachystroma longifolium (Nees) I.M.Johnst.	Tree		X	ssf
Sapium glandulosum (L.) Morong	Tree	SPSF, 25151	III, X, XIII	cer, ssf, rp
FABACEAE				
Aeschynomene racemosa Vogel	Shrub		III, X	cer
Albizia niopoides (Spruce ex Benth.) Burkart	Tree		VII, X	rp
Andira anthelmia (Vell.) Benth.	Tree		III, VI, X	cer, ssf, rp
Andira fraxinifolia Benth.	Tree	MBM, 207659	III, X, XIII	cer
Andira humilis Mart. ex Benth.	Tree, Shrub	CGMS, 43980	VI, XIII	cer, ssf
Andira inermis (W.Wright) DC.	Tree		I, X	ssf
Andira vermifuga (Mart.) Benth.	Tree	UEC, 44042	XIII	cer
Bauhinia holophylla (Bong.) Steud.	Shrub	SPSF, 17378	III, X, XIII	cer
Bowdichia virgilioides Kunth	Tree		III, X	cer, ssf
Camptosema spectabile (Tul.) Burkart	Climbing	SPSF, 20842	XIII	cer
Canavalia picta Mart. ex Benth.	Climbing	HRCB, 52658	IV, IX, XIII	cer
Cassia ferruginea (Schrad.) Schrad. ex DC.	Tree	UEC, 25224	I, II, X, XIII	ssf, rp
Centrolobium tomentosum Guillem. ex Benth.	Tree		I, II, V, X	cer, ssf, rp
Centrosema sagittatum (Humb. & Bonpl. ex Willd.) Brandegee	Climbing	HRCB, 68020; UEC, 170139	IX, XIII	ssf
Chamaecrista flexuosa (L.) Greene	Shrub	HRCB, 52452	III, IV, X, XIII	cer
Copaifera langsdorffii Desf.	Tree		I, II, III, V, VI, VII, X	cer, ssf, rp
Dahlstedtia muehlbergiana (Hassl.) M.J.Silva & A.M.G. Azevedo	Tree		I, X	ssf, rp
Dalbergia miscolobium Benth.	Tree		III, X	cer
Desmodium affine Schltdl.	Shrub	HRCB, 52293	IV, XIII	ssf
Desmodium distortum (Aubl.) J.F.Macbr.	Shrub	HRCB, 52507	IV, XIII	cer, ssf
Desmodium uncinatum (Jacq.) DC.	Shrub	HRCB, 52391	IV, XIII	cer, ssf
Dimorphandra mollis Benth.	Tree	HRCB, 71802	III, VI, X, XIII	cer, ssf
Dioclea violacea Mart. ex Benth.	Climbing	HRCB, 68021	IX	ssf
Enterolobium contortisiliquum (Vell.) Morong	Tree		X	ssf
Enterolobium gummiferum (Mart.) J.F.Macbr.	Tree		III, X	cer
Erythrina falcata Benth.	Tree		III, X	cer, ssf, rp
Holocalyx balansae Micheli	Tree		II, X	ssf, rp
Hymenaea courbaril L.	Tree	HUSC, 11451	I, X, XIII	ssf, rp
Hymenaea stigonocarpa Mart. ex Hayne	Tree		III, X	cer
Inga edulis Mart.	Tree		I, X	ssf
Inga laurina (Sw.) Willd.	Tree	INPA, 205844	I, II, X, XIII	ssf, rp

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Family/Species	Life form	Voucher	Source	Veg. type
Inga marginata Willd.	Tree	SPSF, 27342; UB, 128870	I, II, V, X, XIII	ssf, rp
Inga striata Benth.	Tree	UEC, 49402; UB, 128891	I, II, V, VI, X, XIII	cer, ssf, rp
Inga vera subsp. affinis (DC.) T.D.Penn.	Tree	HRCB, 62049	VII, X, XIII	rp
Leptolobium dasycarpum Vogel	Tree	SPSF, 24697	III, VI, X, XIII	cer, ssf
Leptolobium elegans Vogel	Tree	UEC, 7418; CGMS, 43984	III, X, XIII	cer
Lonchocarpus cultratus (Vell.) A.M.G.Azevedo & H.C.Lima	Tree		VII	rp
Machaerium aculeatum Raddi	Shrub, Climbing		V, VI	cer, ssf
Machaerium acutifolium Vogel	Tree		III, X	cer
Machaerium brasiliense Vogel	Tree, Shrub, Climbing		I, X	ssf, rp
Machaerium hirtum (Vell.) Stellfeld	Tree		VII	rp
Machaerium nyctitans (Vell.) Benth.	Tree	UEC, 49387; UB, 142145	II, X, XIII	ssf, rp
Machaerium stipitatum Vogel	Tree		III, X	cer, ssf
Machaerium villosum Vogel	Tree		I, II, III, VI, X	cer, ssf, rp
Myroxylon peruiferum L.f.	Tree		X, XIII	ssf, rp
Ormosia arborea (Vell.) Harms	Tree	MBM, 189660; IAC, 54532	I, X, XIII	ssf, rp
Peltophorum dubium (Spreng.) Taub.	Tree	SPSF, 49081	III, VI, VII, X, XIII	cer, ssf, rp
Plathymenia reticulata Benth.	Tree		III, X	cer
Platycyamus regnellii Benth.	Tree		I, X	ssf
Platypodium elegans Vogel	Tree	CGMS, 43971	III, VI, X	cer, ssf
Pterogyne nitens Tul.	Tree		II, X	ssf, rp
Rhynchosia melanocarpa Grear	Climbing	UEC, 170127; FUEL, 33424	XIII	cer, ssf
Rhynchosia phaseoloides (Sw.) DC.	Climbing	HRCB, 68022; SPSF, 25897	IX, XIII	cer, ssf
Senegalia lowei (L.Rico) Seigler & Ebinger	Climbing		III, X	cer
Senegalia polyphylla (DC.) Britton & Rose	Tree	SPSF, 49080; UEC, 109268	I, II, III, V, VI, VII, X, XIII	cer, ssf, rp
Senna macranthera (DC. ex Collad.) H.S.Irwin & Barneby	Tree		III, X	cer, ssf, rp
Senna multijuga (Rich.) H.S.Irwin & Barneby	Tree		X	ssf
Senna pendula (Humb.& Bonpl.ex Willd.) H.S.Irwin & Barneby	Tree, Shrub	UEC, 44044	III, X, XIII	cer, ssf
Senna rugosa (G.Don) H.S.Irwin & Barneby	Shrub	SPSF, 25935; HUEFS, 202006	III, IV, X, XIII	cer, ssf
Senna silvestris (Vell.) H.S.Irwin & Barneby	Tree, Shrub	UEC, 44054	III, X, XIII	cer, ssf
Stryphnodendron polyphyllum Mart.	Tree		III, X	cer
Stylosanthes viscosa (L.) Sw.	Shrub	IAC, 21993	XIII	cer, ssf, rp
Tachigali aurea Tul.	Tree		III, X	cer, ssf
Zornia latifolia Sm.	Shrub	APO, 33	IV	cer, ssf
GENTIANACEAE				
Voyria aphylla (Jacq.) Pers.	Herb	HRCB, 52305	IV, XIII	cer, ssf
HYMENOPHYLLACEAE				
Crepidomanes pyxidiferum (L.) Dubuisson & Ebihara	Herb	HRCB, 71765	XIII	ssf
IRIDACEAE				
Cipura paludosa Aubl.	Herb	GMM,798	XIII	cer
LACISTEMATACEAE				
Lacistema hasslerianum Chodat	Shrub	SPSF, 49083; UEC, 25118	I, III, V, VI, VII, X, XIII	cer, ssf, rp

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Family/Species	Life form	Voucher	Source	Veg. type
LAMIACEAE				
Aegiphila integrifolia (Jacq.) Moldenke	Tree	MBML, 45129	III, VI, X, XIII	cer, ssf
Aegiphila verticillata Vell.	Tree, Shrub	SPSF; 25933	III, X, XIII	cer
Cantinoa mutabilis (Rich.) Harley & J.F.B.Pastore	Shrub	CEN, 85801	IV, XIII	ssf
Hyptis campestris Harley & J.F.B. Pastore	Shrub	CEN, 85804	IV, XIII	cer, ssf
Marsypianthes chamaedrys (Vahl) Kuntze	Shrub	APO, 32	IV	cer, ssf
Ocimum carnosum (Spreng.) Link & Otto ex Benth.	Shrub	CEN, 85860; FUEL, 53549	IV, XIII	ssf
Vitex cymosa Bertero ex Spreng.	Tree		II, X	ssf, rp
Vitex megapotamica (Spreng.) Moldenke	Tree	INPA, 266948; SPSF, 49088	VII, XIII	rp
LAURACEAE				
Cryptocarya moschata Nees & Mart.	Tree		I, X	ssf
Endlicheria paniculata (Spreng.) J.F.Macbr.	Tree	SPSF, 20773	I, II, III, V, X, XIII	cer, ssf, rp
Nectandra megapotamica (Spreng.) Mez	Tree	HRCB, 62086; HUEFS, 227999	I, II, III, V, VII, X, XIII	cer, ssf, rp
Nectandra nitidula Nees	Tree	MBM, 128256; UEC, 40205	III, X, XIII	cer, ssf
Ocotea acutifolia (Nees) Mez	Tree		III, X	cer
Ocotea corymbosa (Meisn.) Mez	Tree	HRCB, 58790; UEC, 40302	III, V, VI, X, XIII	cer, ssf
Ocotea indecora (Schott) Mez	Tree		VII	rp
Ocotea nutans (Nees) Mez	Tree		VI	cer, ssf
Ocotea oppositifolia S.Yasuda	Tree		II	rp
Ocotea pulchella (Nees & Mart.) Mez	Tree	HRCB, 52511; UB, 150238	III, VI, X	cer, ssf
Ocotea velutina (Nees) Rohwer	Tree	HRCB, 71803	VI, VII, XIII	cer, ssf, rp
Persea willdenovii Kosterm.	Tree		III, X	cer
LECYTHIDACEAE				
Cariniana estrellensis (Raddi) Kuntze	Tree		I, II, X	ssf, rp
Cariniana legalis (Mart.) Kuntze *	Tree	HRCB, 74506	I, II, X, XIII	ssf, rp
LOGANIACEAE				
Spigelia beyrichiana Cham. & Schltdl.	Herb	UEC, 9311	IV, XIII	cer, ssf
Strychnos parvifolia A.DC.	Shrub		I	ssf
Strychnos pseudoquina A.St.-Hil.	Shrub	UEC, 25119	III, X, XIII	cer
LORANTHACEAE				
Tripodanthus acutifolius (Ruiz & Pav.) Tiegh.	Herb	UEC, 9390	XIII	cer
LYGODIACEAE				
Lygodium volubile Sw.	Climbing	HRCB, 68050	IV, IX, XIII	cer, ssf, rp
LYTHRACEAE				
Diplusodon virgatus Pohl	Tree, Shrub	APO, 14	III, IV, X	cer
Lafoensia pacari A.St.-Hil.	Tree	SPSF, 27378	III, X, XIII	cer
MALPIGHIACEAE				
Banisteriopsis adenopoda (A.Juss.) B.Gates	Climbing	SP, 470763	IV, IX, XIII	cer
Banisteriopsis argyrophylla (A.Juss.) B.Gates	Climbing	SP, 470760	IV, IX, XIII	cer, ssf
Banisteriopsis latifolia (A.Juss.) B.Gates	Tree	HRCB, 68025	IX	cer
Banisteriopsis malifolia var. malifolia (Nees & Mart.) B.Gates	Shrub, Climbing	HRCB, 68026	IV, IX	cer, ssf
Banisteriopsis oxyclada (A.Juss.) B.Gates	Climbing	HRCB, 68027	IX	cer, ssf
Banisteriopsis stellaris (Griseb.) B.Gates	Shrub, Climbing	HRCB, 68028	IV, IX, XIII	cer
Banisteriopsis variabilis B.Gates	Shrub, Climbing	HRCB, 68029	IV, IX, XIII	cer, ssf

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Family/Species	Life form	Voucher	Source	Veg. type
Byrsonima coccolobifolia Kunth	Tree, Shrub		III, X	cer
Byrsonima intermedia A.Juss.	Shrub	SP, 470813	III, IV, V, VI, X, XIII	cer, ssf
Byrsonima laxiflora Griseb.	Tree	SPSF, 17497	XIII	cer
Carolus chlorocarpus (A.Juss.) W.R.Anderson	Climbing	SP, 470892	XIII	cer, ssf
Diplopterys pubipetala (A.Juss.) W.R.Anderson & C.C.Davis	Climbing	FUEL, 53523	IV, IX, XIII	cer
Heteropterys umbellata A.Juss.	Shrub	JAL, 8089	IV, IX	cer, ssf
Mascagnia cordifolia (A.Juss.) Griseb.	Climbing	SP, 470891; UEC, 10048	IV, IX	cer
Niedenzuella lucida (A.Juss.) W.R.Anderson	Climbing	HRCB, 68034	IX	ssf
Niedenzuella multiglandulosa (A.Juss.) W.R.Anderson	Climbing	SP, 470871; HRCB, 68032	IV, IX, XIII	cer, ssf
Stigmaphyllon lalandianum A.Juss.	Climbing	HRCB, 68033	IX	ssf
MALVACEAE				
Callianthe fluviatilis (Vell.) Donnel	Shrub	UEC, 44041	XIII	ssf
Ceiba speciosa (A.St.-Hil.) Ravenna	Tree		I, X	ssf, rp
Christiana macrodon Toledo	Tree, Shrub	SPSF, 49089	I, X, XIII	ssf, rp
Eriotheca candolleana (K.Schum.) A.Robyns	Tree	SPSF, 25432	I, II, X, XIII	ssf, rp
Eriotheca gracilipes (K.Schum.) A.Robyns	Tree	SPSF, 20782	III, X, XIII	cer
Guazuma ulmifolia Lam.	Tree	HRCB, 71797	I, III, X, XIII	cer, ssf
Helicteres brevispira A.St.-Hil.	Shrub	UEC, 14815	XIII	cer, rp
Helicteres macropetala A.St.-Hil.	Tree, Shrub		III, X	cer
Heliocarpus popayanensis Kunth	Tree	UEC, 25137	XIII	ssf
Luehea divaricata Mart. & Zucc.	Tree	SPSF, 49112	I, II, VI, VII, X, XIII	cer, ssf, rp
Luehea grandiflora Mart. & Zucc.	Tree	HUEFS, 201978; UEC, 43389	III, VI, X, XIII	cer, ssf
Pavonia nemoralis A.St.-Hil.	Shrub	JAL, 8079	IV	ssf
Pavonia sepium A.St.-Hil.	Shrub	FUEL, 53518	IV, XIII	ssf
Pseudobombax grandiflorum (Cav.) A.Robyns	Tree	HRCB, 71798	I, VI, X, XIII	cer, ssf
Pseudobombax longiflorum (Mart.) A.Robyns	Tree		III, X	cer
Sida cordifolia L.	Shrub	FUEL, 53517	IV, XIII	cer, ssf
Sida linifolia Cav.	Shrub	APO, 15	IV	cer, ssf
Sida rhombifolia L.	Herb	FUEL, 53519	IV, XIII	ssf
Sida urens L.	Shrub	APO, 105	IV	ssf
Wissadula hernandioides (L.Hér.) Garcke	Shrub	FUEL, 53521	IV, XIII	cer, ssf
MARANTACEAE				
Goeppertia eichleri (Petersen) Borchs. & S.Suárez	Herb	UNOP, 3703	IV, XIII	ssf
Goeppertia flavescens (Lindl). Borchs. & S.Suárez	Herb	MBML, 48122	IV, XIII	ssf
Goeppertia sellowii (Körn.) Borchs. & S. Suárez	Herb	UEC, 168472	XIII	ssf
MELASTOMATACEAE				
Leandra aurea (Cham.) Cogn.	Shrub	SPSF, 25986; UEC, 172881	III, X, XIII	cer
Miconia affinis DC.	Tree	HUEFS, 176684; SPSF, 25907	V, VI, XIII	cer, ssf
Miconia albicans (Sw.) Triana	Tree, Shrub	SPSF, 49124; MBM, 204234	III, V, X, XIII	cer, ssf
Miconia chamissois Naudin	Shrub	SPSF, 25928	XIII	cer, ssf
Miconia collatata Wurdack	Tree, Shrub	SPSF, 49090; UEC, 50534	VII, XIII	rp
Miconia discolor DC.	Tree	UPCB, 71216; SPSF, 25930	IV, XIII	cer, ssf
Miconia eugenioides Triana	Tree, Shrub	UB, 133972	I, II, X, XIII	cer, rp
Miconia ibaguensis (Bonpl.) Triana	Tree, Shrub	SPSF, 25927; UEC, 49409	XIII	cer
Miconia jucunda (DC.) Triana	Tree, Shrub	UEC, 49404	XIII	rp
Miconia latecrenata (DC.) Naudin	Tree, Shrub	SPSF, 16626; MBM, 169217	III, X, XIII	cer, ssf
Miconia ligustroides (DC.) Naudin	Tree, Shrub	SPSF, 25274; UEC, 172872	III, VI, X, XIII	cer, ssf
Miconia nervosa (Sm.) Triana	Shrub	SPSF, 25929; FUEL;,39778	IV, XIII	cer
Miconia paucidens DC.	Tree, Shrub	SPSF, 25989; UEC, 172869	III, IV, V, X, XIII	cer, ssf
Miconia rubiginosa (Bonpl.) DC.	Tree, Shrub	SPSF, 25982; UB, 134163	III, VI, XIII	cer, ssf
Miconia stenostachya DC.	Shrub	SPSF, 20790; UEC, 40240	III, IV, X, XIII	cer
Pleroma stenocarpum (Schrank et Mart. ex DC.) Triana	Tree	SPSF; 20841	III, X, XIII	cer

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Family/Species	Life form	Voucher	Source	Veg. type
MELIACEAE				
Cabralea canjerana (Vell.) Mart.	Tree		I, X	ssf, rp
Cedrela fissilis Vell. *	Tree		V, VI, X	cer, ssf, rp
Guarea guidonia (L.) Sleumer	Tree	HRCB, 74504	I, II, X, XIII	ssf, rp
Guarea kunthiana A.Juss.	Tree	UEC, 34654	I, II, V, X, XIII	ssf, rp
Guarea macrophylla Vahl	Tree	SPSF, 25520; INPA, 266940	V, VII, XIII	ssf, rp
Trichilia casaretti C.DC.	Tree	FUEL, 5498	VI, VII, XIII	cer, ssf, rp
Trichilia catigua A.Juss.	Tree	SPSF, 49078; UEC, 49395	I, II, III, V, VII, X, XIII	cer, ssf, rp
Trichilia clausseni C.DC.	Tree	SPSF, 49111; FUEL, 45515	I, II, V, VII, X, XIII	ssf, rp
Trichilia elegans A.Juss.	Shrub	SPSF, 19729; UEC, 43388	XIII	ssf, rp
Trichilia hirta L.	Tree	SPSF, 22821	XIII	rp
Trichilia pallida Sw.	Tree	SPSF, 49128; UEC, 185068	I, III, V, VI, VII, X, XIII	cer, ssf, rp
MENISPERMACEAE				
Cissampelos pareira L.	Climbing	FUEL, 53511	IV, IX, XIII	cer
MONIMIACEAE				
Mollinedia widgrenii A.DC.	Tree	SPSF, 25977; FUEL, 39753	I, II, V, X, XIII	cer, ssf, rp
MORACEAE				
Brosimum gaudichaudii Trécul	Shrub	SPSF, 20791	III, X, XIII	cer, ssf
Dorstenia vitifolia Gardner	Herb	CEN, 85746	XIII	cer, ssf
Ficus citrifolia Mill.	Tree	SPSF, 49086	III, VII, VIII, X, XIII	cer, ssf, rp
Ficus guaranitica Chodat	Tree	HRCB, 71800	III, V, VI, X, XIII	cer, ssf, rp
Maclura tinctoria (L.) D.Don ex Steud.	Tree		VI, X	cer, ssf
Sorocea bonplandii (Baill.) W.C.Burger et al.	Tree	SPSF, 25924	V, VII, XIII	ssf, rp
MYRISTICACEAE				
Virola sebifera Aubl.	Tree	MBM, 287583; SPSF, 27382	III, V, VI, X, XIII	cer, ssf
MYRTACEAE				
Blepharocalyx salicifolius (Kunth) O.Berg	Tree, Shrub		III, X	cer, ssf, rp
Campomanesia guazumifolia (Cambess.) O.Berg	Tree	HRCB, 71784	X, XIII	ssf
Campomanesia pubescens (Mart. ex DC.) O.Berg	Tree, Shrub	UEC, 11668	III, X, XIII	cer, ssf
Eugenia astringens Cambess.	Tree		I, II, X	ssf, rp
Eugenia aurata O.Berg	Tree, Shrub		III, X	cer
Eugenia bimarginata DC.	Shrub		III, X	cer
Eugenia brasiliensis Lam.	Tree		I, X	ssf
Eugenia brevistyla D.Legrand	Tree	ESA, 118281	XIII	ssf, rp
Eugenia dodonaeifolia Cambess.	Tree	SP, 338775; UEC, 45226	XIII	rp
Eugenia florida DC.	Tree	HUEFS, 227997	III, V, VI, VII, X, XIII	cer, ssf, rp
Eugenia francavilleana O.Berg	Tree	UEC, 45225	V, XIII	ssf
Eugenia handroana D.Legrand	Tree	SPSF, 49100	VII, XIII	rp
Eugenia ligustrina (Sw.) Willd.	Tree		V	ssf
Eugenia livida O.Berg	Shrub		III, X	cer
Eugenia longipedunculata Nied.	Tree	SPSF, 49074	VII, XIII	rp
Eugenia mansoi O.Berg	Tree, Shrub	SPSF, 49077; INPA, 266945	VII, XIII	rp
Eugenia pruniformis Cambess.	Tree, Shrub		II, X	ssf, rp
Eugenia repanda O.Berg	Tree, Shrub	SPSF, 49073	I, VII, X, XIII	ssf, rp
Eugenia speciosa Cambess.	Tree		V	ssf

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Family/Species	Life form	Voucher	Source	Veg. type
Eugenia sphenophylla O.Berg	Tree, Shrub	SPSF, 25908; BHCB, 150372	XIII	rp
Eugenia subterminalis DC.	Tree		X	ssf, rp
Eugenia verticillata (Vell.) Angely	Shrub		II, X	ssf, rp
Myrcia albotomentosa DC.	Shrub	SPSF, 25964	III, X, XIII	cer
Myrcia bella Cambess.	Shrub		III, VI, X	cer, ssf
Myrcia glomerata (Cambess.) G.P.Burton & E.Lucas	Tree		V, VII, XIII	cer, ssf, rp
Myrcia guianensis (Aubl.) DC.	Tree	SPSF, 25406	III, VI, X, XIII	cer, ssf
Myrcia hebepetala DC.	Tree		II, III, X	cer, rp
Myrcia lasiantha DC.	Shrub		III, X	cer
Myrcia multiflora (Lam.) DC.	Tree, Shrub	SPSF, 10654; UEC, 40239	I, II, III, V, X, XIII	cer, ssf, rp
Myrcia neolucida A.R.Lourenço & E.Lucas	Tree		I, X	ssf, rp
Myrcia splendens (Sw.) DC.	Tree	UEC, 40165	I, III, VI, VII, X, XIII	cer, ssf, rp
Myrcia tomentosa (Aubl.) DC.	Tree	SPSF, 25844; INPA, 172201	III, VI, X, XIII	cer, ssf
Myrcia venulosa DC.	Tree	SPSF, 25984; UEC, 12123	VI, XIII	cer, ssf
Myrcianthes pungens (O.Berg) D.Legrand	Tree		VII	rp
Myrciaria floribunda (H.West ex Willd.) O.Berg	Tree	HRCB, 74505	II, X, XIII	ssf, rp
Myrciaria tenella (DC.) O.Berg	Tree	IAC, 54946	VII, XIII	rp
Plinia cauliflora (Mart.) Kausel	Tree		I, X	ssf, rp
Psidium grandifolium Mart. ex DC.	Shrub	SPSF, 25268	XIII	cer
Psidium guineense Sw.	Tree, Shrub	UEC, 12340	III, X, XIII	cer, ssf
Psidium rufum Mart. ex DC.	Tree	SPSF, 20853	III, VI, X, XIII	cer, ssf
Siphoneugena densiflora O.Berg	Tree		VII	rp
NYCTAGINACEAE				
Guapira noxia (Netto) Lundell	Tree	HRCB, 71794	III, X, XIII	cer
Guapira opposita (Vell.) Reitz	Tree		III, X	cer, ssf
Neea theifera Oerst.	Tree, Shrub		III, X	cer
OCHNACEAE				
Ouratea castaneifolia (DC.) Engl.	Tree	HRCB, 58787	III, VI, X	cer, ssf
Ouratea spectabilis (Mart.) Engl.	Tree		III, X	cer
OPILIACEAE				
Agonandra excelsa Griseb.	Tree, Shrub		V	ssf
ORCHIDACEAE				
Acianthera macuconensis (Barb.Rodr.) F.Barros	Herb	HRCB, 62376	VIII	ssf
Acianthera pubescens (Lindl.) Pridgeon & M.W.Chase	Herb	HRCB, 62034	IV, VIII	ssf, rp
Acianthera recurva (Lindl.) Pridgeon & M.W.Chase	Herb	HRCB, 62390	VIII	rp
Acianthera saundersiana (Rchb.f.) Pridgeon & M.W.Chase	Herb	HRCB, 62015	VIII	rp
Anathallis obovata (Lindl.) Pridgeon & M.W.Chase	Herb	HRCB, 62907	VIII	rp
Aspidogyne argentea (Vell.) Garay	Herb	HRCB, 62022	XIII	rp
Bulbophyllum epiphytum Barb.Rodr.	Herb	HRCB, 62378	VIII	ssf
Bulbophyllum tripetalum Lindl.	Herb	GMM, 208	VIII	rp
Campylocentrum crassirhizum Hoehne	Herb	HRCB, 62038	VIII	cer, ssf, rp
Campylocentrum grisebachii Cogn.	Herb	HRCB, 62373	VIII	rp
Campylocentrum sellowii (Rchb.f.) Rolfe	Herb		VIII	rp
Catasetum fimbriatum (C.Morren) Lindl.	Herb	HRCB, 62037	VIII	cer, ssf

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Family/Species	Life form	Voucher	Source	Veg. type
Cattleya cernua (Lindl.) Van den Berg	Herb	HRCB, 62909	VIII	ssf
Cattleya loddigesii Lindl.	Herb	HRCB, 63646	VIII	rp
Cattleya lundii (Rchb.f. & Warm.) Van den Berg	Herb	HRCB, 62375	VIII	ssf
Cattleya walkeriana Gardner *	Herb	HRCB, 62908	VIII	rp
Christensonella neowiedii (Rchb.f.) S.Koehler	Herb	HRCB, 62014	VIII	ssf
Corymborkis flava (Sw.) Kuntze	Herb	HRCB, 62047	XIII	rp
Cyclopogon elatus (Sw.) Schltr.	Herb	HRCB, 62013	XIII	rp
Dryadella aviceps (Rchb.f.) Luer	Herb	HRCB, 62036	VIII	ssf, rp
Encyclia patens Hook.	Herb		VIII	rp
Epidendrum latilabrum Lindl.	Herb	HUFU, 72366	VIII	rp
Epidendrum rigidum Jacq.	Herb	HUFU, 72316	VIII, XIII	rp
Eurystyles actinosophila (Barb.Rodr.) Schltr.	Herb	HRCB, 62369	VIII	rp
Ionopsis utricularioides (Sw.) Lindl.	Herb	IAC, 52898	IV, VIII, XIII	cer, ssf, rp
Isabelia virginalis Barb.Rodr. *	Herb		VIII	ssf
Isochilus linearis (Jacq.) R.Br.	Herb	HRCB, 62384	VIII	ssf, rp
Laelia gloriosa (Rchb.f.) L.O.Williams	Herb	HRCB, 63669	VIII	rp
Liparis nervosa (Thumb.) Lindl.	Herb	HRCB, 62372	XIII	rp
Maxillaria marginata (Lindl.) Fenzl	Herb	HRCB, 63317	VIII	ssf, rp
Mesadenella cuspidata (Lindl.) Garay	Herb	UEC, 160185	IV, XIII	rp
Miltonia flavescens (Lindl.) Lindl.	Herb	HUFU, 72315	VIII, XIII	ssf, rp
Notylia hemitricha Barb.Rodr.	Herb	HRCB, 62377	VIII	ssf
Octomeria warmingii Rchb.f.	Herb	GMM, 181	VIII	ssf, rp
Pelexia laxa (Poepp. & Endl.) Lindl.	Herb	HRCB, 62021	XIII	rp
Polystachya concreta (Jacq.) Garay & Sweet	Herb	HUEFS, 224143	VIII, XIII	ssf, rp
Rodriguezia decora (Lem.) Rchb.f.	Herb	HRCB, 62901	VIII	cer
Trichocentrum pumilum (Lindl.) M.W.Chase & N.H.Williams	Herb	HRCB, 62024	VIII	rp
Vanilla chamissonis Klotzsch	Herb	HRCB, 62032	VIII	rp
OXALIDACEAE				
Oxalis barrelieri L.	Herb	JAL, 8077	IV	rp
Oxalis physocalyx Zucc. ex Progel	Shrub	UEC, 45224	III, X, XIII	cer
PASSIFLORACEAE				
Passiflora alata Curtis	Climbing	UNOP, 8279	IV, IX, XIII	ssf
Passiflora miersii Mast.	Climbing	HRCB, 71788	IV, IX, XIII	cer
Passiflora pohlii Mast.	Climbing	SPSF, 20847; MO, 100510557	XIII	cer, ssf
Passiflora suberosa L.	Climbing	APO, 02	IV, IX	cer
Passiflora tenuifila Killip	Climbing	UEC, 40164; HURB, 2457	XIII	ssf
PERACEAE				
Pera glabrata (Schott) Poepp. ex Baill.	Tree	SPSF, 20846	III, V, VI, X, XIII	cer, ssf, rp
PHYLLANTACEAE				
Phyllanthus tenellus Roxb.	Herb	CEN, 85800	IV, XIII	ssf
Savia dictyocarpa Müll.Arg.	Tree		I, X	ssf, rp
PHYTOLACCACEAE				
Gallesia integrifolia (Spreng.) Harms	Tree		X	ssf
Phytolacca dioica L.	Tree	SPSF, 20851	XIII	cer
PICRAMNIACEAE				
Picramnia ramiflora Planch.	Tree	SPSF, 25996; UEC, 25467	II, X, XIII	ssf, rp
Picramnia sellowii Planch.	Tree, Shrub	SPSF, 49091; INPA, 266939	VII, XIII	rp

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Family/Species	Life form	Voucher	Source	Veg. type
PIPERACEAE				
Peperomia alata Ruiz & Pav.	Herb	HRCB, 62033; SPSF, 231353	IV, VIII	ssf
Peperomia arifolia Miq.	Herb	JAL, 7725	IV	rp
Peperomia campinasana C.DC.	Herb	HRCB, 62902	VIII	rp
Peperomia circinnata Link	Herb	HRCB, 62008	VIII	ssf, rp
Peperomia duartei Yunck.	Herb	JAL, 7680	IV	ssf
Peperomia nitida Dahlst.	Herb	HRCB, 62012	VIII	ssf
Peperomia rhombea Ruiz & Pav.	Herb	HRCB, 62019	IV, VIII	ssf, rp
Peperomia rotundifolia (L.) Kunth	Herb	HRCB, 62026	IV, VIII	ssf, rp
Piper amalago L.	Shrub	JAL, 7713	IV, V, VII	cer, ssf, rp
Piper arboreum Aubl.	Shrub	JAL, 7775	I, IV, V, X	cer, ssf
Piper corcovadensis (Miq.) C.DC.	Shrub	SPSF, 25931	XIII	ssf
Piper glabratum Kunth	Shrub	RON, 9106; FUEL, 53524	IV, XIII	cer, ssf
Piper mikanianum (Kunth) Steud. var. mikanianum	Shrub	JAL, 8081	IV	cer, ssf
Piper ovatum Vahl	Shrub	JAL, 7695	IV	cer, ssf
POACEAE				
Chloris elata Desv.	Herb	SP, 441340	IV, XIII	cer, ssf
Echinolaena inflexa (Poir.) Chase	Herb	UEC, 16836	XIII	cer
Hildaea pallens (Sw.) C.Silva & R.P.Oliveira	Herb	SP, 441351	IV, XIII	cer, ssf
Homolepis glutinosa (Sw.) Zuloaga & Soderstr.	Herb	SP, 441339	IV, XIII	cer, ssf
Homolepis villaricensis (Mez) Zuloaga & Soderstr.	Herb	JAL, 7672	IV	ssf
Lasiacis ligulata Hitchc. & Chase	Herb	HUEFS, 201968, SP, 441335	IV, XIII	cer, ssf
Olyra humilis Nees	Herb	JAL, 7703	IV	cer, ssf
Olyra latifolia L.	Herb	SP, 441346	IV, XIII	cer, ssf
Oplismenus hirtellus subsp. hirtellus (L.) P.Beauv.	Herb	HUEFS, 201967	IV, XIII	cer, ssf
Parodiolyra micrantha (Kunth) Davidse & Zuloaga	Herb	FUEL, 53525; SP, 441327	IV, XIII	cer, ssf
Paspalum conjugatum P.J.Bergius	Herb	SP, 441329	XIII	ssf
Pharus lappulaceus Aubl.	Herb	SP, 441337	IV, XIII	cer, ssf
Rugoloa pilosa (Sw.) Zuloaga	Herb	JAL, 7674	IV	ssf
Setaria scabrifolia (Nees) Kunth	Herb	UNOP, 8269; SP, 441338	IV, XIII	ssf
Setaria vulpiseta (Lam.) Roem. & Schult.	Herb	SP, 441345	IV, XIII	cer, ssf
Streptochaeta spicata Schrad. ex Nees	Herb	UEC, 173870; SP, 441336	IV, XIII	ssf
POLYGALACEAE				
Bredemeyera floribunda Willd.	Shrub, Climbing	HRCB, 68035	III, IV, IX, X, XIII	cer, ssf
*Securidaca rivinifolia var. rivini*folia A.St.-Hil. & Moq.	Shrub, Climbing	SPSF, 20780	XIII	cer
Securidaca tomentosa A.St.-Hil. & Moq.	Shrub, Climbing	HRCB, 68065	IX	cer
POLYGONACEAE				
Polygonum acuminatum Kunth	Herb	UEC, 45231	XIII	cer
POLYPODIACEAE				
Campyloneurum crispum Fée	Herb		XI	ssf, rp
Campyloneurum repens (Aubl.) C.Presl	Herb	UEC, 62329	IV, XI, XIII	ssf, rp
Microgramma lindbergii (Mett.) de la Sota	Herb	BHCB, 141935; HRCB, 62009	IV, VIII, XI, XIII	ssf, rp
Microgramma persicariifolia (Schrad.) C.Presl	Herb	HRCB, 63001	VIII, XI	ssf, rp
Microgramma squamulosa (Kaulf.) de la Sota	Herb	BHCB, 141922; HRCB, 62011	IV, VIII, XI, XIII	cer, ssf, rp
Microgramma vacciniifolia (Langsd. & Fisch.) Copel.	Herb	HRCB, 62903	VIII	rp
Pleopeltis minima (Bory) J. Prado & R.Y. Hirai	Herb	JAL, 7773	IV, VIII, XI	cer, ssf, rp
Pleopeltis pleopeltifolia (Raddi) Alston	Herb	BHCB, 141928	IV, VIII, XI, XIII	cer, ssf, rp
Serpocaulon catharinae (Langsd. & Fisch.) A.R.Sm.	Herb		VIII, XI	cer
Serpocaulon latipes (Langsd. & Fisch.) A.R.Sm.	Herb	BHCB, 141924	XI, XIII	cer
Serpocaulon vacillans (Link) A.R.Sm.	Herb	HRCB, 62040	VIII	cer, ssf

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Family/Species	Life form	Voucher	Source	Veg. type
PRIMULACEAE				
Geissanthus ambiguus (Mart.) G.Agostini	Shrub	UEC, 34652	I, II, V, X, XIII	ssf, rp
Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	Tree	SPSF, 49123; UEC, 49382	I, II, III, V, VI, VII, X, XIII	cer, ssf, rp
Myrsine gardneriana A.DC.	Tree, Shrub	HRCB, 71799	VII, XIII	rp
Myrsine guianensis (Aubl.) Kuntze	Tree		I, III, X	cer, ssf
Myrsine lancifolia Mart.	Shrub		I, II, III, X	cer, ssf, rp
Myrsine loefgrenii (Mez) Imkhan.	Tree	MBM, 273802; SPSF, 25912	XIII	rp
Myrsine umbellata Mart.	Tree	SPSF, 20848; UEC, 45232	I, III, VI, X, XII	cer, ssf
Stylogyne warmingii Mez	Shrub	UEC, 49388; UEC, 49388	I, X, XIII	ssf
PROTEACEAE				
Roupala montana Aubl.	Tree, Shrub		III, VI, X	cer, ssf
PTERIDACEAE				
Adiantopsis radiata (L.) Fée	Herb	BHCB; 141921	IV, XI, XIII	cer, ssf
Adiantum diogoanum Glaz. ex Baker	Herb		XI	ssf, rp
Adiantum platyphyllum Sw.	Herb	BHCB, 153384	IV, XIII	ssf
Adiantum raddianum C.Presl	Herb		XI	ssf, rp
Doryopteris concolor (Langsd. & Fisch.) Kuhn.	Herb		XI	ssf, rp
Hemionitis tomentosa (Lam.) Raddi	Herb		XI	ssf
Pteris denticulata Sw.	Herb	BHCB, 141941	IV, XI, XIII	ssf
Pteris quadriaurita Retz.	Herb		XI	ssf
RHAMNACEAE				
Gouania virgata Reissek	Climbing	HRCB, 68037	IV, IX	cer, ssf
Rhamnidium elaeocarpum Reissek	Tree	UEC, 40210	III, X, XIII	cer, ssf
ROSACEAE				
Prunus myrtifolia (L.) Urb.	Tree	SPSF, 25900	I, III, VI, X, XII	cer, ssf, rp
Rubus brasiliensis Mart.	Shrub	SPSF, 20793	XIII	cer
RUBIACEAE				
Amaioua guianensis Aubl.	Tree, Shrub	SP, 360420	I, II, V, VI, X, XIII	cer, ssf, rp
Borreria cupularis DC.	Herb	JAL, 8078	IV	cer
Chomelia sericea Müll.Arg.	Tree, Shrub		I, X	ssf
Coccocypselum lanceolatum (Ruiz & Pav.) Pers.	Herb	JAL, 8100	IV	rp
Cordiera rigida (K.Schum.) Kuntze	Shrub	SPSF, 49096	VII, XIII	rp
Cordiera sessilis (Vell.) Kuntze	Shrub		I, III, V, VI, X	cer, ssf
Coutarea hexandra (Jacq.) K.Schum.	Tree, Shrub		II, X	ssf, rp
Emmeorhiza umbellata (Spreng.) K.Schum.	Climbing	UEC, 44040	XIII	ssf
Eumachia cephalantha (Müll. Arg.) Delprete & J.H. Kirkbr.	Shrub		V	ssf
Faramea stipulacea (Cham. & Schltdl.) DC.	Shrub	HRCB, 71795	XIII	ssf
Galianthe hispidula (A.Rich. ex DC.) E.L.Cabral & Bacigalupo	Herb	UEC, 44060	XIII	ssf
Galianthe laxa (Cham.	Herb	UNOP, 8272; RON, 9091	IV, IX, XIII	cer, ssf
Genipa americana L.	Tree		I, II, VII, X	ssf, rp
Geophila repens (L.) I.M.Johnst.	Herb	JAL, 7701	IV	cer, ssf
Guettarda viburnoides Cham. & Schltdl.	Tree, Shrub		III, X	cer, ssf
Hamelia patens Jacq.	Tree, Shrub	SPSF, 20778	XIII	rp
Ixora brevifolia Benth.	Tree, Shrub	UEC, 40281	I, VI, X, XIII	cer, ssf

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Family/Species	Life form	Voucher	Source	Veg. type
Ixora venulosa Benth.	Shrub	NY, 779196; UEC, 353229	III, X, XIII	cer, ssf
Manettia cordifolia Mart.	Climbing	HRCB, 68038	IV, IX, XIII	cer, ssf
Mitracarpus hirtus (L.) DC.	Herb	APO, 31	IV	cer, ssf
Palicourea croceoides Ham.	Shrub	SPSF, 27345; IAC, 45367	IV, XIII	rp
Palicourea rigida Kunth	Shrub		III, X	cer
Palicourea sessilis (Vell.) C.M. Taylor	Shrub	UEC, 34795	I, V, X	cer, ssf
Palicourea violacea (Aubl.) A.Rich.	Shrub	IAC, 45362; JAL, 7694	IV, V, XIII	cer, ssf
Psychotria carthagenensis Jacq.	Tree, Shrub	SPSF, 25926; JAL, 8092	IV, VII, XIII	rp
Psychotria deflexa DC.	Shrub	UNOP, 8271	IV, XIII	cer, ssf
Psychotria gracilenta Müll.Arg.	Shrub	FUEL, 53532; JAL, 7698	IV	cer, ssf
Psychotria hastisepala Müll.Arg.	Shrub		V	ssf
Psychotria hoffmannseggiana (Willd. ex Schult.) Müll.Arg.	Shrub	SPSF, 25846; IAC, 45365	IV, XIII	cer, ssf
Psychotria tenuifolia Sw.	Shrub	APO, 78	IV	ssf
Psychotria trichophora Müll.Arg.	Shrub	UEC, 13949	IV, XIII	cer, rp
Randia armata (Sw.) DC.	Tree		III, X	cer, ssf
Rudgea jasminoides (Cham.) Müll.Arg.	Tree, Shrub	UEC, 35267	V, VII, XIII	ssf, rp
Rudgea minor (Cham.) Standl. *subsp. minor*	Shrub		I, X	ssf
Rudgea viburnoides (Cham.) Benth.	Tree, Shrub	SPSF, 20824; UEC, 14110	III, VI, X, XIII	cer, ssf
Simira sampaioana (Standl.) Steyerm.	Tree	SPSF, 20840	X, XIII	rp
Tocoyena formosa (Cham. & Schltdl.) K.Schum.	Shrub	UEC, 40274	III, X, XIII	cer
RUTACEAE				
Conchocarpus pentandrus (A. St.-Hil.) Kallunki & Pirani	Tree, Shrub	UEC, 25135	XIII	ssf
Conchocarpus ruber (A.St.Hil.) Bruniera & Groppo	Shrub	SPSF, 20834	XIII	ssf
Esenbeckia febrifuga (A.St.-Hil.) A. Juss. ex Mart.	Tree	SPSF, 49095	I, II, VII, X, XIII	cer, ssf, rp
Esenbeckia grandiflora Mart.	Tree		I, X	ssf
Galipea jasminiflora (A.St.-Hil.) Engl.	Tree	SPSF, 49101; HUEFS, 224121	I, II, VII, X, XIII	cer, ssf, rp
Metrodorea nigra A.St.-Hil.	Tree	SPSF, 49097; INPA, 266936	I, II, V, X, XIII	ssf, rp
Pilocarpus pauciflorus A.St.-Hil.	Tree	SPSF, 27334; FUEL, 39994	XIII	ssf
Zanthoxylum acuminatum (Sw.) Sw.	Tree	UEC, 25223	I, II, III, X, XIII	cer, ssf, rp
Zanthoxylum fagara (L.) Sarg.	Tree		III, V, X	cer, ssf
Zanthoxylum monogynum A.St.-Hil.	Tree	SPSF, 29009	V, XIII	ssf
Zanthoxylum rhoifolium Lam.	Tree		III, VI, X	cer, ssf, rp
Zanthoxylum riedelianum Engl.	Tree		I, II, X	cer, ssf, rp
SALICACEAE				
Casearia decandra Jacq.	Tree, Shrub		III, V, X	cer, ssf
Casearia gossypiosperma Briq.	Tree	SPSF, 24696	I, II, III, V, VI, VII, X, XIII	cer, ssf, rp
Casearia grandiflora Cambess.	Tree, Shrub	INPA, 78026	XIII	rp
Casearia sylvestris Sw.	Tree, Shrub	IAC, 52464; SPSF, 49127	I, II, III, V, VI, VII, X, XIII	cer, ssf, rp
Prockia crucis P.Browne ex L.	Tree, Shrub	SPSF, 49084; HRCB, 71790	X, XIII	rp
SANTALACEAE				
Phoradendron crassifolium (Pohl ex DC.) Eichler	Herb	SPSF, 27335; RON, 9102	IV, XIII	cer, ssf

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Family/Species	Life form	Voucher	Source	Veg. type
SAPINDACEAE				
Allophylus racemosus Sw.	Shrub	HRCB, 71792	XIII	ssf
Allophylus semidentatus (Miq.) Radlk.	Tree		I, II, VI, X	cer, ssf, rp
Cardiospermum grandiflorum Sw.	Climbing	HRCB, 68039	IX	ssf
Cupania vernalis Cambess.	Tree	SPSF, 17376; UEC, 44049	III, V, VI, X, XIII	cer, ssf, rp
Diatenopteryx sorbifolia Radlk.	Tree		I, X	ssf
Matayba elaeagnoides Radlk.	Tree	SPSF, 49079; INPA, 204885	V, VII, XIII	cer, ssf, rp
Matayba guianensis Aubl.	Tree	SPSF, 17375	I, II, III, X, XIII	cer, ssf, rp
Paullinia rhomboidea Radlk.	Shrub, Climbing	RON, 9096	IV, IX, XIII	cer, ssf, rp
Serjania communis Cambess.	Climbing	FUEL, 53531; UNOP, 8275	IV, IX, XIII	cer
Serjania fuscifolia Radlk.	Climbing	HUEFS, 201964; RON, 9095	IV, IX, XIII	cer, ssf
Serjania laruotteana Cambess.	Climbing	HRCB, 68041	IX	cer
Serjania lethalis A.St.-Hil.	Climbing	RON, 9094	IV, IX, XIII	cer
Serjania meridionalis Cambess.	Climbing	UNOP, 8274; FUEL, 53543	IV, IX, XIII	ssf
Serjania paradoxa Radlk.	Climbing	RON, 9093	IV, IX, XIII	cer
Serjania pinnatifolia Radlk.	Climbing	HRCB, 68055; FUEL, 53513	IV, IX, XIII	cer, ssf
Serjania reticulata Cambess.	Climbing	APO, 48	IV, IX	cer, ssf
Urvillea laevis Radlk.	Climbing	RON, 9092; UNOP, 8273	IV, IX, XIII	cer, ssf
SAPOTACEAE				
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	Tree	SPSF, 49087	I, II, VII, X, XIII	ssf, rp
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	Tree, Shrub	SPSF, 20833	III, V, VI, X, XIII	cer, ssf
Pouteria ramiflora (Mart.) Radlk.	Tree, Shrub		III, X	cer, ssf
SIPARUNACEAE				
Siparuna guianensis Aubl.	Tree	UEC, 35283	III, V, VI, X, XIII	cer, ssf, rp
SMILACACEAE				
Smilax elastica Griseb.	Climbing	HRCB, 68043; RON, 9099	IV, IX, XIII	cer
Smilax fluminensis Steud.	Climbing	HRCB, 68058	IV, IX	cer
SOLANACEAE				
Capsicum flexuosum Sendtn.	Shrub	SPSF; 25610	XIII	ssf
Cestrum mariquitense Kunth	Shrub	SPSF, 25845	XIII	cer
Cestrum pedicellatum Sendtn.	Shrub	UEC, 44039	III, X, XIII	cer
Solanum acerifolium Dunal	Shrub	BHCB, 141929	IV, XIII	cer, ssf
Solanum americanum Mill.	Herb	JAL, 7664	IV	ssf
Solanum campaniforme Roem. & Schult.	Shrub	UEC, 44059	XIII	ssf
Solanum granulosoleprosum Dunal	Tree	SPSF, 20786; FUEL, 31988	XIII	cer
Solanum lantana Sendtn.	Shrub	SPSF, 20827; HUEFS, 201965	IV, XIII	cer, ssf
Solanum lycocarpum A.St.-Hil.	Tree, Shrub	SPSF, 27344; BHCB, 141930	III, IV, X, XIII	cer, ssf
Solanum paniculatum L.	Shrub	SPSF, 25899	III, X, XIII	cer
Solanum swartzianum Roem. & Schult.	Tree	JAL, 7687	I, III, IV, V, X	cer, ssf
Solanum uncinellum Lindl.	Climbing	HRCB, 71796	XIII	ssf
STYRACACEAE				
Styrax acuminatus Pohl	Tree		V, VI	cer, ssf
Styrax camporum Pohl	Tree	UEC, 40658; IAC, 54616	III, VI, X, XIII	cer, ssf
Styrax ferrugineus Nees & Mart.	Tree, Shrub	FUEL, 53529; RON, 9104	VI, XIII	cer, ssf
Styrax pohlii A.DC.	Tree, Shrub		III, X	cer, ssf

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Family/Species	Life form	Voucher	Source	Veg. type
SYMPLOCACEAE				
Symplocos pubescens Klotzsch ex Benth.	Tree, Shrub	SPSF, 25271; UEC, 14966	XIII	cer
Symplocos uniflora (Pohl) Benth.	Tree, Shrub	MBM, 256486; HUFU, 43053	III, X, XIII	cer
TALINACEAE				
Talinum fruticosum (L.) Juss.	Herb	HUEFS, 201976	IV, XIII	ssf
TECTARIACEAE				
Tectaria incisa Cav.	Herb		XI	ssf
THELYPTERIDACEAE				
Christella dentata (Forssk.) Brownsey & Jermy	Herb		XI	cer, ssf
Christella grandis (A.R. Sm.) A.R. Sm.	Herb		XI	ssf
Christella hispidula (Decne.) Holttum	Herb	UEC, 62340	XI, XIII	ssf
Christella patens (Sw.) Pic.Serm.	Herb	BHCB, 60864	XI, XIII	ssf, rp
Cyclosorus interruptus (Willd.) H. Ito	Herb		XI	cer, rp
Goniopteris jamesonii (Hook.) Salino & T.E.Almeida	Herb	BHCB, 69394	XI, XIII	ssf
Goniopteris lugubris (Mett.) Brade	Herb	BHCB, 141919	IV, XI, XIII	ssf
URTICACEAE				
Cecropia glaziovii Snethl.	Tree	SPSF, 20796	XIII	cer
Cecropia pachystachya Trécul	Tree		III, VI, X	cer, ssf
Urera baccifera (L.) Gaudich. ex Wedd.	Tree, Shrub	JAL, 7747	I, IV, X	cer, ssf
Urera caracasana (Jacq.) Griseb.	Tree, Shrub	FUEL, 53512; RON, 9103	IV, XIII	rp
VERBENACEAE				
Aloysia virgata (Ruiz & Pav.) Juss.	Tree, Shrub	UEC, 44056	III, X, XIII	cer, rp
Lippia brasiliensis (Link) T.R.S.Silva	Shrub	UEC, 25494	IV, XIII	cer, ssf
Lippia origanoides Kunth	Shrub	SPSF, 20822	III, IV, X, XIII	cer, ssf
VIOLACEAE				
Pombalia atropurpurea (A.St.-Hil.) Paula-Souza	Shrub	HUEFS, 201966; HRCB, 71793	I, II, IV, X, XIII	ssf, rp
VITACEAE				
Cissus erosa Rich.	Climbing	HRCB, 68045	IV, IX, XIII	cer, ssf
Cissus tinctoria Mart.	Climbing	HRCB, 68046	IV, IX	ssf
Cissus verticillata (L.) Nicolson & C.E.Jarvis	Climbing	HRCB, 68047	IX	ssf
VOCHYSIACEAE				
Qualea cordata Spreng.	Tree	SPSF, 20829; UEC, 145446	III, VI, X, XIII	cer, ssf
Qualea dichotoma (Mart.) Warm.	Tree, Shrub	SPSF, 24703	III, VI, X, XIII	cer, ssf
Qualea grandiflora Mart.	Tree, Shrub		III, VI, X	cer, ssf
Qualea multiflora Mart.	Tree, Shrub		I, III, X	cer, ssf
Qualea parviflora Mart.	Tree, Shrub		III, X	cer
Vochysia magnifica Warm.	Tree	IAC, 54531; SPSF, 17391	XIII	ssf
Vochysia tucanorum Mart.	Tree	SPSF, 17498; FUEL, 53526	I, II, III, V, VI, X, XIII	cer, ssf, rp

JAL= collections of J.A. Lombardi; APO= collections of A.P. Oliveira; GMM= collections of G.M. Marcusso; I to XIII - species reporded by: I= Bertoni 1984; II= Bertoni & Martins 1987; III= Bertoni et al. 2001; IV= Oliveira 2012; V= Osaco 2012; VI= Sabino 2013; VII= Konopczyk 2014; VIII= Marcusso et al. 2016; IX= Vargas et al. 2018; X= São Paulo 2003; XI= Colli et al. 2003; XII= Dickfeldt et al. 2013; XIII= present study; Asterisks indicate threatened species according to the "Livro Vermelho da Flora do Brasil" by CNCFlora (Martinelli & Moraes 2013) and the list of threatened flora of São Paulo State (SMA Resolution 2016); Veg. type: vegetation types of occurrence; cer= cerradão; ssf: seasonal semideciduous forest; rp: riparian forest.

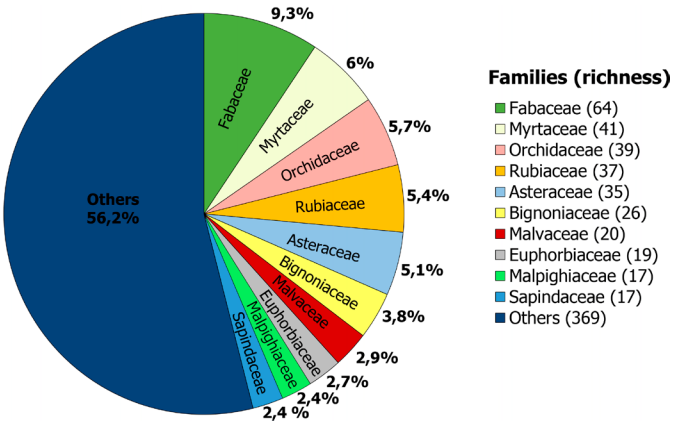


Figure 3. The most species-rich families in the Porto Ferreira State Park, Porto Ferreira, São Paulo state, southeastern Brazil.

The arboreal habit was the predominant life form in the PFSP (41.8%), followed by herbs (25.7%), shrubs/subshrubs (17.9%) and climbing plants (14.7%) (Figure 4). The results listed 84 species (12.2%) with two or more life forms. Concerning all life forms, 9.6%, 18.8% and 18.5% of the species are exclusive to RP, CER and SSF, respectively. The number of exclusive species for the CER is mainly related to the high number of trees species. However, herbs represented 40% and 50% of the exclusive species found in the SSF and RP, respectively.

The number of species compiled for the lists of the floristic similarity comparison was 2745, of which 1420 (51.7%) are exclusively from a single area (Appendix 2). Only 43 species (1.5%) occurred in 50% or more of the lists, and no species were recorded for all areas (Appendix 3). The dendrogram showed a high coefficient of cophenetic correlation of 0.82. The greater the distance was between areas, the greater the floristic dissimilarities among them. The cluster analysis showed the segregation of three major floristic groups (Figure 5). The first group (1) clustered an ecotone area and two RP (one of which belongs to the same survey as the ecotone); the second group (2) categorized the studies carried out in *Cerrado* vegetation types; and the third group (3) all vegetation types of the PFSP and areas under SSF formation.

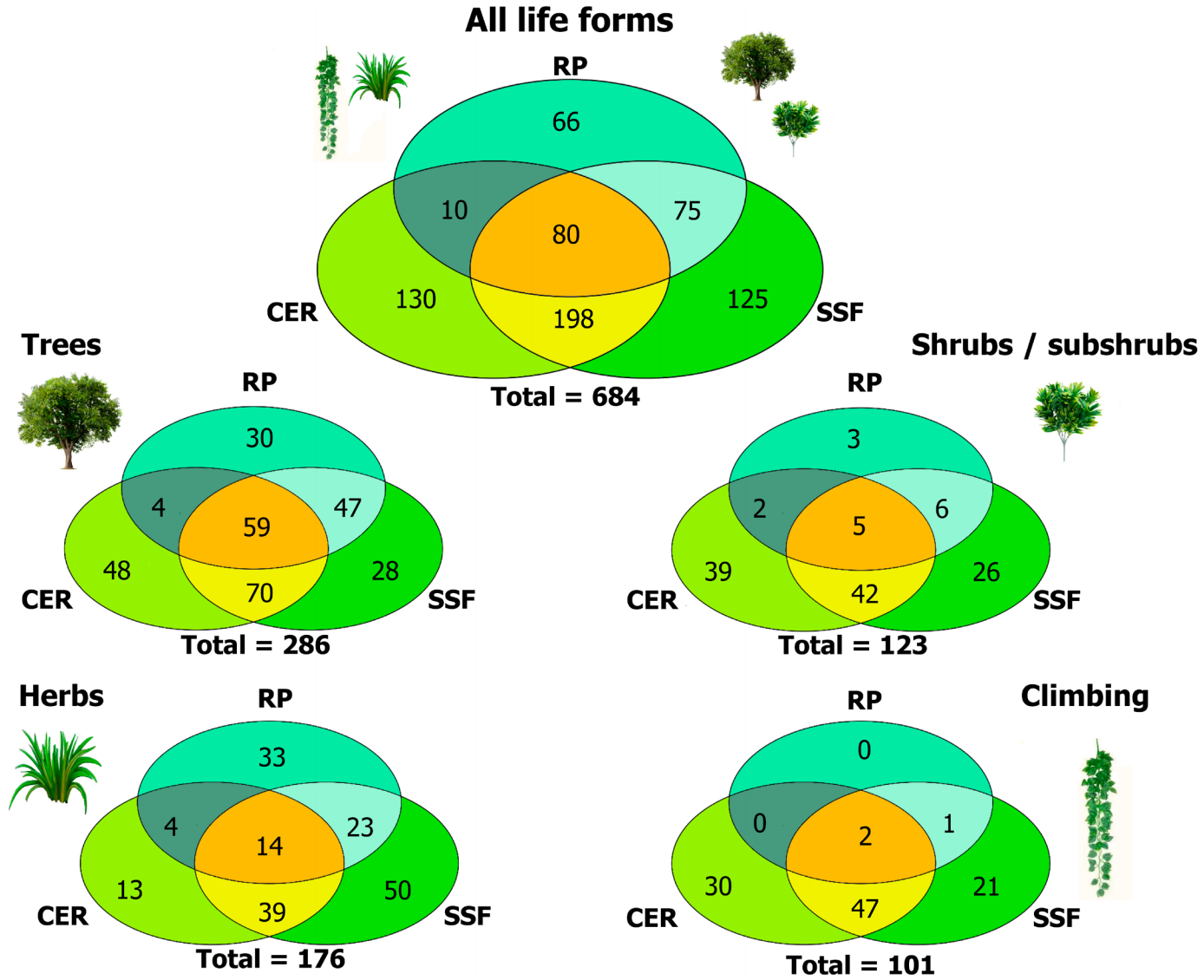


Figure 4. Venn diagrams for vascular plants recorded in Porto Ferreira State Park, Porto Ferreira, São Paulo State, southeastern Brazil. RP: riparian forest, SSF: seasonal semidecidual forest; CER: cerradão.

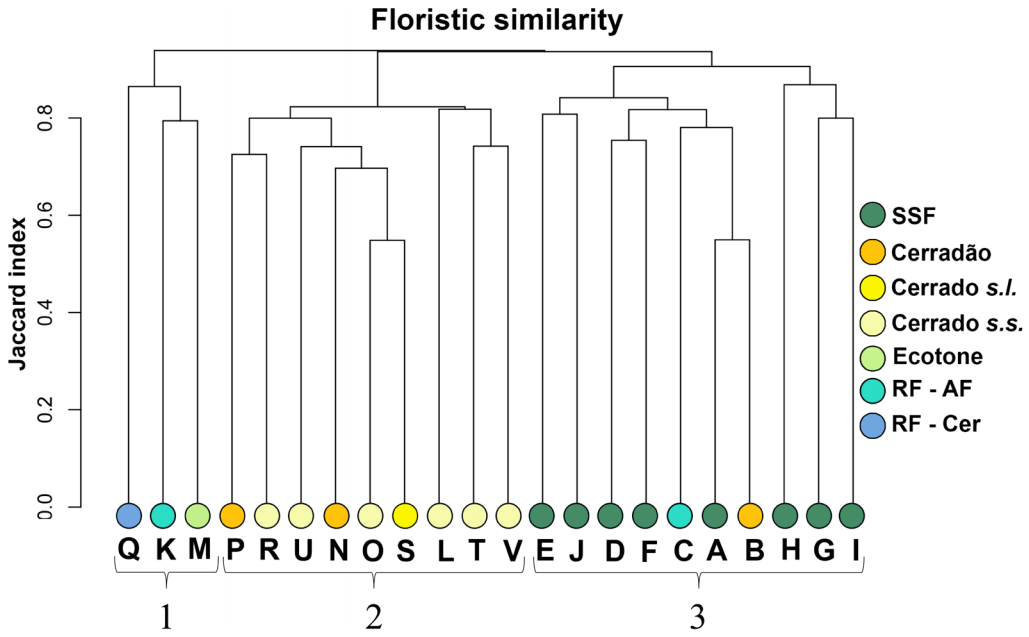


Figure 5. Cluster analysis (UPGMA) using Jaccard index among fifteen studies carried out in *Cerrado,* SSF and riparian forest vegetation. Areas (identified by letters A-V) are given in Table 1. SSF: seasonal semidecidual forest; *Cerrado s.l.*: *Cerrado sensu lato*; *Cerrado s.s.*: *Cerrado sensu stricto*; RF-AF: riparian forest under Atlantic Forest ecoregion; RF-Cer: riparian forest under *Cerrado* ecoregion.

Discussion

The comprehensive checklist of the PFSP allowed us to show that the vascular flora in this ecotonal area is composed of a mixture of elements of both the Atlantic Forest and *Cerrado* biogeographical provinces. The soil features are a possible explanation for the different vegetation types, and variations on a small scale. The overall richness is impressive, considering the small size of park; however, the number of species of each vegetation type recorded is in accordance with previous studies in these vegetation types. An Atlantic Forest similarity was found for the PFSP flora as a whole. The same relationship was found considering the CER and SSF floras independently, demonstrating the strong influence of Atlantic Forest on the area. Perhaps the geographical location of the PFSP, which reaches both biogeographical provinces in the eastern region, could be a reasonable explanation for these results.

The species richness of the PFSP was higher than that found by Cielo-Filho et al. (2015) – with 265 species –, the only vascular flora surveyed in an ecotonal site among *Cerrado* and Atlantic Forest in southeastern Brazil. The overwhelming number of species recorded for the PFSP vascular flora is ranked fourth among studies conducted under seasonal formations, behind only those of Lombardi & Gonçalves (2000), Lombardi et al. (2012) and Forzza et al. (2014). Species richness tends to peak in ecotonal areas (Kark & van Rensburg, 2006), likely because transitional areas hold species from two or more neighboring communities, and due to high spatial heterogeneity (Kark 2012). Furthermore, along with the increase in botanical collection in protected areas, there is an appeal to enhance the importance of these areas to protect threatened species (Colli-Silva et al., 2019). In this sense, we found eight threatened species at regional and national levels. Thus, the ecotonal condition of the PFSP between two biogeographical provinces may contribute to increase the species richness, also being home to important threatened species.

Studies have been emphasizing the need for the expansion of botanical collection in protected areas (Colli-Silva et al. 2016, 2019). The addition of more than 65% of the species number since the last PFSP floristic list (São Paulo, 2003) is significant, showing the importance of continuous research, and fieldwork, to update the knowledge about the flora. Since the Colli-Silva et al. study of 2016, which recorded 292 species for the PFSP, 235 vouchers have been added to the PFSP, most likely due to the digitization of the collections, later available in digital platforms (CRIA, 2019), and to the addition of our own collections. Moreover, notably there are species that we found in the field, such as *Cissus serroniana* (Glaz.) Lombardi (Vitaceae), which had never before been recorded fertile, and, therefore, were not included in the checklist. Even though the PFSP has a significant number of studies concerning its flora, we predict that further collections will increase the number of species in this protected area.

Considering each vegetation type of the PFSP, the richness we found in the SSF averages roughly with that found in other studies (Corrêa et al., 2018; Cielo-Filho et al., 2015; Forzza et al., 2014; Pifano et al., 2013; Rossetto & Vieira, 2013; Lombardi et al., 2012; Guaratini et al., 2008; Lombardi & Gonçalves, 2000). In the CER, the number of species recorded in our study is higher than other *Cerrado* surveys (Cavassan & Weiser, 2015; Cielo-Filho et al. 2015; Carvalho et al., 2010; Ishara et al., 2008; Batalha & Mantovani, 2001; Durigan et al., 1999; Batalha et al., 1997). As for the RP, there are no studies of vascular flora carried out specifically on this vegetation type, but rather inevitably included as a part of a larger work, such as those of Durigan et al. (1999) and Cielo-Filho et al. (2015), making comparison difficult.

The most species-rich families found in our study are also the richest ones for the *Cerrado* as a whole (Souza, et al. 2018), and seasonal forests of the Atlantic Forest (Souza, et al., 2019a). Orchidaceae, Fabaceae, Asteraceae and Myrtaceae are, respectively, the most diverse families in the Atlantic Forest (BFG, 2015).

Thus, Fabaceae, Asteraceae and Orchidaceae constitute the three richest families in the *Cerrado* (Mendonça et al. 2008). The richest genera found in the PFSP – *Eugenia*, *Micona* and *Myrcia* – are ranked as the genera with the highest number of tree species in the *Cerrado* and the Atlantic Forest, under semideciduous formation (Oliveira-Filho & Fontes 2000). Considering Brazilian flora as a whole, *Eugenia*, *Miconia*, *Myrcia*, *Psychotria*, *Solanum* and *Peperomia* are also classified among the 30 most diverse Angiosperm genera (BFG, 2015).

Generalist species, establishing and thriving both in the *Cerrado* and in the Atlantic Forest, generally become very abundant in transition areas between these two biogeographical provinces (Durigan et al. 2012, Morrone, 2014, 2017). All species classified as generalists by Durigan et al. (2012) were found in the PFSP flora [*e.g. Copaifera langsdorffii* Desf., *Cordia trichotoma* (Vell.) Arráb. ex Steud, *Mabea fistulifera* Mart., *Ocotea corymbosa* (Meisn.) Mez, *Platypodium elegans* Vogel, *Senegalia polyphyla* (DC.) Britton & Rose, *Terminalia glabrescens* Mart. and *Vochysia tucanorum* Mart.]. Durigan et al. (2012) also pointed out 20 typical species of SSF, of which 15 were reported in the PFSP flora (*e.g. Aspidosperma polyneuron* Müll.Arg., *Cedrela fissilis* Vell., *Metrodorea nigra* A.St.-Hil. and *Guarea kunthiana* A. Juss.). In a study encompassing most of the *Cerrado* woody vegetation, Ratter et al. (2003) found 38 species with the highest percentage of occurrence, of which 26 (68.4%) occur in PFSP CER (*e.g. Qualea grandiflora* Mart., *Qualea parviflora* Mart., *Bowdichia virgilioides* Kunth, *Dimorphandra mollis* Benth., *Lafoensia pacari* A.St.-Hil., *Connarus suberosus* Planch. and *Hymenaea stigonocarpa* Mart. ex Hayn). These results emphasize the PFSP as a species reservatory of several biogeographical entities, reinforcing its role in conservation.

The trees were the most species-rich life forms in the PFSP, following the patterns of forest vegetation types (IBGE, 2012; Forzza et al., 2014). Regarding the shared species among the vegetation types, trees perform a major contribution to the exclusive species of the CER. The different edaphic physicochemical features among the CER and SSF are the main causes of their differences, even in small scales (Gottsberger & Silberbauer-Gottsberger, 2006; Pinheiro et al. 2009). Edaphic factors, such as water availability in the soil, and soil composition, may play a role in vegetation type differentiation (Haridasan 1992). The heterogeneity of the soil, on a small-scale, can also act as a plant community ecological driver, increasing diversity and promoting structural changes (Souza et al., 2019b). In a study carried out on the PFSP soil and its relationship to the vegetation, Rossi et al. (2005) found several types of soil. The authors also found an association between CER, SSF and RP vegetation and dystrophic oxisols, eutrophic argisols and dystrophic fluvial neosols, respectively.

A substantial number of herbs species were found in the PFSP, including the epiphytic and terricolous habit. The impressive importance of the herbs in the PFSP is most likely due to the contribution of the *Cerrado* elements; usually the number recorded in the AF is lower than the one we recorded here (Vieira et al., 2015). An explanation for this may be the ecotonal feature of the PFSP, and the high number of shared species between the CER and SSF. Thus, even in the *Cerrado* forestry vegetation type, the herbaceous layers must be considered as an important synusia. On the other hand, the high number of exclusive herbaceous species in the RP must be attributed to the microclimatic conditions propitious to the epiphytes' development (Marcusso et al., 2016). The number of species of climbing plants in the present study was lower than that found by Vargas et al. (2018), because we considered only taxa identified at the taxonomic level of species and, occasionally, used the life form classification according to the *Flora do Brasil* (2020). This classification does not always reflect Vargas' et al. (2018) interpretations.

We found an outstanding heterogeneity among the floristic surveys analyzed, in which very few species occurred in 50% or more of the areas, and no species occurred in all areas. This may be due to the addition of surveys from different vegetation types belonging to the *Cerrado* and the Atlantic Forest. Floristic comparisons are usually made between vegetation types within the same biogeographical provinces (*e.g.* Carvalho et al. 2010; Ishara et al., 2008; Guaratini et al., 2008; Pifano et al., 2013). Here, including areas of both *Cerrado* and Atlantic Forest, we found that the areas with the same vegetation type are more inclined to be floristically similar. However, in ecotones, areas with different vegetation types in the same location tend to share more species with each other than areas in which the same vegetation type occurs at a distance from one another. These results have been reported for several studies (*e.g.* Oliveira-Filho & Fontes, 2000; Oliveira-Filho et al., 2015; Dryflor et al., 2016), contrary to the general biogeographic hypothesis that similar species would be shared between regions due to the restriction of their dispersion capacity (Lieberman, 2003). Therefore, the fact that the CER of the PFSP joined in the SSF group might be due to the high spatial proximity correlation between them, suggesting a strong relationship with this matrix (Pinheiro & Monteiro, 2008; Passos et al., 2018), with the SSF exerting more influence over the CER flora.

The PFSP harbours eight threatened species, and a huge number of vascular plant species. We also found a greater floristic similarity within the PFSP, and studies carried out in the Atlantic Forest. There is a lack of floristic studies that include all life forms conducted in ecotonal areas in southeastern Brazil. The reason for this, we believe, is due to the difficulty in recognizing an ecotone, and the negligence on supporting descriptive studies. This is an unprecedented floristic list recorded for the PFSP. The overwhelming diversity and the pool of species found, highlights this remnant as an important protected area. Results shown here can be used as a floristic reference for future conservation measures, and restorative actions in areas under ecotonal influences of the Atlantic Forest and the *Cerrado*.

Supplementary Material

The following online material is available for this article:

Appendix 1 - Excluded species from PFSP species list and the respective reason of exclusion.

Appendix 2 - Number of exclusive species among studies compared with this study.

Appendix 3 - Species occurring at 11 (50%) or more lists among the compared studies and PFSP.

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Author Contributions

Gabriel Pavan Sabino: elaboration of study's concept and design, data collection, analysis and preparation of manuscritpt;

Gabriel Mendes Marcusso: elaboration of study's concept and design, data collection, analysis and preparation of manuscritpt;

Vitor de Andrade Kamimura: elaboration of study's concept and design, data collection, analysis and preparation of manuscritpt;

Renan Borgiani: elaboration of study's concept, data collection and analysis;

Rafael Konopczyk: elaboration of study's concept and data collection;

Ernesto Pedro Dickfeldt: Contribution to data collection;

José Eduardo de Arruda Bertoni: Contribution to data collection;

Sonia Aparecida de Souza Evangelista: Contribution to data collection.

Conflicts of Interest

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

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Thematic Review

Metabarcoding advances for ecology and biogeography of Neotropical protists: what do we know, where do we go?

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Abstract: The Neotropics is one of the most diverse regions of the globe in terms of plants and animal species. Regarding the microbial world, however, little is known about the diversity and biogeography patterns of microorganisms in the Neotropics. The biogeography of several microbial taxonomic groups is still missing and/or incomplete, such as the protists. Despite the hard taxonomic identification of protists, the advance of molecular techniques (e.g., metabarcoding) have allowed to better explore the distribution of several protistan groups. Our goal here was to summarize the available information of Neotropical protists, focusing on metabarcoding studies, to explore what these data evidence on their ecology and biogeography. For this, we reviewed the findings from all articles that focused on or included the terrestrial protists using a metabarcoding approach and identified the gaps and future perspectives in this research field. We found that Neotropical protistan diversity patterns seem to be, at least in part, congruent with that of macro-organisms and, different than plants and bacteria, just weakly explained by environmental variables. We argue that studies with standardized protocols including different ecoregions are necessary, such as temperate forests, grasslands, and savannas from Southern of South America and Northern Atlantic Forest, to fully characterize the ecology and biogeography on Neotropical protists. Furthermore, dismembering evolutionary lineages and functional guilds of protists are important to better understand the relationship between diversity, dispersal abilities, and functionality of particular taxa of protists in their habitats.
Keywords: *Environmental samples; Freshwater protists; High Throughput Sequencing; Neotropics; Microorganism; Operational taxonomic units; Soil protistan biodiversity.*

Ecologia e biogeografia de protistas Neotropicais usando metabarcoding: O que sabemos? Para onde iremos?

Resumo: A região Neotropical é uma das mais diversas regiões do globo em termos de espécies vegetais e animais. Em relação ao mundo microbiano, entretanto, pouco se sabe sobre a diversidade e os padrões biogeográficos dos microrganismos no Neotrópico. Nesse contexto, a biogeografia de diversos grupos taxonômicos microbianos ainda é escasso e/ou incompleto como os protistas, devido à difícil identificação taxonômica de tais microscópicos organismos. Neste contexto, o avanço dos dados moleculares de amostras ambientais (por exemplo, metabarcoding) permitiu explorar a distribuição de vários grupos de protistas. Nosso objetivo aqui foi resumir as informações disponíveis dos protistas neotropicais, com foco em metabarcoding, para explorar o que esses dados evidenciam sobre sua ecologia e biogeografia. Para isso, revisamos os resultados de todos os artigos que enfocavam ou incluíam os protistas terrestres usando uma abordagem de metabarcoding e identificamos as lacunas e as perspectivas futuras neste campo de pesquisa. Os padrões de diversidade dos protistas Neotropicais parecem ser, pelo menos em parte, congruentes com os de macroorganismos e, diferentes das plantas e bactérias, sendo pouco explicados por variáveis ambientais. Estudos com protocolos padronizados incluindo diferentes Ecorregiões são necessários, como em florestas temperadas, campos nativos e savanas no sul da América do Sul e no norte

da Mata Atlântica, para melhor caracterizar a ecologia e biogeografia de protistas Neotropicais. Além disso, é importante diferenciar linhagens evolutivas e guildas funcionais de protistas para entender melhor a relação entre diversidade, capacidade de dispersão e funcionalidade de determinados táxons de protistas em seus habitats.

Palavras-chave: *Amostras ambientais; Biodiversidade do solo; Neotropicos; Sequenciamento de alto desempenho; Microrganismos; Protistas de água doce; Unidades taxonômicas operacionais.*

Introduction

Despite the significant advances in our understanding of biodiversity patterns across a wide spatial scale, the question of whether the same ecological and biogeographical patterns apply to macro and microorganisms remains a discussion topic. Indeed, it was considered one of the 100 fundamental ecological questions (Sutherland et al. 2013). This knowledge gap is worrisome since microorganisms are the richest and more abundant component in any environment (Locey & Lennon 2016, Bar-On et al. 2018), which play a pivotal role in the maintenance of ecosystems (e.g. Petersen & Luxton 1986, Sherr & Sherr 2002, Cuvelier et al. 2010, Steele et al. 2011). To understand the ecology and biogeography of microorganisms is, therefore, crucial to understand these patterns in general. As highlighted by O'Malley & Dupré (2007), the excessive focus on macro-organisms patterns of diversity, ecology and distribution may have distorted several aspects of our understanding about these patterns.

Several studies have compared the diversity patterns of microorganisms with what is known for macro-organisms in a global scale (e.g. Tedersoo et al. 2014, Cameron et al. 2018, Delgado-Baquerizo et al. 2018). However, the study of several taxonomic groups is still missing and/or incomplete, such as the protists. Although some biogeographic patterns of protists in different regions are already known (Geisen et al. 2018, Singer et al. 2021), protists macroecology and biogeography is still in its infancy, and generalizations are difficult to make. It is even worse in the Neotropics, the region that comprises the area from central Mexico to Argentina, including the Caribbean (Morrone 2014). Indeed, until now just two of the articles on Neotropical protists available were used in a compilation of genomic data to test ecological patterns on global terrestrial protists (Oliverio et al. 2020). Furthermore, the hard-taxonomic identification of protists contributes to the lack of sampling in some regions, reflecting the uncertainties on ecological and biogeographic patterns. Advanced molecular techniques such as environmental DNA sampling known as metabarcoding brings promising prospects for protists (Santoferrara et al. 2020). Our goal here was to summarize the findings concerning protistan distribution through metabarcoding data from continental environmental samples in Neotropics to understand the ecological processes underlying the biogeography of the protists in this region. We also identified the main gaps in the Neotropical protists ecology and biogeography and to shed light on the already described patterns and potential prospects in this so promising study group. First, let us introduce this group here, who they are, what is known about their ecology, and then, how molecular techniques such as metabarcoding can bring new advances to the knowledge of this amazing group.

1. The protists

1.1. Who are they? Where do they live? How do they survive?

The protists are a paraphyletic group comprising most lineages in the eukaryotic tree of life (Keeling et al. 2005, Burki 2014). Several groups are closer related with macro-organisms, such the phyla Opisthosporidia, Nucleariida and Fonticula that are inside of the Holozoa, group that comprise Fungi and Metazoa (Burki 2014, Adl et al. 2019). Protists are the non-fungi single cell eukaryotes that are over spread in the tree of life and have the potential to shed light on eukaryotic evolution (Adl et al. 2019). Future perspectives include the deep phylogeny of protists and better characterization of phylogenetic and functional diversity for advance knowledge of this amazing group(s).

Protists inhabit all habitats, from soils, lakes, sea, and the bodies of other organisms (Figure 1). They are mostly known to be vector of diseases such as Malaria (caused by *Plasmodium* sp.), Chagas (caused by *Trypanossoma cruzi*), Giardisis (caused by *Giardia* sp.) and Toxoplasmosis (caused by *Toxoplasma gondii*). However, the protists have a diverse lifestyle from free-living forms to parasites of other animals, plants and even other protists (Adl et al. 2019). Furthermore, they are highly abundant organisms in any given location. For instance, current estimates suggested between 50,000 to 100,000 protist species in the sunlit surface layer of the global ocean, five to ten times more than bacteria and archaea combined (De Vargas et al. 2015). In terrestrial environments, the protists species number is more controversial, with no clear approximation of species number but an estimation of tens of thousands of individuals per gram of bulk soil (Finlay 2002, Stefan et al. 2014). In addition, protists play a key role in the ecosystems, such as the primary production carried out by photosynthetic protists, which is the base of food chains in freshwater and marine environments (Worden et al. 2015), while the heterotrophic protists are crucial in the nutrient recycling through decomposition in water, sediments, and soils (de Araujo et al. 2018). The advance in our knowledge of protistan diversity and distributions in nature is mainly due to the use of molecular approaches that allow sampling of thousands of protists at once.

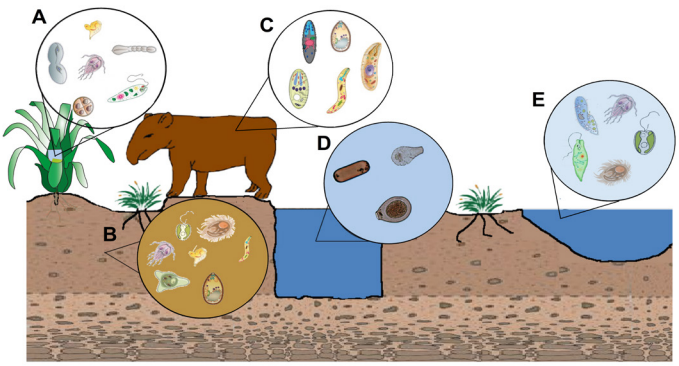


Figure 1. Schematic design of the main groups of protists found in the different environments in Neotropics. The circles represent the zoom showing the most common protists in each environment. A) the phytotelmata of bromeliads plants where was found several Ciliophora and Flagellates; B) soil protists that are mostly represented by Alveolata (mostly Apicomplexa), Dinophycea, Cercozoa and Ciliophora; C) the animal bodies that are occupied by parasitic protists such Apicomplexa; D) river environments that presents several species of Testade Amoebae; and E) lakes with the dominance of Discoba (mainly Euglenidaes), Ciliophora and Ochrophyta.

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2. Molecular approaches to assess protists diversity

The difficulty to sample, identify and test ecological and biogeographical questions in protists (and micro-organisms in general) are mainly due to the hard-taxonomic and time-consuming identification. The taxonomic classification based on morphological characters of almost "invisible" organisms is extremely limited and needs very experienced taxonomists. Several studies on protists using microscopy, incubation and biochemistry-based methods for morphological or functional identification have been done (e.g. Adl & Gupta 2006). However, due to the difficulty of identification, these studies are focused in a limited group such as testate amoebae (e.g. Lansac-Tôha et al. 2014) or planktonic ciliates (e.g. Negreiros et al. 2017).

In this context, high-throughput sequencing (HTS) of environmental DNA have revolutionized the taxonomic identification of microbes in above- and below-ground communities (Bik et al. 2012, Deiner et al. 2017), including protists (Santoferrara et al. 2020). One powerful method for diversity assessment in a given locality is metabarcoding. This technique improves the biodiversity assessment from microbes to mammals and, with that, promises innumerable advances in several fields, including ecology, biogeography and evolution (Compson et al. 2020). These advances follow developments in the identification of barcoding sequences of species and the existence of public and relatively highly populated reference sequence databases.

The idea of DNA barcode is based on that some DNA regions are conserved enough to have little intraspecific variation but variable enough to distinguish species, so the use of a specified DNA sequence provides taxonomic identification for a specimen (Blaxter 2004). The metabarcoding idea is similar, but instead of sequencing the DNA from one specimen, we can use environmental samples, such as soil, water and air to extract all DNA present in these samples to amplify by Polymerase Chain Reaction (PCR). After amplification, we sequencing a specific DNA region, that can be analyzed for all genetic variation with amplicon sequence variants (ASV; Callahan et al. 2017) or can be grouped by a threshold of similarity (usually 97%) in operational taxonomic units (OTUs; Blaxter et al. 2005), to identify a phylogenetic range of organisms from a set of specimens or even entire communities (Taberlet et al. 2018). From these molecular data it is possible to fill gaps about the knowledge of microorganisms in regions with sample deficits, such as the Neotropics, more efficiently, and consequently to better describe the patterns of diversity and distributions of microorganisms on a massive scale.

Material and Methods

We performed the literature review on the bibliographic databases from Web of Science and Google Scholar on April 9, 2019 and updating on August 28, 2020 using the keywords "Eukaryotes" OR "Protists" OR "Protista" AND "metabarcoding" OR "Environmental DNA" AND "Neotropics" OR "Neotropical". Subsequently, the literature was filtered, selecting only metabarcoding studies with continental protists from the Neotropics. We read all the articles resulting from this filtering and selected the important information, chronologically, for new advances in biogeography and ecology of Neotropical protists. In addition, we compiled information about which groups were identified and the locations of the collections, extracting the geographic coordinates of those locations when available.

Results

1. Biogeography of Neotropical Protists: What we know.

In the 90's the idea of microbial biogeography was guided for the famous sentence "everything is everywhere – but the environment selects" (Becking 1934, De Wit & Bouvier 2006). While the first proposition implies that microorganisms have dispersal abilities so high that the effects of past processes are suppressed, the second assumes that current environmental characteristics select different microbial taxa according to their habitat preferences (De Wit & Bouvier 2006). However, the recent advance of genetics allowed a deep sampling of microorganisms and this sentence started to be refuted throughout the world (Finlay & Fenchel 2005, Foissner 2006, Bass et al. 2007, Bates et al. 2013), including some Neotropical representability of samples (Bates et al. 2013, Lentendu, Buosi, et al. 2018). Although both cosmopolitan species were registered (de Vargas et al. 2015) and spatial patterns linked to environmental heterogeneity (Logares et al. 2018) were observed, biogeographical patterns related with long-term climatic and geological processes had already been identified (e.g. Singer et al. 2019). Most of the idea of over-dispersal and cosmopolite occurrence of microorganisms was due to the morphology-based classification that groups several species into a "morphospecies", misidentifying and not identifying some many other species. For instance, using metabarcoding analysis the dispersal limitation was identified in both terrestrial (Singer et al. 2019) and marine environments as the main factor structuring micro-eukaryotes communities (Logares et al. 2020).

The Neotropics presents strong biogeography patterns already recognized for vertebrates and plants (e.g. Alfaro et al. 2015, Esquivel-Muelbert et al. 2017, Carneiro et al. 2018). These biogeographical patterns are related with the highly diverse in both Neotropical biomes and habitats, such as the Andes mountains, tropical rainforests, seasonally flooded areas, savannas, and large dry areas (Hughes et al. 2012, Fig. 2; Olson et al. 2001). Among some of the known biogeographical patterns there are the west-to-east diversity gradient in Amazonia which was suggested been explained by marine incursions (Bates 2001, Lovejoy et al. 2006), bedrock geology (Tuomisto et al. 2017), mountain base formation (Hoorn et al. 2010), soil fertility (ter Steege et al. 2006, Hoorn et al. 2010) and diversification process driven by moisture (Silva et al. 2019). Another pattern is the endemism present in areas of Amazonia (Cracraft 1985, Ribas et al. 2012), Atlantic Forest (Costa et al. 2000, Silva & Vaz-de-Mello 2020) and Cerrado savanna (Azevedo et al. 2016). Other patterns include the high species turnover, the increase of community dissimilarity with geographical distance, also known as the distance-decay relation in the Neotropical forests (Bohlman et al. 2008), body-size habitat specialization (e.g. Hillebrand & Azovsky 2001, Lafferty & Kuris 2002, Woodward et al. 2005, Abades et al. 2010) and tree species density-dependent host-specific predation and parasitism (Janzen 1970, Connell 1971). Although in a limited number, some studies investigate such patterns for Neotropical protists using the metabarcoding approach (Table 1). Below we discuss each study and its advances individually.

Creer et al. (2010) were the first to sample Neotropical soil protists in one of the first environmental metabarcoding studies that evaluated the effectiveness of using Roche/454 sequencing technology to uncover the meiofauna in specific and complex eukaryotic communities in general. They sampled four sites in a secondary plot at La Selva Biological

Station in Costa Rica (Figure 2), as well as marine littoral benthic off the south coast of England. The 18S-rRNA primers that were used were designed to primarily amplify the Nematoda (Porazinska et al. 2009), which was the targeted meiofaunal taxon in this study. Although not designed to amplify all eukaryotes broadly, the primers also amplified numerous protist taxa. In their taxonomic assignment of the OTUs, they lumped all of the OTUs assigned to the protists as "protozoa" but did not break that group down into smaller taxa.

Later, Bates et al. (2013) published the first study targeting protists communities using a metabarcoding approach including the Neotropics being the first with the goal to investigate the diversity and biogeographic patterns of Neotropical soil protists. They sampled several regions in the Americas, including the Neotropics regions of the Caribbean, the Southwest Amazonia in Peru and the Northeast of Argentina (Figure 2). They found a biogeographical pattern for soil protists with just one of the 1,014 OTUs found having a cosmopolitan distribution. Furthermore, they found that the environmental factors, such as edaphic (e.g. pH) and climatic (e.g. temperature) variables, knowing to strongly affect the diversity of plants, animals and soil bacteria had just a moderate effect on soil protistan diversity, while soil moisture was the most important, yet moderate, edaphic variable to explain protistan diversity.

Even with Bates et al. (2013) showing the potential of molecular studies revealing the ecological and biogeographical patterns of protists in Neotropics, the next studies targeting protists were published four years later (Simão et al. 2017, Mahé et al. 2017). Simão et al. (2017) sampled four bromeliads phytotelmata (plant-container habitats) in the Atlantic Forest of Southern Brazil (Figure 2). They used primers to amplify the V9 region of the 18S-rRNA locus (Nolte et al. 2010) in the Illumina DNA sequencing platform to survey the eukaryotic communities, especially ciliates, inhabiting these bromeliads phytotelmata. They found remarkably diverse eukaryotic communities, with Arthropoda and Ciliophora showing the highest abundance. Moreover, a high abundance of both free-living protists (ciliate genera *Tetrahymena* and *Glaucoma*) and animal parasites (the apicomplexan gregarines and the genus *Trypanosoma*) was found. They argue that the high abundance of animal parasitic protists in bromeliad tanks indicates that these organisms and their vectors use phytotelmata as a common habitat. Their results showed a hidden diversity of eukaryotes in bromeliad phytotelmata, even with limited sampling (just four phytotelmatas), shedding light on the studies of plant-protist-animal interactions.

Mahé et al. (2017) sampled multiple lowland tropical rainforests with the aim of uncovering protistan diversity in Neotropical soils. They

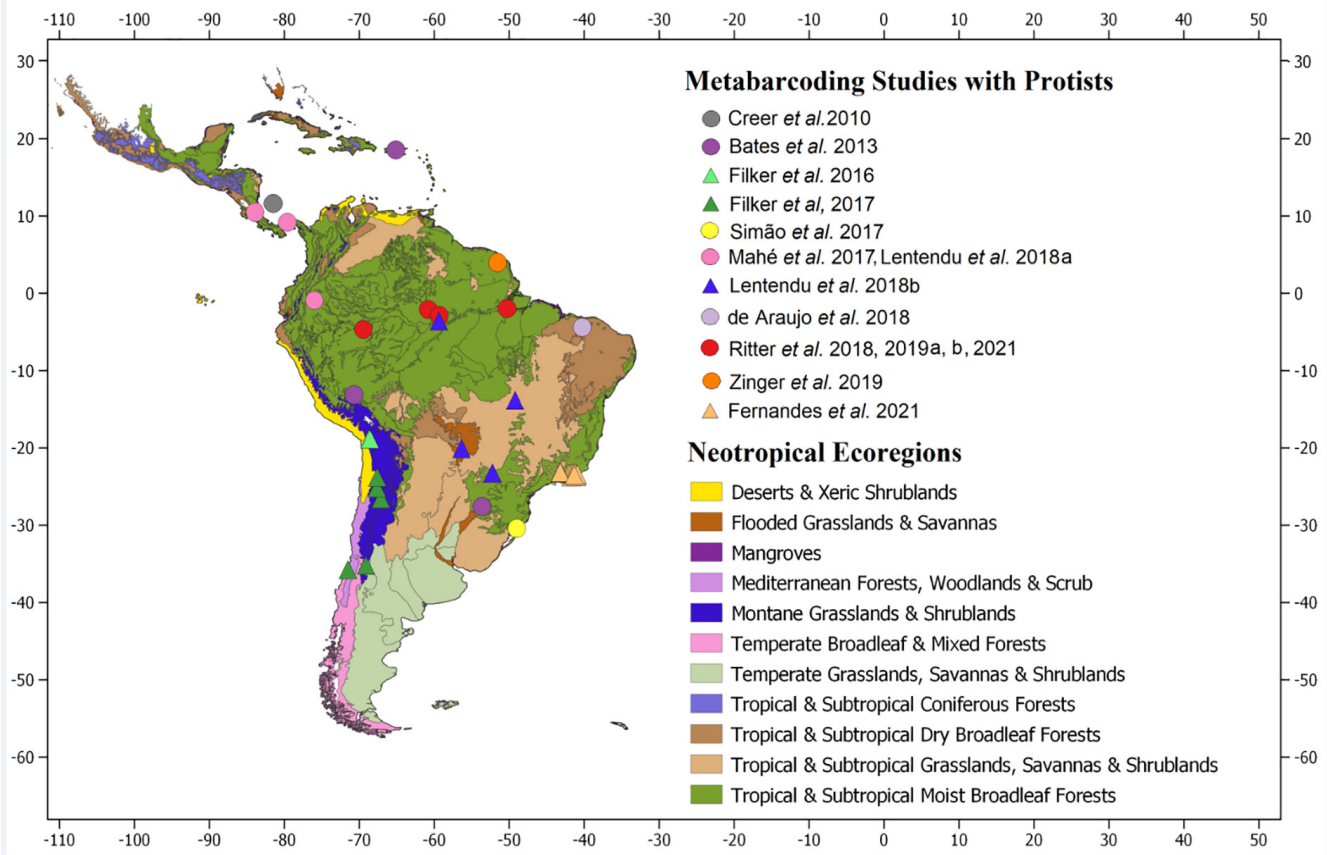


Figure 2. Neotropical Ecoregions with the areas that samples protists. The circles represent the studies location. Studies that used the same data are cited a by the side of the other. The yellow circle that represents Creer et al. (2010) is the side of Mahé et al. (2017) because they are done at the same station but not with the same methodology and the exact same locations. Squares represent terrestrial and triangles the aquatic studies. It is possible to observe the little number of studies on Neotropics with a concentration on forests. A big gap on sampling of other ecoregions such as Andes, dry areas, tempered Neotropical regions, deserts and xeric vegetation is notable. Ecoregions shape file from Dinerstein et al. (2017) licensed under CC-BY 4.0 (https://creativecommons.org/licenses/by/4.0/). Map was created with QGis v.3.6.2 (https://www.qgis.org/) licensed under CC-BY-SA 3.0 (https://creativecommons.org/licenses/by-sa/3.0/).

Table 1. Studies using metabarcoding approach that includes Neotropical protists. All studies amplified the nuclear ribosomal 18S rRNA small subunit (18S) gene, but different regions of this gene. The protistan taxa sampled are variable, and with the limited number of studies, type of sample and DNA region, generalization are hard.

Authors and year	Sample	Marker	DNA region	Protistan taxa
Creer et al. 2010	Soil	18S	not specified	Protozoa not specified
Bates et al. 2013	Soil	18S	not specified	Alveoata; Archaeplastida; Rhizaria; Stramenopiles
Filker et al. 2016	Lakes	18S	V4	Alveolata; Archaeplastida; Cryptophyta; Heterokonta; Stramenopiles
Filker et al. 2017*	Lakes	18S	V4	Archaeplastida; Amoebozoa; Apusozoa; Centroheliozoa; Cryptophyta; Excavata; Hacrobia; Haptophyta; Heterokonta; Opisthonka; Rhizaria; Stramenopiles; Telonemia
Mahé et al. 2017	Soil	18S	V4	Alveolata; Amoebozoa; Apusomonadidae; Archaeplastida; Centroheliozoa; Discoba; Hilomonadae; Opisthokonta; Perkinsea; Rizharia; Stramenopiles
Simão et al. 2017	Bromeliads	18S	V9	Alveolata; Archaeplastida; Discoba; Rhizaria; Stramenopiles
deAraujo et al. 2018	Soil	18S	V9	Alveolata; Amoebozoa; Archaeplastida; Excavata; Opisthokonta; Rhizaria; Stramenopiles
Lentendu et al. 2018a	Soil	18S	V4	Apicomplexa, Rhizaria
Lentendu et al. 2018b	Rivers	18S	V3	Alveolata; Archaeplastida; Centroheliozoa; Discoba; Opisthokonta; Perkinsea; Rizharia; Stramenopiles
Ritter et al. 2018	Soil and Litter	18S	V7	Alveolata; Amoebozoa; Archaeplastida; Rhizaria; Stramenopiles
Ritter et al. 2019a	Soil and Litter	18S	V7	Alveolata; Amoebozoa; Archaeplastida; Rhizaria; Stramenopiles
Ritter et al. 2019b	Soil, Litter and Insects	18S	V7	Alveolata; Amoebozoa; Archaeplastida; Rhizaria; Stramenopiles
Zinger et al. 2019	Soil	18S	V7	Protozoa not specified
Fernandes et al. 2021	freshwater and brackish	18S	V4	Alveolata (Ciliophora)
Ritter et al. 2021	Soil and Litter	18S	V7	Alveolata; Amoebozoa; Archaeplastida; Rhizaria; Stramenopiles

*Filker *et al.* 2017 did not split protistan sampled in Neotropical lake from African and European Lakes.

sampled over two years in older growth plots in La Selva Biological Station, Barro Colorado Island in Panama, and Tiputini Biodiversity Station in Ecuador (Figure 2). The primers that were used were designed to amplify the hypervariable V4 region of the 18S-rRNA locus in all eukaryotes. The protistan soil communities in all three countries were found to be dominated by OTUs taxonomically assigned to the parasitic Apicomplexa, which are all parasites of animals (Rueckert et al. 2019). Although some of these apicomplexans are from the Haemosporida, which includes *Plasmodium* and close relatives that infect arthropods and vertebrates, most of the apicomplexans are from the Gregarinasina the predominantly infect arthropods and other invertebrates (Adl et al. 2019).

Mahé et al. (2017) suggested that this massive diversity of apicomplexans could potentially contribute to more animal species coexisting together in the tropical forests because of density-dependent parasitism. This "Mahé-Dunthorn" hypothesis for animals mirrors the Janzen-Connell hypothesis (Janzen 1970, Connell 1971) for density-dependent in host-specific predation and parasitism contributing to more tropical tree species being able to coexist. It should be noted that there are other hypotheses for high animal species coexistence in tropical forests, but these have focused on how the increased number of plant species affects herbivorous insects, and to a lesser extent other arthropods (Novotny et al. 2006, Basset et al. 2012, Becerra 2015). However, not all of the high animal diversity in tropical forests can be explained or predicted by plants alone. In contrast to the apicomplexans, there were few parasitic oomycetes OTUs in the protists soil communities in three countries. Mahé et al. (2017) argued that there were too few oomycetes to be an important group for the density-dependent host-specific parasitism under the Janzen-Connell hypothesis. Although oomycetes were long thought to be major host-

specific parasites (Freckleton & Lewis 2006), they were also not found to have an effect on plant communities in a fungicide- and insecticide-study in Belize (Bagchi et al. 2014).

Using the same data as Mahé et al. (2017), Lentendu et al. (2018) evaluated the taxa-area relationships and the distance-decay relationships on soil Neotropical protists (Figure 2). While taxa-area relationships measure the increasing number of species or richness with the increase of sampled area (Arrhenius 1921, Drakare et al. 2006), distance-decay relationships focus on community composition and measures the increase of communities' dissimilarity with the increase of distance (Soininen et al. 2007, Morlon et al. 2008). These patterns were tested in macro-organisms in tropical forests showing a high alpha (local - Condit et al. 1996, Basset et al. 2012) and low beta (regional - Plotkin et al. 2000, Condit et al. 2002) diversity. For the parasitic and free-living protists, a similar high alpha and low beta diversity pattern was found among Neotropical forests (Lentendu, Mahé, et al. 2018). These results showed the congruence with Neotropical biogeographic patterns between macro and microorganisms and indicate that these organisms are spatially structured, at least in part, for the same general process. Yet, which process molds this Neotropical diversity patterns should be further investigated.

de Araújo et al. (2018) sampled Neotropical soils protists from transitions zones between the Tropical Dry Forests and the Brazilian Cerrado (Figure 2), the most diverse savanna in the world in terms of animals and plants (Furley 1999, Myers et al. 2000). They sampled four vegetation zones in the Sete Cidades National Park, Brazil. They also used Illumina sequencing technology with the aim of uncovering protistan diversity and co-occurrence in Neotropical savanna. The primers used were designed to amplify the hypervariable V9 region of the 18S-rRNA locus in all eukaryotes. Considering the vegetation coverage, the Brazilian Cerrado can be classified in four vegetation succession zones: from grass, grass and shrub, shrub and tree, and tree-dominated climax vegetation zone (Coutinho 1978, Furley 1999). These zones show a plant diversity gradient (de Araujo et al. 2018) and are also related with animal diversity (da Silva & Bates 2002, Mares & Ernest 2019) but see Nogueira et al. (2009) that shows a mismatch between vegetation and animal diversity in the Cerrado. Using this vegetation zone classification, de Araujo et al. (2018) compared soil protists richness and microbiome complexity, combining protists with prokaryotic and fungal sequences, through co-occurrence network analysis. Both protistan richness and microbial complexity were higher in tree-dominated zones (de Araujo et al. 2018). Also, the soil protists composition was different between zones with the plant-parasites and omnivores being more abundant in grass zones and animal parasites in grass-shrub zones (de Araujo et al. 2018). They suggested that protists are key soil microbial components and that vegetation succession towards climax vegetation, and consequently higher animal and plant diversity, is stimulated by higher loads of animal and plant pathogens. Furthermore, the authors suggested higher system stability with an increase in microbial complexity.

Ritter et al. (2019) also compared patterns between animals and plants with soil Neotropical microorganisms. They sampled litter and soils in 39 plots at four localities across a large longitudinal range in Brazilian Amazonia (Figure 2). Localities were selected to maximize west-to-east diversity gradient in Amazonia (ter Steege et al. 2003, Bass et al. 2010, Hoorn et al. 2010, Zizka et al. 2018) and the number of vegetation (habitat) types with characteristic biota and environmental conditions (ter Steege & Hammond 2001, Haugaasen & Peres 2006, Assis et al. 2015, Adeney et al. 2016, Myster 2016). These habitats include, in a decreasing macro-organisms' diversity gradient: non-flooded rainforests (terra-firme), forests seasonally flooded by fertile white waters (várzeas) or by unfertile black waters (igapós), and naturally open areas associated with white sand soils (campinas). They found that microorganisms' richness (including protists) and community composition differ significantly among localities and habitats, and that habitat type strongly structured microbial composition than locality. Ritter et al. (2019) detected a different habitat gradient from the expected, but as expected they found a west-to-east longitudinal gradient for microbial richness and community composition. The authors, in another study, explicitly tested the birds and tree diversity against protists (and other microorganisms) diversity (Ritter, Faurby, et al. 2019) showing that the currently accepted diversity patterns in Amazonia just partially match for macro and microorganisms.

Furthermore, these data were used to test soil chemical-physical variables to explain the richness and diversity of Amazonian microorganisms (Ritter et al. 2018). They found a positive correlation for pH and a negative correlation for soil organic carbon content with respect to microbial diversity, suggesting that physicochemical soil properties can predict, to some extent, microbial soil, and litter diversity in Amazonia. However, the author did not test physicochemical soil properties directly with just protistan diversity. In another study, the authors explored the ecological network of these soil and litter organisms and the importance of soil properties in the co-occurrence and co-exclusion patterns (Ritter et al. 2021). They found that mostly protists were specialists (occurring in just one habitat type), yet they were registered in the co-occurrence networks. Most protists recovered in the networks belong to the supergroup SAR (mostly Rhizaria, followed by Alveolata, and Stramenopiles) followed by Amebozoa (Ritter et al. 2021). The networks were dominated by bacteria, what can explain the highest predominance of protists that feed on bacteria and some on fungi (or both), with few eukaryotic parasites (Ritter et al. 2021). The soil properties do not explain protists co-occurrence neither their co-exclusion, although several soil properties are important factor in the co-exclusion networks considering all soil organism (bacteria, chloroplastida, fungi, metazio, and protists; Ritter et al. 2021).

Zinger et al. (2019) explored the role of environmental selection (i.e., soil properties, biotic interactions) and stochastic distance-dependent neutral processes (i.e., demography, dispersal) in shaping soil communities, including protists (Table 1), considering the effect of body sizes. Body size is known to be important to determine ecological and biogeographical patterns in the organisms (e.g. Hillebrand & Azovsky 2001, Lafferty & Kuris 2002, Woodward et al. 2005, Abades et al. 2010). In this study, they sampled 1,132 soils from a 12 ha Neotropical forest plot in Nouragues Ecological Research Station, French Guiana (Figure 2). They found that the distribution of protists is primarily stochastic, suggesting that, at least on a regional scale (12 ha), neutral processes are important factors to shape the protistan soil community. Other weak but significant drivers of the soil protistan richness and composition include aluminum, topography, and plant species. Together, these studies showed a mix of deterministic and stochastic factors shaping Neotropical protistan biogeography and ecology. However, such scale does not include historical factors and some biotic variation as

temperature and precipitation. It highlights the need of more extensive studies to understand the patterns and drivers of the distribution of Neotropical protists.

It is also worth mentioning that even more scarce is the knowledge about the biogeography of aquatic protists in the Neotropics. As far as we know, only four articles published so far have explored distribution patterns of Neotropical protists in continental waters through metabarcoding (Filker et al. 2016, 2017, Lentendu, Buosi, et al. 2018, Fernandes et al. 2021). Filker et al. (2016) studied planktonic protists of high-mountain lakes in the Chilean Altiplano using the V4 region of the 18S-rRNA locus, and Lentendu et al. (2018a) studied planktonic protists in Brazilian lakes using the V3 region of the 18S-rRNA locus. In these two articles, the authors have found that the freshwater protists were not globally distributed, but that different communities exhibited particular taxonomic compositions both within the Neotropical (Lentendu, Buosi, et al. 2018) and when compared with other regions of the globe (Filker et al. 2016). The third article explored the distribution of halophilic aquatic protists, using the V4 region of the SSU rDNA locus, in shallow salt ponds with different degrees of salinity from South America and Europe (Filker et al. 2017). In this study, differently from Eastern Antarctica (Logares et al. 2018), salinity was more important than geography in structuring protistan communities. Moreover, a high rate of endemism was observed. Recently, Fernandes et al. (2021) investigated the diversity of ciliates in freshwater and brackish environments along the Atlantic Forest using the hypervariable V4 region of the 18S-rRNA. They found that ciliate communities are more diverse in freshwater than in brackish environments, in agreement with Filker (2017). Interestingly, they also showed that a considerable fraction of the diversity of Atlantic Forest ciliate species detected by HTS is not represented in the molecular databases currently available, since they recorded 409 taxonomic units of ciliate at a 97% similarity level, but could attributed in only 144 species (Fernandes et al. 2021).

Discussion

1. Gaps and prospects: where do we go?

Although more than 350 articles using metabarcoding approaches that include protists are published until now (Santoferrara et al. 2020), for our knowledge, there are just 11 articles including terrestrial protists in the Neotropics (Figure 2). Among them, we have several sampling designs, different primers set and sequencing methods that make comparisons impossible (Table 1). To grasp the protistan biogeographic and ecological patterns, studies with standardized methods across the different ecoregions comparing the geographical and environmental distance are essential (Martiny et al. 2006).

Several factors are important to consider when using molecular tools in biodiversity assessments, including sampling design, DNA extraction protocols, choice of genetic marker, sequencing method, and data analysis procedures (Ritter, Häggqvist, et al. 2019, Zinger, Bonin, et al. 2019, Compson et al. 2020). For instance, a serious caveat for using a metabarcoding approach for protists biodiversity assessments is the primer choice that oversample some groups and under-sample others. Indeed, although the most used marker to sample protists with metabarcoding is the nuclear ribosomal 18S rRNA small subunit (18S) gene, many different primers in various combinations, targeting different 18S gene regions were used (Geisen et al. 2019, Santoferrara et al. 2020). Although just 11 studies are made for Neotropical protists, at least three regions of 18S gene were used. It is important to standardize the gene region and primers used to allow a more truthful comparison between studies.

Beyond standardizing primer to study in a broader scale Neotropical protists, new techniques, yet underexplored in the Neotropics, can help to unveil protistan biogeography and ecology and may overcome some biases of PCR. For instance, metatranscriptomics, the RNA sequencing of environmental samples, uses a primer-free approach that can pick up different parts of the same gene and uncover taxa not amplified by common amplicons (Geisen et al. 2015, Cristescu 2019). Other techniques include PCR-free DNA targeted-sequencing (Shokralla et al. 2016, Giebner et al. 2020), non-targeted, reduced-representation of whole genome (Hand et al. 2015), and whole-genome skimming (Coissac et al. 2016). In addition, single-molecule DNA sequencing technologies such as Oxford Nanopore and Pacific Biosciences (PacBio) can sequence bigger fragments allowing a better taxonomic resolution (Thompson & Milos 2011, Jamy et al. 2020, Ritter et al. 2020). The advances in molecular based studies have the potential to allow further investigation of the distribution of Neotropical protists and their drivers.

Another problem is the lack of sequence reference databases for several taxonomic groups, especially for the tropical regions (Zinger et al. 2020). Without such reference databases, the recovered sequences cannot be matched to resolved taxonomic levels (Fernandes et al. 2021). However, phylogenetic placement of lineages without sequence reference can uncover this caveat. For instance, lineages of short-branch Microsporidia were recently uncovered in a re-analysis of a metabarcoding study of Neotropical rainforest soils (Bass et al. 2018). Short-branch Microsporidia are a parasitic group, and it is expected that these environmental lineages are also parasitic, but no information about their ecology are available. Even so, using co-occurrence network analysis Doliwa et al. (2020) identified potential hosts of these lineages, showing that high-throughput DNA sequencing studies of biodiversity assessment form a powerful tool to explore entire communities and to understand their biotic/abiotic interactions.

Although it is hard to differentiate environmental filters from species interaction using co-occurrence network analysis (Blanchet et al. 2020), it could help to unravel the patterns and drivers of Neotropical protists diversity and distributions (Mikhailov et al. 2019). For instance, de Araujo et al. (2018) showed the relationship between plants and protists, adding the influence of different environmental zones and the co-occurrence patterns between microorganisms. Also, Ritter et al. (2021) showed a high co-occurrence of protists bacterivorous with bacteria in Amazonian soils. The study by Simão et al. (2017) reveals an important point for advances in studies of Neotropical protists, showing a hidden diversity of eukaryotes in phytotelmata of bromeliads, which can be explored in future studies covering other biotic interactions as well as comparing differences on environmental factors that affect these interactions along Neotropical ecoregions. These studies reveal the importance of studies embracing different interactions between protists and other organisms, as well as between environments as key components of the ecosystem. Therefore, there is still a gap to be filled in relation to these issues, representing good perspectives for future studies.

The Neotropical biogeographic patterns in protists seem to be, at least in part, congruent with that of macro-organisms (Lentendu, Mahé,

et al. 2018) despite the enormous difference between these groups. These similarities can be explained by similar filters or by biotic interactions, for instance, parasitic protists must have similar distribution of their hosts. These findings are extremely important and should be further investigated to understand whether they represent the same processes at work or if different processes lead to the same patterns between these groups. Common themes in Neotropical biogeography of macro-organisms, such as the impact of uplifting the Andes on the distribution and evolution of biotas (Hoorn et al. 2010) and the Great American Biotic Interchange (Stehli & Webb 2013, Antonelli et al. 2018) remain unexplored for Neotropical protists. In addition, there is a huge difference within the group itself, which deserves to be better explored.

Protists are a highly diverse group not just in terms of the number of species but also in terms of functional ecology that may affect their distribution (e.g. Weisse 2017, Adl et al. 2019). Then, which differences can we expect in the ecological and biogeographical patterns between different groups of protists? This type of approach would be remarkably interesting for the field. It is possible to explore the differences between biogeographic patterns in protists with different types of mobility (e.g. ciliate versus flagellate), reproduction (several types of asexual and sexual reproduction cycles), cell shape (several types of cell wall/theca), cell organization (unicellular, filamentous, and colonial) metabolism (heterotrophic, autotrophic and mixotrophic) and preferences habitat (wetlands, aquatic, terrestrial, and in association with other organisms).

In addition, phototrophs protists dominated freshwater systems while consumers dominated soil ecosystems (Logares et al. 2018, 2020). Yet, the extent importance of historical, geographical, and ecological factors to determine both aquatic and terrestrial protists is an important issue to be investigated to understand patterns and drivers of protists distribution. Considering the several types of continental aquatic ecosystems (freshwater and salt reservoirs, ponds, lakes, and rivers), it is important to compare the protistan diversity and composition in these environments in order to fully characterize this group in the Neotropics. Furthermore, protists are great models to generate new insights of Neotropical ecology and biogeography due to some species having high dispersal rates (Geisen et al. 2014) that allow quantifying the relative importance of niche and stochastic in structuring biological communities. On the other hand, endemic protists (Ryšánek et al. 2015) can be great models for testing the role of speciation, local adaptation and dispersal limitation (Singer et al. 2019, Logares et al. 2020). Also, due to their short generation time and consequently high speciation rates, they can potentially lead to the convergence of ecological and evolutionary time scales.

Another important gap to be filled in biogeographic studies of Neotropical protists is the sample coverage throughout this widely diverse region. Much of the tropical rainforest region of eastern South America (covering the North of the Atlantic Forest) still needs to be sampled and studied, in terms of metabarcoding (Figure 2). In addition, the temperate regions of the Neotropics also lack biogeographic studies using molecular protist approaches (Figure 2). It will also be important to fill the study gaps in Neotropical savannas, which have their only sampling in the Cerrado savannas as well as the Dry Forests. The altitude gradient, that strongly structure macro-organisms (Mateo et al. 2012, Li et al. 2019, Veintimilla et al. 2019, Villamarín et al. 2020) and some micro-organisms (Meng et al. 2013, Siles & Margesin 2016, Peay et al. 2017, Shen et al. 2020) may be widely tested for protists in Neotropical regions as these sample gaps are filled with metabarcoding studies.

Beyond the improvement in taxonomic and spatial coverage, it is also important to include abundance metrics since density-dependent factors are crucial to understand the biogeographic and ecological patterns (Martiny et al. 2006). Density-dependent factors include competition, predation and parasitism (Ricklefs 2008). Even so, most evidence for density dependence diversity control is plant-based (e.g. Hector et al. 1999, Hooper et al. 2005). However, a study showed that while niche complementarity and density-dependent effects can produce a diversity-productivity saturation curve in plants, soil-transmitted microorganisms were the major determinants of the relationship (Schnitzer et al. 2011). On the other hand, diversity in biological communities is also a historical product of immigration, diversification and extinction (Fukami & Morin 2003, Fukami et al. 2007). However, these processes are still poorly studied in protists, even less so in the Neotropical region. Therefore, we highlight the need for more extensive studies to understand the patterns and drivers of the distribution of Neotropical protists, covering these regions with gaps, as well as the points highlighted above.

Conclusions

Here we review the available information of metabarcoding for Neotropical protists and put it together to better understand their ecological and biogeographical patterns. Together our review shows that: 1) much more information is needed to explore the Neotropical protists diversity, ecology and biogeography; 2) Neotropical protists diversity patterns seem to be, at least in part, congruent with that of macro-organisms; 3) studies with focus on protist that split at least the main groups that could identify lineages and guilds are important to better understanding the ecosystem function of each group in their habitats; and 4) environmental variables weakly explain protists distribution in both regional to more broad scale, however, standardized studies including different biomes are necessary to better address these patterns.

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Author Contributions

Camila Duarte Ritter: Responsible for the concept and design of the study; collected, analyzed, and interpreted the data; write and reviewed the manuscript contributing to critical review, adding intellectual content

Arielli Fabrício Machado: Collected, analyzed, and interpreted the data; write and reviewed the manuscript contributing to critical review, adding intellectual content

Karine Felix Ribeiro: Collected, analyzed, and interpreted the data; write and reviewed the manuscript contributing to critical review, adding intellectual content

Micah Dunthorn: Responsible for the concept and design of the study; write and reviewed the manuscript contributing to critical review, adding intellectual content.

Conflicts of Interest

The authors declare no conflict of interest.

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Thematic Review

Research trends on elasmobranchs from the Brazilian Amazon Coast: a four-decade review

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Abstract: Elasmobranchs exhibit the biggest population declines among vertebrates, being considered one of the groups with the highest risk of extinction. The Brazilian Amazon Coast (BAC) is considered a priority area for elasmobranch conservation, as many species are endemic to the region, and most of them are threatened with extinction. The present study made a scientometric analysis using the IRAMUTEQ method (***I****nterface de* ***R*** *pour les* ***A****nalyses* ***M****ultidimensionnelles de* ***T****extes et de* ***Q****uestionnaires*) to evaluate the trends of research with elasmobranchs in BAC in the last four decades. Ten research trends were identified, highlighting "Biodiversity", "Reproduction", "Trophic Ecology" and "Conservation". However, most of the publications found are aimed at understanding the diversity and abundance of species in the region, with the number of studies focused on reproduction, feeding and other aspects of the biology and ecology of elasmobranchs in the BAC being less expressive. Although the research area "Conservation" stood out in the search, the amount of relevant information so that management and conservation measures can be implemented is still low. Lastly, despite following the global trend of studies with elasmobranchs between 2000 and 2010, investigations into the BAC need to advance, especially considering the poor level of basic information on most species (Biology and population dynamics) and the incomplete knowledge of specific composition of elasmobranch species in the entire area, aspects relevant to conservation and more applied studies that rely on more recent methodologies and technologies.
Keywords: *Biodiversity; Chondrichthyes; conservation; scientometric analysis.*

Tendências de pesquisa sobre elasmobrânquios na Costa Amazônica Brasileira: uma revisão de quatro décadas

Resumo: Elasmobrânquios apresentam os maiores declínios populacionais entre os vertebrados, sendo considerado um dos grupos com maior risco de extinção. O Litoral Amazônico Brasileiro (BAC) é considerado uma área prioritária para conservação de elasmobrânquios, pois várias espécies são endêmicas da região, e a maioria delas estão ameaçadas de extinção. O presente estudo fez uma análise cientométrica aplicando o método IRAMUTEQ (***I****nterface de* ***R*** *pour les* ***A****nalyses* ***M****ultidimensionnelles de* ***T****extes et de* ***Q****uestionnaires*) para avaliar as tendências de pesquisas com elasmobrânquios no BAC nas últimas quatro décadas. Dez tendências de pesquisa foram identificadas, destacando-se "Biodiversidade", "Reprodução", "Ecologia trófica" e "Conservação". Entretanto, a maioria das publicações encontradas é voltada para o conhecimento da diversidade e abundância das espécies na região, sendo o número de estudos voltados para a reprodução, alimentação e outros aspectos da biologia e ecologia de elasmobrânquios do BAC menos expressivo. Apesar da área de investigação "Conservação" ter se destacado na busca, a quantidade de informações relevantes para que medidas de manejo e conservação possam ser implementadas ainda é baixa.

Por fim, apesar de seguir a tendência mundial de estudos com elasmobrânquios entre 2000 a 2010, as investigações sobre o BAC precisam avançar, especialmente considerando o baixo nível de informações básicas sobre a maioria das espécies (biologia e dinâmica populacional) e o conhecimento incompleto da composição específica das espécies de elasmobrânquios em toda a área, aspectos relevantes para a conservação e estudos mais aplicados e que contem com metodologias e tecnologias mais recentes.

Palavras-chave: *Biodiversidade; Chondrichthyes; conservação; análise cientométrica.*

Introduction

Elasmobranchs are cartilaginous fish represented by sharks and batoids with about 1,200 species currently described (Weigmann 2016) distributed in tropical, subtropical, temperate, and cold waters. Species can be found from coastal regions to great depths across the planet (Compagno et al. 2005, Last et al. 2016, Nelson et al. 2016). Due to their high position in the aquatic food webs, sharks and batoids are important for ecosystem balance through lower-trophic level population control (Heithaus et al. 2010). They also contribute to food security in underdeveloped and developing countries, as well as generate income for traditional communities through fishing and tourism (Rigby et al. 2019). However, elasmobranchs suffer intense anthropic pressure, mainly due to overexploitation, bycatch, habitat loss, climate change, and pollution (Dulvy et al. 2017, Pacoureau et al. 2021). Due to their biological characteristics, such as low growth rates, late maturation, low fertility, and long gestation periods with small litters, sharks and batoids exhibit low population recovery potential (Vooren & Klippel 2005).

Brazil has one of the largest coastal zones on the planet, with approximately 8.500 km in length, of which 2.975 km are part of the Brazilian Amazon Coast (BAC), composed by the states of Amapá, Pará, and Maranhão (Pereira et al. 2009, Brazil 2018). The BAC is one of the most important fishing centers in the country due to its high productivity (Stride et al. 1992, Lessa et al. 1999a, Marceniuk et al. 2019). In 2011, BAC's fishing productivity was 138,864 tons, representing 25% of the national production (553,670 tons) (Brazil 2011). The BAC is also a global hotspot for maintaining and preserving elasmobranch stocks, mainly due to the high irreplaceable values of endemic species calculated for the region (Dulvy et al. 2014). Currently, 34 species of sharks and 36 species of batoids are found within the BAC (Marceniuk et al. 2019), highlighting endemic species at high risk of extinction, such as the Daggernose shark, *Isogomphodon oxyrhynchus* (Müller & Henle, 1839), and the Wingfin stingray, *Fontitrygon geijskesi* (Boeseman, 1948) (Wosnick et al. 2019), both occurring mainly on the Amazon Coast and listed respectively as Critically Endangered (CR) and Not Evaluated (NE) by the Chico Mendes Institute for Biodiversity Conservation (ICMBio 2018).

Understanding elasmobranchs' population dynamics in the region is imperative for management plans and conservation policies aiming at the recovery of Amazonian stocks and sustainability of local fisheries (Lessa et al. 2016). Therefore, the assessment of research trends helps to understand the evolution of scientific knowledge, the rise of new technologies, and to track new challenges for conservation. Globally, the most significant research trend in the last 15 years has been growth rate estimates and basic biometric data (Awruch et al. 2018), both relevant to demographic analysis, population status assessment, and stock assessments. Considering only South America, the main research trends were impacts of fishing, reproductive aspects, and taxonomy (Awruch et al. 2018). In Brazil, the activities proposed by the National Action Plan for the Conservation of Endangered Marine Sharks and Rays (PAN-tubarões) (ICMBio 2021) were based on information available from published studies and reports, and rely on specific actions aiming to improve fisheries management in the country to minimize the impacts on threatened species and raise awareness on fishers and civil society on the importance of elasmobranch conservation. Despite the great amount of information for BAC fauna, studies focused on elasmobranchs are still scarce, and inventories are outdated, posing an extra challenge for the implementation of management measures appropriate to the current scenario. As management/conservation strategies depend on the knowledge available, the present study aimed to survey available data to detect temporal research trends and to identify the knowledge gaps as a way to guide future studies and decision-making at the regional level.

Material and Methods

Past data from Bibliometric Indicators (IBs) were compiled from "white literature" (79%) obtained from indexing and reference databases using the keywords "Chondrichthyes", "Elasmobranch" "Amazon". The search also considered "gray literature" (21%), represented by publications with restricted distribution or without an editorial board, among them scientific-technical reports, academic monographs, and Master thesis (e.g., Almeida et al. 1998, Paz & Almeida 2003, Santos 2004). Studies from other countries that are part the Amazon coast were disregarded, to direct regional management and future studies focusing on the Brazilian territory. A total of 110 studies were selected (Supplementary material).

Data were analyzed using the software IRAMUTEQ (***I****nterface de* ***R*** *pour les* ***A****nalyses* ***Mu****ltidimensionnelles de* ***T****extes et de* ***Q****uestionnaires*) (Kami et al. 2016), to support data processing and statistical analysis through encoding and compartmentalization of literature, leading to the visual and graphical representation of essential information contained in the text (Camargo & Justo 2013). The software creates a dictionary of words through Chi-square tests ($\chi 2$), revealing the associative strength between words and their respective class.

The associative strength is considered to be significant when the test is greater than 3.84, representing p<0.0001 (Souza et al. 2018).

The analyzes of studies carried out with elasmobranchs within the BAC in the last four decades (1976-2020) was carried out in three stages: the definition of the textual corpus, established by compiling the 110 abstracts of the documents considered; the establishment of the Initial Context Units (ICU), and the establishment of the Elementary Context Units (ECU) (i.e., text fragments that are scaled by the software itself according to the size of the textual corpus and that are obtained from the ICUs). The units were set considering each document category (e.g., scientific articles, scientific-technical reports, or texts) and according to the scope of each study.

Next, a Descending Hierarchical Classification (DHC) was applied, compiling the data in a dendrogram that illustrates the similarities and differences between the word classes. This analysis aims to obtain UCE classes that, at the same time, have similar vocabulary, and vocabulary different from the UCE of other classes (Camargo & Justo 2013). A Similitude Analysis to detect co-occurrences and connections between the words, and a Word Cloud to simplify the vocabulary distribution through graphical representations based on word grouping with the highest number of repetitions were also used.

Results

1. Overall distribution and research trends

A total of 10 research trends were identified in the 110 studies considered. For some studies, more than one research trend was identified, totaling 134 entries for the textual analysis. The scope Biodiversity was the most significant (43.3%; n = 58), followed by Reproduction (14.9%; n = 20), Diet and Feeding Ecology (11.2%; n = 15), Conservation (10.4%; n = 14), Morphometry (5.2%; n = 7); Genetics (4.5%; n = 6), Fisher Ecological Knowledge (4.5%; n = 6), Age and Growth (3.0%; n = 4), Biochemistry (1.5%; n = 2), and Accidents with Fishers (1.5%; n = 2). This pattern indicates that Biodiversity, Reproduction, Diet and Feeding Ecology and Conservation were the most relevant research trends in the past four decades (Figure 1).

More specifically, in the first temporal window (1970-1980), most studies published (n = 8) were on Biodiversity, followed by Reproduction (n = 4), and Morphometry (n = 1). As for the second temporal window (1990), the same research trend was observed, with studies on Biodiversity (n = 10), Reproduction (n = 4) and Diet/Feeding Ecology (n = 3) being the most prevalent. One study on Morphometry was also retrieved, as well as two studies on Age and Growth. Considering the third temporal window (2000-2009), more research areas were covered, with a prevalence of studies on Biodiversity (n = 20), followed by Diet and Feeding Ecology (n = 11), Reproduction (n = 8), and Morphometry (n = 4). The remaining portion referred to Age and Growth (n = 2), Conservation (n = 2), and Genetics (n = 1). Lastly, for the fourth temporal window (2010-2020), studies on all research areas, except Age and Growth were performed, with the prevalence of Biodiversity (n = 20) and Conservation (n = 12), followed by Fisher Ecological Knowledge (n = 6), Genetics (n = 5), Reproduction (n = 4), Accidents with Fishermen (n = 2), Biochemistry (n = 2), and lastly Morphometry and Diet/Feeding Ecology (one study each).

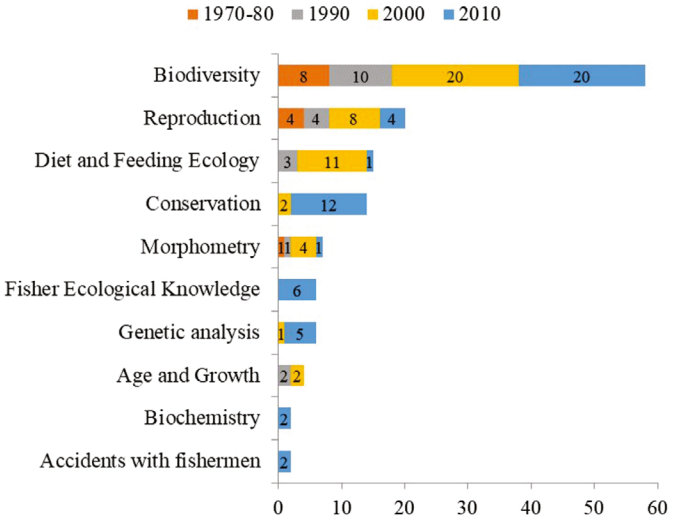


Figure 1. Research trends with focus on the scope of the literature published in the past four decades. Data is presented in number of trends (n = 10).

2. Descending Hierarchical Classification (DHC)

The corpus used in the DHC was categorized into 450 Text Segments (ECU), 15.572 occurrences (i.e., repeated words), 2.634 stemmed words (i.e., reduced forms that unite all the inflections of a verb), and 2.161 active forms (i.e., significant words). Of the 450 ECU, 381 were actively used, with a recovery rate of 84.67%, that is, the ECU that was used for DHC, and which continued under analysis. A percentage of use of 70% or more is necessary as if the retention is lower, the corpus is not adequate for this type of analysis, or that its content is very diverse, not allowing hierarchize the textual content (Souza et al. 2018).

The corpus was divided into two subcorpus and the dendrogram generated five classes based on similar vocabulary and the grouping of statistically significant words. Subcorpus 1 was divided into two distinct clusters: Class 1 + Class 5, and Class 3 + Class 4. Both clusters were formed from the classification of text segments according to their respective vocabularies and divided based on the frequency of reduced forms (words already lemmatized), obtaining ECU classes that present similar vocabulary to each other, and vocabulary different from UCE from other classes. In the cluster 1-5, the words with the greatest statistical association were: “Brazil”, “Maranhão”, “shark”, “tropical”, “coast”, “occurrence”, “elasmobranch” (19.2%; class 1), and “catch”, “longline”, “net”, “vessel” and “artisanal” (23.1%; class 5). This cluster indicates that 42.3% of the research carried out with elasmobranchs from the BAC were based on data from artisanal fisheries (Figure 2).

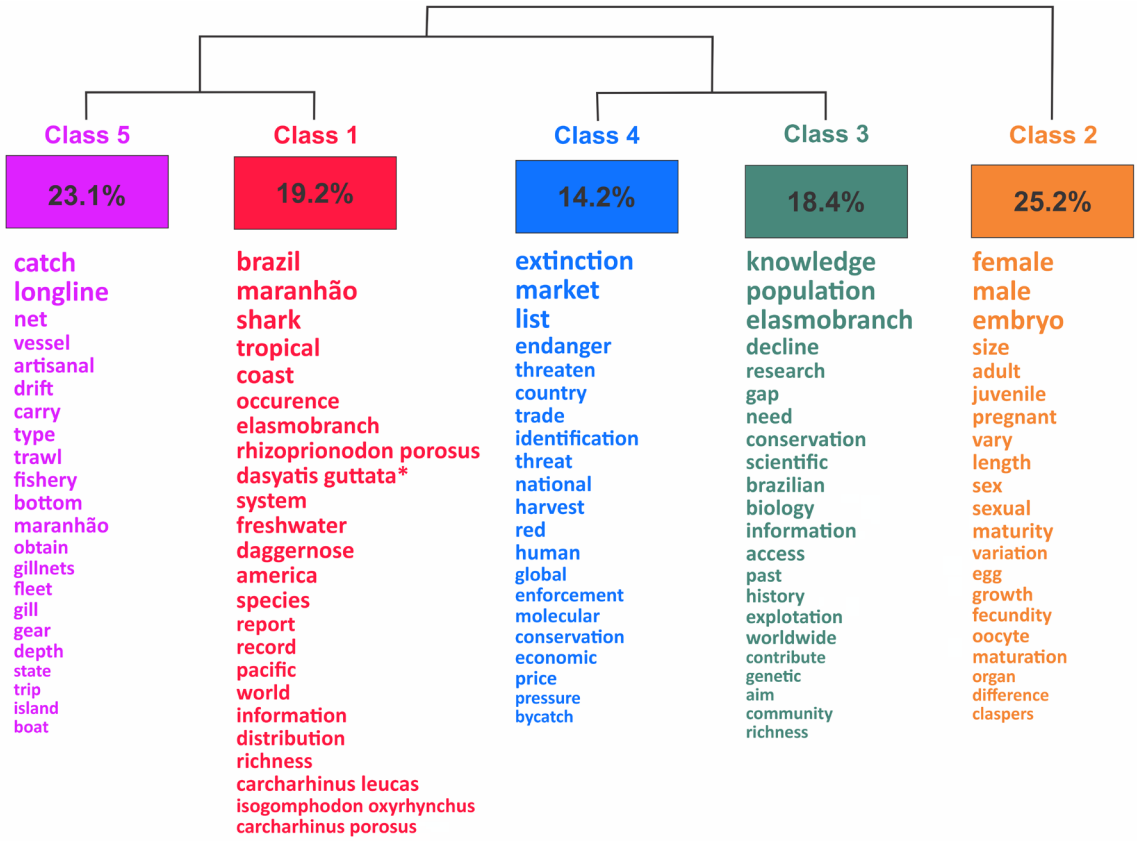


Figure 2. Dendrogram of the Descending Hierarchical Classification (DHC) of the words with the highest number of repetitions. *Reclassified as *Hypanus guttatus*.

In the cluster 3-4, the words with the greatest statistical association were: “knowledge”, “population”, “elasmobranch”, “decline”, “research” (18.4%; class 3), and “extinction”, “market”, “list”, “endanger”, “threaten”, “country”, “trade” e “identification” (14.2%; class 4). According to this cluster, 32.6% of research conducted with elasmobranchs from the BAC collected data relevant to threatened species management/conservation, based mostly on information available from commercial fisheries and local trade markets (Figure 2). Lastly, Subcorpus 2 was composed by a single Class (2), in which the words with the greatest statistical association were “female”, “male”, “embryo”, “size”, “adult”, “juvenile” and “pregnant”. This set of words indicates that 25.2% of the research carried out with elasmobranchs on the BAC aimed to elucidate basic reproductive aspects of species commonly caught by the artisanal fleet of the region (Figure 2).

3. *Similitude analysis*

Trough the Similarity Analysis it was possible to identify the connection between words distinguishing common parts from specificities in terms of significant words in the text. Thus, the tree of maximum similarity showed a high degree of connectedness between the words: “shark”, “Maranhão”, “Brazil”, “coast”, “female” and “male”. The highest occurrence was registered for the word “shark” (120), followed by the words - “Maranhão” (88), “Brazil” (87), “coast” (86), “female” (71) and “male” (60) (Figure 3). Moreover, there was a strong connection between the words - “species”, “fish”, “shark”, Maranhão” and “coast”, evidenced by the thickness of the connecting lines between them (Figure 3). These results also corroborate the research trends evidenced by class 2, represented by the strong connection between the words “female” and “male”, both being directly correlated with the words - “embryo”, “adult”, “juvenile”, “size” and “sexual” (Figure 3 and Figure 4).

In addition, the central block presents a set of the words most frequently associated in the literature analyzed, highlighting “fishery”, “specimen”, “capture”, “elasmobranch”, “study”, “*Rhizoprionodon porosus*”, “*Carcharhinus leucas*”, “*Carcharhinus porosus*”, “*Isogomphodon oxyrhynchus*”, “*Sphyrna tiburo*”, “*Dasyatis guttata*” (reclassified as *Hypanus guttatus*) and “*Aetobatus narinari*” (Figure 3). More specifically, it was possible to identify research trends at the species level, indicating which elasmobranchs were the main focus of investigations within the BAC so far. However, conclusions must be drawn with caution since most studies in the region rely on artisanal fishing, thus, it is likely that the most studied species are the result of opportunistic sampling, rather than preference for scientific investigations or priorities for conservation (Figure 3 and Figure 4).

4. *Word cloud*

The Word Cloud analysis allowed to group the words according to their frequency, corroborating both the DHC and the Similarity Analysis and reinforcing the research trends “Biodiversity” (e.g., elasmobranch, shark and study), “Reproduction” (e.g., female, male and reproductive) and “Conservation” (e.g., management, endanger, threat, and extinction) for the elasmobranchs of the BAC (Figure 4).



Figure 3. Connectedness of the most recurrent words in the literature analyzed based on the Similitude Analysis. Thicker lines represent more connectivity between words, and larger words represent greater occurrence.

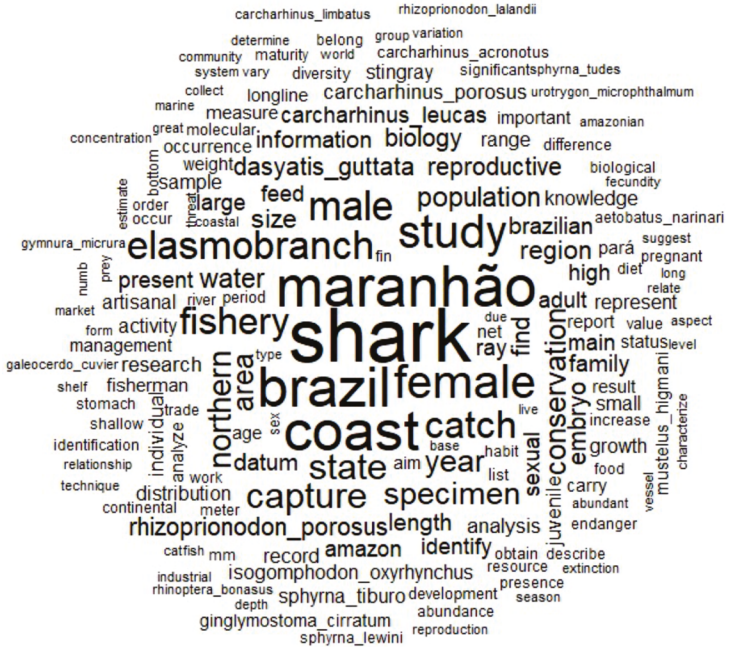


Figure 4. Word cloud with the most frequent words of the textual corpus. The size of the word indicates its frequency of occurrence, with larger words being the most representative.

Discussion

The analyzes performed in the present study showed a greater concentration of research trends within the fields of Biodiversity, Reproductive Biology, Feeding Ecology and Conservation, with different approaches over 44 years that will be discussed briefly next. Furthermore, considering the historical importance of the studies performed in the BAC for the Brazilian elasmobranch research scenario, and the status of the region as a global hotspot for elasmobranch conservation, our discussion will revisit some important milestones.

Studies on the diversity and abundance of species that occur in the region were predominant in relation to other areas of investigation during the entire temporal window evaluated in the present study. Even though it has been carried out since the 70s, studies on elasmobranch biodiversity reached its peak in the 2000s, and continue to be the main research trend in the region. In the global context of research trends with cartilaginous fish (Awruch et al. 2018), the topic biodiversity is not evident, but rather diluted into different subcategories within the identified clusters (i.e., population dynamics and spatial ecology). This indicates that at the BAC, the main research trend is different from that observed at the global level, being less applied and more focused on basic survey that have ceased to be a trend in other parts of the globe in recent decades. However, considering the challenges for elasmobranch research and conservation in Brazil, the need for baseline studies such as those prevalent in the BAC is understandable, especially in a scenario of lack of public investment for research and biodiversity conservation (Magnusson et al. 2018).

As for the second main research trend (i.e., Reproduction) there was a temporal constancy in the publications, with a peak in the 2000s. However, considering the diversity of species found in the region and the importance of reproduction data for management measures, the region still lack data for most species. Considering the global research scenario, the BAC follows the same trend, however, to a lesser extent. Interestingly, reproduction studies at the global level also peaked in the 2000s (i.e., 2002-2006), however, there was a very significant drop from 2011 onwards, indicating that this is no longer a global research trend (Awruch et al. 2018). In Brazil, and consequently also in the BAC, reproduction and diet studies are predominant (personal communication from the authors). Collecting basic biological data is imperative to guide conservation measures (Stroud & Thompson 2019) and also to pave the way for future studies using non-lethal methodologies (Awruch et al. 2008). However, few advances have been observed in this regard, since in the BAC, to date, reproduction data of studied species have not translated into guidelines for proper management. Thus, it is imperative that this topic continues to be investigated, but also be directed to policy makers in order to bring subsidies for species conservation.

Similar trend was observed to the topic "Feeding Ecology", with a peak in the 2000s that is also observed at the global scenario (Awruch et al., 2018). Despite being a traditional research area, it was only in the 1990s that the first study of diet for elasmobranchs was published in the BAC. In addition, the number of publications is negligible, configuring a large knowledge gap regarding trophic interactions and feeding patterns for most species that occur in the region. Moreover, to date, molecular studies (i.e., DNA barcoding of the stomach) that do not require the sampling effort of traditional studies (i.e., stomach content analysis) have not been carried out in the region, going against the global trend of elasmobranch feeding ecology. Thus, it is clear that, even identified as a research trend, more studies on this topic should be carried out, aiming to increase knowledge about the natural history of the species found in the BAC.

Lastly, although Conservation has stood out as a research trend at BAC, the amount of relevant information so that management and conservation measures can be implemented is still incipient. As noted for the global trend (Awruch et al., 2018), it was only from 2010 onwards that the topic "Conservation" started to represent a significant portion of published studies, indicating that BAC, despite generating few data towards conservation, follows the global trend. Interestingly, despite housing a large number of Conservation Units (i.e., Maranhão state) (IMESC 2020), and "Marine Protected Areas" being is a very relevant subtopic in the "Conservation cluster" of the global scenario, so far, no investigation on the importance of BAC marine protected areas for elasmobranchs was carried out, configuring a large knowledge gap about the effectiveness of this management strategy for sharks and batoids conservation. Furthermore, considering the identified subtopics in the global scenario (e.g., taxonomy, phylogeny, paleobiology, genetics, physiology, and parasites) (Awruch et al. 2018), the BAC is a region that still lacks studies, especially those that rely on more advanced methodologies and techniques. Furthermore, even though artisanal fishing is the main threat to elasmobranchs in the region, few studies focused on fisher's experiences and knowledge have been carried out, pointing to a historical neglect of traditional ecological knowledge.

As for specific information on BAC elasmobranchs, the first published studies date from 1976 and 1978 with a focus on exploring fishery resources in general. These studies, carried out by the Northeast Development Agency (SUDENE) and the Superintendence of Fisheries Promotion (SUDEPE), aimed to boost commercial fishing in the area, in addition to characterizing the profile of the artisanal fleet in the Maranhão State (SUDEPE 1976) and on the BAC continental shelf (SUDENE 1976), as well as to access the regional production chain (Emerenciano 1978). In this context, SUDENE carried out exploratory/experimental fishing campaigns and detected a great diversity and abundance of fish species with potential commercial value, including elasmobranchs. This suggested sustainable potential was based on the abundance of juveniles caught in coastal waters, highlighting *Galeocerdo cuvier* (Péron & Lesueur, 1822), *Ginglymostoma cirratum* (Bonnaterre, 1788), *Carcharhinus* spp., and *Sphyrna* spp. (SUDEPE 1976, Emerenciano 1978). The expectation was that juveniles were part of a larger stock in the high seas (SUDENE 1976). During this period, oceanic motorized fishing (back then with only a few adapted boats) began to explore deeper regions, with reports of large volumes of adults of *G. cuvier, Carcharhinus leucas* (Müller & Henle, 1839), *C. limbatus* (Müller & Henle, 1839) and *C. obscurus* (Lesueur, 1818) (SUDENE 1976). Such capture volumes strengthened the idea that shark fishing could be quite profitable.

It was in the 1980s that studies on elasmobranch abundance began to stand out, indicating that research groups realize that the artisanal fishing landing could be an opportunity to investigate this group of vertebrates with increasing commercial interest. The same occurred worldwide, but at a faster rate. Researchers from several countries began to focus their efforts on understanding the impacts of fishing through data from commercial landings (Thorson 1987), in addition to investing efforts in assessing regional diversity and abundance, so that temporal analyzes of fish stocks could be carried out (Wosnick et al. 2020a).

At the BAC, the first inventory registered 1.732 individuals of 22 species (belonging to former 13 shark and 9 batoid orders) (Lessa 1986). For sharks, the families Carcharhinidae and Sphyrnidae represented 77.4% and 18% (respectively) of the total captured, with higher occurrence of *C. porosus* (Ranzani, 1839) (43%) and *S. tiburo* (Linnaeus, 1758) (9.4%). For batoids, the catch in number was lower (4.6%). This inventory was very important as it expanded our knowledge on BAC diversity, being the first record of *C. porosus*, *C. acronotus* (Poey, 1860), *Hypanus guttatus* (Bloch & Schneider, 1801) (in figure 3 as former *Dasyatis guttata*) and *F. geijskesi* in the region. During this period, the suggested sustainable potential for shark capture was 23.500 tonnes/year (65%) of a total of 36.000 tonnes/year for fish in general (SUDENE 1984, Stride 1988) given the high biomass detected (Lessa 1986). This condition would depend on a series of factors to achieve this productivity, such as the gear used in the captures (e.g., gillnets and longlines, bait used and hook size). Concomitantly, Martins-Juras et al. (1987) published a list of estuarine fish from the state of Maranhão, with elasmobranchs representing 16.7% of the region's species richness. Studies on reproductive aspects also started in the 80s, generating relevant data for *C. porosus* (Lessa 1986-87), *I. oxyrhynchus* (Lessa 1987), and *Rhizoprionodon lalandii* (Müller & Henle, 1839) (Lessa 1988). Addressing fertility, growth rates, sexual maturation size, and minimum/maximum catch sizes is essential to ensure fisheries management and population recruitment (Lessa 1986, Awruch et al. 2018). However, in Brazil, management and conservation plans were not yet discussed at that time, as the impacts of fishing were not yet observed.

In the 90s, diversity studies were complemented by investigations about the population dynamics bringing new information on habitat use, population estimates, and basic biology data such as morphometry, diet, and age and growth (Almeida 1991, Batista & Silva 1995, Lessa & Almeida 1997, Lessa & Almeida 1998, Lessa & Santana 1998, Lessa et al. 1999a, Lessa et al. 1999b). The species list was once again updated, with the first report for *Urotrygon* spp. (Stride et al. 1992). During this period, the high productivity of shark fishing in the dry period has been reported, and guidelines for reducing juvenile catches through the use of larger meshes have been suggested (Stride et al. 1992). In fact, the use of smaller meshes was very harmful, particularly for *C. porosus* (Lessa et al. 1999a), a small-sized shark that uses the BAC as a nursery area (Lessa et al. 1999b).

While commercial fishing continued to benefit from the bycatch of *Rhizoprionodon porosus* (Poey, 1861) and *C. porosus* (Almeida & Carneiro 1999), studies on the reproductive aspects of *Sphyrna tiburo* (Silva & Lessa 1991, Lessa & Silva 1992, Menni & Lessa 1998), *S. tudes* (Valenciennes, 1822), *S. lewini* (Griffith & Smith, 1834) (Stride et al. 1992, Menni & Lessa 1998, Almeida et al. 2011), *C. acronotus* (Menni & Lessa 1998, Almeida et al. 2011) and *C. limbatus* (Stride et al. 1992, Menni & Lessa 1998, Almeida et al. 2011) were initiated. At the same time, in the global scenario, the first conservation measures were proposed (i.e., IPOA-Sharks, FAO), pointing to a growing concern of the international community regarding the sustainability of elasmobranch fishing.

In the early 2000s, the global research trends further diversified, with new technologies and methodologies being used (e.g., genetics and physiology). Additionally, studies of taxonomy and anatomy stood out, aiming at updating the group's phylogeny. In contrast, in South America (from 2002 to 2006), studies on reproductive biology and age and growth still prevail (Awruch et al. 2018). At the BAC, the 2000s were the most representative, with 46.2% of the total of studies being published in this period. The studies still focused on species diversity (Almeida & Vieira 2000, Alencar et al. 2001, Nunes et al. 2005) and reproductive aspects (Machado et al. 2000, Santos et al. 2000, Motta et al. 2009) but also diet (Silva & Almeida 2001, Costa & Almeida 2003) and aspects increasingly related to conservation (Almeida et al. 2006). The REVIZEE Program has also generated results causing an incalculable increase in the information available for elasmobranchs across the country, including the BAC. It was also in this decade that oceanic species were first described in the region, among them *Prionace glauca* (Linnaeus, 1758), *Isurus oxyrhincus* (Rafinesque, 1810), *I. paucus* (Guitart, 1966), *Alopias superciliosus* (Lowe, 1841), *A. vulpinus* (Bonnaterre, 1788), *Pseudocarcharias kamohara*i (Matsubara, 1936) and *Mitsukurina owstoni* (Jordan, 1898) (Asano-Filho et al. 2007, Almeida et al. 2008, Holanda & Asano-Filho 2008).

Also, it was in the 2000s that papers related to shark fishing as bycatch, the trade of threatened species, and industrial fisheries began to be published (Pinheiro & Frédou 2004, Lessa et al. 2006, Oliveira et al. 2007). More specifically, incidental capture in fisheries targeting *Scomberomorus brasiliensis* Collette, Russo & Zavala-Camin, 1978, *Cynoscion acoupa* (Lacepède, 1801), and *C. leiarchus* (Cuvier, 1830) also impacted elasmobranch populations mainly due to the low selectivity of fishing apparatus and large volumes of neonates and juveniles caught (Almeida et al. 2006). It was during this period that the Brazilian academic community established measures to deal with the reported declines, most of them resumed in the National Action Plan for the Conservation and Management of Elasmobranch stocks in Brazil (SBEEL 2005). Governmental measures also emerge, highlighting the Normative Instructions of the Ministry of the Environment (MMA) nº 05 (21/05/2004), nº 52 (08/11/2005), nº 166 (18/07/2007), nº 05 (MPA/MMA 15/04/2011), nº 14 (MPA/MMA 26/12/2012), nº 29 (MAPA 23/09/2015), and Ordinances nº 125 (04/12/2014), nº 445 (17/12/2014), nº 163 (08/06/2015), and nº 73 (26/03/2018).

In the last decade (2010 to 2020), new methodologies have emerged, with studies focused on spatial ecology (Feitosa et al. 2020), and the impacts of environmental pollution on BAC elasmobranchs (Chaves 2019, Wosnick et al. 2021a, Wosnick et al. 2021b). Social demands and food safety issues also stood out, with studies aiming to assess accidents with marine stingrays involving artisanal fishers (Dias et al. 2016, Carvalho et al. 2019) and the potential risks of shark meat consumption to human health (Souza-Araujo et al. 2021, with data collected in 2017). Furthermore, the use of molecular techniques enabled the identification of endangered species such as *G. cirratum* (VU), *Sphyrna mokarran* (Rüppell, 1837) (EN), *Mustelus canis* (Mitchill, 1815) (EN), *S. tiburo* (CR), *C. porosus* (CR), *S. lewini* (CR), *S. tudes* (CR) and *I. oxyrhynchus* (CR) being sold in the region (Feitosa *et al.* 2018). Besides, molecular studies aiming to assess the commercialization of batoids also indicated that threatened species were sold indiscriminately (Rodrigues-Filho et al. 2020). More recently, studies on population genetics and conservation physiology started, aiming to evaluate the effects of fishing on the genotypic and phenotypic diversity of species threatened with extinction in the region.

Given the absence of official fisheries statistics programs in the country, alternative approaches such as access to traditional knowledge from fishing communities (Martins et al. 2018) and participatory monitoring of landings or of catches are becoming more and more popular (Aragão et al. 2019, Shiffman et al. 2020, Giareta et al. 2021). In fact, management measures based on traditional knowledge, the socioeconomic and cultural demands of fishing communities, and the inclusion of fishers in research activities have proved to be promising tools for the conservation of threatened elasmobranchs (Martins et al. 2018, Wosnick et al. 2020b, Giareta et al. 2021). Moreover, data recently obtained with artisanal fishers at BAC brought important discoveries on spatial ecology and physiological tolerance of Amazonian species (Feitosa et al. 2016, Feitosa et al. 2019, Feitosa & Nunes 2020), emphasizing the importance of traditional knowledge not only for fisheries data access but also to guide future studies based on non-lethal methodologies (e.g., eDNA, Telemetry, BRUV's) (Awruch et al. 2018, Rigby et al. 2019; Shiffman et al. 2020).

Conclusion

The Brazilian Amazon Coast is a priority area for elasmobranch conservation at a global level. So, it is imperative that previous published data be easily available to stakeholders and decision-makers as a subsidy for the management of Amazonian species. Papers focused on basic reproductive aspects, which are extremely relevant data for adequate fisheries management, were a trend between the 1970s and 1990s, and along with data on diversity and abundance were the most common/traditional studies with BAC elasmobranchs. Along with the global trend to guide threatened species conservation, from the 1980s onwards, there was an increasing interest to collect fisheries data, in addition to assessing the local production chain and the commercial potential of elasmobranch fishing. From the 1990s, the impacts of commercial fishing in the region began to be quantified, indicating that elasmobranch fishing could not be as sustainable as initially proposed.

The panorama of studies presented here can assist researchers and managers, directing their efforts towards knowledge gaps that hinder decision-making and the effective conservation of threatened species. Much remains to be done, as the BAC is home to endemic species at high risk of extinction and also species listed as DD, for which information for proper risk assessment are not available. Moreover, the overall level of basic biology on species described in the region is low. Thus, future studies must consider research areas still neglected (i.e., fisheries management, spatial ecology, conservation physiology, local ecological knowledge, and applied conservation), specific demands for the creation of recovery plans (i.e., survival rates, sublethal effects of capture and alternative options to mitigate incidental capture and associated mortality) and also in generating basic biology data for species found in the region. Even though many data needed for proper conservation are lacking, it is imperative that the region starts to mobilize efforts to implement management measures, as waiting until the necessary data are available may be too late for some species, as is the case of *I. oxyrhynchus*, *S. tudes, C. por*osus and many others.

Lastly, as the REVIZEE Program was one of the reasons for the improvement in the available information on BAC elasmobranchs, it is imperative that initiatives as REVIZEE be promoted. Furthermore, current knowledge of most commonly employed fishing modalities (i.e., trawling and gillnetting) cannot be overestimated as the information is either scarce or out-of-data as most information was collected several decades ago, thus emphasizing the importance of resuming monitoring programs.

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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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Use of road underpasses by terrestrial tetrapods inside a protected area in the southeastern part of the State of São Paulo, Brazil

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Abstract: Roads, despite playing a key role in economy, begin or aggravate processes of forest fragmentation and lead to several species losing their natural habitats, acting as filters and barriers that impose challenges to animal locomotion. Wildlife crossings seek to reestablish the connectivity of the landscape. In general, after being installed, these passages need to be evaluated regarding their functioning. In this study, we present the results of monitoring the underpasses on Serra da Macaca Park Road (SP-139), which crosses Carlos Botelho State Park. The underpasses, constituted by bridges and culverts, were constructed after a license obtained to restore this section of the road. Camera traps were installed inside all crossing structures, and systematic samples were obtained through four field expeditions, with sampling efforts of 10 days each, between March 2018 and February 2019. The footprints found around the intersection structures were also considered. A two-sided Student's t-test was applied to verify differences in richness between the underpasses that have distinct types of margins. Differences in abundance were analyzed through the non-parametric Mann-Whitney test. A Whittaker diagram was generated according to the order of the species, from the most common to the rarest, while their diversity was estimated through Simpson's Diversity Index ($1 - D$). The Pearson correlation coefficient was used to study the interaction between diversity and altitude variation. We observed a richness of 16 species of terrestrial tetrapods, without any statistically significant differences between underpasses with dry or flooded margins. *Cuniculus paca* was the most abundant species, and higher altitudes presented the most diversity. We concluded that the underpasses located inside Permanent Preservation Areas (PPAs) of watercourses are essential to maintain the flow of animals beneath the road.
Keywords: *Wildlife crossing, mitigation, connectivity, PPA of watercourses.*

Uso de pontes e galerias rodoviárias por tetrápodes terrestres em uma área protegida na região sudeste do Estado de São Paulo

Resumo: As rodovias, apesar de exercerem um papel fundamental na economia, instauram ou agravam processos de fragmentação florestal e levam à perda de habitat. Atuam como filtros e barreiras, dificultando a movimentação animal. As passagens de fauna buscam restabelecer a conectividade na paisagem. Geralmente, após serem implantadas procede-se à avaliação do seu funcionamento. Nesse artigo nós apresentamos os resultados de um monitoramento do uso das passagens inferiores de fauna da Estrada Parque Serra da Macaca (SP-139), que atravessa o Parque Estadual Carlos Botelho. As passagens inferiores, representadas por pontes e galerias hidráulicas, foram concebidas através do licenciamento das obras de revitalização do trecho rodoviário. Armadilhas fotográficas foram instaladas no interior de todas as estruturas, e as amostragens sistemáticas ocorreram por meio de quatro expedições a campo, com um esforço amostral de 10 dias cada, entre março de 2018 e fevereiro de 2019. Os rastros encontrados no perímetro das estruturas de transposição também foram considerados. Os dados foram submetidos ao teste T de Student bicaudal, para verificar a diferença de riqueza entre as passagens inferiores com tipos distintos de margens. As diferenças de abundância foram analisadas pelo teste não paramétrico de Mann-Whitney. O diagrama de Whittaker foi gerado pela ordenação das espécies, a partir das mais comuns para as mais raras, enquanto a diversidade de espécies foi estimada pelo índice de Simpson ($1 - D$). O coeficiente de correlação de Pearson foi empregado para estudar a interação entre a diversidadade e a variação de altitude. Detectamos uma riqueza de 16 espécies de tetrápodes terrestres e não houve diferença significativa entre as passagens com margens secas e alagadas. *Cuniculus paca* foi a espécie mais abundante. Altitudes mais elevadas concentraram as maiores diversidades. Concluímos que as passagens inferiores alocadas em APPs de curso d'água são essenciais para manter o fluxo da fauna sob a rodovia.
Palavras-chave: *Passagem de fauna, mitigação, conectividade, APP de curso d'água.*

Introduction

The construction of wildlife crossings has gained traction recently (Van der Grift et al. 2013). There are two distinct groups of wildlife crossings: underpasses (e.g., culverts, linear tunnels) and overpasses (e.g., green bridges and canopy bridges). This type of measure seeks to restore connectivity between sectioned habitats (Ascensão & Mira 2007); in addition, fences are built to direct vertebrate species towards underpasses (Dodd et al. 2004, Abra et al. 2020).

Roads may isolate these populations, affecting migrations and increasing mortality due to collisions with vehicles (Lesbarrères & Fahrig 2012). Furthermore, roads act as barriers for animal movement and may lead to genetic impoverishment of many species (Holderegger & Digiulio 2010). The combined use of wildlife crossings and guiding fences is considered the best method to decrease roadkill rates (Mastro et al. 2008).

Other solutions with less proven effectiveness have been described, including repellents, awareness campaigns, installation of roadway lighting, population control of target species, reduced speed limits, caution signs, and the use of animal detection systems (Mastro et al. 2008, Glista et al. 2009, Grilo et al. 2010). The cost of implementation is one of the main criteria to choose measures to mitigate collisions (Glista et al. 2009), but inconsistent proposals may be imprudent and hence aggravate the problem (Bager & Fontoura 2013).

Several factors influence the effectiveness of crossing structures. Vegetation covering their entrances has a positive effect as it favors the approach of animals (Ascensão & Mira 2007), and the conditions inside (luminosity, humidity, temperature, soil, and noise) also affect their behavior (Glista 2009). It is ideal that the underpasses be implemented on locations already identified as animal crossing spots in the roads, such as trails (Foster & Humphrey 1995, Grilo et al. 2008).

Yanes et al. (1994) analyzed the movements of vertebrates across 17 culverts distributed along roads and railroads for a period of one year in central Spain. They found that smaller passages inhibited the movement of medium-and large-sized mammals. Sawaya et al. (2013) described a learning curve for some species to find wildlife crossings and start using them. In a long-term monitoring performed in the Banff National Park, brown bears and wolves took years to feel comfortable using the structures to move around (Clevenger & Waltho 2003).

This study aims to assess the use of underpasses across Serra da Macaca Park Road (SP-139) by terrestrial tetrapods and to compare the richness and abundance of vertebrates between two types of wildlife crossing structures.

Materials and Methods

1. Study area

Carlos Botelho State Park (PECB) (24° 08' S; 47° 58' W) is located in the southeastern part of the State of São Paulo, Brazil (Figure 1) and covers an area of 37.644 ha of tropical rainforest (Veloso et al., 1991, Lima et al., 2011). The uneven topography of the area ranges from 30 to 1.000 m above sea level (Dias, 2005). Serra da Macaca Park Road (SP-139), within the jurisdiction of the Department of Roads and Highways of the State of São Paulo (DER/SP), is a popular name for the 33-km section of the road that crosses the PECB. A project for paving and improving this road has been discussed in the scope of a management plan of the Park, which was approved considering that the project would contribute to supervision and visitation in the Protected Area. The redevelopment project of the road network used a type of eco-friendly paving system, composed of interlocked concrete blocks that allow the rainwater to drain, trap less heat, and produce noise from the friction between tires and pavement to scare the fauna away. Additionally, the project implemented a drainage system, regularized the condition of hillsides, and installed metallic defenses. Work on the project started in October 2013 and finished in November 2015. Serra da Macaca Park Road (SP-139), being inside a region of great environmental concern, received a broad set of measures to help prevent collisions between animals and vehicles. Therefore, in order to ensure the sustainability of the local traffic of vehicles, the region has 16 overpasses, in the form of canopy bridges suspended by a system of interlaced cables and ropes (Teixeira et al. 2013), 12 underpasses (eight bridges and four culverts), 30 speed bumps distributed throughout the section, adequate vertical signaling, and speed limits of 40 km/h, in addition to two fixed OCR (Optical Character Recognition) devices to help monitor the road, one at the entrance and the other at the exit of PECB. Moreover, the road is closed during the night.

2. Data collection and analysis

This study was approved by the Ethics Committee on the Use of Animals of the School of Veterinary Medicine and Animal Science at the São Paulo State University (UNESP / Campus Botucatu), approval n. CEUA 0127/2019. The project was also approved by the techno-scientific committee of the Forestry Institute State of São Paulo – Letter Cotec n. 485/2019 – and is properly included in the Brazilian National Management System of the Genetic Heritage and Associated Traditional Knowledge – Register SisGen n. A18FA6A. All statistical analyses were performed using the software "R" v. 3.5.1 (R Core Team 2020).

Data collection was performed in four field expeditions distributed from March 2018 to February 2019. Samplings were carried out in the dry and wet seasons. A systematic sampling of terrestrial tetrapods in 12 wildlife crossings (Figure 2) was performed through camera traps. In addition, footprints found by chance inside or around the structures were considered as evidence of locomotion of medium-and large-sized mammals. In order to avoid biases, footprint records were not considered as a valid method for the estimates of abundance and diversity.

Underpasses in Serra da Macaca Park Road (SP-139) are waterway crossings with height exceeding 1 m, resulting in a group of eight bridges and four culverts (Figure 2) of varied shapes and sizes. The underpasses were subdivided in two categories according to the characteristics of their margins: dry (P5, P6, P7, P8, P10, and P11) and flooded (P1, P2, P3, P4, P9, and P12).

A camera trap (Bushnell Model ZT820) was positioned at each sampling location. The cameras were screwed to the inner walls of the underpasses at 40 cm above the ground and programmed to function continuously during the entire sampling period. The cameras were installed for 10 days per expedition, totalling a sampling effort of 480 cameras/days.

Videos of a single species obtained from the same camera trap in intervals below 20 minutes were considered as a single record of the species (except when the images captured showed two or more individuals together).

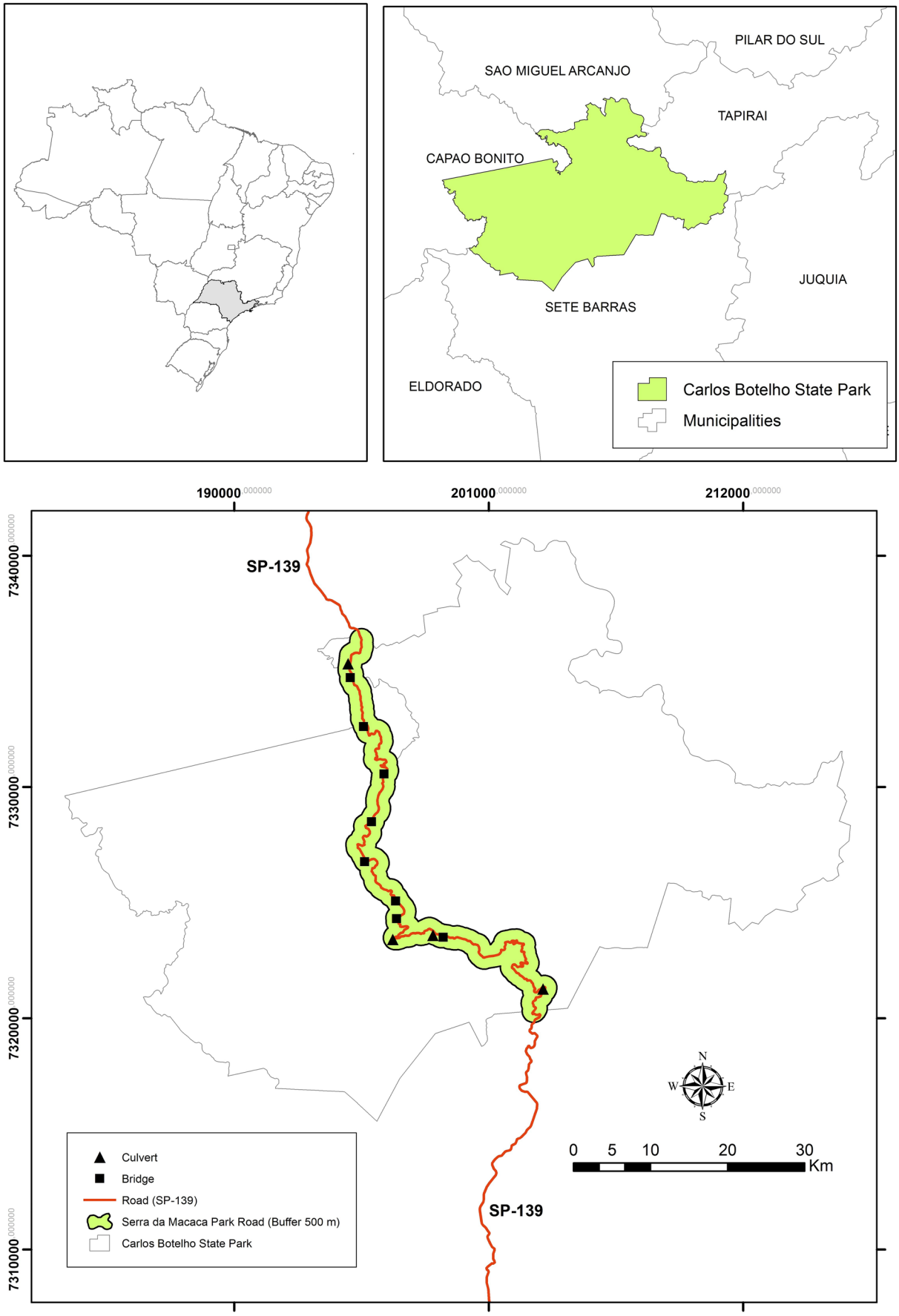


Figure 1. Location of the 12 wildlife crossings along Serra da Macaca Park Road (SP-139), which crosses Carlos Botelho State Park (PECB).



Figure 2. Existing wildlife underpasses along Serra da Macaca Park Road (SP-139). P1 – Circular culvert (Km 46+800), P2 – bridge (Km 56+200), P3 – rectangular culvert (Km 56+620), P4 – rectangular culvert (Km 58+714), P5 – bridge (Km 60+300), P6 – bridge (Km 61+300), P7 – bridge (Km 64+660), P8 – bridge (Km 67+100), P9 – bridge (Km 69+710), P10 – bridge (Km 73+850), P11 – bridge (Km 76+200), and P12 – circular culvert (Km 76+860).

A two-sided Student's t-test was applied to verify the differences in richness between underpasses with distinct types of margins, considering a 5% significance level. Assumptions of normality and homogeneity of the variances were also evaluated. The difference in abundance was analyzed based on the same parameters through a non-parametric Mann-Whitney test, as the data go against the normal distribution.

A Whittaker diagram was created to sort the species from the most common to the rarest, whereas species diversity in the underpasses was estimated according to Simpson's Diversity Index ($1 - D$). Pearson's correlation coeficiente was applied to study the interaction between species diversity and variations in elevation from the sea level. The P1 site was removed from this analysis, because there are no replicates for low altitudes.

The scientific names followed Piacentini et al. (2015), Abreu et al. (2021), and SBH (2021). Animals were identified based on existing literature (Sigrist 2009, Reis et al. 2006, Forlani et al. 2010). The conservation status of the species is in accordance with the List of Endangered Species of the State of São Paulo (São Paulo, 2018).

Results

We detected an abundance of 105 individuals in the underpasses during the study period, 8.57% of which were reptiles, whereas 15.24% were birds and 76.19% mammals. There were no records of amphibians. We observed a total richness of 16 species (Table 1 and Figure 3).

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Table 1. Taxonomic list (class, order, family, and species), registration method, abundance of individuals, richness of species, and Simpson's Diversity Index (1 – *D*) for the terrestrial tetrapods sampled in the wildlife crossings of Serra da Macaca Park Road (SP-139). Ct = Camera traps, F = Footprints. *Conservation status in the State of São Paulo (São Paulo 2018).

Taxon	Wildlife Crossings											
	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12
	Altitude (m)											
	101	570	582	629	711	737	772	770	755	753	703	712
REPTILIA												
Squamata												
Teiidae												
Salvator merianae (Duméril & Bibron, 1839)											Ct	
BIRDS												
Galliformes												
Odontophoridae												
Odontophorus capueira (Spix, 1825)								Ct				
Gruiformes												
Ralidae												
Aramides saracura (Spix, 1825)			Ct					Ct			Ct	
Passeriformes												
Formicariidae												
Chamaeza campanisona (Lichtenstein, 1823)					Ct			Ct				
Turdidae												
Turdus rufiventris Vieillot, 1818			Ct		Ct	Ct						
MAMMALIA												
Didelphimorphia												
Didelphidae												
Chironectes minimus (Zimmermann, 1780)			Ct	Ct		Ct						
Didelphis aurita Wied-Neuwied, 1826							F		F			
Philander quica (Temminck, 1824)			Ct	Ct	Ct	Ct			Ct	Ct	Ct	Ct
Cingulata												
Dasypodidae												
Dasypus novemcinctus Linnaeus, 1758										F	Ct	
Carnivora												
Felidae												
Leopardus pardalis (Linnaeus, 1758)*		Ct				F		Ct, F				
Mustelidae												
Lontra longicaudis (Olfers, 1818)*						F						Ct
Procyonidae												
Procyon cancrivorus Cuvier, 1798			Ct	Ct				Ct	F			
Perissodactyla												
Tapiridae												
Tapirus terrestris (Linnaeus, 1758)*								Ct		F	F	
Cetartiodactyla												
Cervidae												
Mazama sp.						F		Ct				
Rodentia												
Sciuridae												
Guerlinguetus brasiliensis (Gmelin, 1788)						Ct				Ct		
Cuniculidae												
Cuniculus paca (Linnaeus, 1766)	F	Ct	Ct	Ct	Ct	F	F	Ct	Ct, F	Ct	Ct	Ct
Abundance of individuals	**0**	**6**	**28**	**7**	**7**	**9**	**0**	**10**	**3**	**4**	**26**	**5**
Richness of species	**1**	**2**	**6**	**4**	**4**	**8**	**2**	**8**	**4**	**5**	**6**	**3**
Simpson's Diversity Index (1 – *D*)	**0.00**	**0.44**	**0.67**	**0.61**	**0.69**	**0.64**	**0.00**	**0.86**	**0.44**	**0.62**	**0.74**	**0.64**



Figure 3. Images of tetrapods obtained in the wildlife crossings along Serra da Macaca Park Road (SP-139). *Leopardus pardalis* (a), *Aramides saracura* (b), *Procyon cancrivorus* (c), *Chamaeza campanisona* (d), *Odontophorus capueira* (e), *Tapirus terrestris* (f), *Mazama* sp. (g), *Cuniculus paca* (h), *Lontra longicaudis* (i), *Philander quica* (j), *Salvator merianae* (k), *Turdus rufiventris* (l), *Chironectes minimus* (m).

The Whittaker diagram (Figure 4) shows that the most abundant species in the underpasses were *Philander quica* (Temminck, 1824) (n = 32) and *Cuniculus paca* (Linnaeus, 1766) (n = 28). *Cuniculus paca* also presented the highest distribution, being recorded in all crossing structures.

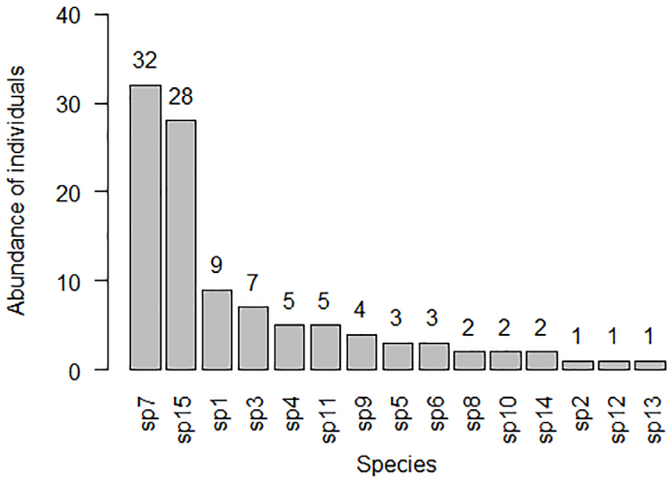


Figure 4. Whittaker diagram for the species of tetrapods sampled in the wildlife crossings along Serra da Macaca Park Road (SP-139): sp1 = *Salvator merianae*, sp2 = *Odontophorus capueira*, sp3 = *Aramides saracura*, sp4 = *Chamaeza campanisona*, sp5 = *Turdus rufiventris*, sp6 = *Chironectes minimus*, sp7 = *Philander quica*, sp8 = *Dasypus novemcinctus*, sp9 = *Leopardus pardalis*, sp10 = *Lontra longicaudis*, sp11 = *Procyon cancrivorus*, sp12 = *Tapirus terrestris*, sp13 = *Mazama* sp., sp14 = *Guerlinguetus brasiliensis*, sp15 = *Cuniculus paca.*

Among all underpasses studied, P1 and P7 showed the lowest Simpson Diversity Index, whereas P8 presented the highest (Table 1).

The underpasses with dry margins presented an average of ~2.2 more species than the passages with flooded margins (Figure 5), but this result is not statistically significant according to the t-test (t = -1.813, g.l.= 10, p = 0.100). There were also no statistically significant differences between the two types of passage regarding abundance (p = 0.574) (Figure 6).

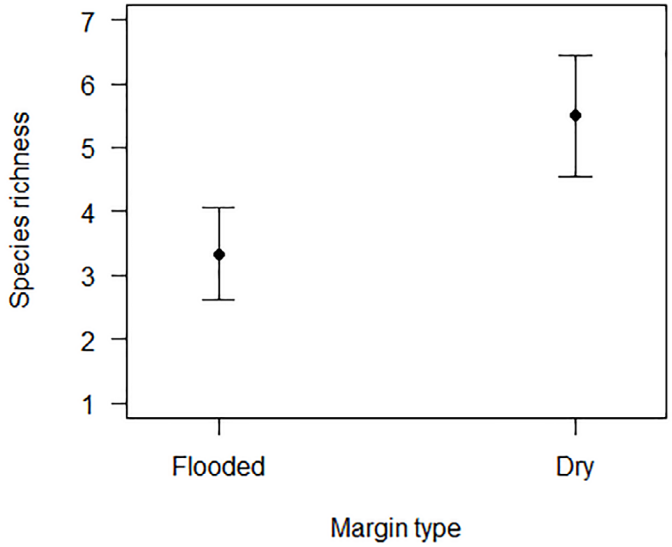


Figure 5. Mean (dot) and standard deviation (bar) for the richness of tetrapod species observed in the wildlife crossings along Serra da Macaca Park Road (SP-139), according to the type of margin. The differences are not statistically significant according to the t-test (t = -1.813, g.l. = 10, p = 0.100).

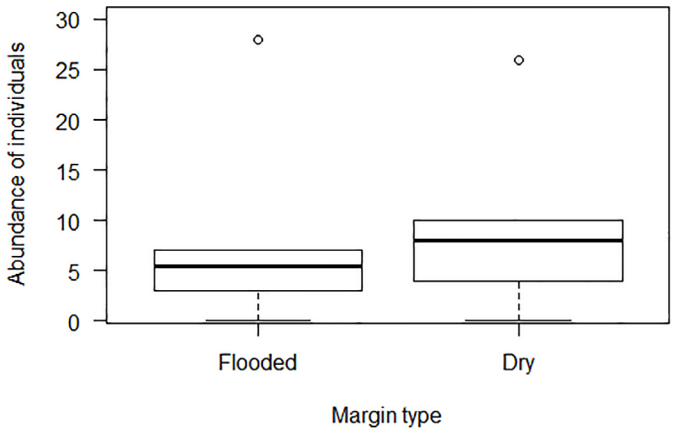


Figure 6. Boxplot of the variation in the abundance of individuals registered in the two groups of underpasses analyzed in Serra da Macaca Park Road (SP-139). The differences are not statistically significant according to the Mann-Whitney test (p = 0.574).

Based on the data obtained, we didn't observe correlation between diversity and altitude variables for the underpasses (Figure 7).

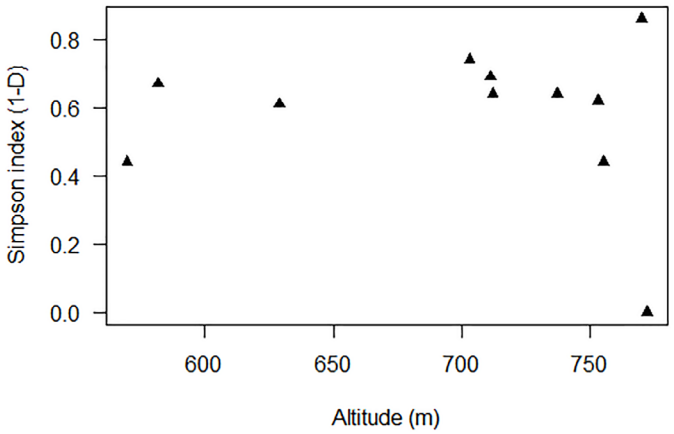


Figure 7. Correlation between the diversity of species and the altitude of the underpasses along Serra da Macaca Park Road (SP-139): r = -0.107 and p > 0.05.

Discussion

A bridge is a type of structure built to connect two points separated by valleys. Its main function is to facilitate the drainage of waterways and improve the flow. Secondarily, it allows the passage of animals beneath the roads (Van der Ree et al. 2007). Likewise, culverts and drainage galleries serve the same purpose for the local fauna (Clevenger et al. 2001).

One common characteristic to the underpasses of Serra da Macaca Park Road (SP-139) is the environment in which they are inserted. The structures were constructed in Permanent Preservation Areas (PPAs) of rivers and permanent streams, whose margins are valuable for connecting animal populations and consequently maintaining gene flow (Coutinho et al. 2013).

Even in the flooded crossing structures, the water level remained low during the samplings (0.15 m), and we believe this may explain why no statistically significant differences were observed when comparing the underpasses with dry and flooded margins regarding the abundance of individuals and richness of species.

The most expressive results obtained for medium and large mammals, when compared with other terrestrial tetrapods, are related to the sampling methods chosen.

Regarding the conservation status of recorded taxa, two of the species sampled are considered Vulnerable to extinction in the State of São Paulo: *Leopardus pardalis* (Linnaeus, 1758) and *Lontra longicaudis* (Olfers, 1818). *Tapirus terrestris* (Linnaeus, 1758) is Endangered, whereas *Odontophorus capueira* (Spix, 1825), *Chironectes minimus* (Zimmermann, 1780), and *Cuniculus paca* are Near Threatened.

Concerning the most abundant species, agoutis (*Cuniculus paca*) typically inhabit forested areas, living near watercourses. They have the habit of burrowing in hillsides and are common in locations where hunting them is forbidden (Reis et al. 2006). The southeastern four-eyed opossum (*Philander quica*) is also a forest species, positively associated to litter cover and watercourses (Moura et al. 2005).

The underpasses of Serra da Macaca Park Road (SP-139) do not have any guiding fences to direct animal passage through them. The choice for not installing this accessory measure was to prevent medium and large mammals from having their escape routes towards the PPAs blocked, during the day. At night the road is closed to traffic.

Simpson's Diversity Index measures the probability of two individuals, randomly chosen from the community, belonging to different species (Melo, 2008). According to this index, P1 and P7 were the underpasses with the lowest diversity. We recorded only one mammal species at P1, through the footprint method. A possible explanation for this result is the tourism in the location, which is easily accessible and highly sought in PECB.

Brocardo et al. (2012) stated that the high portion of PECB shows a lesser degree of anthropization in comparison with the rest of the protected area, which faces illegal extraction of heart of palm and hunting as the main challenges to the conservation of its biota. The greatest diversities were observed in the underpasses P8 and P11 respectively, both located in the highest parts of the mountain range. However, as shown, we did not find a correlation between the diversity of species and the altitude where the structures are located.

These results highlight the ecological importance of having underpasses on roads crossing Permanent Preservation Areas (PPAs) along watercourses. The presence of a thin layer of water on the ground of the crossing structures did not interfere with their use by the tetrapods, but it is worth noting that this type of environment was more favorable for species with higher affinity to wet areas. Therefore, we highlight the need to implement dry causeways inside flooded passages. Abra et al. (2020) found that some species of Brazilian mammals exclusively used passages with running water, whereas others preferred dry ones.

If, on the one hand, the absence of fencing did not inhibit the use of the bridges and culverts by the animals, on the other human presence in the crossing structures may compromise their functionality.

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Author Contributions

Francisco de Assis Alves: Substantial contribution towards the idealization and design of the study; contribution in collection, analysis and interpretation of the data; contribution in the preparation of the manuscript.

Carlos Roberto Teixeira: Contribution towards the idealization and design of the study; contributions with critical reviews, aggregating intellectual content.

Luciano Barbosa: Contribution in the analysis and interpretation of the data; contributions with critical reviews of the analyses.

Jairo Alves Júnior: Contribution with data collection.

Conflicting Interests

The authors declare they have no conflicting interests in what pertains to the publication of this manuscript.

Ethics

This study did not envolve experimentation with or collection of animals.

Data Availability

All information necessary to replicate this study is present in the text of the manuscript.

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