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Inventory

Fishes from Yarinacocha lake: an emblematic Amazonian ecosystem in the lower Ucayali River basin, Pucallpa, Peru

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Abstract: The Yarinacocha lake is an emblematic ecosystem of the Peruvian Amazon, representing the main point of fish landing and a tourist attraction in the city of Pucallpa. The wide fauna diversity in this area has made it the target of various studies, although for fish species most of them were focused on commercial species. In this work, we carried out the first ichthyofauna species inventory of the Yarinacocha lake, sampling throughout the entire lake during the rainy and dry seasons and considering also all previously recorded species deposited in the Ichthyological Collection of the MUSM with the same locality. A total of 164 fish species were recorded, representing 10 orders (plus Eupercaria), 34 families and 116 genera. Characiformes was the order with more species (68 spp., 41.5%) followed by Siluriformes (59 spp., 36%), Cichliformes (17 spp., 10.5%), and Gymnotiformes (8 spp., 4.9%). The most highly represented families, including almost 55.5% of the total diversity obtained, were Characidae (23 spp., 14%), followed by Cichlidae (17 spp., 10.4%), Loricariidae (14 spp., 8.5%), Pimelodidae (13 spp., 7.9%), Doradidae (13 spp., 7.4%) and Anostomidae (12 spp., 7.3%). From the total fish species recorded in this study, only 22 are considered protected species following the IUCN criteria and 109 species have commercial importance, including 90 ornamental species (54.8%). Our results contribute to the knowledge of the ichthyofauna of the Yarinacocha lake and can be used as a starting point for its conservation and sustainable management over time.

Keywords: *Amazon; Ichthyofauna; Inventory; Neotropical; South America.*

Peixes do lago Yarinacocha: um ecossistema amazônico emblemático na bacia do baixo rio Ucayali, Pucallpa, Peru

Resumo: O lago Yarinacocha é um ecossistema emblemático da Amazônia peruana, representando o principal ponto de desembarque de peixes e também uma atração turística da cidade de Pucallpa. A grande diversidade faunística nesta área a tornou alvo de vários estudos, embora para as espécies de peixes a maioria deles tenha sido focada em espécies comerciais. Neste trabalho, realizamos o primeiro inventário da ictiofauna do lago Yarinacocha, amostrando todo o lago durante as estações chuvosa e seca, e também considerando todas as espécies depositadas na Coleção Ictiológica do MUSM dessa localidade. Um total de 164 espécies de peixes foram registradas, representando 10 ordens (mais Eupercaria), 34 famílias e 116 gêneros. Characiformes foi a ordem com mais espécies (68 espécies, 41,5%), seguida por Siluriformes (59 espécies, 36%), Cichliformes (17 espécies, 10,5%) e Gymnotiformes (8 espécies, 4,9%). As famílias mais representadas, incluindo quase 55,5% da diversidade total obtida, foram Characidae (23 spp., 14%), seguido por Cichlidae (17 spp., 10,4%), Loricariidae (14 spp., 8,5%), Pimelodidae (13 spp., 7,9%), Doradidae (13 spp., 7,4%) e Anostomidae (12 spp., 7,3%). Do total de espécies de peixes registradas neste estudo, apenas 22 são consideradas espécies protegidas seguindo os critérios da IUCN e 109 espécies têm importância comercial, incluindo 90 espécies ornamentais (54,8%). Nossos resultados contribuem para o conhecimento da ictiofauna do lago Yarinacocha e podem ser utilizados como ponto de partida para sua conservação e manejo sustentável ao longo do tempo.

Palavras-chave: *Amazonia; América do Sul; Ictiofauna; Inventário; Neotropical.*

Introduction

The Peruvian Amazonian ichthyofauna has been the object of numerous and in-depth studies, which register more than 800 species (Ortega et al. 2012). Among lotic water bodies, the most important assessments include the Amazon (Goulding et al. 2003), Huallaga (Ortega et al. 2007), Madre de Dios (Barthem et al. 2003), Aguaytía (Quezada et al. 2017) and Las Piedras (Carvalho et al. 2011) River basins. Likewise, the lentic aquatic ecosystems of the Peruvian Amazon play an important ecological role and contribute to the support of economic activities of the local population (García-Vásquez et al. 2009) due to its value as a source of hydrobiological resources. This is partially the consequence of oxbows migration, which promotes this enormous diversity forming sinuous rivers and lakes during the course changes (Nagel et al. 2022), and the flood pulses that comprise annual oscillations of the average water level (Junk et al. 1989), allowing the interconnection of lakes and small water bodies during the floods (Bartletta et al. 2010).

The Yarinacocha lake, located in the district of Yarinacocha, department of Ucayali, known regionally as “cocha” or “tipishca” by shipibo-conibo populations, is approximately 20 km long, with an area of 13.4 km^2, a maximum depth of 19 m and average width of 650 m (Campbell et al. 2017). Its meandering origin formed by the erosion of Ucayali River banks (Neuendorf et al. 2005) has allowed the occurrence of an enormous diversity, not yet fully monitored, but which supports important fishing activities in the region, local consumption and tourist destination (García-Dávila et al. 2018). During the floods of the Ucayali River in January, February and March, the entire lake acts as a riverside highway for trade and transportation (Campbell et al. 2017). The rest of the year it is supplied with water from small tributaries that can be streams or “caños”, which are small channels that connect the lake with other water bodies and represents a key habitat for many species of fish reproduction (MINAM 2021). However, as a result of the human populations growth on the riverbanks (hamlets, communities and the population of the Yarinacocha district), restaurants and tourism, the use of toxic substances in illegal fishing and by hospital wastewater that fail biodiversity and human health (personal comments by José Riofrío), this ecosystem is highly polluted by sewage and solid waste that could affect biodiversity (Rondon-Espinoza et al. 2022). These characteristics and threats as a whole, give Yarinacocha lake an emblematic meaning covering cultural, economic and ecological aspects worthy of being preserved and studied.

Scientific knowledge of the fish species composition at Yarinacocha lake is limited. A recent study reports that the diversity of fish species that arrives at the Yarinacocha lake landing stage, including a large part of the Utuquinía and Callería sub-basins, and to a lesser extent Loreto and Aguaytía-San Alejandro (Salazar-Ramirez et al. 2021). In their results, 63 species between 2015 and 2019 were reported, being the most abundant “carachama” (Loricariidae), “piro” (Doradidae), “palometa” (*Mylossoma* spp.) and “sardina” (*Triportheus* spp.) all of them recorded only as common names that may include several species. Other studies include monitoring of fishing landings in the city of Pucallpa (Vela et al. 2016) and characterization of commercial fisheries in the Ucayali River basin (Zorrilla et al. 2016), without offering precise data on the ichthyofauna of the lake. Also, these studies focus on large fishes with commercial interest, while neglecting the smaller species that contain the highest biomass (Barletta et al. 2010) and to date, no other publication has reported the total diversity of the ichthyofauna of the Yarinacocha lake.

This lack of monitoring and rapid identification tools for the fish fauna of Yarinacocha lake encourages the existence of erroneous records in fishing statistics (García-Dávila et al. 2018) and could be covering up the depredation of the fish populations.

For the above stated, we have formulated as the main purpose of this work to present the first fish species checklist of Yarinacocha Lake, updating the information of continental catalogs (Reis et al. 2003), species threatened status (IUCN 2022) and economic importance of species reported.

Material and Methods

A total of 15 sampling sites were evaluated (Fig. 1, Table 1), covering variable environments inside Yarinacocha lake including streams, water channels and shores (Fig. 2).

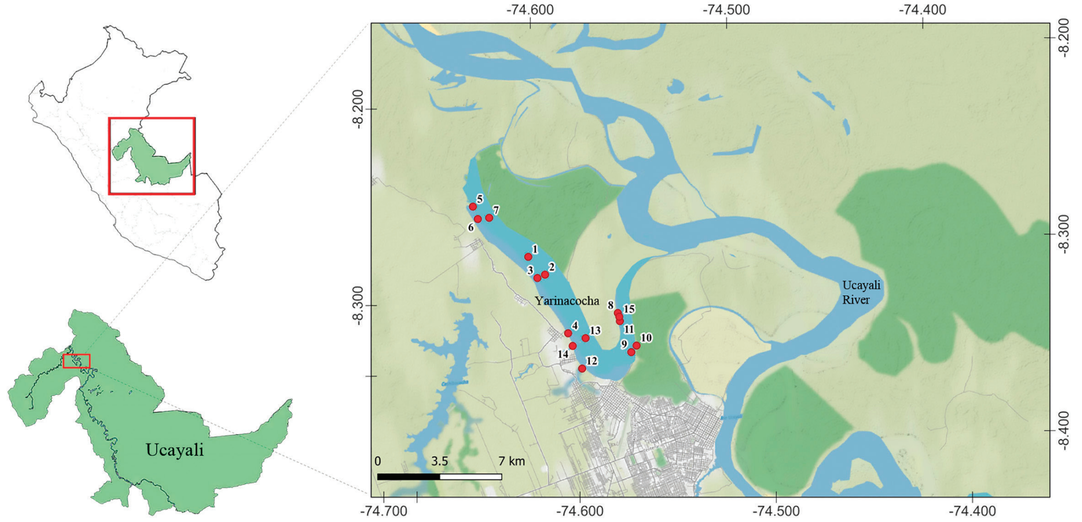

Figure 1. Map of Yarinacocha lake, Ucayali, Peru showing each collecting site (red circles). Numbers follow Table 1 and Fig. 2.

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Table 1. Sampled localities in the Yarinacocha lake.

Site	Latitude	Longitude	Hábitat
1	–8.283635°	–74.613530°	Shore
2	–8.293595°	–74.605929°	Shore
3	–8.294893°	–74.610005°	Lake
4	–8.324666°	–74.597307°	Shore
5	–8.255102°	–74.639067°	River canal
6	–8.261677°	–74.637215°	Lake
7	–8.261672°	–74.631376°	Stream
8	–8.317004°	–74.570915°	Lake
9	–8.337667°	–74.566134°	Shore
10	–8.334606°	–74.563095°	Stream
11	–8.321236°	–74.570293°	Lake
12	–8.343393°	–74.592056°	Stream
13	–8.328085°	–74.588685°	Pool
14	–8.331376°	–74.595665°	Shore
15	–8.318975°	–74.570368°	Shore

Sampling efforts occurred during the start of the rainy season in October 2020 and in the dry season in July 2022, mostly during daylight. The collection of specimens involved bottom trawls of 10 and 20 m nets with 5 mm internodes, used on the beaches and areas with vegetation, trunks and leaves; cast nets of 15 m in open areas and channels; and gillnets of 30 m, blocking the passage of fish during the beginning of the day. Obtained specimens were anesthetized in a clove oil solution, muscle tissues were fixed in 96% ethanol (for molecular studies), vouchers and other specimens were fixed in 10% formalin by 48 hours and then preserved in 70% ethanol. Expeditions had a Fish Collection Permit for research purposes under PRODUCE license number 132/2021.

Species identifications to the lowest taxonomic level were conducted consulting the taxonomic literature (Galvis et al. 2006, Queiroz et al. 2013, van der Sleen & Albert 2018) and identification keys for Characiformes (Géry, 1977; Vari, 1991; Malabarba, 2004), Siluriformes (Burgess, 1989; Albert, 2001; Littmann et al. 2021), Cichliformes (Kullander, 1986; Kullander and Ferreira, 2006; Arbour et al. 2014) and Gymnotiformes (Mago-Leccia, 1994; Crampton et al. 2016; de Santana et al. 2019); and valid names were confirmed following Fricke et al. (2022). Classification follows the

Figure 2. Sampled localities in Yarinacocha lake. Numbers 1–12 follows Table 1.

current phylogenetic arrangement of bony fishes sensu according to Betancur et al. (2017) and for Characiformes the classification proposed by Oliveira et al. (2011). To corroborate geographical distribution of species we used CLOFFSCA (Reis et al. 2003), digital platforms like SpeciesLink (http://www.splink.org.br/) and FishNet2 (http://www.fishnet2.net/) and Nijssen and Isbrücker (1986) for additional taxonomic revisions and species descriptions. Vouchers were deposited in the Ichthyology Collection of Museo de Historia Natural of the Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM).

Specimens collected in the Yarinacocha lake by previous expeditions and deposited in the MUSM Fish Collection, were also recorded after their identifications were verified. In our results, only native species were included without considering invasive or exotic species because they lacked vouchers in the scientific collection; however, its presence was discussed due to previous reports from the Ministerio del Ambiente (MINAM).

The commercial species were classified into ornamental fish (IIAP 2011, García-Dávila et al. 2020) and fish for consumption (García-Dávila et al. 2018). The threatened status of the species was derived from IUCN (2022) criteria available in https://www.iucnredlist.org/.

Results and Discussion

The total of previously reported species is 63 (Vela et al. 2016; Zorrilla et al. 2016; Salazar-Ramirez et al. 2021) reporting only Characiformes and Siluriformes. However, as indicated above, those studies did not include precise data on the location of capture, making impossible a comparison of the total richness previously reported in relation to the results presented here which only include fishes from Yarinacocha lake.

Our contribution carries a very high value due to the fact of representing the first ichthyofauna inventory of Yarinacocha lake in its entire extension, assessing a wide range of habitats, including almost all possible species, not only those with commercial value (Fig. 3). In this manner, a total 164 fish species were recorded (Table 2) representing 10 orders (plus Eupercaria), 34 families and 116 genera.

The order with the most species richness was Characiformes with 68 species (41.5%) followed by Siluriformes with 59 species (36%), Cichliformes with 17 species (10.5%) and Gymnotiformes with eight species (4.9%). These orders represent 92.6% of the total species (Fig. 4). Clupeiformes, with four species, and remaining five orders (plus Eupercaria), with one or two species for each, represent 7.4% of total species. The most highly represented family was Characidae with 23 species (14%), followed by Cichlidae with 17 species (10.4%), Loricariidae with 14 species (8.5%), Pimelodidae with 13 species (7.9%), Doradidae with 13 species (7.4%) and Anostomidae with 12 species (7.3%); together represent 55.5% of the total species (Fig. 5). As in the Neotropical freshwater habitats, the ichthyofauna belongs to the Ostariophysi and in South America mostly represented by Characiformes, Siluriformes and Gymnotiformes (Reis et al. 2016). In the Peruvian Amazon, the families Characidae, Loricariidae y Cichlidae, concentrate the greatest diversity of species (Ortega et al. 2012) and represent some of the dominant families in the composition of Amazonian species (Dagosta & de Pinna 2019).

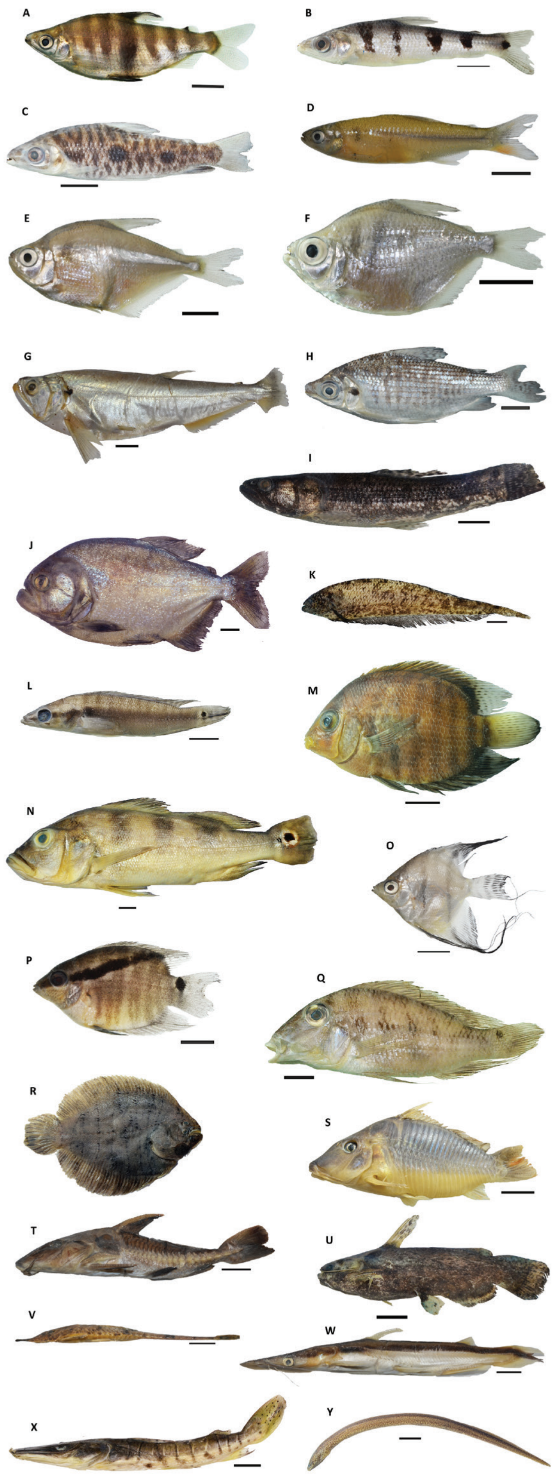

Figure 3. Some fish species collected in Yarinacocha lake, Ucayali basin, Peru. Scale bar 1 cm. **A)** *Abramites hypselonotus,* **B)** *Schizodon fasciatus,* **C)** *Leporinus* cf. *parae,* **D)** *Aphyocharax pusillus,* **E)** *Ctenobrycon hauxwellianus,* **F)** *Tetragonopterus argenteus,* **G)** *Hydrolycus scomberoides,* **H)** *Prochilodus nigricans*, **I)** *Hoplias malabaricus,* **J)** *Pygocentrus nattereri,* **K)** *Adontosternarchus balaenops,* **L)** *Crenicichla proteus,* **M)** *Heros efasciatus,* **N)** *Cichla monoculus,* **O)** *Pterophyllum scalare,* **P)** *Mesonauta mirificus,* **Q)** *Satanoperca jurupari*, **R)** *Hypoclinemus mentalis*, **S)** *Corydoras multiradiatus*, **T)** *Oxydoras niger*, **U)** *Trachelyopterus galeatus*, **V)** *Hemiodontichthys acipenserinus*, **W)** *Sorubim lima*, **X)** *Pseudoplatystoma punctifer*, **Y)** *Synbranchus marmoratus.*

Table 2. Fish fauna recorded for the Yarinacocha lake. The list includes the Peruvian common name, economic importance of the species as ornamental fish (O) according to IIAP (2011) and García Dávila et al. (2021), or fish for consumption (C) according to García-Dávila et al. (2018), IUCN category (LC = Least Concern, DD = Data Deficient, NT = Near Threatened, CR = Critically Endangered, EN = Endangered, VU = Vulnerable). In addition, the catalog number of the voucher specimens deposited in the MUSM fish collections is also being considered.

Taxon	Peruvian common name	Economic importance	IUCN	Voucher MUSM
CLASS ACTINOPTERYGII				
BELONIFORMES				
Belonidae				
Potamorrhaphis guianensis (Jardine, 1843)	pez aguja	–	–	MUSM 7466
Pseudotylosurus angusticeps (Günther, 1866)	pez aguja	–	–	MUSM 70497
CHARACIFORMES				
Acestrorhynchidae				
Acestrorhynchus abbreviatus (Cope, 1878)	peje zorro	O	LC	MUSM 7424
Acestrorhynchus microlepis (Jardine, 1841)	pez cachorro	O	LC	MUSM 1778
Anostomidae				
Abramites hypselonotus (Günther, 1868)	san pedrito	O	–	MUSM 2056, 70030
Leporellus vittatus (Valenciennes, 1850)	lisa	O	–	MUSM 7447
Leporinus aff. *amazonicus* Santos & Zuanon, 2008	lisa	–	–	MUSM 10307
Leporinus jamesi Garman, 1929	lisa	–	–	MUSM 70419
Leporinus niceforoi Fowler, 1943	lisa	–	–	MUSM 2351
Leporinus cf. *parae* Eigenmann, 1907	lisa	C	–	MUSM 59645, 69652, 69884, 70137, 70175, 70204
Leporinus pearsoni Fowler, 1940	lisa	–	LC	MUSM 70420
Leporinus striatus Kner, 1858	lisa	–	LC	MUSM 69704
Leporinus subniger Fowler, 1943	lisa	–	–	MUSM 69704
Megaleporinus trifasciatus (Steindachner, 1876)	lisa	C	–	MUSM 69876
Rhytiodus microlepis Kner, 1858	lisa	C	–	MUSM 15769, 15914
Schizodon fasciatus Spix & Agassiz, 1829	lisa	C	–	MUSM 481, 6269, 15298, 15769, 15813, 15914, 15917, 59644, 70033, 70048, 70136
Characidae				
Aphyocharax pusillus Günther, 1868	mojarita	O	–	MUSM 7421, 15381, 15804, 59640, 70037, 70041, 70131, 70171
Astyanax bimaculatus (Linnaeus, 1758)	mojara	O	–	MUSM 1887, 2371, 2985, 3453, 5494, 15325
Astyanax maximus (Steindachner, 1876)	mojara	–	–	MUSM 70056, 70138
Brachychalcinus copei (Steindachner, 1882)	palometita	O	LC	MUSM 70207
Charax tectifer (Cope, 1870)	dentón	O	–	MUSM 70467
Ctenobrycon hauxellianus (Cope, 1870)	mojara	O	–	MUSM 59293, 69868, 70039, 70054, 70145, 70170
Cynopotamus amazonum (Günther, 1868)	dentón	–	–	MUSM 69875
Galeocharax gulo (Cope, 1870)	dentón	–	–	MUSM 70031
Moenkhausia barbouri Eigenmann, 1908	mojara	–	–	MUSM 70154
Moenkhausia collettii (Steindachner, 1882)	mojara	O	–	MUSM 5490
Moenkhausia aff. *dichroura* (Kner, 1858)	mojara	–	–	MUSM 59288, 70023, 70055, 70144
Moenkhausia intermedia Eigenmann, 1908	mojara	O	–	MUSM 69649, 70052, 70148

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Taxon	Peruvian common name	Economic importance	IUCN	Voucher MUSM
Moenkhausia grandisquamis (Müller & Troschel, 1845)	mojara	–	–	MUSM 7417, 7425
Moenkhausia oligolepis (Günther, 1864)	mojara	O	–	MUSM 2195, 6280
Odontostilbe fugitiva Cope, 1870	mojarita	O	–	MUSM 5492, 69881
Prionobrama filigera (Cope, 1870)	mojara	O	–	MUSM 1392, 2194, 2272, 3458, 5487, 7422, 10881, 15323, 15800, 17787, 69880, 70034, 70050, 70142, 70153
Protocheirdodon pi (Vari, 1978)	pez vidrio	O	–	MUSM 70418
Psalidodon fasciatus (Cuvier, 1819)	mojarra	O	–	MUSM 2273
Roeboides affinis (Günther, 1868)	dentón	O	–	MUSM 10235, 15717, 15771, 15324, 59286, 70140, 70209
Roeboides myersi Gill, 1870	dentón	O, C	LC	MUSM 15201, 39575, 59289, 70210
Stethaprion erythrops Cope, 1870	palometita	O	–	MUSM 3528, 15328
Tetragonopterus argenteus Cuvier, 1816	mojara	O	–	MUSM 5488, 7418, 7423, 8568, 15297, 15411, 39577, 59290, 70038, 70053,70134, 70164, 70206
Serrapinnus heterodon (Eigenmann, 1915)	mojarita	–	–	MUSM 5493
Crenuchidae				
Characidium zebra Eigenmann, 1909	mojarita	O	–	MUSM 70491
Curimatidae				
Curimatella meyeri (Steindachner, 1882)	chio chio	C	–	MUSM 5213, 69742, 69759
Potamorhina altamazonica (Cope, 1878)	yahuarachi	C	–	MUSM 858, 5134, 15088
Potamorhina latior (Spix & Agassiz, 1829)	llambina	C	–	MUSM 70463
Psectrogaster amazonica Eigenmann & Eigenmann, 1889	ractacara	C	–	MUSM 7462, 15203, 69741, 69758, 70165
Psectrogaster rutiloides (Kner, 1858)	ractacara	C	–	MUSM 2076, 2108, 5133, 7465, 15205, 69743, 69757, 70162
Steindachnerina dobula (Günther, 1868)	julilla	–	–	MUSM 5227, 15322, 70043, 70146
Steindachnerina leucisca (Günther, 1868)	julilla	–	–	MUSM 5228, 15924, 70045, 70129
Cynodontidae				
Cynodon gibbus (Spix & Agassiz, 1829)	chambira	O, C	–	MUSM 69761
Hydrolycus scomberoides (Cuvier, 1819)	chambira	O, C	–	MUSM 69875
Rhaphiodon vulpinus Spix & Agassiz, 1829	chambira	O, C	–	MUSM 7054
Erythrinidae				
Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)	shuyo	O, C	–	MUSM 69755
Hoplias malabaricus (Bloch, 1794)	fasaco	O, C	LC	MUSM 5123, 5497, 15299, 15915, 69752, 69753, 69871, 69887, 70151
Gasteropelecidae				
Thoracocharax stellatus (Kner, 1858)	pechito	O	–	MUSM 7463, 15399, 15806, 17756, 17785, 70211

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Taxon	Peruvian common name	Economic importance	IUCN	Voucher MUSM
Hemiodontidae				
Anodus elongatus Agassiz, 1829	julilla	C	–	MUSM 7055
Hemiodus aff. *microlepis* Kner, 1858	julilla	–	–	MUSM 69745
Hemiodus amazonum (Humboldt, 1821)	julilla	–	–	MUSM 7451
Prochilodontidae				
Prochilodus nigricans Agassiz, 1829	boquichico	C	–	MUSM 47, 50, 2001, 2023, 2111, 2190, 7455, 7467, 8575, 10302, 15327, 15768, 15803, 17755, 19711, 19721, 59643, 69653, 69874, 69885, 70040, 70159
Parodontidae				
Parodon pongoensis (Allen, 1942)	julilla	O	–	MUSM 70495
Serrasalmidae				
Colossoma macropomum (Cuvier, 1816)	gamitana	C	–	MUSM 62
Mylossoma albiscopum (Cope, 1872)	palometa	C	–	MUSM 59646, 70043
Mylossoma aureum (Spix & Agassiz, 1829)	palometa	O, C	–	MUSM 5489, 17843
Piaractus brachypomus (Cuvier, 1818)	paco	O, C	–	MUSM 1814, 70044
Pygocentrus nattereri Kner, 1858	paña roja	O, C	–	MUSM 84, 15410, 39581, 69740, 69762, 70202
Serrasalmus rhombeus Linnaeus, 1776	paña moteada	O, C	–	MUSM 70462
Triportheidae				
Triportheus albus Cope, 1872	sardina	–	–	MUSM 2384, 5226, 10301, 15766, 15801, 15808, 15918, 69639, 69648, 70114, 70132, 70156
Triportheus angulatus (Spix & Agassiz, 1829)	sardina	C		MUSM 2341, 2374, 7416, 7420, 10300, 15921, 15522, 15810, 15921, 17750, 59281, 70115, 70139, 70155
Triportheus curtus (Garman, 1890)	sardina	–		MUSM 70464
Triportheus rotundatus (Jardine, 1841)	sardina	–	LC	MUSM 575, 70465
CLUPEIFORMES				
Engraulidae				
Anchoviella guianensis (Eigenmann, 1912)	sardina	–	–	MUSM 70205
Anchoviella hernanni Loeb, Varella & Menezes, 2018	sardina	–	–	MUSM 70490
Jurengraulis juruensis (Boulenger, 1898)	sardina	–	–	MUSM 70163
Lycengraulis batesii (Günther, 1868)	sardina	–	–	MUSM 70169
Pristigasteridae				
Pellona castelnaeana Valenciennes, 1847	panshin, bacalao	C	LC	MUSM 5111, 5275
Pristigaster cayana Cuvier, 1829	pechito	–	LC	MUSM 5, 15776, 70171
GYMNOTIFORMES				
Apteronotidae				
Apteronotus bonapartii (Castelnau, 1855)	macana	O	–	MUSM 3027, MUSM 3030
Adontosternarchus balaenops (Cope, 1878)	macana	O	–	MUSM 70485

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Taxon	Peruvian common name	Economic importance	IUCN	Voucher MUSM
Gymnotidae				
Electrophorus varii de Santana, Wosiacki, Crampton, Sabaj, Dillman, Mendes–Júnior & Castro e Castro, 2019	anguila eléctrica	O	–	MUSM 70128
Hypopomidae				
Brachyhypopomus bennetti Sullivan, Zuanon & Cox Fernandes, 2013	macana	O	–	MUSM 70493
Sternopygidae				
Eigenmannia humboldtii (Steindachner, 1878)	macana	O	–	MUSM 3020
Eigenmannia limbata (Schreiner & Miranda Ribeiro, 1903)	macana	–	–	MUSM 70184
Eigenmannia virescens (Valenciennes, 1836)	macana	O	–	MUSM 3019, 70190
Sternopygus macrurus (Bloch & Schneider, 1801)	macana	O	–	MUSM 3018, 70189
CICHLIFORMES				
Cichlidae				
Aequidens tetramerus (Heckel, 1840)	bujurqui	O	–	MUSM 70494
Astronotus ocellatus (Agassiz, 1831)	acahuarazu	O, C	–	MUSM 19724
Bujurquina megalospilus Kullander, 1986	bujurqui	–	–	MUSM 70486
Chaetobranchus flavescens Heckel, 1840	bujurqui	C	–	MUSM 940
Cichla monoculus Agassiz, 1831	tucunare	O, C	–	MUSM 7392, 8571, 69739, 70150
Cichlasoma amazonarum Kullander, 1983	bujurqui	O	–	MUSM 5486, 7391, 15345, 15378, 70146
Crenicara punctulata (Günther, 1863)	bujurqui	O	–	MUSM 2538
Crenicichla cyanonotus Cope, 1870	añashua	–	–	MUSM 59279, 70178
Crenicichla proteus Cope, 1872	añashua	O	–	MUSM 5482, 7394, 7399, 69654, 700051, 70148, 70180
Crenicichla sedentaria Kullander, 1986	añashua	–	LC	MUSM 15379, 70179
Heros efasciatus Heckel, 1840	bujurqui	O, C	–	MUSM 5484, 6272, 7395, 7400, 15073, 15140, 15375, 15781, 59280, 70025, 70147, 70203
Hypselecara temporalis (Günther, 1862)	bujurqui	O, C	–	MUSM 916, 7396
Mesonauta festivus (Heckel, 1840)	bujurqui	O	–	MUSM 1021
Mesonauta insignis (Heckel, 1840)	bujurqui	–	–	MUSM 5483
Mesonauta mirificus Kullander & Silfvergrip, 1991	bujurqui	O	LC	MUSM 3049, 7401, 7403, 10294, 15397, 70027, 70149
Pterophyllum scalare (Schultze, 1823)	pez angel	O	–	MUSM 982, 984, 1041, 1209, 3451, 3469, 5485, 7398, 9124, 10297, 15247, 15376, 15772, 19725, 70026, 70157
Satanoperca jurupari (Heckel, 1840)	bujurqui	O, C	–	MUSM 957, 5503, 7402, 7415, 8572, 10295, 15383, 59282, 70172
EUPERCARIA sensu Betancur et al. 2017				
Scianidae				
Plagioscion squamosissimus (Heckel, 1840)	corvina	O, C	–	MUSM 790, 2110

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Taxon	Peruvian common name	Economic importance	IUCN	Voucher MUSM
PLEURONECTIFORMES				
Achiridae				
Achirus achirus (Linnaeus, 1758)	panga raya, lenguado	O	LC	MUSM 15807, 59292
Hypoclinemus mentalis (Günther, 1862)	panga raya, lenguado	O	LC	MUSM 898, 59641, 69650
OSTEOGLOSSIFORMES				
Arapaimidae				
Arapaimas gigas (Schinz, 1822)	paiche	O, C	DD	MUSM 104
SILURIFORMES				
Auchenipteridae				
Ageneiosus inermis (Linnaeus, 1766)	bocón	O, C	–	MUSM 7045
Epapterus dispilurus Cope, 1878	maparate	O	–	MUSM 17782, 70181
Trachelyopterus galeatus (Linnaeus, 1766)	bocón	O, C	–	MUSM 70474
Trachelyopterus isacanthus (Cope, 1878)	bocón	–	–	MUSM 7457
Trachelyopterus porosus (Eigenmann & Eigenmann, 1888)	bocón	–	–	MUSM 70475
Tympanopleura atronasus (Eigenmann & Eigenmann, 1888)	bocón	–	–	MUSM 70472
Tympanopleura longipinna Walsh, Ribeiro & Rapp Py-Daniel, 2015	bocón	–	–	MUSM 70473
Aspredinidae				
Bunocephalus aleuropsis Cope, 1870	banjo, sapo cunshi	O	–	MUSM 70499
Callichthyidae				
Callichthys callichthys (Linnaeus, 1758)	coridora, shirui	–	–	MUSM 3481
Corydoras leucomelas Eigenmann & Allen 1942	coridora, shirui	O	LC	CAS 36561
Corydoras multiradiatus (Orcés V, 1960)	coridora, shirui	O	LC	MUSM 69877
Corydoras splendens (Castelnau 1855)	coridora, shirui	O	LC	MUSM 69878
Corydoras stenocephalus Eigenmann & Allen, 1942	coridora, shirui	–	LC	CAS 36386
Corydoras trilineatus Cope, 1872	coridora, shirui	O	–	MUSM 7458
Dianema longibarbis Cope, 1872	shirui	C	–	MUSM 1790
Hoplosternum littorale (Hancock, 1828)	shirui	–	–	MUSM 69756
Doradidae				
Acanthodoras aff. *spinosissimus* (Eigenmann & Eigenmann, 1888)	pirillo	O	–	MUSM 15486
Agamyxis pectinifrons (Cope, 1870)	pirillo	O	–	MUSM 2804, 5116
Anadoras grypus (Cope, 1872)	pirillo	O	LC	MUSM 15485, 33335
Hemidoras stuebelii (Steindachner, 1882)	pirillo	–	–	MUSM 5127, 70501
Nemadoras humeralis (Kner, 1855)	pirillo	O	–	MUSM 5122, 5128, 5163, 15484
Ossancora asterophysa Birindelli & Sabaj Pérez, 2011	pirillo	–	–	MUSM 70177
Ossancora eigenmanni (Boulenger, 1895)	pirillo	O	–	MUSM 5130, 15499, 32674

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Taxon	Peruvian common name	Economic importance	IUCN	Voucher MUSM
Ossancora punctata (Kner, 1855)	pirillo	–	–	MUSM 596, 1982, 5105, 5120, 5126, 5159, 5160, 5161, 5501, 7042, 15413, 19714, 70047, 70176
Oxydoras niger (Valenciennes, 1821)	turushuqui	O, C	–	MUSM 2902, 5119, 70183
Platydoras armatulus (Valenciennes, 1840)	rafles	O	–	MUSM 70200
Platydoras costatus (Linnaeus, 1758)	rafles	O	–	MUSM 5103, 5115, 19713
Pterodoras granulosus (Valenciennes, 1821)	cahuara	C	–	MUSM 1637, 1980, 5102, 5114, 15513
Heptapteridae				
Pimelodella cristata (Müller & Troschel, 1849)	cunshi, bagre	–	–	MUSM 5500
Pimelodella cyanostigma (Cope, 1870)	cunshi, bagre	–	–	MUSM 69873, 70036, 70166, 70195
Pimelodella gracilis (Valenciennes, 1835)	cunshi, bagre	–	–	MUSM 5500, 15811, 70049, 70133, 70167
Rhamdia quelen (Quoy & Gaimard, 1824)	cunshi, bagre	O	–	MUSM 70028
Loricariidae				
Ancistrus alga (Cope, 1872)	carachama	–	–	MUSM 69869, 70194
Farlowella amazonum (Günther, 1864)	shitari aguja	–	–	MUSM 69872, 70182
Hemiodontichthys acipenserinus (Kner, 1853)	shitari	O	–	MUSM 7452, 15764, 17753, 70191
Hypoptopoma gulare Cope, 1878	carachamita	O	–	MUSM 15146, 15206, 15237, 15341, 69879, 69886, 70130, 70160, 70197
Hypoptopoma psilogaster Fowler, 1915	carachamita	–	–	MUSM 70141, 70174
Hypoptopoma thoracatum Günther, 1868	carachamita	O	–	MUSM 15349, 69882, 70199
Hypostomus ericius Armbruster, 2003	carachama	–	LC	MUSM 69870, 70173, 70198
Limatulichthys griseus (Eigenmann, 1909)	shitari	–	–	MUSM 1776
Loricaria simillima Regan, 1904	shitari	O	–	MUSM 7453, 70042, 70188
Loricariichthys maculatus (Bloch, 1794)	shitari	–	–	MUSM 70502
Pterygoplichthys pardalis (Castelnau, 1855)	carachama	O	–	MUSM 59278, 69746, 70036, 70152, 70187
Rineloricaria sp.	shitari	–	–	MUSM 70024, 70193
Rineloricaria wolfei Fowler, 1940	shitari	–	LC	MUSM 70192
Sturisoma nigrirostrum Fowler, 1940	shitari	O	LC	MUSM 10106, 70186
Pimelodidae				
Brachyplatystoma platynemum Boulenger, 1898	mota flemosa	O, C	–	MUSM 1813
Calophysus macropterus (Lichtenstein, 1819)	mota	O, C	–	MUSM 7056
Hemisorubim platyrhynchos (Valenciennes, 1840)	toa	O, C	–	MUSM 70498
Hypophthalmus edentatus Spix & Agassiz, 1829	maparate	C	–	MUSM 1505, 1506, 1509, 3249, 12777
Hypophthalmus oremaculatus Nani & Fuster de Plaza, 1947	maparate	–	–	MUSM 69744
Phractocephalus hemioliopterus (Bloch & Schneider, 1801)	peje torre	O, C	–	MUSM 1518
Pimelodina flavipinnis Steindachner, 1876	bagre	C	–	MUSM 10014

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Taxon	Peruvian common name	Economic importance	IUCN	Voucher MUSM
Pimelodus blochii Valenciennes, 1840	cunshi, bagre	O	–	MUSM 15783, 15797, 15814, 17789, 59291, 59642, 69651,70135, 70168, 70196
Pimelodus maculatus Lacepède, 1803	cunshi, bagre	O	–	MUSM 15250, 17751, 17851
Pimelodus pictus Steindachner, 1876	cunshi, bagre	O	–	MUSM 1742, 3465, 5107, 5118, 6288, 15809
Pseudoplatystoma punctifer (Castelnau, 1855)	doncella	O, C	–	MUSM 70496
Sorubim elongatus Littmann, Burr, Schmidt & Isern, 2001	shiripira	–	–	MUSM 70477
Sorubim lima (Bloch & Schneider, 1801)	shiripira	O, C	–	MUSM 643, 681, 5053, 5158, 10105, 15449, 19720, 70201
SYNBRANCHIFORMES				
Synbranchidae				
Synbranchus marmoratus Bloch, 1795	atinga	O	–	MUSM 3057, 12711
TETRAODONTIFORMES				
Tetraodontidae				
Colomesus asellus (Müller & Troschel, 1849)	pez globo	O	–	MUSM 1949

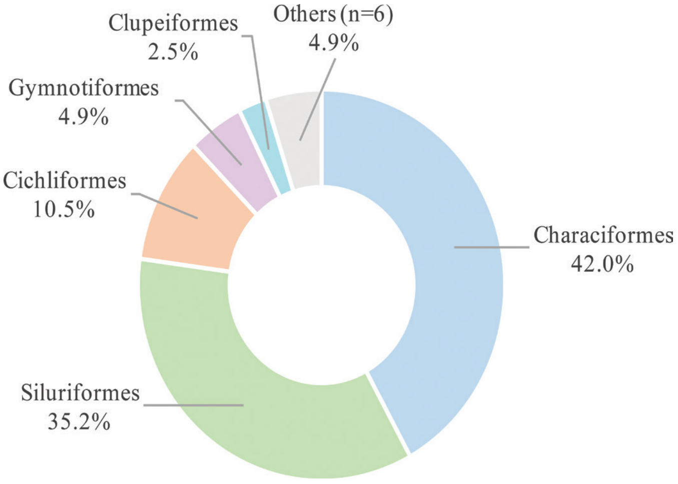

Figure 4. Richness of fish species for orders/series recorded in Yarinacocha lake.

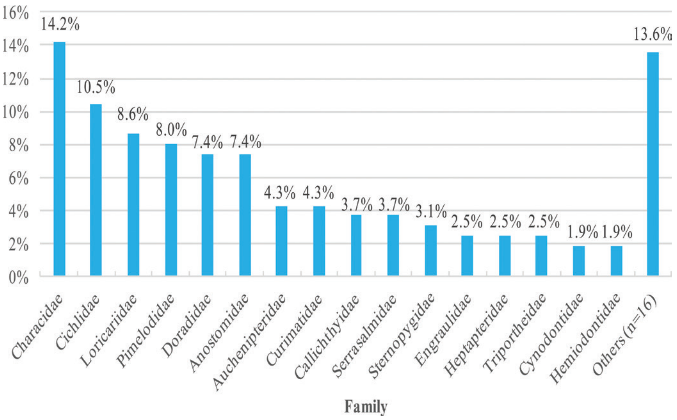

Figure 5. Richness of fish species for families recorded in Yarinacocha lake.

Another interesting novelty is *Leporinus subniger*, with distribution in the Upper Amazon Basin (Colombia and Ecuador) (Britski & Birindelli 2008), species not previously reported by previous peruvian inventories (Ortega et al. 2012, Meza-Vargas et al. 2021, Chuctaya et al. 2022) representing a new record for the department of Ucayali.

The following species could not be identified to the species level *Hemiodus* aff. *microlepis* belongs to the *Hemiodus microlepis* species group, previously reported for the Ucayali River, being a species not formally described (Nogueira et al. 2021), *Leporinus* cf. *parae*, a member of the *Leporinus friderici* species complex (Silva-Santos et al. 2018), and *Leporinus* aff. *amazonicus* represents putative undescribed species. *Leporinus* is the most species-rich genus within Anostomidae and is considered one of the richest genera within Characiformes (Garavello and Britski 2003, Ramirez et al. 2016) and a thorough taxonomic review of this group is needed (Silva-Santos et al. 2018). *Rineloricaria* sp. could only be identified to the genus level without coinciding with *R. morrowi* or *R. wolfei*, the two species described for the region by Fowler (1940), further studies will be needed to classify these specimens. *Moenkhausia* aff. *dichroura* belongs to the *M. dichroura* species group, because it's distributed only in the La Plata basin (Paraguay and lower Paraná rivers) and the morphotype found in the Amazon basin would be a possible new species (Britzke 2011). Several species have the same color pattern, such as *M. dichroura*, *M. intermedia*, *M. barbouri*, *M. bonita* and also the species *Schultzites axelrodi*, which in some cases may make it difficult to correctly identify this species group.

Regarding the species of economic importance, 109 species have commercial importance, of which 90 species (54.8%) are ornamentals, 26 species are used for both purposes and 20 species only for consumption, including *Prochilodus nigricans* (boquichico) which contributes the highest percentage of catches (Riofrío 1998, Riofrío 2002, Wasiw et al. 2012, Salazar-Ramirez et al. 2021) and large migratory catfish, with high commercial value, such as *Pseudoplatystoma punctifer* (doncella) and *Phractocephalus hemioliopterus* (peje torre), whose presence indicates the importance of this ecosystem in its migratory route, since this type of whitewater ecosystems are the most important for commercial migratory species (Duponchelle et al. 2021). Therefore, the majority of species recorded for Yarinacocha lake (66.7%) represent important economic resources. Nevertheless, the abundances of these resources can decline due to human impacts including habitat alteration, water pollution, overfishing, exotic species introduction and other factors (van der Sleen & Albert 2021).

The reduction in landings in Yarinacocha lake has been reported in recent years (Salazar-Ramirez et al. 2021). Species of consumption of high commercial demand such as *Colossoma macropomum* (gamitana) and *Piaractus brachypomus* (paco) have almost disappeared from landings, being replaced by small-sized species (Riofrío 1998, Wasiw et al. 2012, Salazar-Ramirez et al. 2021). This evidences the decrease of fish populations for consumption due to overexploitation.

The global ornamental fish industry is a market expansion grid, and moves approximately US$ 15 billion/year, including equipment, accessories, supplies and publications (Cheong 1996). There are 350 to 400 million ornamental fish sold, where 70% are produced in captivity and 63% are exported by developing countries generating about U.S. $ 202 million/year (Chao et al. 2001). This market is dominated by freshwater fishes and the Amazon basin is a key supplier of wild freshwater fishes to the ornamental trade (Moreau and Coomes 2007). In the Peruvian Amazon, most of these resources are the product of direct extraction from the natural environment (MINAM 2021) and Yarinacocha lake is one of the leading regions for ornamental fish extraction in the Ucayali department (PNIPA 2021). Although the collection of fish from tropical lentic environments can be carried out almost throughout the entire year, this activity can lead to direct depletion of wild populations (Andrews 1990).

In recent years, the global trade for freshwater specimens has led to the overexploitation of native species, and the destruction of these habitats by invasive species (Chang et al. 2009). An example of an exotic species found in Peru would be *Trichopodus trichopterus* (Pallas 1770), order Anabantiformes, family Osphronemidae, that was reported in Yarinacocha in 2016, in the La Restinga fishing area (MINAM 2021). This species is a tropical freshwater fish native to Southeast Asia, known as the three spot gourami, and has a specialized organ (organ labyrinth) that allows them to breathe oxygen from the air (Blank & Burggren 2014), helping them to adapt to an environment of low oxygen concentration in the water (Degani et al. 2021). Specimens of this group were introduced in 1970 for ornamentation (Ortega et al. 2007) and have been reported for the city of Iquitos (department of Loreto, Peru) (Meza-Vargas et al. 2021). The effects of exotic species on lentic water bodies can be complex (Ortega and Hidalgo 2008), although the impact of *T. trichopterus* on native species is uncertain, the introduction of exotic species may imply a risk of co-introduction of parasites, especially with phylogenetically similar native fauna (Trujillo-González et al. 2018), and generate problems of predation, competition for food and occupation of niches (Meza-Vargas et al. 2021). Therefore, *T. trichopterus* can be detrimental to native fish and further studies are required to assess the real impact on native species.

Freshwater fish may currently be one of the most threatened vertebrate groups, mainly based on the more than 5,000 species assessed by the IUCN, where the main threats include habitat modification, fragmentation and destruction; the introduction of invasive species; fisheries overexploitation; environment pollution; and climate change (Reid 2013). Thus, in the long term, it is estimated that 20% of the world's freshwater fish should be in the vulnerable, threatened or extinct category in recent decades (Revenga et al. 1998).

In this study, 22 species are considered protected species (13.4%) following the IUCN criteria. One species, *Arapaima gigas*, was categorized as "Data deficient" (DD), therefore the knowledge about the biology and ecology of this species is limited, in particular the structure of its natural populations (Vitorino et al. 2017) and further information on the species is required. The natural populations of this species have historically been reduced or even eradicated near the main cities (Castello et al. 2011). Currently, its landing in Yarinacocha lake is almost nil (Salazar-Ramírez et al. 2021). The other 21 species are considered "Least concern" (LC), which means that after being evaluated, it doesn't meet any of the criteria that define the other categories. Most of the registered species lack information that allows them to be classified in some category, therefore further studies are necessary for an adequate evaluation of these species and of the Peruvian ichthyofauna in general.

Overall, Yarinacocha lake is an ecosystem with a high diversity of fish species that are valuable resources for the local people. Nonetheless, these resources are vulnerable to pollution, overexploitation and the presence of exotic species that affect native populations. Our study contributes to the knowledge of the ichthyofauna of the Yarinacocha lake and can be used as a starting point for its conservation and sustainable management over time.

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Hernán Ortega: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to critical revision, adding intelectual content.

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Ricardo Britzke: 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

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

Ethics

Authors have complied with the guidelines established by the ethics committees of their respective research institutions.

Data Availability

Supporting data are available at: Britzke, Ricardo, 2022, “Fishes from Yarinacocha lake: an emblematic Amazonian ecosystem in the lower Ucayali River basin, Pucallpa, Peru”, https://doi.org/10.48331/scielodata.4FNJMY, SciELO Data, DRAFT VERSION.

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The drift effect on nestedness of Ephemeroptera, Trichoptera and Plecoptera orders in the Xingu River

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Abstract: The drift movement consists of the displacement of the organisms inside the water column which allows its passive locomotion. This movement will result in a variation of the communities of organisms along the river, generating spatial patterns. Based on this, we tested the hypotheses a) the drift of individuals in an upstream-downstream direction creates a nestedness pattern, when the upstream is a subset of downstream communities of aquatic insects; b) there will be an increase in the number of individuals and genera as we approach the most downstream point. The present study was carried out in seven sampling points distributed along the Xingu River. The sampling occurred at night in the central area of the river. The number of genera along the river remained constant, and the nestedness distribution of the communities in the upstream-downstream gradient was not observed. Based on the results, it is possible to visualize a turnover of genera in the longitudinal gradient of the river, but with an accumulation of genera in the downstream region. Organisms that are transported by the flow of the water current respond to the characteristics of the body of water by adapting to the type of environment in which they are found.
Keywords: *Dispersion; Aquatic Insects; Amazonian River; Upstream-downstream movement.*

O efeito da deriva no aninhamento das ordens Ephemeroptera, Trichoptera e Plecoptera no Rio Xingu

Resumo: O movimento de deriva consiste no desprendimento dos organismos dentro da coluna de água, o que permite a sua locomoção passiva. Este movimento resultará numa variação das comunidades de organismos ao longo do rio, gerando padrões espaciais. Com base nisto, testamos as hipóteses a) o movimento de indivíduos em direção montante-jusante criará um padrão aninhado, no qual as comunidades de insetos aquáticos a montante são um subconjunto das comunidades a jusante; b) haverá um aumento no número de indivíduos e gêneros à medida que nos aproximamos do ponto mais a jusante. O presente estudo foi realizado em sete pontos de amostragem distribuídos ao longo do rio Xingu. A amostragem ocorreu durante a noite no canal central do rio. O número de gêneros ao longo do rio se manteve constante, e não observamos uma distribuição de aninhamento das comunidades no gradiente ascendente e descendente do rio. Com base nos resultados, é possível visualizar uma substituição dos gêneros no gradiente longitudinal do rio, porém ocorrendo um acúmulo de gêneros na região mais a jusante. Os organismos que são transportados pelo fluxo da corrente de água respondem as características do corpo de água adaptando-se ao tipo de ambiente em que se encontram.
Palavras-chave: *Dispersão; Insetos Aquáticos; Rio Amazônico; Movimento montante-jusante.*

Introduction

Water flow plays a major role in the dynamics of lotic environments (e.g., rivers and streams) and is related to the stability of biological populations (Poff & Ward 1991). The movement of water promotes the drift of organisms, which consists of their transport using the water flow. The drift behavior is related to several factors, such as current velocity, water chemistry, period of the year and photoperiod (Fierro et al. 2015). The drift can be classified as active, when the organism is cast into the water column in order to escape from predation, competition, or seek food; or passive when the organism is involuntarily thrown into the water column (Brittain & Eikeland 1988, Poff & Ward 1991, Castro et al. 2013a).

The study of the drift movement is fundamental to understand the transport of these organisms through the water flow, to understand the process of colonization and recolonization of habitats, as well as to identify the functional ecosystem role of different species. The drift movement of aquatic insects can be responsible for the stability and structure of the communities existing in each environment through the process of repopulating localities (Vellend 2010). There is this dependence because the distribution of the species is also linked to the environmental variables and to the physiological tolerance of each organism (Godoy, Queiroz, et al. 2022, Vellend 2010). Thus, studies on drift movement are being used to understand the distribution of organisms in order to determine the connection between localities (Poff & Ward 1991, Anholt 1995, Covich 2006).

The flow of water into a river is unidirectional, so it is expected in an upstream-downstream direction for the transport of organisms carried by the stream. This will generate a pattern of species distribution, of species addition in the upstream-downstream gradient. The pattern generated may also be of the nestedness type, in which the upstream communities are a subset of those found downstream (Covich 2006, Almeida-Neto et al. 2008). The concept of nestedness was created to explain the communities of island colonized by species from mainland, wherein the better disperses colonize the great portion of islands, independent of the distance (Darlington 1966). In other hand, the poor disperses occur only in the more connected island, creating a nested pattern of species occurrences, based in the species incidence. The knowledge about nestedness distribution is important to understand the patterns of community composition in ecosystems and based on this knowledge create strategies for preservation and conservation of the environment (Ulrich 2009). However, most of the studies on drift movement are concentrated in streams, resulting in a knowledge gap in relation to large rivers that present a differentiated dynamic, with a more intense water flow and variation between environments.

The aquatic insects are strongly influenced by the water dynamics of the water bodies and, in order to establish themselves in the environment, use adapted mechanisms to the conditions to which they are submitted (Mazzucco et al. 2015). In addition to the water flow, these organisms suffer interference from the substrate type, and rocky substrates have a differentiated community when compared to sandy environments (Bispo et al. 2004). The availability of food and predation will also be limiting factors and may define the population density of each locality (Ciborowski 1983, Hay et al. 2008, Godoy et al. 2016). Environments with high population density show an increase in biotic interactions, causing the escape of individuals who are forced into the water column. The active dispersal movement occurs more intensely during the night period, where the lack of luminosity provides a protection against the predators, guaranteeing a greater success during the displacement in the water column (Bishop 1969, Koetsier 2005). There are many studies with the orders Ephemeroptera, Plecoptera and Trichoptera (EPT) about their distribution and life cycle (Godoy, Valente-Neto, et al. 2022, Godoy, Queiroz, et al. 2022, Merritt et al. 2008, Sarremejane et al. 2020). In addition, they are orders with high environmental sensitivity, wide distribution within the lotic environments, high abundance and each order presents high richness and complexity (Godoy et al. 2019), which allows its use as model organisms for studies of the drift process.

The Xingu River is characterized as a large river, presenting along its length a high environmental heterogeneity, characterized as a river of high complexity. Its landscapes are composed by waterfalls and rapids, where in these localities the speed of the current appears very varied. In addition to this variation of the current, there will be a variation of the biological communities within its course, resulting in a distribution of varied species within each environment. The lack of studies in large-scale rivers undermines understanding of ecosystem dynamics and how changes in water flow alter the structure of aquatic insect communities. Thus, in this study we tested the following hypotheses: 1) there will be a nesteness distribution of the genera Ephemeroptera and Trichoptera in an upstream-downstream gradient along the Xingu River; 2) there will be an increase in the abundance and richness of genera as we approach the most downstream point on the Xingu River, and c) the community of aquatic insects moves upstream.

Material and Methods

1. *Study area*

The study was carried out on the Xingu River (02°51′33.1″S and 52°19′28″W), near the city of Altamira, Pará, during the flood period, April 2015 (Figure 1). The Xingu River belongs to the Amazon River

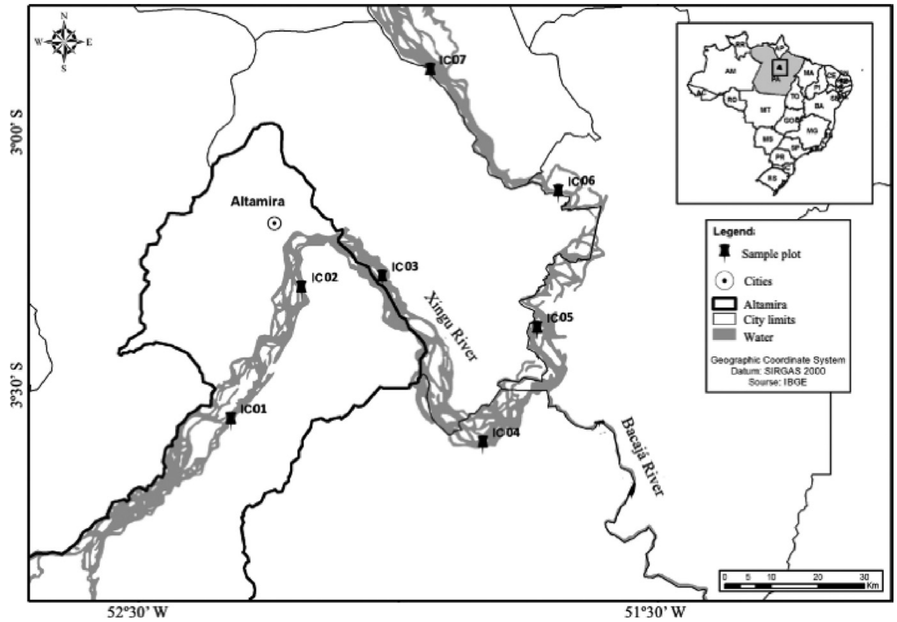

Figure 1. Sampling points of aquatic insects on the Xingu River in the period of April 2015. The sample units are symbolized by the P code.

Basin, located on the right side of the river. With an extension of 1500 km from its source in the Brazilian Central Plateau until its mouth in the Amazon River, it drains an area of 540 km^2. The pH ranges from 5.5 to 7.0 with a mean conductivity of 30 µS/cm^{-1}, as well as high concentrations of oxygen resulting from the large volume of water (Sioli 1957, Salomão et al. 2007).

The average flow rate during the flood period varies from 8,000 to 10,000 m^3/s and in the dry period the average is 2000 m^3/s (Norte-Energia 2016). The flood period occurs between December and April and the dry season occurs between July and November. Because it is located near the equator, the Xingu River basin presents a warm climate and according to Köppen classification the climate is tropical and predominantly humid (Am, Sheffield et al. 2006). The mean annual temperature in the Altamira-PA region is 27°C, the rainy season starts in November and the dry season in July.

2. *Sampling*

The sampling occurred in seven locations on the Xingu River during the night period. We sampled two times in the central region of the river in each location. However, for our study we jointed the two samples. At each sampling point we measured abiotic variables (pH, OD, conductivity, temperature and current velocity). We used a plankton net with a 50 cm diameter ring and 1.5 m in length, with a mesh opening of 300 µm (Bialetzki et al. 1999). We attached a weight to the net, aiming at its balance in the water column. A flowmeter was attached to the net to determine the amount of filtered water and at the end of the net a collecting cup was added. We performed the samplings with the aid of a motorized canoe, which during the collection was kept on with low acceleration, with the bow upstream of the river. The net was positioned against the current, at an average depth of 2 meters, for a period of 10 minutes, adapting methodologies previously used in works with aquatic insects (Waters 1972, Castro et al. 2013a, b). The sampled individuals were preserved in 70% ethanol and identified to the genus level (Wiggins 1977, Domingues & Fernandez 2001, Pes et al. 2005, Oliveira 2006).

3. *Data analysis*

To verify the relationship between the number of genera and the abundance of individuals with the upstream-downstream gradient of the points sampled, a linear regression was performed, using the ordering of the samples in this gradient as a predictor variable. We used NODF (Nestedness metric based on Overlapping and Decreasing Fill) (Almeida-Neto et al. 2008), to observe a nestedness pattern in the upstream-downstream gradient for the aquatic insect community within the river course. This metric works in a range between 0-100, with 100 representing a perfectly nesteness set. The data are organized in an array of rows and columns, where the columns are the genera and in the rows are the points sampled, the NODF is calculated in pairs of subsequent rows and columns, if the previous row has lesser or equal number of genera than the after, the value of the NODF will be zero. However, if the previous line has higher number of genera than the posterior one, the index uses the common occurrence in both lines to generated the value of the NODF. This calculation is performed for both rows and columns and at the end the overall mean will be achieved resulting in the general NODF (Milesi & Melo 2014, Pinha et al. 2016). In order to calculate the NODF in our study, we maintained the order of the sampling sites by fixing the points in the upstream-downstream direction, generating the real distribution of the genera of aquatic insects in the studied gradient. We performed the T test to compare the observed NODF values with the estimated distribution in a null model of 1000 iterations for the NODF values.

The dispersion among the communities of the points sampled was determined by the dispersion coefficient of the biogeographic direction, using the DD3 index (Legendre & Legendre 1984). This index determines in what direction the movement of species is occurring between communities of locations that are geographically connected (Borcard et al. 1995, Legendre & Legendre 1984). For the analysis, the Vegan package was used (Oksanen et al. 2013) available in the R program (R Development Core Team 2020).

Results

We collected 1760 individuals in total, divided into 13 families and 34 genera. The order Ephemeroptera consisted of 1614 individuals divided into 6 families and 21 genera. The order Trichoptera presented 146 individuals distributed in 7 families and 13 genera. The most abundant genera were *Lachlania*, *Camelobaetidius*, *Hydrosmilodon* and *Cloeodes* (Table 1). The families that obtained the highest representation were Baetidae (31.2%), Oligoneuriidae (29.01%) and Leptophlebiidae (22.26%). The values of physical and chemical variables showed low variability between the locations (Table 2).

Table 1. Aquatic insects' genera, abundance and occurrence in samples collected in the channel of Xingu River, during the flood period (April/2015).

Family	Genera	Individuals	%	Sampling Points
Oligoneuriidae	*Lachlania*	448	25.45	1, 2, 3, 4, 5, 6, 7
Baetidae	*Camelobaetidius*	374	21.25	1, 2, 3, 4, 5, 6, 7
Leptophlebiidae	*Hydrosmilodon*	261	14.82	1, 2, 3, 4, 5, 6, 7
Baetidae	*Cloeodes*	145	8.23	1, 2, 3, 4, 5, 6, 7
Leptophlebiidae	*Needhamella*	116	6.59	1, 2, 3, 4, 5, 6, 7
Polymitarcyidae	*Campsurus*	79	4.48	1, 2, 3, 4, 5, 6, 7
Hydropsychidae	*Leptonema*	70	3.97	1, 2, 4, 5
Oligoneuriidae	*Oligoneuria*	63	3.57	1, 2, 4, 5, 6
Leptohyphidae	*Tricorythopsis*	49	2.78	1, 2, 3, 4, 5, 6, 7
Leptohyphidae	*Leptohyphes*	25	1.42	2, 4, 5, 6

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Family	Genera	Individuals	%	Sampling Points
Baetidae	*Spiritiops*	20	1.13	1, 2, 4, 5
Hydropsychidae	*Centromacronema*	19	1.07	1, 3, 6
Hydropsychidae	*Macrostemum*	19	1.07	1, 3, 5
Hydropsychidae	*Smicridea*	13	0.73	1, 6
Leptophlebiidae	*Farrodes*	9	0.51	1, 3
Baetidae	*Baetodes*	6	0.34	1
Helicopsychidae	*Helicopsyche*	6	0.34	3, 6
Hydropsychidae	*Synoestropsis*	5	0.28	2, 5
Leptohyphidae	*Tricorythodes*	5	0.28	1
Leptoceridae	*Oecetis*	4	0.22	1, 4, 5
Polycentropodidae	*Cyrnellus*	4	0.22	3, 4, 5
Baetidae	*Aturbina*	3	0.17	2, 6
Baetidae	*Cryptonympha*	2	0.11	1, 5
Leptophlebiidae	*Askola*	2	0.11	1, 6
Leptophlebiidae	*Ulmeritoides*	2	0.11	1
Philopotamidae	*Chimarra*	2	0.11	1, 6
Polymitarcyidae	*Asthenopus*	2	0.11	1, 3
Caenidae	*Caenis*	1	0.05	5
Ecnomidae	*Austrotinodes*	1	0.05	6
Hydroptilidae	*Hydroptila*	1	0.05	4
Hydroptilidae	*Neotrichia*	1	0.05	4
Leptoceridae	*Nectopsyche*	1	0.05	5
Leptophlebiidae	*Hagenulopsis*	1	0.05	6
Leptophlebiidae	*Tikuna*	1	0.05	3

Table 2. Coordinates and physical and chemical variables in the sampled locations.

Points	Latitude	Longitude	Water velocity ($m.s^{-1}$)	Water temperature (ºc)	Dissolved oxygen (ppm)	Electrical conductivity ($\mu S.cm^{-2}$)	pH
1	03°34.807’	52°23.683’	6.34	28.2	7.3	13	7.3
2	03°12.826’	52°11.248’	10.11	28.1	7.2	14	7.4
3	03°19.260’	52°02.154’	9.78	27.5	7.8	15	7.5
4	03°35.753’	51°50.262’	8.33	27.2	8.2	14	6.4
5	03°23.312’	52°43.967’	19.15	27.7	6.5	15	6.5
6	03°07.745’	51°41.479’	6.96	28.3	7.4	15	7.6
7	03°53.014’	51°57.535’	13.91	28.1	7.8	16	7.2

The number of genera between the sampling points did not differ significantly, except for the last sampling point located downstream, where there was a reduction in the number of genera (F1,5 = 1.99, p = 0.28). However, this reduction should not be interpreted as an indication of decay, since the pattern is not clear, and more collections are needed before we can even visualize this distribution. The same pattern was observed for the abundance of individuals following the downstream gradient (F1,5 = 0.01, p = 0.90).

The distribution of the genera showed a turnover pattern (NODF observed: 28.88; NODF estimated: 58.51; T = 7.97, $p < 0.01$), wherein a genera substitution and each sampling point there is a differentiated community. The genera *Needhamella*, *Lachlania*, *Hydrosmilodon, Cloeodes, Campsurus, Camelobaetis, Tricorythopsis* were the most expressive in the abundance being present at all sampling points, whereas the genera *Anacroneuria, Austrotinodes, Chimarra, Hagenulopsis, Caenis, Cryptonympha, Nectopsyche, Hydroptila, Neotrichia, Tikuna, Ulmeritoides* and *Tricorythodes* occurred at only one sampling point.

The result of the dispersion coefficient (DD3 index) indicated a possible existence of a dispersion pattern in the downstream direction of the river, where the organisms move following the current flow. Individuals were found to carry out a dispersion movement directed towards the last sampling point located further downstream (Figure 2). The positive values in the table indicate that the displacement is occurring in a downstream direction while negative values indicate that a reverse movement occurs (Table 3).

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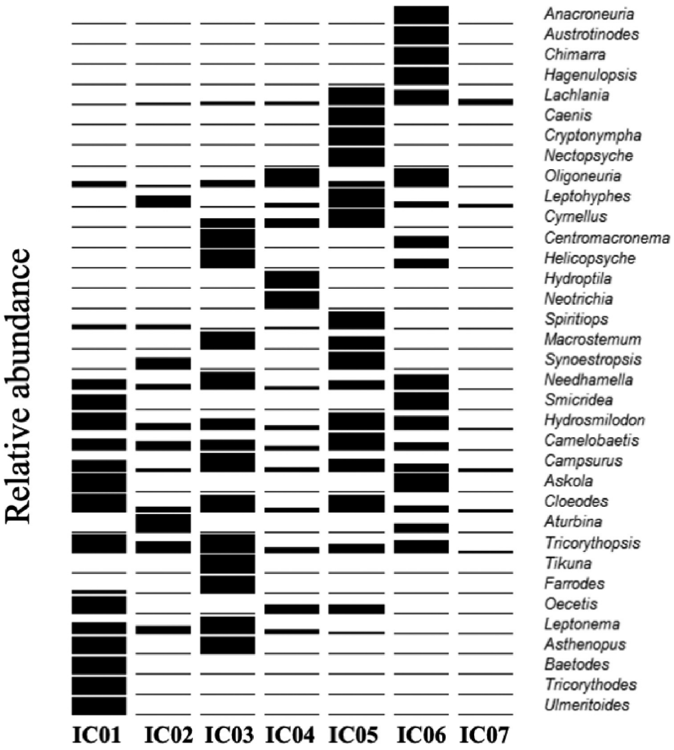

Figure 2. Relative abundance of the aquatic insects at the sampling points int the Xingu River.

Table 3. Dispersion between communities of the Xingu River in a downstream gradient. At the top of the table are the values for index DD3, while at the bottom are the associated p values. Bold values indicate p < 0.05

Sampling Points		Destination (Upstream – Downstream)						
		1	2	3	4	5	6	7
Origin	1		0.18	–0.07	0.12	–0.16	–0.06	0.06
	2	0.13		–0.20	0.09	–0.19	–0.18	0.11
	3	0.57	0.37		0.17	–0.11	–0.03	0.12
	4	0.37	0.43	0.77		–0.14	–0.19	0.14
	5	1.00	0.05	0.57	0.27		0.13	0.13
	6	1.00	0.13	0.60	0.44	1.00		0.16
	7	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	

Discussion

The dispersion movement within aquatic insect communities is responsible for the interaction between communities from different localities, resulting in the colonization of environments and increasing local diversity. The physical and chemical characteristics of each locality will generate different organizations of aquatic insects, where the most adapted to a certain condition will be able to establish themselves (Rodrigues-Filho et al. 2015). The aquatic insect communities that perform their locomotion through the water column in the Xingu River did not demonstrate a nestedness distribution, refuting our first hypothesis. In order to occur a nestedness distribution, the community of aquatic insects found downstream should be a subset of the community found downstream, however we observed a species substitution for each sampling point, a pattern normally observed when the environment is relevant to the community structure (Heino 2009).

The results obtained in this study showed no variation in the number of insect genera along the course of the river, resulting in a uniformity in the community of aquatic insects. The environmental variables don`t showed a relevant variation between the sample points, and the marginal vegetation surround the river is well preserved. The marginal vegetation is a great driver in the chemical conditions of the water (Salomão et al. 2007, Sawakuchi et al. 2015), and the lack of major alterations in the course of sampling points and due to this uniformity in the environment, may be results in the stability of aquatic insect communities. As water level rises, there will be a greater interconnection between the environments facilitating the movement of dispersion between the environments (Wilson & McTammany 2016, Barbosa et al. 2015).

However, the variability of environmental conditions in the Xingu River is related to the seasonality (Salomão et al. 2007, Sawakuchi et al. 2015). During the rainy season the river showed an increase of environmental heterogeneity, because large portions of the bottom of the river (included big stones and mud stretch) were exposed out of the water. In other hand, during the period of flood occurs a uniformity of the environments, because the water covers great portion of the margins, and in the period of drought the environment becomes more heterogeneous with the emergence of rocky outcrops that will make the flow of water be varied (Sawakuchi et al. 2015). It was found in this study that during the flood period the structure of the aquatic insect community does not show large changes between the sampling points, and studies are needed to compare how insect community structuring occurs during the dry season.

Our results indicated the last downstream point as the destination of the genera. All genera observed at the most upstream points are scattering to this location, generating a drift pattern of genera that tend to follow the flow of the river. The dispersion movement is necessary for the colonization of new areas, in view of the fact that communities are interlinked to the dispersion movement and aim to establish the equilibrium of populations in the environment, keeping population sizes in line with environmental support capacity (Waters 1972, Mazzucco et al. 2015). However, that statement is need to be tested using other methods to verify the locomotion of individuals, like mark-recapture methods. In addition, we need caution to interpret the result of our study, because the reduced number of sample locations (seven) may be representing a relevant, but limited, source of information about this aquatic community.

The presence of aquatic insects in the water column has ecological relevance, such as food for larger organisms such as fish, processing of organic matter and provides energy within the trophic web. The location of the occurrence of aquatic insects in the regions of the river column may be related to the life strategies of the animals, where they can counterbalance the food encounter with the dispersion and leakage capacity provided by the water flow, in the water column due to poor fixation on the substrate. Understanding how the dispersion movement occurs is necessary so that we can understand patterns of distribution, richness and interaction between species from different localities (Junior & Suarez 2015).

The EPT orders have a wide global distribution and there are many studies with this group about its ecology and bionomics characteristics (Marques et al. 1999, Baumgartner et al. 2004, Galdean et al. 2001, Gualdoni & Oberto 2012, Godoy, Valente-Neto, et al. 2022, Godoy, Queiroz, et al. 2022). We can better understand the dynamics of dispersion and drift when we observe the characteristics of each order separately. The order Ephemeroptera is strongly influenced by the organic matter present in association with this type of material (Hamada et al. 2019). The samplings were carried out during the flood period when there is a large quantity of organic matter. The high level of the river transports the organic matter present in the marginal region to the channel resulting in an increase in the passive drift of these organisms, besides this factor, we have the high-water flow that exerts strong pressure for the detachment of these organisms from the substrate. Due to these conditions, the order Ephemeroptera was the most abundant and diverse in our samples (Bauernfeind & Moog 2000, Barbosa et al. 2015). Ephemeroptera presents a high diversity in lotic environments, where some genera have preference for places with higher current velocity (Hamada et al. 2019, Sawakuchi et al. 2015). This ability to adapt to this type of environmental condition is related to its body structure that has as characteristic the flattened and elongated body, besides the presence of abdominal gills that aid in the displacement, most of the collected individuals are filterers and adapt easily to this type of environment, due to these characteristics occurred an expressive number of individuals obtained (Castro et al. 2013a).

During the dry season, the Xingu River provides an environment with high heterogeneity, with the presence of riffles in some localities, which will be used for fixation by organisms of the order Trichoptera (Spies et al. 2006, Braun et al. 2014). This study was carried out during the flood period characterized by high water level and uniformity in the landscape, however, even when submerged the riffles serve as shelter for the genera of the order Trichoptera, which has the capacity to build shelters with sediment and suspended material. These shelters are normally fixed to the substrate and are not easily carried by the stream, reducing the probability to found individuals of these group present in the water column (de Moor & Ivanov 2007). The beginning of the dispersion movement may be related to the population density that the increase of density forcing individuals to disperse in the water column, like other organisms, aquatic or not (Munday et al. 2001, Munday 2004, Yu et al. 2001).

Since this relationship exists between the flow of a river and the processes of dispersion and drift, changes in the water dynamics of a river can drastically alter the distribution of aquatic insects, since these spatial patterns are directly related to the drift movement. In order to generate energy, Hydroelectric Power Plants are being built all over Brazil, however such developments cause great changes in the natural course of the river. As there is a relationship between aquatic insects and water flow, these modifications will alter the structure of communities, generating a new equilibrium in the environment (Fearnside 2016). Understanding how the environment is in its pristine state is essential to create conservation strategies for ecosystem processes, allowing the maintenance and use of natural resources (Oldmeadow et al. 2010). In addition, it is necessary to establish parameters to be used in monitoring human-modified environments (Gray et al. 2011, Hauer et al. 2012).

Our study demonstrates an organization of these organisms in an environment without major changes. However, the Belo Monte hydroelectric plant is being built on the Xingu River, which is modifying the original landscape of the river, in which some parts of the river were closed for the construction of a reservoir. These changes directly influence the community of aquatic insects that depend on the flow of the river. The barriers that have been created will make some communities isolated and over time this may result in changes in population genetics in these communities, as well as loss of diversity due to loss followed by non-replenishment of individuals of the species. This study will serve as a reference on how the community of aquatic insects was structured before the changes occurred in the river, being necessary the monitoring to observe how the community will be structured by the changes in the environment.

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Author Contributions

Leal TB and Godoy BS conceived the ideas, designed methodology; Leal TB collected and analyzed the data; Leal TB, Oliveira RRS, Giarrizzo T and Godoy BS wrote the original manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of Interest

The authors declare that they have no conflict of interest.

Data Availability

Supporting data are available at <https://doi.org/10.5281/zenodo.7186623>

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Mapping threatened canga ecosystems in the Brazilian savanna using U-Net deep learning segmentation and Sentinel-2 images: a first step toward conservation planning

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PEREIRA, E.O., WAGNER, F.H., KAMINO, L.H.Y., CARMO, F.F. **Mapping threatened canga ecosystems in the Brazilian savanna using U-Net deep learning segmentation and Sentinel-2 images: a first step toward conservation planning**. Biota Neotropica 23(1): e20221384, 2023. https://doi.org/10.1590/1676-0611-BN-2022-1384

Abstract: Canga ecosystems are iron-rich habitats and pose a challenge for conservation and environmental governance in Brazil. They support high levels of biodiversity and endemism and, at the same time, have suffered intense losses and degradation due to large-scale iron ore mining. The Peixe Bravo River Valley in the Brazilian savanna is one of the last natural canga areas that has yet to face the irreversible impacts of mining. However, there are vast gaps in data on the vegetation cover, location, spatial distribution, and area of occurrence of this ecosystem. Therefore, more information is needed on the appropriate scale, without which it is difficult to establish conservation planning and strategies to prevent, mitigate or compensate for impacts on canga ecosystems. In this study, we provide the first map of canga ecosystems in Brazil using the U-Net deep learning model and Sentinel-2 images. In addition, we estimate the degree of direct threat faced by ecosystems due to the spatial overlap of the mapped cangas and the location of mining concession areas for iron ore exploitation. The deep learning algorithm identified and segmented 762 canga patches (overall accuracy of 98.5%) in an area of 30,000 ha in the Peixe Bravo River Valley, demonstrating the high predictive power of the mapping approach. We conclude that the direct threat to canga ecosystems is high since 99.6% of the observed canga patches are included in mining concession areas. We also highlight that the knowledge acquired about the distribution of cangas through the application of an effective method of artificial intelligence and the use of open-source satellite images is especially important for supporting conservation strategies and environmental public policies.

Keywords: *Conservation policies; ecosystem monitoring; ironstone; remote sensing; artificial intelligence.*

Mapeamento de ecossistemas de canga ameaçados no Cerrado brasileiro utilizando deep learning segmentação U-Net e imagens Sentinel-2: um primeiro passo para o planejamento de conservação

Resumo: Os ecossistemas de Canga, habitats com elevadas concentrações de ferro, são um desafio para conservação e governança ambiental no Brasil. Eles sustentam uma alta biodiversidade e endemismo, e sofreram intensas perdas e degradações de áreas naturais devido à mineração de ferro em larga escala. O Vale do Rio Peixe Bravo, localizado no Cerrado brasileiro, é uma das últimas regiões com ecossistemas de canga que ainda não sofreu impactos irreversíveis da mineração. Mas ainda há ausência de dados sobre a cobertura vegetal, localização, distribuição geográfica e a área de ocorrência desse ecossistema. Portanto, a ausência de informações em escala adequada dificulta o planejamento em conservação e as estratégias para prevenir, mitigar ou compensar os impactos nos ecossistemas de canga. Neste estudo, nós fornecemos o primeiro mapa de ecossistemas de canga no Brasil elaborado a partir de deep learning segmentação U-Net e imagens de satélite Sentinel-2. Além disso, nós estimamos o grau de ameaça direta dos ecossistemas devido a sobreposição espacial das manchas de cangas preditas e a localização dos títulos de concessão minerária para exploração do minério de ferro. O algoritmo de aprendizado profundo identificou 762 manchas de canga (acurácia acima de 98,5%) em uma área de 30.000 ha no Vale do Rio Peixe Bravo, demonstrando o alto poder preditivo do método de mapeamento. Nós estimamos que há um alto grau de ameaça direta aos ecossistemas de canga, uma vez que 99,6% das manchas de cangas preditas estão incluídas em áreas de concessão de mineração. Nós também destacamos que o conhecimento adquirido sobre a distribuição das cangas por meio da aplicação de um método eficaz de inteligência artificial e do uso de imagens de satélite de código aberto é especialmente importante para apoiar estratégias de conservação e políticas públicas ambientais.

Palavras-chave: *Políticas de conservação; monitoramento de ecossistemas; campos rupestres ferruginosos; sensoriamento remoto; inteligência artificial.*

Introduction

The collapse of natural ecosystems due to human activities is a global crisis, with consequences such as decreased biodiversity, species extinction, environmental degradation, resource depletion, pollution, wealth and climate impacts, poverty, and inequality (Cardinale et al. 2012, UNEP 2019). Large-scale mining is an activity that modifies entire landscapes by removing and processing billions of tons of rocky material every year, causing intense and prolonged socioenvironmental impacts (Carmo et al. 2020). Therefore, the ironstone ecosystems stand out as the natural areas most threatened by mining activities. These iron-rich habitats, known as cangas, are found mainly in restricted areas of Brazil and Australia and support high levels of biological diversity – *sensu* Convention on Biological Diversity (MMA 2000) – and many rare and endemic species (Jacobi et al. 2011, English & Keith 2015, Carmo et al. 2018). The main characteristics of canga ecosystems are their anomalous metal contents (especially natural iron and manganese) and insular distributions, which are island-like lateritic duricrusts that are home to specialized edaphic plant communities (Jacobi et al. 2011, Tibbet 2015). Harsh environmental conditions, in addition to the geographic isolation and the antiquity of the cangas duricrusts, likely contributed to the formation of the evolutionary scenarios responsible for the high number of endemic species, the distributions of which are restricted to one or a few localities (Gibson et al. 2010, Carmo & Kamino 2017, Leme et al. 2020).

The global demand for Brazilian iron ore led to the production of this resource increasing to 510 million tons in 2019 (ANM 2020), with extractions occurring in canga ecosystems. Consequently, mining has caused the loss and degradation of iron-rich habitats, with critical outcomes such as the local extinction of rare plant populations and irreversible damage to surface and underground freshwater reserves (Carmo et al. 2018, Salles et al. 2019). In addition, the destruction of canga ecosystems as a result of large-scale mining causes landscape and aesthetic degradation and environmental conflicts with traditional communities (Sánchez et al. 2018, EJatlas 2021a, b). Most regions with canga ecosystems in Brazil have already experienced the intense loss and degradation of natural areas due to dozens of large-scale mining sites, such as those located in the Serra dos Carajás (Amazon Forest), Morraria do Urucum (Pantanal), Caetité (Caatinga), the Serra da Serpentina and the Quadrilátero Ferrífero (Atlantic Forest). The Quadrilátero Ferrífero has already lost up to 50% of its natural canga ecosystem area (Salles et al. 2019), and most canga remnants are found in a very degraded matrix composed of large-scale open pit mines (Jacobi et al. 2011, Sonter et al. 2014).

One of the last natural areas that has not yet irreversible impacts from mining is in the Peixe Bravo River Valley region (Cerrado, Brazilian savanna), southeastern Brazil (Carmo & Kamino 2017). However, in this region, there is still an unexploited iron ore megadeposit, identified as the Nova Aurora Iron District. Currently, there are several large-scale mining projects in the area (Melfi et al. 2016), and the exploitation of these iron-rich deposits is the main direct threat (sensu Salafsky et al. 2008) to canga ecosystems. There are limited data available about the vegetation cover, location, distribution, and area of occurrence of the canga ecosystems in the Peixe Bravo River Valley. This lack of information is due to the challenges of accessing remote regions and the high cost of surveys of geological field camps. These limitations of the data are also related to the scale of existing maps, which is usually smaller than 1:100,000, with some maps on the 1:1,000,000 scale. The smallest linear units that can be mapped on these scales are approximately 150 and 3000 meters, respectively, which is not suitable for identifying most canga outcrops (for details see CODEMIG 2012, Souza et al. 2020, CPRM 2021). The lack of information on the appropriate scale precludes conservation planning and the implementation of measures for the prevention and mitigation of impacts or compensation for damage to biodiversity (Hardner et al. 2015). Therefore, the Peixe Bravo River Valley region represents a unique opportunity to develop solution-based conservation research (Fonseca et al. 2021) that can contribute to the reduction in conflicts between local communities, the mining industry, and environmental policies.

The use of remote sensing and artificial intelligence technologies has great potential for supporting conservation planning, including the indication of critical habitats, ecosystem risk assessments and landscape analysis for large-scale monitoring (Christin et al. 2019, Lamba et al. 2019). In the last decade, a revolution for image classification occurred in 2012 using deep learning techniques that began with AlexNet, a convolutional neural network architecture (Krizhevsky et al. 2017). The field of remote sensing has been using deep learning since 2012 to improve its capacity to automatically classify features in satellite images. Using only raw data, supervised deep convolutional networks automatically learn objects in an image with minimal knowledge about those features (LeCun et al. 1998, 2015). For example, for semantic segmentation, the only necessary input is a mask with labels to aid recognition of the training images (Wagner et al. 2019).

The aims of this study were as follows: 1) to identify and map canga ecosystems using Sentinel-2 images and the artificial intelligence tool U-Net convolutional network; 2) after mapping, to estimate the degree of direct threat faced by ecosystems due to the spatial overlap of cangas and the location of mining concession regimes for iron ore exploitation. We also highlight how the knowledge acquired about the distribution of cangas through the application of the U-Net network and the use of open-source satellite images is especially important to support conservation strategies and environmental public policies.

Materials and Methods

1. *Study area*

The study was conducted in a landscape comprised predominantly of the Cerrado biome (Brazilian savannas) located in the north of the state of Minas Gerais, Brazil, centered at 16°7’ S and 42°42’ W (Figure 1). The

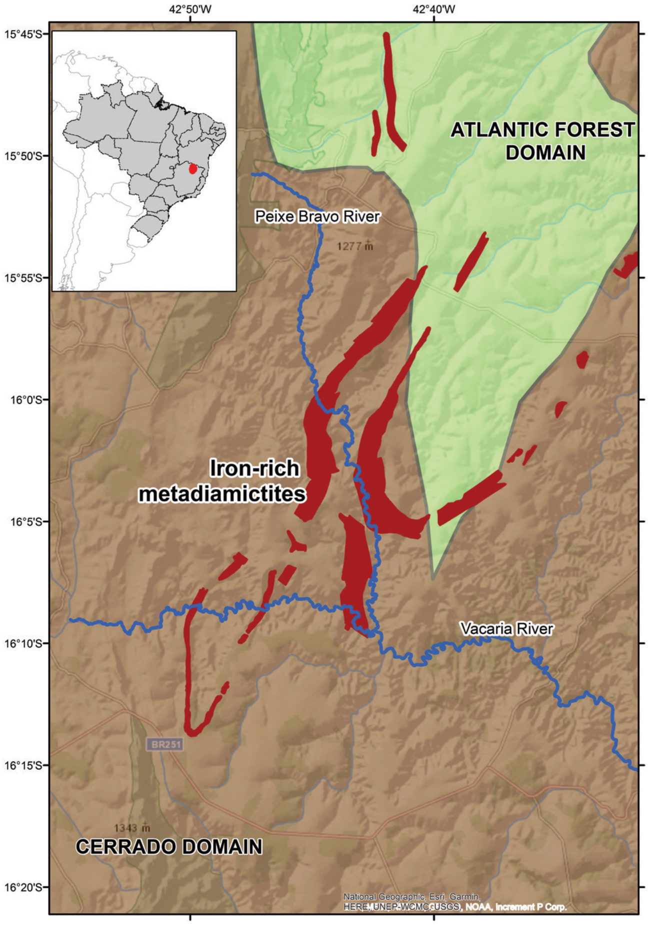


Figure 1. Peixe Bravo River Valley region, North Minas Gerais state, southeastern Brazil. Location of iron-rich metadiamictites from the Riacho Poções Member, in red (Macaúbas Group, Nova Aurora Formation), in the study area. Inset map: South America.

climate in the region is tropical, with a dry winter (Aw type according to Köppen) and an average annual rainfall of approximately 900 mm (Reboita et al. 2015). The canga duricrust is the result of millions of years of weathering of the Neoproterozoic rocks that mainly consist of iron-rich metadiamictites of the Riacho Poções Member (Macaúbas Group, Nova Aurora Formation) (CODEMGE 2018). Extensive plateaus and some hills are the main forms of relief perceived in the landscape. The high topographic heterogeneity of the canga duricrusts forms a set of habitats, such as cracks, depressions, pores, cliffs, puddles and caves, and a corresponding vegetation mosaic (Figure 2).

According to the Technical Manual of Brazilian Vegetation (IBGE 2012), the plant communities associated with canga duricrusts can be defined as relict communities or vegetational refuges, which are adapted to very specific deterministic factors, such as oligotrophic and metalliferous rocky substrates (Carmo & Kamino 2017). Vegetation refuges, therefore, exhibit high sensitivity to any type of intervention since endemic species are abundant. The most frequent phytophysiognomies in canga ecosystems are rocky grasslands and shrublands, known as Campos Rupestres Ferruginosos (Figure 3). This open vegetation occurs in very acidic and oligotrophic metalliferous canga outcrops. Woodland physiognomies can also occur along the canga border and in duricrust cracks and depressions, depending on the topography, soil thickness and moisture (Carmo et al. 2011, Carmo & Kamino 2017).

2. *Classification and mapping of the canga ecosystems*

2.1. Sentinel-2 images and preprocessing

Since 2015, Sentinel-2 is an orbital mission that has been providing continuous global multispectral images with a spatial resolution of 10 meters, thus, can contribute to the mapping of cangas. Furthermore, Sentinel-2 has a revisit rate of up to five days at the equator (ESA 2015),

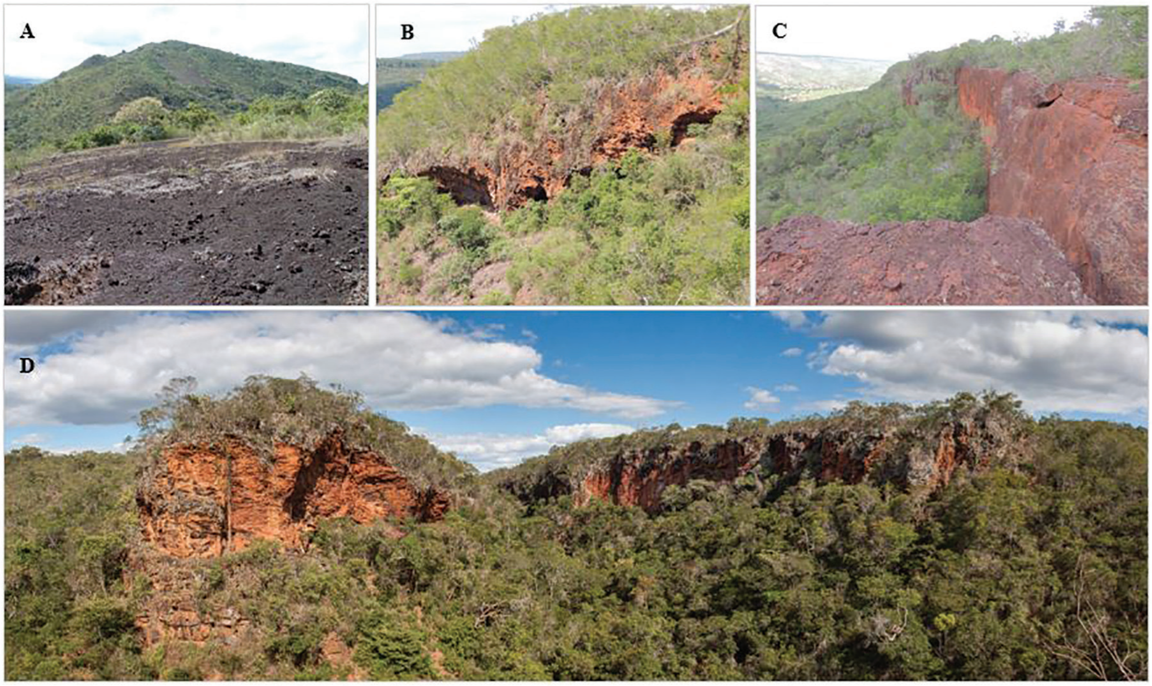


Figure 2. Peixe Bravo River Valley landscape diversity. (A) Hills, (B) caves, (C) cracks and cliffs, and (D) woodland in valleys. Photos: Instituto Prístino.

Figure 3. Canga ecosystems in the Peixe Bravo River Valley, North Minas Gerais state, Brazil. (A) Contrast between the plant communities in iron duricrusts (canga) and the tree matrix outside the canga. (B) Specialized edaphic plant communities in the canga (ironstone) in the foreground and savanna landscape in the background. Photos: Instituto Prístino.

Table 1. Sentinel-2A and Sentinel-2B images used to generate and apply the prediction model for different data corresponding to the passage of the satellite.

Image ID	Original name from Sentinel hub	Date
	Model	
Image 01	S2A_MSIL1C_20190608T130251_N0207_ R095_T23LQC_20190608T143715.tif	06/08/2019
Image 03	S2B_MSIL1C_20190703T130259_N0207_ R095_T23LQC_20190703T161417.tif	07/03/2019
Image 06	S2A_MSIL1C_20160822T130252_N0204_ R095_T23LQC_20160822T130418.tif	08/22/2016
	Prediction	
Image 07	S2A_MSIL1C_20161021T130242_N0204_ R095_T23LQC_20161021T130242.tif	10/21/2016
Image 10	S2A_MSIL1C_20170419T130251_N0204_ R095_T23LQC_20170419T130247.tif	04/19/2017
Image 11	S2A_MSIL1C_20180124T130241_N0206_ R095_T23LQC_20180124T143902.tif	01/24/2018
Image 12	S2A_MSIL1C_20180504T130251_N0206_ R095_T23LQC_20180626T123252.tif	06/26/2018
Image 13	S2A_MSIL1C_20190119T130241_N0207_ R095_T23LQC_20190119T143228.tif	01/19/2019
Image 14	S2A_MSIL1C_20160713T130431_N0204_ R095_T23LQC_20160713T202929.tif	07/13/2016

which can help to determine the best time to map the cangas. For the training of the model, we used three images of the T23LQC tile from the dry period of this region, which occurs between May and September. As shown in Table 1, these images were sensed on 06/08/2019 and 08/22/2016 from Sentinel-2A (prefix S2A) and 07/03/2019 from Sentinel-2B (prefix S2B). For the model predictions, we selected six from different years and periods, including the rainy season sensed in October (Image 07) and January (images 11 and 13) and others sensed in the dry season in May (Image 10), June (Image 12), and July (Image 14). They were all used to identify the potential of the technique for mapping and monitoring. It is important to note that our prediction was applied for each of the images separately, and the training was constructed using the three cited images together.

The occurrence of cangas was mapped from an initial area of 1250 km^2 (50 km × 25 km), obtained from the delimitation of the lithological iron formations available in mappings of the region (scales from 1:100,000 to 1:1,000,000); details are available in the Minas Gerais Mineral Resources web map (CODEMGE 2018). We used Level 1C, Sentinel-2A and 2B images from the European Space Agency (ESA) (Table 1). The Level 1C product resulted from using a digital elevation model to project the image in coordinates. Radiometric measurements per pixel were held on top of atmosphere reflectances with all parameters aimed at transforming them into radiances. In addition, the Level-1C images were resampled with a constant ground sampling distance of 10, 20 and 60 meters depending on the native resolution of the different spectral bands (ESA 2015). The data were downloaded from the Sentinel Data Hub (2020). The images were organized into tiles that cover 108 × 108 kilometers with 1080 × 1080 pixels. We only used red (665 nm), green (560 nm), blue (490 nm), and infrared (842 nm) spectra, all of them at a spatial resolution of 10 meters. The images were preprocessed so that they could be used for the intended method; preprocessing required rescaling of the digital numbers (DN) from 11 bits to 8 bits. In addition, the bands were unified in a composite band process, borders were inserted around the image, and a cut was made at the limits of the study area. The preprocessing procedures of the scenes were performed in RStudio software (R Core Team 2016). The reference image for the vectorization was Image 01 (Table 1). In addition, Google Earth Pro software (Google 2021) was used to assist with the orientation and verification of canga areas in very high-resolution images.

2.2. U-Net convolutional network

In this study, we used a convolutional network for multiclass image segmentation known as U-nets, with which pixel-by-pixel classification is performed and the probability of each pixel belonging to a particular class is estimated. Details of this architecture can be found in Ronneberger et al. (2015) and Wagner et al. (2019). We adapted the filters to improve performance to reach our aim of classifying a large natural surface and because the sentinel images have a smaller spatial resolution when compared with Ronnerberger et al. (2015) and Wagner et al. (2019). The algorithm for generating the model uses three images from the same region (Table 1). The tests were performed with the composition in the natural color (red, green, blue), as in other works in this field (Wagner et al. 2019, 2020a), and the false-color composition was also tested (infrared, red, green) because of the difference between our target area and regions assessed in other studies. The scripts and data necessary to reproduce the model are available on Zenodo (https://doi.org/10.5281/zenodo.6762185).

To enable the U-Net algorithm to recognize and segment the canga cover, we used a vectorized mask based on an image to indicate the ground truth sample, acquired on 06/08/2019, for training (Table 1). This image was chosen due to the low cloud cover and the greater contrast between the canga vegetation and surrounding vegetation; the incidence of water stress reduced the vegetation cover in the canga ecosystem, while the Brazilian savanna matrix remained unchanged. In addition to vector samples, field data collected in 2015, 2019 and 2020 were used to guide searches and check areas for the occurrence of canga (Figure 4). The field data were obtained using a GPS receiver (Garmin GPS 62S model) with at most ±5 m error and were recorded by a Nikon Coolpix P510 camera and DJI Mavic 2 unmanned aerial vehicle (UAV). We applied the geoprocessing and satellite image interpretation techniques available on 09/23/2003, 08/06/2010, 03/06/2013, 04/23/2014, and 09/12/2019 from Google Earth Pro 7.3.6.9326 (Google LLC. 2022) to extract the polygon (vectorized mask) of the canga areas identified in the field.

Using a script developed in RStudio software (R Core Team 2016), the vector mask was superimposed on Sentinel images 01, 02 and 03 (Table 1). The images were subdivided into 32 × 32 pixel squares. Thus, the value representing canga presence (DN = 1) was assigned only in places where there was overlap between the sample vectors and the images. With the resulting squares, a random draw was made in the remainder of the scene to generate squares with the other types of coverage, which were named background (DN = 0). Thus, squares (tiles) of the object of interest (canga) and their surroundings (background) were obtained, generating two classes for the model. Ultimately, the sample was composed of 927 images containing canga only or canga plus background and 1,134 images containing background only. Eighty percent (1,649) were used for the training, and 20% (412) were used for the independent validation of the U-Net segmentation.

In addition, during the training process, image processing techniques were applied to the input images to artificially increase the number of images in the training sample and to help the model generalize to improve prediction on new images. This data augmentation was applied randomly to the input images of the model, as follows: rotations of 0/90/180/270 degrees, since its direction affects how the algorithm interprets an object; changes in the brightness, saturation and hue; conversion of the RGB to BSH (brightness-saturation-hue); and modulation of the values between 95% and 110% for brightness, between 95% and 105% for saturation and between 95% and 105% for hue. This was done to reduce overfitting (Kim 2020). More details on this process can be found in Wagner et al. (2019).

The training of the model included stages such as analyzing a first result and making subsequent adjustments based on visual verification of the predictions so that the squares containing false-positive data could be identified. Thus, the squares that were visually identified were added to the randomly drawn background (DN = 0). In the subsequent tests of the constructed model, this adjustment was refined until the best result, which was related to the reduction in false positives in this case, was obtained.

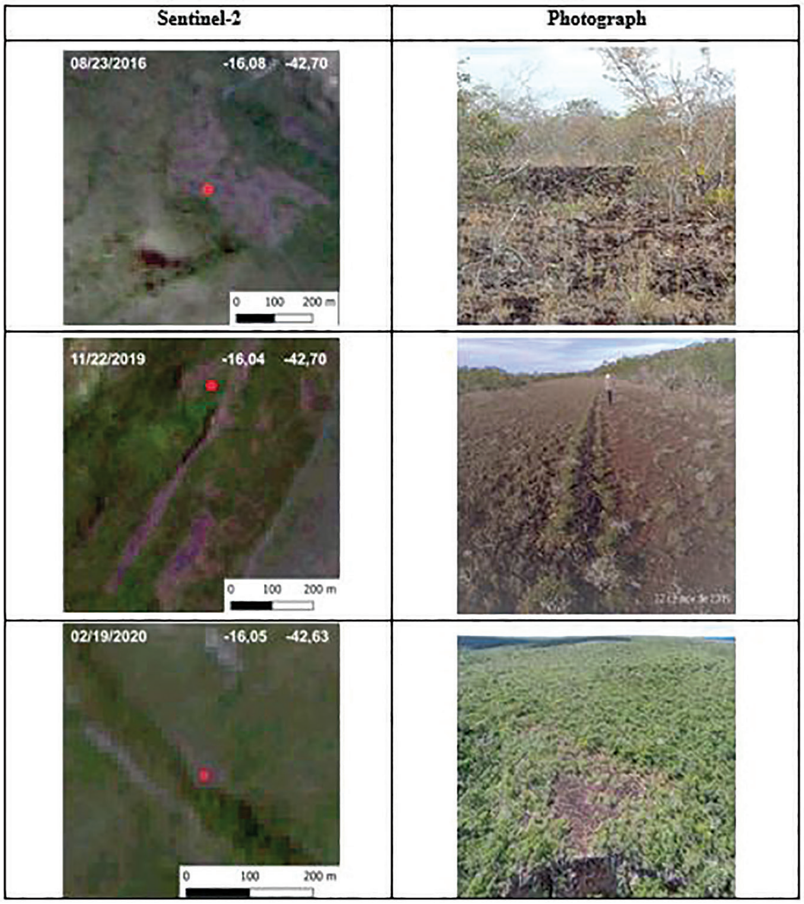


Figure 4. Examples of canga ecosystems observed in Sentinel-2 images and during fieldwork conducted in 2016, 2019 and 2020. Photos: Instituto Prístino.

We randomly sampled images and their associated mask and used 80 percent for training and 20 percent for validation of our classification. Two metrics were estimated for the segmentation accuracy assessment. The first calculates the overall accuracy in terms of percent of well classified pixels (0 or 1), which is implemented by pixelwise assessment. The confusion matrix between the predicted results and the validation sample was generated. The confusion matrix is a table with two rows and two columns that reports the number of canga areas predicted by the U-Net algorithm (correctly predicted), canga predicted where there are no canga (incorrect predicted canga), no canga predicted as no canga (background correctly classified), and no canga predicted as canga (background incorrectly classified). The second metric, the $F1$ score, compares correctly and incorrectly classified segments. The $F1$ score is computed for each class i as the harmonic average of the precision and recall (Equation 1), where precision is the ratio of the number of segments correctly classified as i and the number of all segments (true and false-positive), and recall is the ratio of the number of segments classified correctly as i and the total number of segments belonging to class i (true positive and false negative). This score varies between 0 (lowest value) and 1 (best value).

$$F1_i = 2 \, * \, \frac{precision_i \, * \, recall_i}{(precision_i + recall_i)}$$

Equation 1: $F1$-Score, where i is the number of segments.

To evaluate the prediction and performance of the algorithm, each satellite image (Table 1) was cropped on a regular grid of 320 × 320 pixels, and 64 neighboring pixels were added on each side to create an overlap between the patches. The predictions were made for these images with 384 × 384 pixels, and the resulting images were cropped to 320 × 320 pixels and merged to reconstitute an image of the canga cover to the original extent. This overlapping method was used to prevent prediction artifacts on the image borders, a known problem for the U-Net algorithm (Ronneberger et al. 2015). Classification was made if a pixel prediction value was greater than or equal to 0.5 for a given class. This method is suitable for separating two classes; in this case, a value of 1 was assigned to pixels with canga, and a value of 0 was assigned to background pixels.

The training of the models took approximately 5 hours using the graphics processing unit (GPU) on an Nvidia GeForce GTX-1660Ti with 6 Gb of dedicated memory. The prediction of canga cover in a single image using the GPU took approximately 35 minutes. The model was coded in the R language (R Core Team 2016) with the RStudio interface to Keras (Chollet et al. 2015, Allaire & Chollet 2016) and a Tensor Flow backend (Abadi et al. 2016).

We applied an additional verification to observe convergences of the model prediction with the available geological mapping data in the Peixe Bravo River Valley region because the canga duricrusts are geologically associated with the rocks of the Riacho Poções Member, specifically the hematitic/iron rich metadiamictites and banded iron formations. For this purpose, the locations of some canga patches generated in model prediction to check the field areas in November 2020 and February 2021 were used. Field observations were guided using a Garmin 62S GPS model and recorded by a Nikon Coolpix P510 camera and DJI Mavic 2 UAV. Geological Service (CPRM 2021) and the Minas Gerais Economic Development Company (CODEMIG 2012). Open source QGIS software (QGIS Development Team 2009) was used to validate the delimitations.

3. *Degree of direct threat to canga ecosystems*

The degree of threat was estimated by superimposing the map of the canga ecosystems obtained using the U-Net model with mining concession areas in the Availability and Mining Requirement phases, available on the online platform of the Geographic Information System for Mining (SIGMINE, the acronym in Portuguese) (ANM 2021). In these phases, the mining company must present an economic use plan (PAE, the acronym in Portuguese) to the National Mining Agency (ANM, the acronym in Portuguese), the federal regulatory agency responsible for the management of mineral resources. The PAE produced by the mining company specifies, for example, the volume of mineral extraction, the economics of the enterprise and the description of all the mining and processing structures that will be implemented, thus assessing whether the mining project will be profitable (MPMG 2012). We used the geospatial data related to the polygon areas in the "Availability" and "Mining Requirement" phases obtained from ANM (2021). The overlapping areas were calculated using open source QGIS software (QGIS Development Team 2009).

Results

1. *Classification and mapping of the canga ecosystems*

The segmentation of cangas with the U-Net model in the 1031 images in the validation dataset had an overall accuracy of 98.5% and

Table 2. Numerical evaluation of the models and convergence details.

Model	Epoch	Batch	Sample		Overall accuracy	F1 score	Precision	Recall
			Training	Validation				
Canga cover	240	4	2061	1031	98.5%	0.8235	0.7937	0.855

Table 3. Confusion Matrix.

Confusion Matrix		Predicted label	
		Canga	No-Canga
True label	Canga	True Positive 0.74	False Negative 0.26
	No-Canga	False Positive 0.01	True Negative 0.99

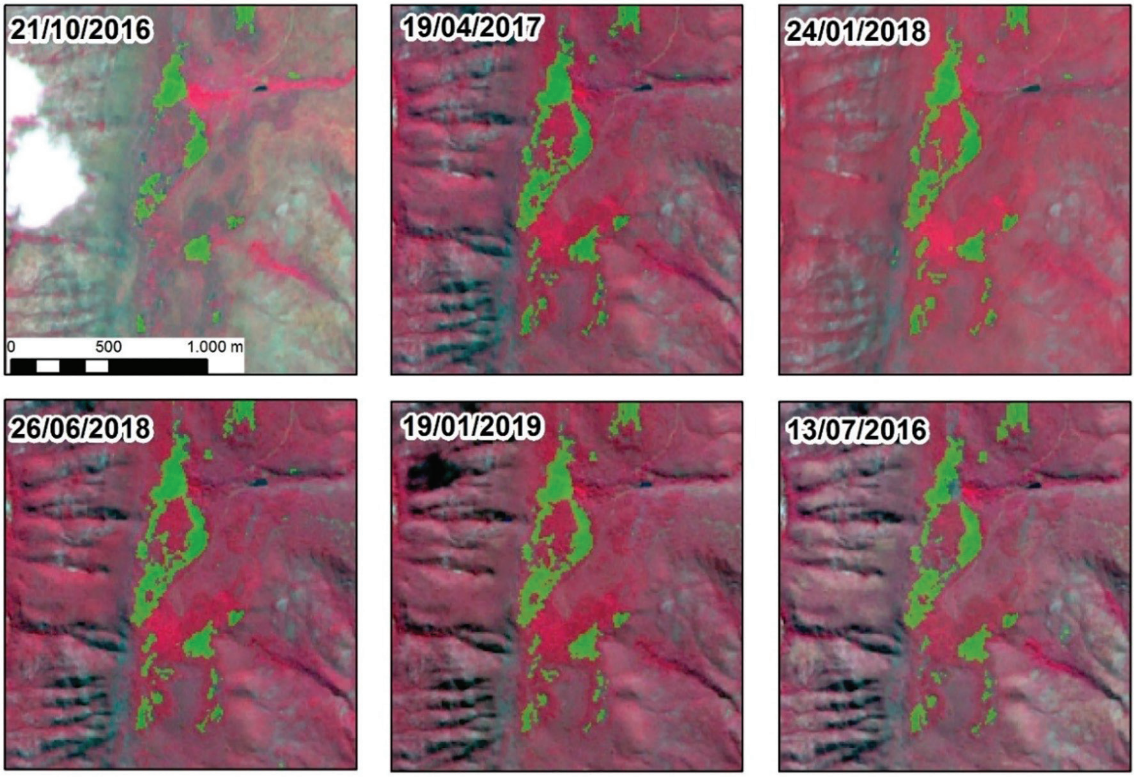


Figure 5. Details of the segmentation process for the six images observed in Sentinel-2 in July and October/2016, April/2017, January and June/2018 and January/2019 to which the model was applied. The green patches in the images represent the predicted "canga patches" on different dates.

an $F1$ score of 0.8235 (precision = 0.7937 and recall = 0.855). The time required for convergence was approximately 12 hours. The best model was obtained after 240 epochs with four images per batch (Table 2). The number of pixels correctly classified as canga as a percentage were 74% (true positive), while 26% were not detected (false negative). For background, defined as all other land covers that are not canga, the matrix indicates that 1% were detected as Canga (false positive), and 99% were classified as background (true negative) (Table 3).

The results of the canga segmentation for the Peixe Bravo River Valley, as seen in Figure 5, showed the delineation of the canga patches among the different Sentinel images. We selected the images using the sentinel metadata, which indicates the percentage of cloud cover. For training the model, we chose zero percent cloud cover. When we performed the classification, we purposely aimed to demonstrate its performance and acquired one image sensed on 10/21/2016, which showed a slightly different prediction result, likely due to a higher cloud cover. Cloud cover increased during the wet season, which occurred between September and March in this region. The surface of the land cover type of interest (a dark rocky substrate and sparse vegetation) posed another challenge because the deep learning technique is usually applied to images with features that reflect in the visible spectrum (i.e., in the RGB channels) (Wagner et al. 2019, 2020a, b). Thus, we adapted the approach for modeling canga surfaces because the infrared frequencies generated a greater contrast with the other covers (shrub and tree vegetation and water). The images were converted to the natural color composition. However, at the time of data and model preparation, removal of the blue band and insertion of the infrared range (IRG), leading to a false color composition (R8G4B2), led to a better visual result for prediction than the natural color images (Figure 5). This result was due to the increased contrast between the target land cover (i.e., the cangas) and the rest of the surfaces (background) when using the near infrared range. In addition, removing the blue wavelengths could have reduced the noise caused by Rayleigh scattering (Jensen & Epiphanio 2011), resulting in better canga predictions.

In our set of images, the largest canga area was predicted in June 2018 (the driest period of the year), with an area of 3,330,484 m² (bottom left corner in Figure 4). In October 2016, however, the observed canga area was only 1,926,891 m² due to the presence of clouds (top left corner in Figure 5). The canga map obtained for 06/26/2018 was used in the following analyses.

The map with a 10 m spatial resolution created using U-Net deep learning allowed the identification of 762 canga patches distributed over an area of 30,000 ha. The canga ecosystems exhibited an insular distribution in the natural landscape and were concentrated in the northern part of the study area, along interfluves and on the moderate slopes of the Peixe Bravo River Valley (Figure 6). Morro Grande was another landscape compartment in which these ecosystems are concentrated; canga ecosystems were found at higher altitudes in this region (1030 m) (white arrow Figure 6), in which the largest canga patch, which was estimated to be nearly 30 ha, was observed. Cangas smaller than 1 ha represented approximately 90% of the 762 patches found in the Peixe Bravo region, and the longest linear distance between two cangas was estimated to be 43 km.

We found that most of the areas (72%) predicted to be canga by the model were associated with the lithostratigraphic unit Riacho Poções Member, represented in the geological maps at scales of 1:100,000 to 1:1,000,000. This lithostratigraphic unit contains iron-rich metadiamictite rocks. During field observations in November

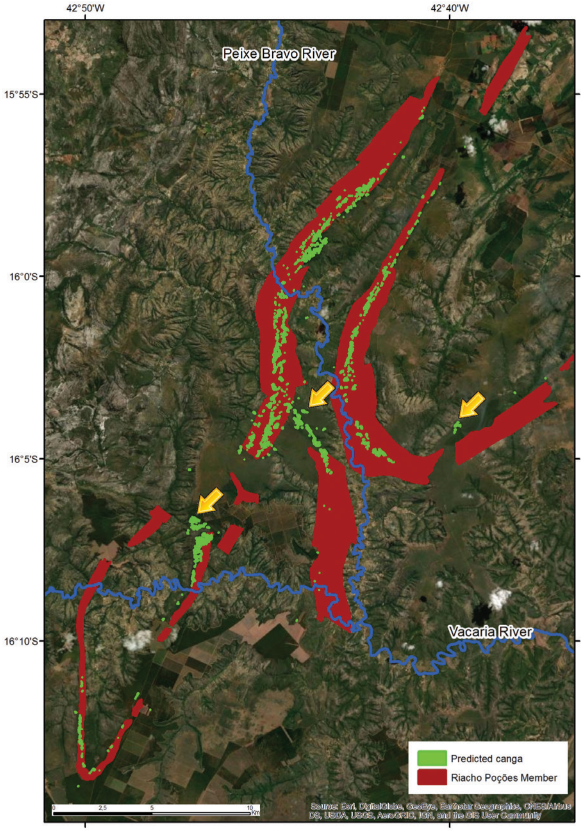


Figure 6. Predicted canga patches (green) in the Peixe Bravo River Valley and the relationship with the lithostratigraphic unit of the Riacho Poções Member/ iron-rich metadiamictites (red) in geological maps (1:100,000 to 1:1,000,000). The yellow arrows indicate the main canga patches that are not yet officially identified on geological maps.

2020 and February 2021, the other canga predicted areas (28%) were verified to also be associated with the Riacho Poções Member but had not yet been identified in the officially available geological maps (Figure 6). Therefore, both the lithostratigraphic unit of the Riacho Poções Member and especially the cangas duricrusts are probably not yet fully represented in geological maps on scales of 1:100,000 to 1:1,000,000. Some canga patches predicted by the segmentation model and validated in the field presented typical cave formations associated with duricrusts (see Figure 2).

2. *Degree of direct threat to canga ecosystems*

Although large-scale iron ore extraction has not yet started, the opening of several access roads to hundreds of geological survey sites has caused some loss and degradation of canga ecosystems (Figure 7). We identified 26 mining concession areas in the Availability and Mining Requirement phases within the Peixe Bravo River Valley, which together cover an area of 25,064 hectares. Most of these mining concession areas were associated with the iron-rich metadiamictites of the Riacho Poções Member and, therefore, the canga duricrusts. We observed that 99.6% of the predicted canga ecosystems were included in areas with a high concentration of mining concessions (Figure 8).

Discussion

In this study, we performed the first canga ecosystem mapping in Brazil at a spatial resolution of 10 m using a U-Net convolutional network. This high-resolution mapping allowed the identification of 762 canga patches distributed in an area of 30,000 ha along the Peixe Bravo River Valley. The deep learning algorithm identified and segmented canga patches with an overall accuracy of 98.5%, demonstrating the

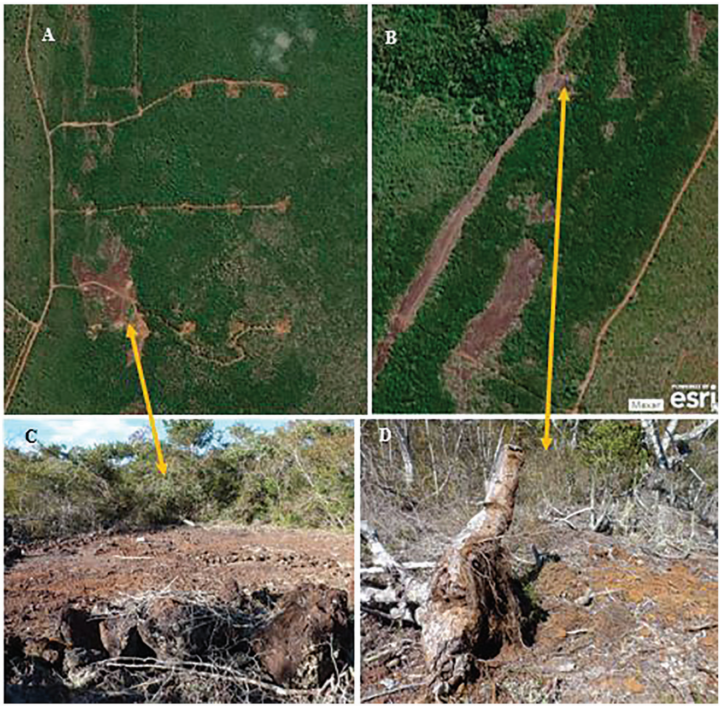
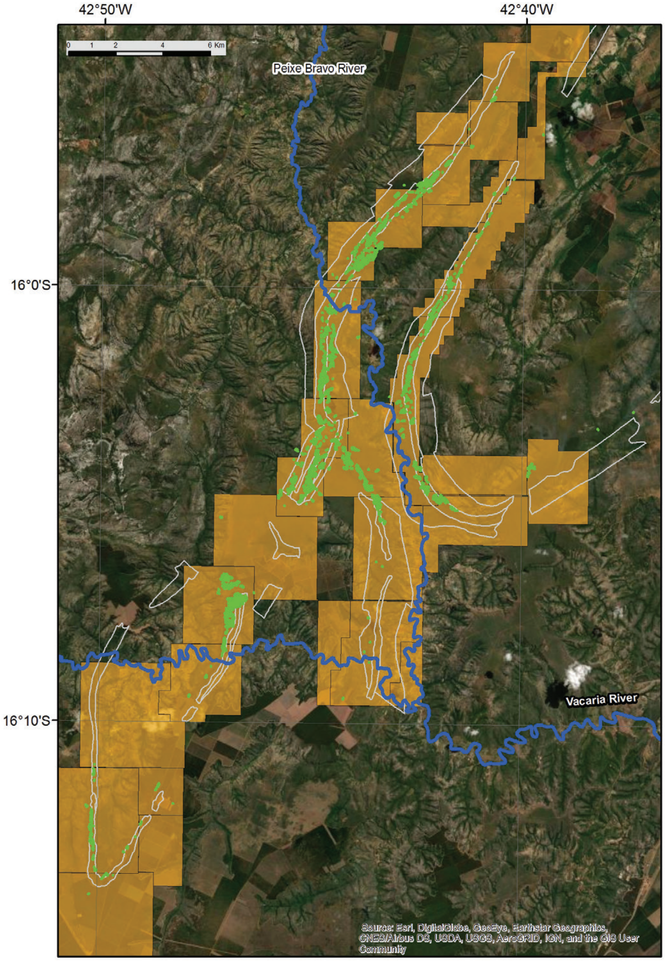


Figure 7. Environmental damage caused by geological survey sites (A and C) and access roads (B and D) resulting in degradation in canga ecosystems in the Peixe Bravo River Valley, North Minas Gerais state, southeastern Brazil. The yellow arrows indicate the relationship between the satellite images and field photos. Images A and B: Digital Geoenvironmental Atlas. Available in:https://institutopristino.org.br/atlas/municipios-de-minas-gerais/ (accessed 18 June 2022). Photos: Instituto Prístino.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 8. High concentration of mining concessions (orange polygons) in the Availability and Mining Requirement phases overlapping the predicted canga patches (green) in the Peixe Bravo River Valley, North Minas Gerais state, southeastern Brazil.

high predictive power of the map. This high level of accuracy means that for every 100 patches detected by the model, only 1.5 patches are expected to contain an error. For comparison, the accuracy of our map was superior to the overall accuracy of collection 6.0 of the Annual Mapping of Land Use and Land Coverage in Brazil (MapBiomas 2022), which reached less than 75% for Cerrado formations of the Cerrado biome, including classes 2 and 3, which correspond to grasslands and subshrub formations (including the Cerrado rupestre).

We found that obtaining images during the dry period was important for mapping rocky outcrop ecosystems located in regions that experience water stress, as was the case for the present study. During the dry period, several species partially or completely lose their aboveground biomass, while others survive despite almost complete desiccation (Proctor & Tuba 2002), which lowers the greenness of the vegetation and further exposes canga duricrusts. Acquiring images during the wet period is not an impediment; however, for long-term monitoring studies, defining a reference month for images is suggested so that the exposure conditions of the cangas are similar. This could prevent overestimation or underestimation of possible changes, such as the eventual loss or degradation of a habitat.

The mapping and monitoring of habitats and ecosystems is one of the main components of the National Biodiversity Policy (Brasil 2002), which also recognizes that canga ecosystems are unique environments that are highly threatened by mining activities. Moreover, one of the main difficulties in implementing monitoring programs with high-resolution imagery is the high cost, which prevents the mapping of large areas (Flood et al. 2019). Thus, the challenge that our study addressed was the need for an effective but low-cost method using satellite images and free software. Previous studies generally used satellite imagery with high cost and a spatial resolution of <3 meters (Wagner et al. 2019, 2020a, b). Here, we demonstrated that for the canga ecosystem, which can be visually assessed in high-resolution images, maps used for monitoring can be created with open source software (R packages citation and keras) and with free high-resolution multispectral satellite imagery (e.g., Sentinel-2 images, which have a repeat interval of 10 days).

Using geotechnologies and artificial intelligence capable of mapping and monitoring ecosystems with restricted and naturally insular areas is essential for obtaining spatial information at the microscale (<<1 km^2). This is a common need when mapping rocky outcrop ecosystems (Cartwright 2019, Christin et al. 2019, Dang et al. 2022). The present study showed that most canga ecosystems were distributed in patches smaller than 1 ha, and nearly one-third of all predicted canga ecosystems were also associated with the Riacho Poções Member but not yet identified in the officially available geological maps. These small outcrops are essential, both because they represent exclusive habitats for endemic species (Hopper et al. 2021) and because they contribute to connectivity, serving as connection points (i.e., stepping stones) for the ecological flow between areas (Chetkiewicz et al. 2006). Thus, our results may also support conservation strategies based on studies involving spatial dynamics in plant populations and landscape ecology, including connectivity analysis (Salles et al. 2019, Ghehi et al. 2020).

In addition, Brazil has the highest plant biodiversity in the world, and Minas Gerais state has the greatest number of rare plants found in rocky outcrops (sensu lato Campos Rupestres). Because of this high conservation value and the low quality or absence of spatial occurrence data for plant species, there are enormous challenges related to monitoring the conservation status of the species in these ecosystems and conducting risk assessments for extinction (Martinelli & Mores 2013). Thus, the use of remote images with high spatial resolution and U-Net deep learning to map canga patches is a promising approach to improve our understanding of, for example, connectivity and gene flow; identify the main anthropogenic threats to conservation targets; develop appropriate guidelines and goals to prevent biodiversity losses and the degradation of ecosystem services; and determine the extent of occurrence and area of occupancy of plant populations with restricted distributions (Kiesecker et al. 2009, Pettorelli et al. 2014).

A real-world scenario in which our results could be applied is to support an evaluation of the extinction risk categories of a rare bromeliad species, *Orthophytum minimum* (Leme & O.B.C. Ribeiro), recently described in the Peixe Bravo River Valley. This rare bromeliad is endemic to canga and has a very restricted geographic distribution, being found in only one location known as Morro do Capim (Leme et al. 2020). The taxonomists who described *O. minimum* were not able to determine the extent of the canga ecosystems, and therefore, there is no information on the geographic distribution and population size of this species. Thus, *O. minimum* is considered a “data deficient” (DD) species since the available data are not sufficient for an assessment of its risk of extinction. Specifically, for the Morro do Capim location, the present study mapped canga patches totaling less than 1 km^2. Thus, our study contributed directly to the application of the IUCN geographic distribution criteria (IUCN 2022) used to evaluate the threat category of a species. Another important contribution of this mapping effort is that it reduces the costs of field work associated with botanical inventories, thus making resources available to investigate more canga rather than using them to search an area of 30,000 ha. The increase in the collection effort in canga ecosystems is necessary and promising, considering that the only a floristic study published for the region (Mota et al. 2017) indicated four new species to science.

Salafsky et al. (2008) conceptualized “direct threats” as synonymous with sources of stress and proximal pressures, representing human activities that have caused, are causing, or may cause the destruction, degradation, and/or biodiversity loss. In this context, we determined there to be a high degree of direct threat to canga ecosystems in the Peixe Bravo River Valley according to the estimate that 99.6% of canga patches are included in mining concession areas (in the availability and requirement phases). This situation makes the deposits of iron ore technically and economically usable because mineral research has already been conducted and approved by the ANM (Brasil 2018). Mining entrepreneurs already have satisfied the legal conditions for initiating an environmental licensing request. In fact, there are three different mining companies that have signed protocols of intention with the State of Minas Gerais for the large-scale exploitation of iron ore over extensive natural areas. At least one mining company has already begun the application for environmental licensing in the Peixe Bravo River Valley region. This requirement is linked to a project that predicts an annual production of 27 million tons of iron ore concentrate, with the installation of open pits, tailings dams, mineral processing plants and pipelines (Minas Gerais 2021, GESTA 2022). These projects have already catalyzed socioenvironmental conflicts in a region that has not yet planned suffered major human interventions due to its rugged relief and primary land use and occupation, which is restricted to family farming distributed in small properties and traditional communities and Quilombo remnants (Carmo et al. 2011, EJatlas 2021a, Palmares Cultural Foundation 2021).

There are still no protected areas for canga ecosystems in the Peixe Bravo River Valley. Thus, our mapping could also contribute to the implementation of public policies aimed at indicating priority conservation areas (PCAs), promoting the sustainable use of resources and sharing biodiversity benefits (MMA 2021). One of the premises of the National Biodiversity Policy (Brasil 2002) is the expansion of the capacity to monitor and evaluate the impacts of natural areas with transparency, greater participation and social control. In addition, broad adherence to systematic PCA procedures is based on the adoption of ecological criteria, participatory decision-making, and the use of geotechnological tools, which are fundamental in scenarios of increasingly scarce financial resources (Margules et al. 2002, McIntosh et al. 2017). Therefore, identifying conservation targets, such as natural habitats that contain relevant biodiversity plots, provide ecosystem services and ensure the livelihood of traditional peoples and communities, is a fundamental part of the process of defining PCAs (Brasil 2005).

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Flávio Fonseca do Carmo: Project administration; writing – original draft, review & editing.

Conflicts of Interest

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

Ethics

This study did not involve human beings and/or clinical trials that would require approval by an Institutional Committee.

Data Availability

The datasets generated during and/or analyzed during the current study are available at: https://doi.org/10.5281/zenodo.6762185

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Article

Ephemeroptera (Insecta) from the metropolitan region of Santarém, Pará, Brazil

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Abstract: With the objective of improving the knowledge about Ephemeroptera in the North region of Brazil, the group's first survey was carried out for the metropolitan region of Santarém, Pará, Brazil. The specimens analyzed were collected from 2019 to 2020 in 27 aquatic environments distributed in the region. The nymphs were captured in the streams with aquatic entomological nets, in addition to manual collection on the substrates. Adults were collected using light traps and flight intercept traps. To complement the inventory, a bibliographic survey of species previously recorded in the area was carried out. For this, the Taxonomic Catalog of Fauna of Brazil, the website Ephemeroptera in South America and scientific articles were consulted. As a result, eight families, 23 genera and 31 species/morphospecies were recorded for the region, with 13 new records for Pará and 19 for the metropolis of Santarém. This study demonstrates the relevance of surveys for the knowledge of biodiversity and for understanding the geographic distribution of taxa.

Keywords: *Diversity; Aquatic Insects; Survey.*

Ephemeroptera (Insecta) da região metropolitana de Santarém, Pará, Brasil

Resumo: Com o objetivo de aprimorar o conhecimento sobre Ephemeroptera na região Norte do Brasil, foi realizado o primeiro levantamento do grupo para a região metropolitana de Santarém, Pará, Brazil. Os espécimes analisados foram coletados de 2019 a 2020 em 27 ambientes aquáticos distribuídos na região. As ninfas foram capturadas nos riachos com redes entomológicas aquáticas, além da coleta manual nos substratos. Os adultos foram coletados por meio de armadilhas luminosas e armadilhas de interceptação de voo. Para complementar o inventário, foi realizado o levantamento bibliográfico das espécies previamente registradas na área. Para isso, foram consultados o Catálogo Taxonômico da Fauna do Brasil, o site Ephemeroptera na América do Sul e artigos científicos. Como resultado, oito famílias, 23 gêneros e 31 espécies/morfoespécies foram registradas para a região, sendo 13 novos registros para o Pará e 19 para a metrópole de Santarém. Este estudo demonstra a relevância dos levantamentos para o conhecimento da biodiversidade e para a compreensão da distribuição geográfica dos táxons.

Palavras-chave: *Diversidade; Insetos Aquáticos; Levantamento.*

Introduction

Ephemeroptera (Insecta) is one of the most important groups of aquatic insects. Representatives of this order are found in lotic and lentic freshwater ecosystems, associated with various substrate types, and participate actively in nutrient cycling and energy flow. In general, they need clean, cold, and well-oxygenated waters for their survival and permanence in the place (Alba-Tercedor 2015), being considered excellent indicators of good water quality because they are sensitive to environmental disturbances (Barbola et al. 2011).

The order is widely distributed on the terrestrial globe, and there are about 3,500 valid species in 450 genera and 42 families (Sartori & Briittain 2015). According to the Brazilian Fauna Taxonomic Catalog (in Portuguese: Catálogo Taxonômico da Fauna do Brasil), about 432 species distributed in 84 genera and 10 families are registered from Brazil. For Pará state, there were 41 species distributed in 33 genera and nine families (Salles et al. 2022).

The knowledge concerning mayflies (Ephemeroptera: Insecta) in Brazil has increased considerably in the last years. With the increase of taxonomic papers and published geographical distribution, the number of species reported from the country almost doubled in two decades (Da-Silva & Salles 2012, Salles et al. 2022). However, this knowledge is concentrated in some regions (Salles et al. 2022). Most of the studies on the order conducted with material collected in Pará were directed to descriptions of species of some families (e.g., Dias et al. 2007, Gonçalves 2010, Souto et al. 2016, Boldrini et al. 2017). This situation not only hampers any attempts to uncover the diversity of the aquatic biota in the region, but also prevents directly applicable studies, such as biomonitoring for example.

The metropolitan region of Santarém in Para state, Brazil, has been suffering anthropic impacts for years, including deforestation for the planting of soybeans, rice and corn, pisciculture, the release of untreated sewage in water bodies and channeling rivers (Da Trindade & Cordeiro 2011, Soares et al. 2016, Gomes et al. 2017). Therefore, understanding of Ephemeroptera biodiversity in this region is priority and can contribute to the realization of future actions in the face of these impacts, especially in decision making and public policies for conservation of natural habitats.

Material and Methods

1. *Study area*

Santarém metropolitan region is in the west of Pará state, comprising the cities of Santarém, Mojuí dos Campos and Belterra, covering a territory of 27,285.426 km² (Figure 1). It has a tropical monsoon climate and an average temperature of 25.6 °C, with an average relative humidity of 80% and annual rainfall of 2,000 mm (Fapespa 2015, De Andrade 2017). The sampled sites are distributed between the Tapajós and Mojuí rivers basins (Lima 2012), including streams, waterfalls, rivers and lakes ecosystems. The region also has a conservation unit – the Floresta Nacional do Tapajós (Tapajós National Forest), an area of approximately 527,319 hectares, covering the following cities: Aveiro, Belterra, Placas and Rurópolis (ICMBIO 2019).

2. *Collection, Identification and illustrations*

The collections were carried out at 27 points distributed in the metropolitan region of Santarém-PA, being 18 in Santarém, seven in Belterra and five in Mojuí dos Campos. The mayflies were collected between June/2019 and October/2020. Nymphs were collected with aquatic entomological nets in addition to manual collection with forceps directly from de substrates. At each collection point, the largest number of possible substrates (sand, gravel, bottom litter, stones, marginal vegetation) was sampled. Imagos and subimagos were collected with light traps (white sheet illuminated with a 15W emergency lamp, Pennsylvania trap and Malaise trap). The subimagos collected alive were kept for about twelve hours in empty microtubules, until they moulted to the imago stage, and then they were fixed in 80% ethanol.

The identifications were based on taxonomic keys (e.g., Domínguez et al. 2006, Salles 2006, Salles et al. 2018) and updated articles for each group (e.g., Boldrini et al. 2018, Araújo & Dias 2020, Oliveira et al. 2020). When needed, structures of the bodies were dissected and mounted between slide and coverslip, using Euparal® as the mounting medium. The specimens are deposited in the Laboratory of Ecology and Taxonomy of Aquatic Invertebrates (UFOPA).

Multilayer photographs were obtained using a Leica M165C stereomicroscope in conjunction with Leica DFC 420 image capturing equipment and LED dome lighting for uniform reflection of light on

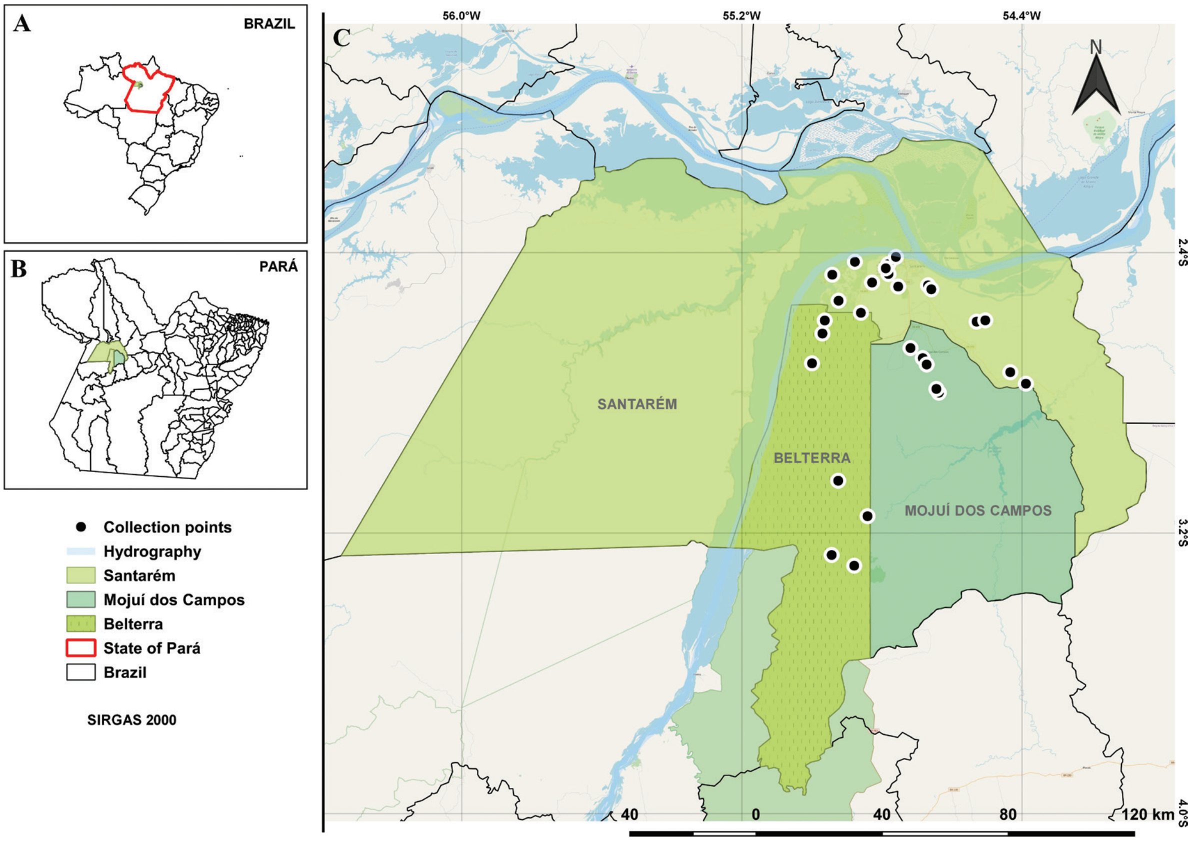

Figure 1. (A-C) Maps. (A) Brazil. (B) Pará state in detail. (C) Metropolitan Region of Santarém with the location of the sampled sites.

the specimens (Kawada and Buffington 2016) and an Olympus BX51 compound microscope in conjunction with an Olympus digital image acquisition system (DP 72 model using the Cell D program). The final images were generated using Digital Leica Application Suite v.3.7 and Helicon Focus (6.7.1 Pro) software.

3. *Geographical distribution and material examined*

The geographic distribution of the taxa collected in the present study was compiled from the Brazilian Fauna Taxonomic Catalog (Salles et al. 2022), from the Ephemeroptera in South America website and from several articles using data of collections carried out in the region. The new records for Pará state were marked with a positive symbol (+) and the new records only for the metropolis of Santarém were marked with a black asterisk (*).

Results

Based on the literature and new samples, a total of eight families, 23 genera and 31 species/morphospecies have been compiled for the metropolitan region of Santarém, with 13 new records for Pará and 19 new records for the metropolitan region of Santarém (Table 1).

Family Baetidae

Aturbina georgei Lugo-Ortiz & McCafferty, 1996

Geographic distribution. North: Pará, Amazonas, Acre, Roraima. Northeast: Bahia, Pernambuco. Midwest: Mato Grosso. Southeast: Espírito Santo, Minas Gerais, São Paulo, Rio de Janeiro.

Comment. Species described by Lugo-Ortiz & McCafferty (1996a) based on material collected in Paraná do Tapará, near Santarém, but not collected during the sampling of the present study.

Aturbina maculata Salles, Boldrini & Shimano, 2011

Figure 2A, E

Material Examined. Pará, Santarém: Guaraná stream (02°46'25.9"S; 54°23'20.5"W), 06/iii/2020, Oliveira, LA. col: 2 imagos ♂, 2 imagos ♀. Pará, Mojuí dos Campos: Mojuí dos Caboclos stream (02°42'03.0"S; 54°41'01.0"W), 05/vii/2020, Oliveira, LA. col: 30 imagos ♂, 35 imagos ♀.

Geographic distribution. North: Amazonas, Pará$^{+}$.

Comment. Until now, this species was registered only for its type-locality (Amazonas) (Salles et al. 2011). According to the description presented in Salles et al. (2011), the costal area of the anterior wing of *A. maculata* has four veins. However, based on the material collected in this study, it was observed that this characteristic is variable, with specimens also showing five veins (Figure 2E). This is the first record of this species for Pará state.

Callibaetis gelidus Cruz, Salles & Hamada, 2014

Figure 2B

Material Examined. Pará, Santarém: Amarjuá stream (02°26'56.2"S; 54°47'53.9"W), 13/ix/2019, Oliveira, LA. col: 1 imago ♀.

Geographic distribution. North: Amazonas, Roraima, Rondônia, Pará$^{+}$.

Comment. This is the first record of this species for Pará state.

Callibaetis gonzalezi (Navás, 1934)

Figure 2C

Material Examined. Pará, Santarém: Tapajós river - CDP port (02°25'03.0"S; 54°44'34.0"W), 05/iii/2020, Sousa, CAL. col: 2 imagos ♀.

Table 1. Ephemeroptera (Insecta) recorded for the Metropolitan Region of Santarém. New records: (+) new record for the state; (*) new record for the metropolitan region of Santarém; (?) locality not specified.

Species	Records
Baetidae	
Aturbina georgei Lugo-Ortiz & McCafferty, 1996	
Aturbina maculata Salles, Boldrini & Snimano, 2011	+
Callibaetis gelidus Cruz, Salles & Hamada, 2014	+
Callibaetis gonzalezi (Navás, 1934)	+
Callibaetis nigracyclus Cruz, Salles & Hamada, 2014	*
Cloeodes sp.	+
Camelobaetidius labiosus (Boldrini & Salles, 2017)	
Cryptonympha copiosa Lugo-Ortiz & McCafferty, 1998	
Paracloeodes binodulus Lugo-Ortiz & McCafferty, 1996	
Tupiara ibirapitanga Salles Lugo-Ortiz, Da-Silva & Francischetti, 2003	+
Waltzoyphius roberti Thomas & Perú, 2002	+
Caenidae	
Brasilocaenis mendesi Malzacher, 1998	+
Caenis cuniana Froehlich, 1969	+
Caenis reissi Malzacher, 1986	
Coryphoridae	
Coryphorus aquilus Peters, 1981	
Ephemeridae	
Hexagenia (Pseudeatonica) albivitta (Walker, 1853)	?
Euthyplociidae	
Campylocia demoulini Gonçalves & Salles, 2017	?
Leptohyphidae	
Amanahyphes saguassu Salles & Molineri, 2006	*
Tricorythopsis similis Oliveira, Salles & Couceiro, 2021	+
Macunahyphes australis (Banks, 1913)	*
Leptophlebiidae	
Askola emmerichi Domínguez, Molineri & Mariano, 2009	+
Farrodes xingu Domínguez, Molineri & Peters, 1996	*
Hermanellopsis arsia Savage & Peters, 1983	+
Hydrosmilodon gilliesae Thomas & Perú, 2004	*
Miroculis (Atroari) duckensis Savage & Peters, 1983	+
Simothraulopsis demerara (Traver, 1947)	
Simothraulopsis inaequalis Nascimento, Salles & Hamada, 2017	
Simothraulopsis plesius Kluge, 2007	
Polymitarcyidae	
Campsurus essequibo Traver, 1947	*
Campsurus latipennis (Walker, 1853)	
Campsurus lucidus Needham & Murphy, 1924	+

Geographic distribution. North: Amazonas, Rondônia, Pará$^{+}$. Northeast: Bahia, Pernambuco.

Comment. This is the first record of this species for Pará state.

Figure 2. Baetidae adults. (A) *Aturbina maculata* (male imago). (B) *Callibaetis gelidus* (female imago). (C) *Callibaetis gonzalezi* (female imago). (D) *Callibaetis nigracyclus* (male imago). (E) *Aturbina maculata* (male imago), anterior wing.

Callibaetis nigracyclus Cruz, Salles & Hamada, 2014

Figure 2D

Material Examined. Pará, Mojuí dos Campos: Terra Preta stream (02°43'09.1"S; 54°40'20.7"W), 31/vii/2020; 24/ii/2020, Oliveira, LA. col: 5 imagos ♂, 1 imago ♀. Água Fria stream (02°47'19.7"S; 54°38"40.9"W), 24/ix/2020, Oliveira, LA. col: 7 imagos ♂, 2 imagos ♀.

Geographic distribution. North: Amazonas, Pará*. Northeast: Piauí.

Comment. Species described by Cruz et al. (2014) based on material from Pará (Parauapebas - Flona do Carajás). This is the first record of this species for the metropolis of Santarém.

Camelobaetidius labiosus (Boldrini & Salles, 2017)

Geographic distribution. North: Pará.

Comment. Boldrini et al. (2017) described *Tapajobaetis labiosus* (a new genus and species) based on material collected in Pará. Recently, in a phylogenetic study (Nieto et al. 2020), this genus was recovered as a synonym for *Camelobaetidius*, and a new combination was proposed for this species. In addition, after analyzing the coordinates provided in Boldrini et al. (2017), it was found that the collection area is in Belterra municipality, instead of Santarém, as described in the original article. This taxon was not collected during the sampling of the present study.

Cloeodes sp.

Figure 3A

Material Examined. Pará, Santarém: Rai stream (02°35'35.3"S; 54°30'18.1"W), 13/xi/19, Oliveira, LA. col: 2 nymphs. Pará, Belterra: stream km-115 (03°17'34.8"S; 54° 52'45.6"W), 20/i/20, Oliveira, LA. col: 1 nymph. Jatuaranã stream (03°15'44.7"S; 54° 56'37.5"W), 11/ii/20, Oliveira, LA. col: 1 nymph.

Geographic distribution. North: Pará$^{+}$.

Comment. Despite being a genus widely distributed in Brazil, this is the first record for Pará. The specific identification of this morphospecies is in analysis.

Figure 3. Baetidae nymphs. (A) *Cloeodes* sp. (B) *Cryptonympha copiosa.* (C) *Tupiara ibirapitanga*. (D) *Waltzoyphius roberti*.

Cryptonympha copiosa **Lugo-Ortiz & McCafferty, 1998**

Figure 3B

Material Examined. Pará, Santarém: Guaraná stream (02°46'25.9"S; 54°23'20.5"W), 06/iii/2020, Oliveira, LA. col. (UFOPA): 31 nymphs. Jatobá stream (02°34'17.9"S; 54°51'36.8"W), 10/x/2020, Oliveira, LA. col: 2 nymphs.

Geographic distribution. Brazil: North: Pará, Amazonas, Acre, Roraima, Rondônia. Northeast: Bahia, Maranhão. Midwest: Mato Grosso. South: Rio Grande do Sul and Santa Catarina.

Comment. Species described by Lugo-Ortiz & McCafferty (1998) based on material collected in the surroundings of Santarém.

Paracloeodes binodulus **Lugo-Ortiz & McCafferty, 1996**

Geographic distribution. North: Pará, Amazonas, Roraima, Amapá. Northeast: Maranhão. Midwest: Mato Grosso.

Comment. Species described by Lugo-Ortiz & McCafferty (1996b) based on material collected in the vicinity of Santarém and Belterra, but not found during the sampling of the present study.

Tupiara ibirapitanga **Salles Lugo-Ortiz, Da-Silva & Francischetti, 2003**

Figure 3C

Material Examined. Pará, Santarém: Rocha Negra waterfall (02°29'48.5"S; 54°45'13.3"W), 24/ix/2020, Oliveira, LA. col: 1 nymph.

Geographic distribution. North: Amazonas, Pará$^{+}$. Southeast: Espírito Santo, Minas Gerais, Rio de Janeiro.

Comment. This is the first record of the genus and species for Pará state.

Waltzoyphius roberti **Thomas & Perú, 2002**

Figure 3D

Material Examined. Pará, Santarém: Guaraná stream (02°46'25.9"S; 54°23'20.5"W), 06/iii/2020, Oliveira, LA. col: 50 nymphs. Cajutuba stream (02°27'39.1"S; 54°46'53.5"W), 11/x/2020, Oliveira, LA. col: 1 nymph.

Geographic distribution. North: Amazonas, Roraima, Rondônia, Pará$^{+}$. Northeast: Bahia. Midwest: Mato Grosso, Goiás.

Comment. This is the first record of this species for Pará state.

Family Caenidae

Brasilocaenis mendesi **Malzacher, 1998**

Figure 4A

Material Examined. Pará, Mojuí dos Campos: Mojuí dos Caboclos stream (02°42'03.0"S; 54°41'01.0"W),11/xi/2020, Oliveira, LA. col: 133 imagos ♂, 36 imagos ♀.

Geographic distribution. North: Pará$^{+}$. Midwest: Mato Grosso.

Comment. This is the first record of this species for the Pará state.

Caenis cuniana **Froehlich, 1969**

Figure 4B

Material Examined. Pará, Santarém: Amarjuá stream (02°26'56.2"S; 54°47'53.9"W), 13/ix/2019, Oliveira, LA. col: 4 imagos ♂.

Geographic distribution. North: Roraima, Pará$^{+}$. Northeast: Pernambuco. Midwest: Mato Grosso. Southeast: Espírito Santo, São Paulo, Rio de Janeiro.

Comment. This is the first record of this species for the state.

Figure 4. Caenidae adults. (A) *Brasilocaenis mendesi* (male imago). (B) *Caenis cuniana* (male imago).

Figure 5. *Coryphorus aquilus*, male imago. (A) Dorsal view. (B) Genitalia, ventral view.

Caenis reissi **Malzacher, 1986**

Geographic distribution. North: Pará.

Comment. Species described by Malzacher (1986) based on material collected in Belterra municipality, but not found during the sampling of the present study.

Family Coryphoridae

Coryphorus aquilus **Peters, 1981**

Figure 5

Material Examined. Pará, Mojuí dos Campos: Mojuí dos Caboclos stream (02°42'03.0"S; 54°41'01.0"W), 11/xi/2020, Oliveira, LA. col. 3 imagos ♂, 1 imago ♀.

Geographic distribution. North: Amapá, Amazonas, Pará, Roraima, Tocantins. Midwest: Mato Grosso.

Comment. Species described by Peters (1981) based on material collected in the vicinity of Santarém.

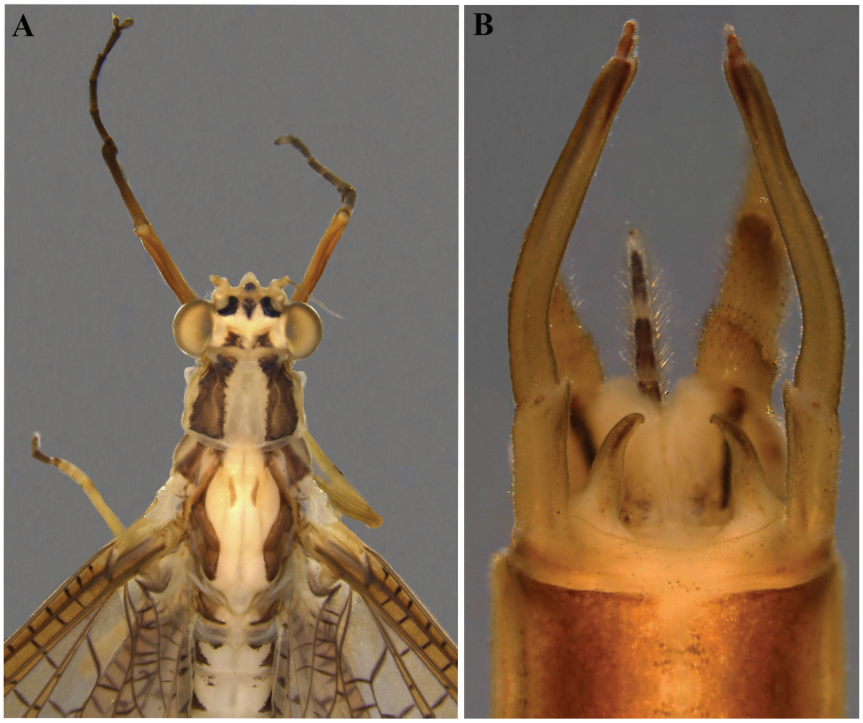

Figure 6. *Hexagenia (Pseudeatonica) albivitta* male imago. (A) Head, thorax and partial region of the abdomen, dorsal view. (B) Genitalia, ventral view.

Family Ephemeridae

***Hexagenia* (*Pseudeatonica*) *albivitta* (Walker, 1853)**

Figure 6

Material Examined. Pará, Santarém: Tapajós river – CDP port (02°25'03.0"S; 54°44'34.0"W), 21/viii/ 2020, Sousa, CAL. col: 2 imagos ♂, 7 imagos ♀.

Geographic distribution. North: Amazonas, Pará. Northeast: Bahia. Midwest: Goiás. Southeast: Espírito Santo, São Paulo, Rio de Janeiro. South: Paraná, Rio Grande do Sul.

Comment. Species registered for Pará by Walker (1853), however, more accurate data on the collection sites were not provided in the original article.

Family Euthyplociidae

***Campylocia demoulini* Gonçalves & Salles, 2017**

Figure 7

Material Examined. Pará, Belterra: stream km-115 BR-316 (03°17'34.8"S; 54°52'45.6"W), 23/vii/2020; 11/xii/2020, Oliveira, LA. col: 1 imago ♂.

Geographic distribution. North: Pará, Amazonas, Roraima, Tocantins. Midwest: Mato Grosso, Distrito Federal.

Comment. Species registered for Pará state in Gonçalves et al. (2017), however, more specific data about the collection site were not provided in the original work.

Figure 7. *Campylocia demoulini,* male imago. (A) Dorsal view. (B) Genitalia, ventral view.

Family Leptohyphidae

***Amanahyphes saguassu* Salles & Molineri, 2006**

Figure 8A

Material Examined. Pará, Mojuí dos Campos: stream km-115 (03°17'34.8"S; 54°52'45.6"W), 23/x/2019, Oliveira, LA. col: 10 subimagos ♂, 4 subimagos ♀. Pará, Belterra: stream at the exit of Flona do Tapajós (03°03'02.6"S; 54°55'30.1"W), 20/x2019, Oliveira, LA. col: 2 subimagos ♂, 5 nymphs.

Geographic distribution. North: Pará*, Amazonas, Amapá. Northeast: Maranhão. Midwest: Mato Grosso.

Comment. This species was previously registered for Pará state by Gonçalves & Da-Silva (2010), for Parauapebas municipality. This is the first record for the metropolitan region of Santarém.

Tricorythopsis similis **Oliveira, Nascimento & Couceiro, 2021**
Figure 8B

Material Examined. Pará, Santarém: stream Ponte do Juá (02°26'41"S; 54°47'21"W), 06/xii/2019, Santos, SE. col: 1 nymph. Pará, Mojuí dos Campos: stream Mojuí dos Caboclos (02°42'03"S; 54°41'01"W), 05/vii/2020, Oliveira, LA. col: 1 nymph.

Geographic distribution. North: Pará$^{+}$

Comment. This species was first described and recorded for the state of Pará by Oliveira et al. (2021), based on material collected in Santarém and Mojuí dos Campos.

Macunahyphes australis **(Banks, 1913)**
Figure 8C

Material Examined. Pará, Santarém: Tapajós river – Ufopa port (02°25'03.0"S; 54°44'34.0"W), 19/vi/2020, Oliveira, LA. col: 6 imagos ♂.

Geographic distribution. North: Amazonas, Roraima, Amapá, Pará*. Midwest: Mato Grosso. Southeast: Espírito Santo. South: Paraná.

Comment. This species was registered for Pará for the first time by Molineri (2002) as *Tricorythodes australis*, for Altamira municipality. Later, Dias et al. (2005) proposed a new genus to allocate this species and recorded its occurrence for Oriximiná (PA). This is the first record for the metropolitan region of Santarém.

Family Leptophlebiidae
Askola emmerichi **Domínguez, Molineri & Mariano, 2009**
Figure 9A

Material Examined. Pará, Belterra: stream km-115 (03°17'34.8"S; 54°52'45.6"W), 23/x/2019, Oliveira, LA. col: 1 subimago ♂, 1 subimago ♀. Stream at the exit of Flona do Tapajós (03°03'02.6"S; 54°55'30.1"W), 20/x/2019, Oliveira, LA. col: 1 subimago ♂, 2 imagos ♀.

Geographic distribution. North: Amazonas, Roraima, Pará$^{+}$. Northeast: Bahia, Pernambuco, Maranhão.

Comment. This is the first record of this species for Pará state.

Farrodes xingu **Domínguez, Molineri & Peters, 1996**
Figure 9B

Material Examined. Pará, Santarém: Cavada waterfall (02°35'48.9"S; 54°31'47.3"W), 13/xi/2019, Oliveira, LA. col: 1 subimago ♂, 3 imagos ♀. Débora stream (02°35'48.9"S; 54°31'47.3"W), 21/x/2019, Oliveira, LA. col: 1 subimago ♂. Pará, Belterra: stream km-115 (03°17'34.8"S; 54°52'45.6"W), 23/x/2019, Oliveira, LA. col: 1 subimago ♂.

Figure 8. Leptohyphidae. (A) *Amanahyphes saguassu* (male imago). (B) *Tricorythopsis silimis* (nymph). (C) *Macunahyphes australis* (male imago), lateral view.

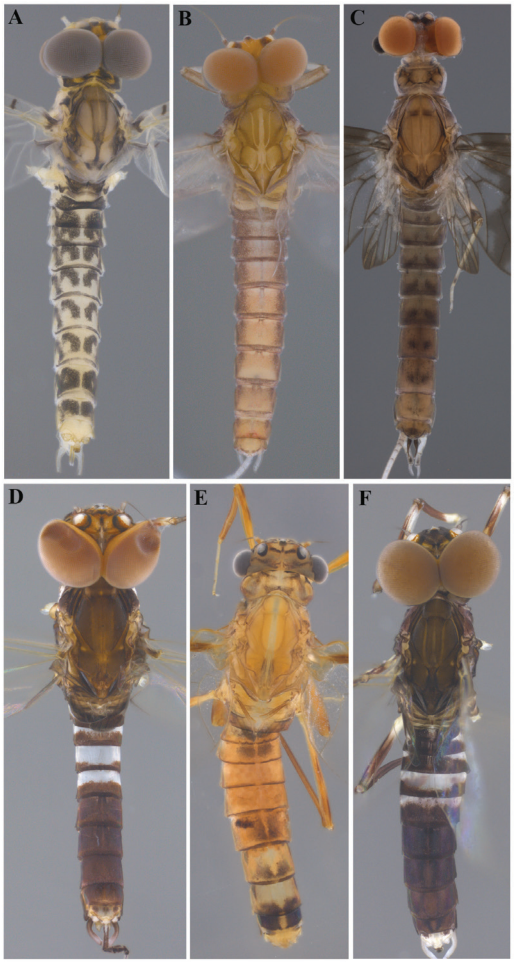

Figure 9. Leptophlebiidae adults. (A) *Askola emmerichi* (male subimago). (B) *Farrodes xingu* (male imago). (C) *Miroculis* (*Atroari)duckensis* (male imago). (D) *Simothraulopsis demerara* (male imago). (E) *Simothraulopsis inaequalis* (female imago). (F) *Simothraulopsis plesius* (male imago).

Geographic distribution. North: Pará*. Northeast: Maranhão. Midwest: Goiás.

Comment. Species described by Domínguez et al. (1996) based on material collected in Altamira (PA) municipality. This is the first record for the metropolitan region of Santarém.

Hermanellopsis arsia **Savage & Peters, 1983**

Figure 10A

Material Examined. Pará, Mojuí dos Campos: Mojuí dos Caboclos stream (02°42'03.0"S; 54°41'01.0"W), 21/i/2020, Oliveira, LA. col:15 imagos ♂, 1 nymph.

Geographic distribution. North: Amazonas, Roraima, Pará$^{+}$. Northeast: Maranhão.

Comment. This is the first record of the genus and species for Pará state.

Hydrosmilodon gilliesae **Thomas & Perú, 2004**

Figure 10B

Material Examined. Pará, Santarém: Guaraná stream (02°46'25.9"S; 54°23'20.6"W), 05/iii/2020, Oliveira, LA. col: 4 imagos ♂, 2 imagos ♀, 20 nymphs. Sonrizal stream (02°32'13.6"S; 54°55'26.6"W), 09/viii/2019, Oliveira, LA. col: 1 imago ♂, 4 imagos ♀, 21 nymphs. São Braz stream (02°29'07.0"S; 54°49'41.9"W), 26/vii/2019, Oliveira, LA. col: 1 imago ♂, 8 imagos ♀, 2 nymphs. Diamantino stream (02° 30'16.2"S; 54°39'32.9"W), 06/ix/2019, Oliveira, LA. col: 1 imago ♂. Mararu stream (02°29'35.9"S; 54°40'06.6"W), 28/viii/2019, Oliveira, LA. col: 1 imago ♂. Pará, Mojuí dos Campos: Santa Júlia stream (02°40'19.7"S; 54°43'06.9"W),09/xii/2019, Oliveira, LA. col: 15 imagos ♂, 14 imagos ♀, 27 nymphs. Mojuí dos Caboclos stream (02°42'03.0"S; 54°41'01.0"W), 21/i/2020, Oliveira, LA. col: 15 imagos ♂, 2 imagos ♀, 21 nymphs. Terra de areia stream (02°47'58.7"S; 54°38'15.6"W), 24/i/2020, Oliveira, LA. col. 14 imagos ♂, 5 imagos ♀, 24 nymphs. Pará, Belterra: stream at the exit of the Flona do Tapajós (03°03'02.6"S; 54°55'30.1"W), 20/x/2019, Oliveira, LA. col: 9 imagos ♂, 2 subimagos ♂, 10 imagos ♀, 3 subimagos ♀. Antônio Leite stream (03°09'06.2"S; 54°50'28.7"W), 18/x/2019, Oliveira, LA. col. 1 nymph. Ailton stream (02°35'36.7"S; 54°57'48.4"W), 06/xi/2019, Oliveira, LA. col: 2 imagos ♂. Stream km-115 (03°17'34.8"S; 54°52'45.6"W), 07-14/xii/2019, Oliveira, LA. col: 1 subimago ♂, 3 subimagos ♂.

Geographic distribution. North: Amazonas, Roraima, Pará*. Northeast: Bahia, Pernambuco, Maranhão. Midwest: Mato Grosso. Southeast: Espírito Santo.

Comment. This is the first record of the genus and species for Pará state.

Miroculis **(*Atroari*)** ***duckensis*** **Savage & Peters, 1983**

Figure 9C

Material Examined. Pará, Belterra: stream km-115 (03°17'34.8"S; 54°52'45.6"W), 23/x/2019, Oliveira, LA. col: 2 subimagos ♂, 1 subimago ♂, 2 subimagos ♂, 45 subimagos ♂. Stream at the exit of Flona do Tapajós (03°03'02.6"S; 54°55'30.1"W), 20/x/2019, Oliveira, LA. col: 1 imago ♂, 1 subimago ♂, 1 imago ♂.

Geographic distribution. North: Amazona, Pará$^{+}$. Northeast: Bahia, Maranhão.

Comment. This is the first record of this species for Pará state.

Simothraulopsis demerara **(Traver, 1947)**

Figure 9D

Material Examined. Pará, Santarém: Tapajós river – CDP port (02°24'50.8"S; 54°44'15.0"W), 05/iii/2020, Sousa, CAL: 1 imago ♂, 3 imagos ♂, 2 subimagos ♀. Tapajós river - Ufopa port (02°25'03.0"S; 54°44'34.0"W), 19/vi/2020, Oliveira, LA. col: 4 imagos ♂, 2 imagos ♂. Tapari lake (02°26'36.1"S; 54°53'53.5"W), 05/vi/2019, Oliveira, LA. col: 2 nymphs.

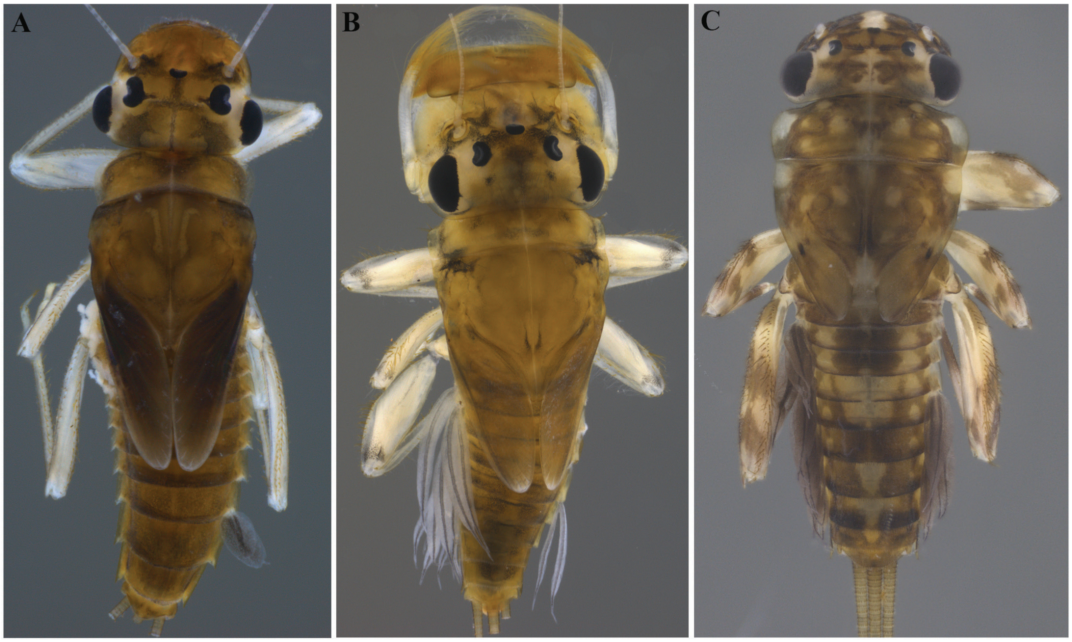

Figure 10. Leptophlebiidae nymphs. (A) *Hermanellopsis arsia*. (B) *Hydrosmilodon gilliesae.* (C) *Simothraulopsis inaequalis.*

Geographic distribution. North: Pará, Amazonas, Acre, Amapá, Rondônia. Northeast: Ceará, Bahia, Piauí, Pernambuco. Maranhão: Midwest: Mato Grosso, Goiás. Southeast: Espírito Santo. South: Paraná.

Comment. This species was previously registered for Pará state by Nascimento et al. (2017), occurring in Santarém.

***Simothraulopsis inaequalis* Nascimento, Salles & Hamada, 2017**

Figure 9E, 10C

Material Examined. Pará, Santarém: Sonrizal stream (02°32'13.6"S; 54°55'26.6"W), 09/viii/2019, Oliveira, LA. col: 1 nymph. Diamantino stream (02°30'16.2"S; 54°39'32.9"W), 06/ix/2019, Oliveira, LA. col: 1 imago ♀. Pará, Mojuí dos Campos: stream km-115 (03°17'34.8"S; 54°52'45.6"W), 23/x/2019, Oliveira, LA. col: 1 I ♀, 3 nymphs. Pará, Belterra: CEL Batista stream (02°37'50.6"S; 54°58'12.4"W), 08/xi/2019, Oliveira, LA. col: 1 imago ♀.

Geographic distribution. North: Pará, Amazonas.

Comment. Species described by Nascimento et al. (2017) based on material collected in Santarém municipality.

***Simothraulopsis plesius* Kluge, 2007**

Figure 9F

Material Examined. Pará, Santarém: Tapari lake (02°26'36.1"S; 54°53'53.5"W), 05/vi/2019, Oliveira, LA. col: 5 nymphs. Pará, Mojuí dos campos: Mojuí dos Caboclos stream (02°42'03.0"S; 54°41'01.0"W), 05/vi/2019, Oliveira, LA. col: 1 imago ♂, 1 subimago ♂, 2 subimagos ♀.

Geographic distribution. North: Pará, Amazonas.

Comment. This species was previously registered for Pará state by Nascimento et al. (2017), for Alter do Chão, Santarém district.

Family Polymitarcyidae

***Campsurus essequibo* Traver, 1947**

Figure 11A

Material Examined. Pará, Santarém: Tapajós river – Ufopa port (02°25'03.0"S; 54°44'34.0"W), 04/v/2020, Oliveira, LA. col: 3 imagos ♂. Tapajós river – CDP port (02°25'03.0"S; 54°44'34.0"W), 19/vi/2020, Sousa, CAL. col: 1 imago ♂.

Geographic distribution. North: Pará*, Amazonas, Roraima.

Comment. This species was registered for Pará state by Molineri & Salles (2017), for Tucuruí municipality. This is the first record for the metropolitan region of Santarém.

***Campsurus latipennis* (Walker, 1853)**

Geographic distribution. North: Pará, Tocantins. Southeast: Espírito Santo.

Comment. This species was registered for the municipality of Santarém by Lestage (1923); however, it was not found during the sampling of the present study.

***Campsurus lucidus* Needham & Murphy, 1924**

Figure 11B

Material Examined. Pará, Santarém: Tapajós river – CDP port (02°25'03.0"; S 54°44'34.0"W), 05/iii/ 2020, Sousa, CAL. col: 1 subimago ♂.

Figure 11. Polymitarcyidae adults. (A) *Campsurus essequibo* (male imago). (B) *Campsurus lucidus* (male subimago).

Geographic distribution. North: Roraima, Pará $^{+}$. Midwest: Mato Grosso do Sul. South: Santa Catarina.

Comment. This is the first record of this species for Pará state.

Discussion

Ephemeroptera is a group of aquatic insects well studied in some locations due to the permanence of researchers in local institutions and because this is a key group in studies of environmental quality (Alba-Tercedor 2015). Despite the great ecological importance of the group, most of applied studies deal with Ephemeroptera only at the level of genus or family (Chen et al. 2017, Nicacio et al. 2020).

The metropolitan area of Santarém presented a representative diversity of Ephemeroptera for the state, which may be related to the variety of habitats among the sampled sites, mainly in places far from the urban areas of the city. Environmental heterogeneity is considered one of the main factors to explain the high richness of taxa in an area (Chisholm et al. 2011), as they provide more resources and niches for species (Bazzaz 1975). However, it is important to emphasize that the metropolitan region of Santarém is experiencing great anthropic pressures (Sousa et al. 2020) and that a large part of the natural environments is at risk of destruction.

Until the completion of this study, a total of 41 species, distributed in 33 genera and nine families were registered for Pará, of these, only 10 species, 16 genera and six families were registered for the metropolis of Santarém. After this research, Pará state is now represented by 54 species/morphospecies, 36 genera and nine families; the metropolis of Santarém is now represented by 31 species/morphospecies, 23 genera and eight families. Thus, with the present study, there was an increase of 23% in the number of new records of Ephemeroptera registered for Pará state and an increase of 65% in what there was registered for the metropolitan area of Santarém (Table 1). And the metropolitan region of Santarém becomes the area with the largest number of Ephemeroptera records in the state. Significant numbers, especially because the study area comprises only 2.19% of the state territory (IBGE 2021).

Baetidae and Leptophlebidae were the most representative families in the metropolitan region of Santarém, with 11 and eight species/morphospecies, respectively, followed by Caenidae (n=3), Polymitarcidae (n=3), Leptohyphidae (n=3), Euthyplocidae (n=1), Ephemeridae (n=1) and Coryphoridae (n=1). This pattern is in line with general studies on the order Ephemeroptera in Brazil, where Baetidae is always identified as the most representative family, followed by Leptophlebiidae and Leptohyphidae (e.g., Francischetti 2007, Salles et al. 2010, Shimano et al. 2011, Lima et al. 2012).

Cloeodes, Hermanellopsis and *Tupiara* stand out as the first records for the state of Pará. Even if recorded for some Brazilian states (Salles & Boldrinni 2022), on a more precise geographic scale, we still see gaps in their distributions, probably because of sampling being concentrated in certain locations.

Although the three cities are seen as a single region, *Hydrosmilodon gilliesae* and *Simothraulopsis inaequalis* were the only species sampled in the three cities. *Callibaetis gelidus*, *Caenis cuniana* and *Campsurus lucidus* (and others), for example, were sampled in only one of the cities. Likewise, some taxa registered in previous (ecological) studies carried out in the region were not collected in the present study.

Some points were sampled several times to obtain nymphs or adults for the complete identification of the species. Even so, despite the efforts, it was not possible to obtain the necessary stage. These observations underscore the importance of constant surveys with increased sampling efforts to obtain complete knowledge about the diversity of Ephemeroptera in the region.

The results presented in this study increased, in general, the knowledge about the diversity and distribution of Ephemeroptera. This knowledge is fundamental for the understanding of aquatic diversity, both in terms of naming the taxa, given future descriptions of new species collected, and for understanding the distribution of these taxa. In addition, the naming of taxa allows greater accuracy in ecological studies, including studies of aquatic biomonitoring in the region.

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Author Contributions

Laura Almeida de Oliveira: contributed to data collection, species identification and article writing.

Sheyla Regina Marques Couceiro: contributed to the data collection and writing of the article.

Jeane Marcelle Cavalcante do Nascimento: contributed to the identification of species and writing of the article.

Conflicts of Interest

The authors declare that there is no conflict of interest related to the publication of this manuscript.

Data Availability

The data used in our analysis is available at Biota Neotropica Dataverse

https://doi.org/10.48331/scielodata.YSVOBZ

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Short Communication

Indirect evidence of following association between golden dorados (*Salminus brasiliensis*) and green anacondas (*Eunectes murinus*) in a clearwater river of Midwest Brazil

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Abstract: On four occasions, the golden dorado (*Salminus brasiliensis*) was recorded following the green anaconda (*Eunectes murinus*) in a clearwater river of Midwest Brazil. These observations were considered as an indirect evidence of a following association known as "nuclear-follower feeding association", a condition in which the follower approach the nuclear when it somehow disturbs the substrate and form sediment clouds while foraging, taking the opportunity to feed during this situation. However, no direct observations of golden dorados getting some benefit from the activity of the green anacondas to feed were made. Nevertheless, as there is a varied list of vertebrates considered as nuclear species in the clearwater rivers of Midwest Brazil, it is to be expected that future observations may provide unusual information about nuclear-follower feeding association between fish and snakes in the Neotropics.

Keywords: *Bryconidae; Boidae; foraging behaviour; opportunistic interaction; Bodoquena Plateau.*

Evidência indireta de associação de seguidor entre dourado (*Salminus brasiliensis*) e sucuri-verde (*Eunectes murinus*) em um rio de águas claras do Centro-Oeste do Brasil

Resumo: Em quatro ocasiões, o dourado (*Salminus brasiliensis*) foi registrado seguindo a sucuri-verde (*Eunectes murinus*) em um rio de águas claras do Centro-Oeste do Brasil. Essas interações foram consideradas como uma evidência indireta de uma associação de seguidor conhecida como "associação de alimentação nuclear-seguidor", uma condição na qual o seguidor se aproxima da espécie nuclear quando esta de alguma forma perturba o substrato e/ou forma nuvens de sedimentos enquanto forrageia, aproveitando a oportunidade para se alimentar durante essa situação. No entanto, observações diretas de dourados obtendo algum benefício da atividade das sucuris para se alimentar não foram feitas. No entanto, como há uma lista variada de vertebrados considerados como espécies nucleares nos rios de águas claras do Centro-Oeste do Brasil, é de se esperar que observações futuras possam fornecer informações incomuns sobre associações do tipo "nuclear-seguidor" entre peixes e serpentes na região Neotropical.

Palavras-chave: *Bryconidae; Boidae; comportamento de forrageamento; interação oportunista; Planalto da Bodoquena.*

Introduction

A large number of fish and even other animals that feed on benthic preys usually through substrate speculation can attract opportunistic species. This type of interaction is known as "following association", "nuclear-follower feeding association" or "following behaviour", and consists of an aquatic animal [or even more than one individual; named as "nuclear(s)"] that excavate or otherwise disturb the substrate while foraging, and one or more opportunistic species [named as "follower(s)"] that capitalize on the small animals and other food types displaced by the foraging activity of the nuclear (Strand 1988, Lukoschek & McCormick 2000, Somaweera & Somaweera, 2021).

This association is well-documented in marine environments, especially for reef dwellers (see Strand 1988 and Sazima et al. 2007 for overviews). However, an increasing number of records of this type of interaction has been reported from freshwater habitats in the Neotropical region (e.g., Sazima 1986, Baker & Foster 1994, Leitão et al. 2007, Teresa & Carvalho 2008, Garrone-Neto & Sazima 2009, Garrone-Neto & Carvalho 2011, Teresa et al. 2014, Sabino et al. 2016, Souza et al. 2019). Nevertheless, no records on the following association between snakes and fish are available in the literature, which constitutes an opportunity to bring up questions of this nature. Thus, in this study we present indirect evidence of a following association between the golden dorado *Salminus brasiliensis* (Cuvier 1816) and the green anaconda *Eunectes murinus* (Linnaeus 1758), and discuss the possible motivations for this type of interspecific interaction and its convergence with observations made for other species.

Material and Methods

The underwater observations were performed in the Olho d'Água River, a clearwater river located in the Bodoquena Plateau, in Midwest Brazil (around 21º26'18''S, 56º26'43''W) (Figure 1). The Olho d'Água River is part of the Paraguay River watershed, and it is directly influenced by the karstic geomorphology of the Bodoquena Plateau, which makes the water naturally highly alkaline and with a very low turbidity (the horizontal water transparency is usually higher than 30 m) (Teresa et al. 2011).

Records were made opportunistically while snorkeling, during a long-term monitoring of the ichthyofauna in the Olho d'Água River. As soon as observed, the following associations were recorded in videos for further analysis. We used the combination of the "ad libitum" and "sequence" sampling rules (Altmann 1974, Martin & Bateson 2007) to describe the interactions, in which the number and size of the nuclear and the follower species, the duration of each behavioural event, the depth and the type of substrate were verified. Size estimates (total length – TL, cm) for *S. brasiliensis* and *E. murinus* were calibrated against objects of known size. Animals were identified *in situ* during the underwater observations, following Marques et al. (2005) and Britski et al. (2007).

Results and Discussion

On four occasions (August 2006, June 2018, November 2019, and June 2021), the golden dorado (*Salminus brasiliensis*) was recorded following the green anaconda (*Eunectes murinus*). Observations were made during daylight, between 09:00 am and 10:30 am, around two meters depth in conditions of full transparency of water.

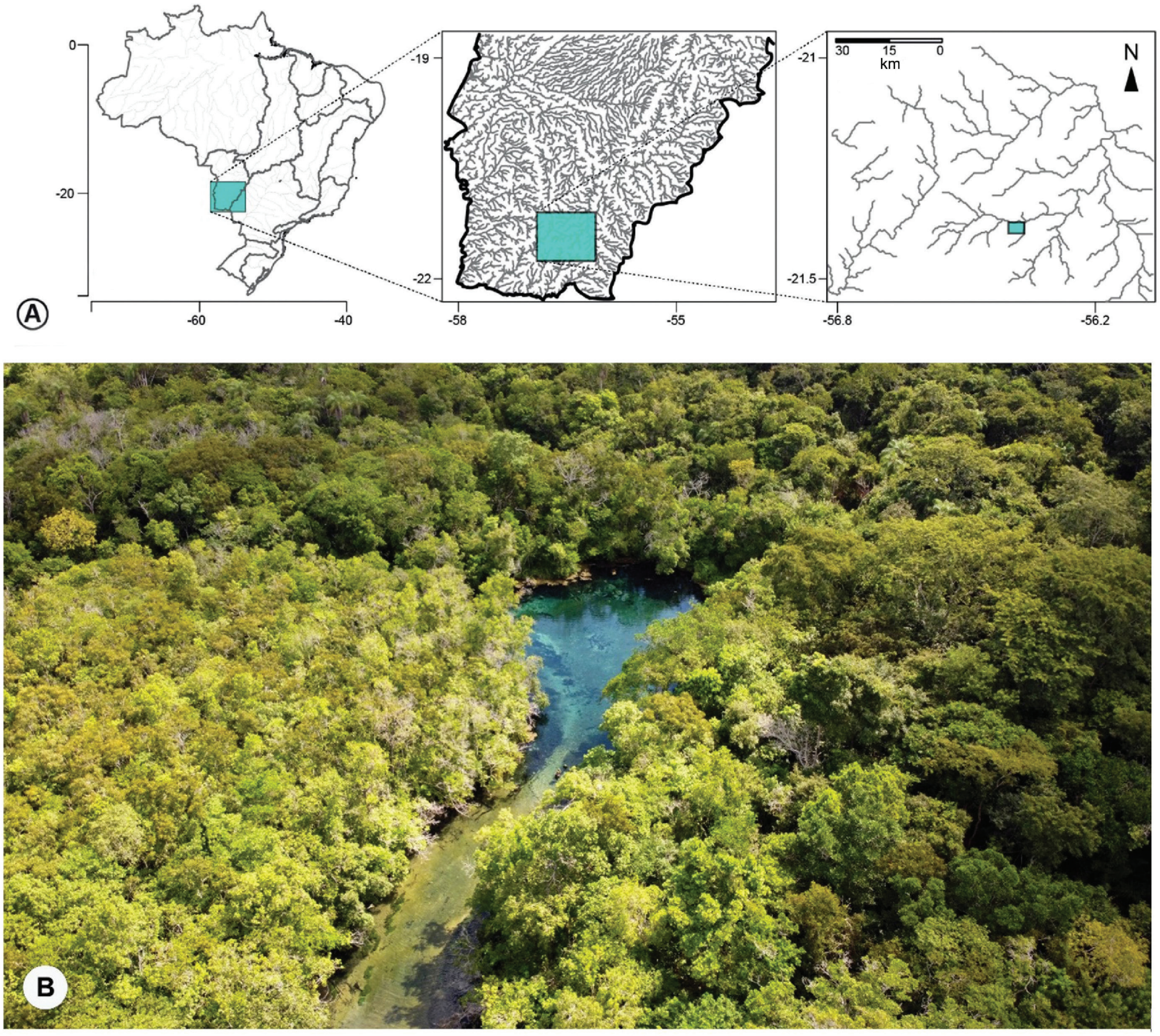

Figure 1. A. Olho d'Água River located in the upper Paraguay River basin, Midwest Brazil. B. Clear water allows observation of the underwater habitats, even in drone photographs.

The interactions were observed when adult and solitary individuals of *S. brasiliensis* (TL ~70 cm) approached to the individuals of *E. murinus* (TL ~400 cm) from the tail. Snakes were moving slowly close to the bottom, composed by sandy substrate, some presence of mud, macrophytes and trunks. Golden dorados remained close to the green anacondas' tails, following the snakes from the posterior region, immediately behind or on one side, never moving forward and approaches the snake's head (Figure 2 and Supplementary Material – Video 1). While moving, some individuals of another species of fish, the piraputanga (*Brycon hilarii*), were observed around or just in front of the green anacondas. Individuals of golden dorados continued to follow the green anacondas, displaying a non-aggressive position in relation to the piraputangas (i.e., a slow swimming, with the dorsal and pectoral fins not arched) (Figure 3). In addition, other fish were also recorded approaching the green anacondas, although in a more temporary way than the piraputangas: tetras (*Astyanax lacustris*), curimbatas (*Prochilodus lineatus*) and piranhas (*Serrasalmus maculatus*) (Supplementary Material – Video 2). No agonistic interactions between *B. hilarii*, *A. lacustris*, *P. lineatus*, and *S. maculatus* and *E. murinus* were observed as well. Observations lasted more than 10 minutes, when the observers stopped following the interactions.

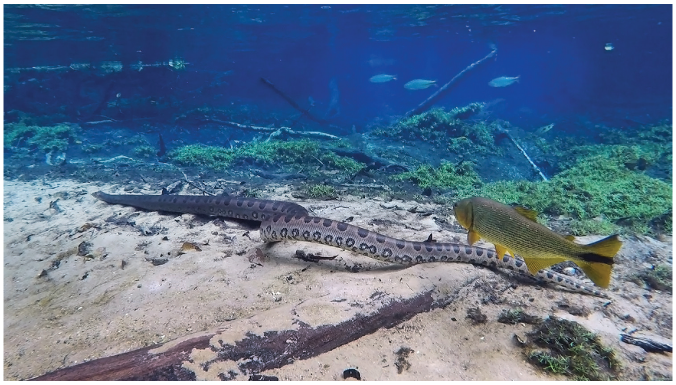

Figure 2. An individual of golden dorado (*Salminus brasiliensis*; TL ~70 cm) following a green anaconda (*Eunectes murinus*; TL ~350 cm) in the Olho d'Água River, Bodoquena Plateau, Midwest Brazil.

Figure 3. Individual of piraputanga (indication in yellow) (*Brycon hilarii*; TL ~40 cm) positioned close to the head of a green anaconda (*Eunectes murinus*; TL ~350 cm). An adult and solitary individual of the golden dorado (indication in white) (*Salminus brasiliensis*; TL ~70 cm) is following the snake, displaying a non-aggressive position in relation to the piraputanga (e.g., pectoral, and dorsal fins not arched).

Although it was not possible to record the golden dorados benefiting from the feeding activity of the green anacondas, most of the observed facts are consistent with following association (sensu Strand 1988), especially in relation to the disturbance in the substrate caused by the movement of the snakes (Supplementary Material – Video 3). Thus, we assume that *S. brasiliensis* can follow *E. murinus* to opportunistically prey mainly on individuals of *B. hilarii* and, eventually, on other species such as tetras (*A. lacustris*), curimbatas (*P. lineatus*) and piranhas (*S. maculatus*).

The fish from the order Characiformes, especially the piraputanga (*B. hilarii*), are in the list of prey of adult individuals of the golden dorado (*S. brasiliensis*) (Bessa et al. 2011). In the streams of the Bodoquena Plateau, Midwest Brazil, adult individuals of *S. brasiliensis* usually attacks individuals of *B. hilarii* in the darker periods of the day, such as the early morning and the dusk (J. Sabino, pers. obs.). This hunting strategy is probably related to the high transparency of the water that is observed in the region, but at the same time makes hinders the stealth action of a visually oriented predator such as *S. brasiliensis*. Thus, when associating with *E. murinus*, *S. brasiliensis* may appear less aggressive to *B. hilarii*, taking the opportunity to prey on this species in a moment of distraction promoted by the movement or the feeding activity of the snake. Besides a possible predation on *B. hilarii*, another possibility is that the movement of *E. murinus* over sandy substrate with mud could dislodge some prey, which could be attacked by *S. brasiliensis*. A similar behaviour occurs when nuclear fish (e.g., *Megaleporinus* and *Prochilodus*) dig into the sand bed and displace small organisms. In this situation, smaller predators such as the cichlids *Crenicichla lepidota* and *C. vitatta* take advantage of the situation to feed on small characins and benthic invertebrates (Teresa et al. 2014, Sabino et al. 2016). To our knowledge, though transient, this is the first documented evidence on the occurrence of this interaction between freshwater fish and aquatic snakes.

Given the absence of photos and videos of green anacondas (*E. murinus*) capturing prey and golden dorados (*S. brasiliensis*) taking advantage of this fact to feed on organisms attracted by the formation of sediment clouds (notably fishes of the order Characiformes), it is not possible to categorically guarantee that the following association occurs between these two species. However, the anecdotal observations presented herein represent rare and uncommon records between two species of South American aquatic predators. With the increase of tourist activities in wild environments, the interaction between scientists and other people through citizen science and with the increase in the offer of less complex tools for the registration of underwater fauna, it is expected that interactions such as following associations start to be registered more frequently. This may help confirm of the hypothesis on the interaction between golden dorados and green anacondas, expanding the knowledge about this type of behaviour in freshwater environments as well as between species from different taxonomic groups.

In addition to following association, the interaction between fish and other organisms can occur for the purpose of cleaning symbiosis, in which the "cleaner" removes ectoparasites and other material from the "host". Although this behaviour could be an alternative to what is being suggested in this study, we don't believe this can be possible. Green anacondas and golden dorados are top predators in the underwater environment that feed mainly on live and medium to large-sized prey in relation to its body. Thus, golden dorados feeding on ectoparasites, mucus or other material does not seem to be feasible. Additionally, a golden dorado searching for protection or chasing an anaconda for predation are also discarded.

Due to the increasing number of records of following associations in the clearwater rivers of the Bodoquena Plateau, Midwest Brazil, including interactions between fishes (Sabino et al. 2016, Souza et al. 2019) and other organisms such as monkeys (*Sapajus apella*), tapirs (*Tapirus terrestris*) and giant otters (*Pteronura brasiliensis*) (Sabino & Sazima 1999, Costa-Pereira 2012), new discoveries like what we are suggesting for golden dorados (*S. brasiliensis*) and green anacondas (*E. murinus*) are possible. One of the main predictors for the occurrence of this type of interaction is the presence of a nuclear species that strongly disturb (directly or indirectly) the substrate while foraging, which attracts a greater variety of followers (Krajewski 2009). In freshwater environments with a predominance of unconsolidated substrate such as sand and mud and with deposit of organic matter, a higher suspension of particles is expected to occur during the feeding activity of nuclear species and, consequently, a greater number of followers must be observed (Teresa et al. 2011, 2014). In streams and rivers of the Neotropical region, especially in the area where our observations were performed, followers are usually represented by benthivorous fishes that form large groups while following the nuclear (Sabino et al. 2016). The golden dorado is a carnivorous fish with a tendency to piscivory that can reach up to 1 meter in length (Moraes Filho & Schubart 1955, Britski et al. 2007). Therefore, we assume that the golden dorado follows the green anaconda in order to catch some fish that eventually escapes from an attempt of predation by the snake or prey on smaller fish that are attracted by a situation in which the snake causes a large disturbance in the substrate. Thus, although transitory, these circumstances may support the idea obtained from the indirect evidence of golden dorados following green anacondas to opportunistically obtain food. As there is a varied list of vertebrates considered as nuclear species in the clearwater rivers of Midwest Brazil, it is to be expected that future observations may provide new information about ecological interactions such as following association between fish and snakes in the Neotropics.

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Associate Editor

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Author Contributions

Jose Sabino: conceived the research.
Domingos Garrone-Neto: conceived the research.
Fernando Maydana: collected and analyzed data.

All authors contributed with ideias, data and information to the text. All authors reviewed and approved the text.

Conflicts of Interest

The authors declare no conflicts of interest.

Ethics

We declare that the procedures used in this study have no conflict with the Brazilian laws regarding the use of vertebrates in scientific research. In addition, this study was performed in compliance with the guidelines for field research inside protected areas in the Mato Grosso do Sul State.

Data Availability

Supporting data are available at:

Video 1: <figshare.com/articles/media/SUCURI1following_association_between_dorado_and_anaconda_mpg/20416020>. DOI: 10.6084/m9.figshare.20416020.

Video 2: <figshare.com/articles/media/SUCURI2following_association_between_dorado_and_anaconda_mov/20422161>. DOI: 10.6084/m9.figshare.20422161.

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Article

The freshwater fishes from the Costa Verde Fluminense region of southeastern Brazil

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***Abstract**:* The region between the Brazilian Shield and the Atlantic Ocean is characterized by the presence of numerous hydrographic basins isolated by mountainous terrain that flow directly into the ocean without forming wide coastal plains. However, knowledge about the diversity and distribution of freshwater fish in several coastal areas is still incipient. One of these areas is the Costa Verde Fluminense region, situated between the municipalities of Mangaratiba and Paraty in the Brazilian State of Rio de Janeiro. In order to eliminate the gap of knowledge about the freshwater fish fauna of this region, we prepared a list of the species, and dichotomous identification keys and illustrations of all species. We examined material from expeditions carried out between 1942 and 2019, deposited in the Ichthyological Collection of the Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil. The material comes from 29 continental coastal rivers and four drainages on Ilha Grande island. We recognized 54 fish species belonging to 16 families and 9 orders. The order Siluriformes was the most diverse with 18 species, followed by Characiformes with 14 species, Cyprinodontiformes with 10 species, Cichliformes with four species, Gobiiformes with three species, Syngnathiformes with two species, and Gymnotiformes, Salmoniformes and Synbranchiformes with one species each. These records include two putative undescribed species and four introduced species. *Phalloceros anisophallos* was the most widely distributed species, recorded in 24 drainages. More than a half (52 %) of the native species occur exclusively in coastal streams, demonstrating the importance of the area for biogeographic and conservation studies.
Keywords: *Angra dos Reis; Mangaratiba; Paraty.*

Os peixes de água doce da região da Costa Verde Fluminense do sudeste do Brasil

Resumo: A região entre o Escudo Brasileiro e o Oceano Atlântico é caracterizada pela presença de inúmeras bacias hidrográficas isoladas por terrenos montanhosos que deságuam diretamente no oceano sem formar amplas planícies costeiras. No entanto, o conhecimento sobre a diversidade e distribuição de peixes de água doce em diversas áreas costeiras ainda é incipiente. Uma dessas áreas é a região da Costa Verde Fluminense, situada entre os municípios de Mangaratiba e Paraty no Estado do Rio de Janeiro. A fim de eliminar a lacuna de conhecimento sobre a ictiofauna de água doce desta região, elaboramos uma lista das espécies, chaves de identificação dicotômicas e ilustrações de todas as espécies. Examinamos material de expedições realizadas entre 1942 e 2019, depositado na Coleção Ictiológica do Museu Nacional da Universidade Federal do Rio de Janeiro, Brasil. O material é proveniente de 29 rios costeiros continentais e quatro drenagens da Ilha Grande. Reconhecemos 54 espécies de peixes pertencentes a 16 famílias e 9 ordens. A ordem Siluriformes foi a mais diversa com 18 espécies, seguida de Characiformes com 14 espécies, Cyprinodontiformes com 10 espécies, Cichliformes com quatro espécies, Gobiiformes com três espécies, Syngnathiformes com duas espécies e Gymnotiformes, Salmoniformes e Synbranchiformes com uma espécie cada. Esses registros incluem duas espécies presumidamente não descritas e quatro espécies introduzidas. *Phalloceros anisophallos* foi a espécie mais amplamente distribuída, registrada em 24 drenagens. Mais da metade (52 %) das espécies nativas ocorrem exclusivamente em córregos costeiros, demonstrando a importância da área para estudos biogeográficos e de conservação.
Palavras-chave: *Angra dos Reis; Mangaratiba; Paraty.*

Introduction

The region between the Brazilian Shield and the Atlantic Ocean is characterized by the presence of numerous hydrographic basins isolated by mountainous terrain. These drainages flow directly into the ocean without forming wide coastal plains and harbor endemic fish populations (Buckup 2011). Most eastern Brazilian coastal basins are small and isolated drainages, characterized by relatively low fish diversity (when compared to the Paraná basin), and high level of endemism (Thomaz & Knowles 2018). One of these areas is the Costa Verde Fluminense region, situated between the municipalities of Mangaratiba and Paraty, which is home to one of the largest remnants of native Atlantic Forest in the Brazilian State of Rio de Janeiro. As for most eastern Brazilian coastal basins, the knowledge about the diversity and distribution of its freshwater fish fauna is still incipient.

The basins of the Costa Verde Fluminense are included in the Fluminense Ecoregion (FEOW352), limited to the north by the Paraíba do Sul (FEOW329) and to the south by Ribeira de Iguape (FEOW330) ecoregions (Abell et al. 2008). This ecoregion is occupied by one of the highest densities of urban occupation in the Atlantic Forest. Despite of the long history of human occupation of the Atlantic coast of Rio de Janeiro, the distribution of freshwater fishes is still poorly known. The first description of a fish species, *Characidium japuhybense*, from a locality situated in the Costa Verde region was published only in the middle of the 20th Century (Travassos 1949) based on material collected in the Japuíba basin, at Angra dos Reis, a few years earlier by George Myers, Paulo Miranda-Ribeiro and Haroldo Travassos. Additional species have been described in recent decades, totaling 11 species described from specimens collected in the Costa Verde region (Table 1), but no comprehensive study of fish composition is currently available (Guimarães et al. 2021).

Bizerril & Primo (2001) provided three lists of fish species from river drainages of Ilha Grande Bay, the largest area in the Costa Verde Fluminense region. Those lists are the most comprehensive ever published for Costa Verde Fluminense, but they are not associated with voucher specimens from museum collection. One of the lists was extracted from an unpublished master's thesis by H. São-Thiago, and included 22 marine and freshwater species from the Parati-Mirim River. The second list (based on "field data" and three unpublished contributions by C. Coutinho, E. Caramaschi, and H. São-Thiago compiled fish diversity from 22 coastal basins, including again the Parati-Mirim. The third list, based on personal communication by R. Mazzoni, presented 18 species of fish that occur in the drainages of the Ilha Grande island.

Here we present a compilation of fish species from the Costa Verde Fluminense region based on voucher specimens deposited in a permanent ichthyological collection. In addition to the list of voucher specimens collected from 33 river basins, we provide identification keys for all species.

Material and Methods

1. *Study area*

The study area comprises the Costa Verde Fluminense region (Figure 1), in the municipalities of Mangaratiba, Angra dos Reis and Paraty, in the Brazilian State of Rio de Janeiro, and São José do Barreiro and Bananal in the Brazilian State of São Paulo. This region includes both continental and insular drainages of the Ilha Grande and Sepetiba Bays, between the rio Itinguçu (22°54'44.16"S, 43°52'47.97"W) in the east and the western border of the State of Rio de Janeiro where it meets the ocean (23°22'06"S, 44°43'27"W). Additionally, we included the small drainages of the Ilha Grande, the largest island inside the Ilha Grande Bay. The continental rivers drain the coastal lowlands and the slopes of the Serra do Mar, locally known as Serra da Bocaina (Francisco & Oliveira 2009), while the headwaters of some of these rivers drain the main plateau of the Bocaina highlands. The sampled coastal rivers were numbered from east to west following the shoreline (Table 2).

2. *Specimens*

For the purpose of inclusion in our list, species were considered as freshwater according to Reis et al. (2003). The list is based on examination of specimens collected between 1942 and 2019 (Supplementary file 1), and deposited at the Ichthyological Collection of the Museu Nacional (MNRJ), Universidade Federal do Rio de Janeiro, Brazil, which harbors the largest collection of freshwater fishes from the Costa Verde Fluminense region. Literature records of species from the region are included in the list and discussed as deemed appropriate, but only when associated with material deposited in a museum collection.

3. *Species*

Specimens were identified to the lowest taxonomic level possible using available literature (e.g., Buckup et al. 2014; Costa 2009; Menezes

Table 1. Freshwater fishes with type-locality located in river drainages of the Costa Verde Fluminense, southeastern Brazil.

Original species	Valid name	Type-locality (Drainage)	Authorship
Rivulus lazzarotoi	*Atlantirivulus lazzarotoi*	Jurumirim	Costa 2007
Rivulus simplicis	*Atlantirivulus simplicis*	Perequê-Açu	Costa 2004
Characidium japuhybense	*Characidium japuhybense*	Japuíba	Travassos 1949
Hemipsilichthys nimius	*Hemipsilichthys nimius*	Perequê-Açu	Pereira, Reis, Souza & Lazzarotto 2003
Listrura costai	*Listrura costai*	Jurumirim	Villa-Verde, Lazzarotto & Lima 2012
Neoplecostomus paraty	*Neoplecostomus paraty*	Perequê-Açu	Cherobim, Lazzarotto & Langeani 2017
Phalloceros anisophallos	*Phalloceros anisophallos*	São Roque	Lucinda 2008
Phalloceros aspilos	*Phalloceros leptokeras*	Parati-Mirim	Lucinda 2008
Phalloceros enneaktinos	*Phalloceros enneaktinos*	Toca do Boi	Lucinda 2008
Callichthys barbatus	*Scleromystax barbatus*	Japuíba	Quoy & Gaimard 1824
Trichomycterus potschi	*Trichomycterus potschi*	Saco (Mangaratiba)	Barbosa & Costa 2003

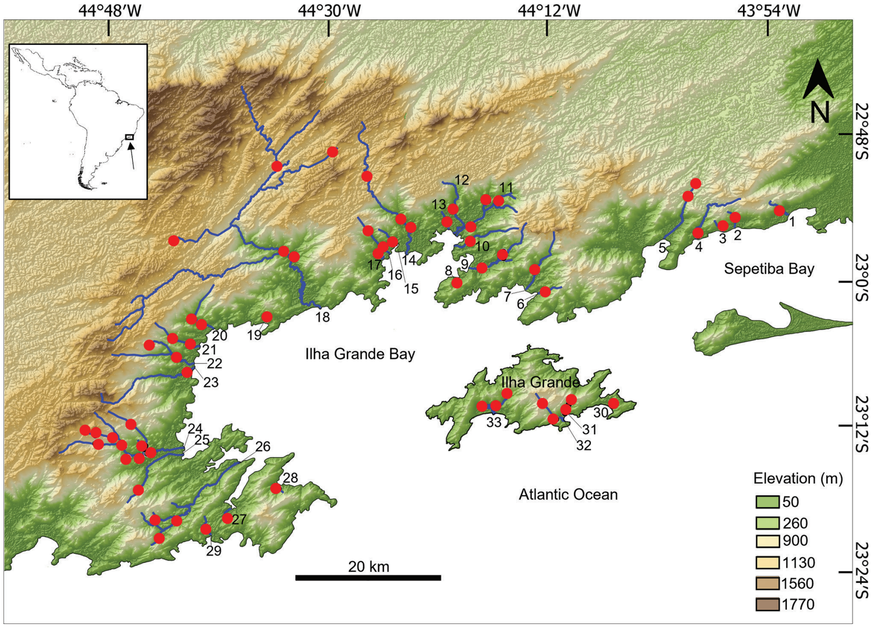

Figure 1. Sampled localities in the Costa Verde Fluminense (Rio de Janeiro) region. River drainages are numbered according to Table 2. Circles may represent more than one sample locality.

Table 2. River drainages sampled in the Costa Verde Fluminense region, numbered from east to west according to the position of their mouth (Figure 1) and coordinates of sampled localities. Drainages 30 to 33 are located on Ilha Grande island. Original geographic coordinates obtained with GPS at collection localities are provided, except for those indicated by an asterisk (*), which are estimated from topographic maps.

Number	River drainage	Latitude	Longitude
1	Itinguçu	22°54'23.7"S	43°53'22.3"W
2	Muriqui	22°55'01.2"S	43°57'10.9"W
3	Praia Grande	22°55'45.1"S	43°58'11.8"W*
4	Sahy	22°56'23.0"S	44°00'08.0"W
5	Saco (municipality of Mangaratiba)	22°52'58.0"S	44°00'44.0"W
		22°52'14.3"S	44°00'21.4"W
6	Monsuaba	23°00'40.6"S	44°12'40.8"W*
7	Jacuecanga	22°58'51.5"S	44°13'30.4"W*
8	Praia do Retiro	22°59'44.6"S	44°19'57.1"W*
9	Japuíba (=Japuhyba or Rio do Meio)	22°57'23.0"S	44°16'06.0"W
		22°57'24.0"S	44°16'07.0"W
		22°57'24.4"S	44°16'06.5"W
		22°57'54.8"S	44°16'07.1"W
		22°58'40.4"S	44°17'42.0"W
10	Caputera	22°56'29.0"S	44°18'41.0"W
		22°56'29.6"S	44°18'38.3"W
11	Jurumirim	22°53'14.0"S	44°17'18.0"W
		22°53'18.0"S	44°16'18.0"W
		22°53'09.0"S	44°16'31.0"W
		22°55'24.0"S	44°18'51.0"W
		22°55'24.0"S	44°18'37.0"W
12	Ariró	22°53'43.9"S	44°20'08.3"W*
13	Floresta	22°55'02.6"S	44°20'34.9"W*
14	Bracuí	22°51'03.0"S	44°27'03.0"W
		22°54'34.0"S	44°24'31.0"W
		22°55'13.6"S	44°23'41.3"W
		22°55'32.0"S	44°27'08.0"W
15	Saco (municipality of Angra dos Reis)	22°56'25.0"S	44°25'11.0"W
16	Grataú	22°56'52.1"S	44°25'57.1"W
17	Ambrósio	22°57'28.0"S	44°26'13.0"W
18	Mambucaba	22°49'00.0"S	44°30'00.0"W
		22°50'13.0"S	44°34'28.0"W
		22°56'00.0"S	44°43'00.0"W
		22°57'06.5"S	44°33'56.8"W
		22°57'24.8"S	44°33'18.7"W
		22°57'31.4"S	44°33'17.8"W
19	Praia Tarituba	23°02'36.6"S	44°35'37.9"W*
20	Taquari	23°02'29.0"S	44°41'38.0"W
		23°02'47.0"S	44°41'05.0"W
21	São Roque	23°04'33.0"S	44°45'06.0"W
		23°04'35.0"S	44°41'51.0"W
		23°04'04.0"S	44°43'14.0"W
22	Barra Grande	23°05'33.0"S	44°43'05.0"W
23	Pequeno	23°06'45.6"S	44°42'09.2"W*
24	Perequê-Açu	23°11'00.0"S	44°46'53.0"W
		23°11'26.0"S	44°50'30.0"W
		23°11'29.0"S	44°50'41.0"W
		23°11'52.0"S	44°49'49.0"W
		23°12'27.0"S	44°49'32.0"W
		23°12'30.0"S	44°49'45.0"W
		23°12'32.0"S	44°49'50.0"W
		23°12'33.0"S	44°47'38.0"W
		23°12'34.0"S	44°47'39.0"W
		23°12'35.0"S	44°47'39.0"W
		23°12'35.0"S	44°47'40.0"W
		23°12'44.0"S	44°46'09.0"W

Continue...

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Number	River drainage	Latitude	Longitude
		23°12'44.0"S	44°47'30.0"W
		23°12'45.0"S	44°47'30.0"W
		23°12'45.0"S	44°47'31.0"W
		23°12'46.0"S	44°47'31.0"W
		23°12'48.0"S	44°45'44.0"W
		23°12'49.0"S	44°47'29.0"W
		23°12'51.0"S	44°47'48.0"W
		23°12'07.0"S	44°48'15.0"W
		23°13'04.0"S	44°45'47.9"W
		23°13'22.0"S	44°45'30.0"W
		23°13'23.0"S	44°45'14.0"W
		23°13'24.0"S	44°45'30.0"W
		23°13'26.0"S	44°45'35.0"W
		23°13'27.0"S	44°45'36.0"W
		23°13'03.0"S	44°45'47.0"W
		23°13'43.0"S	44°47'11.0"W
		23°13'44.0"S	44°47'12.0"W
		23°13'46.0"S	44°46'24.0"W
		23°13'46.0"S	44°46'25.0"W
25	Mateus Nunes	23°16'24.0"S	44°46'21.0"W
26	Parati-Mirim (=Paraty-Mirim)	23°19'00.0"S	44°45'00.0"W
		23°19'03.0"S	44°43'24.0"W
		23°20'27.0"S	44°44'48.0"W
27	Saco do Mamanguá	23°18'43.0"S	44°39'05.0"W
28	Praia Grande de Cajaíba	23°16'28.0"S	44°34'53.0"W
		23°16'30.0"S	44°34'52.0"W
29	Toca do Boi	23°19'44.0"S	44°40'52.0"W
		23°19'44.0"S	44°40'54.0"W
30	Lopes Mendes	23°10'13.0"S	44°07'25.0"W
31	Barra Pequena	23°10'01.0"S	44°10'59.0"W
		23°10'44.0"S	44°11'18.0"W
32	Andorinha	23°10'00.0"S	44°13'00.0"W
		23°11'12.0"S	44°12'02.0"W
		23°11'13.0"S	44°12'02.0"W
		23°05'23.0"S	44°06'44.0"W
33	Sistema Lagunar do Sul e do Leste	23°10'00.0"S	44°17'00.0"W
		23°10'00.0"S	44°18'00.0"W
		23°10'05.0"S	44°17'00.0"W
		23°09'00.0"S	44°16'00.0"W
		24°10'00.0"S	44°16'00.0"W

et al. 2007; Oyakawa et al. 2006) or by direct comparisons with type series or specimens identified by experts. DNA Barcoding methods (sensu Hebert et al. 2003a; Hebert et al. 2003b) were used for species confirmation of Characidae and *Trichomycterus* (data not shown). The taxonomic nomenclature follows Eschmeyer's Catalog of Fishes (Fricke et al. 2022). The species are listed following the order of the classification proposed by Nelson et al. (2016).

The identification keys are provided for the species that occur in the Costa Verde Fluminense region, including exotic species recorded to date. Exotic species are those with origins from any other continent. We first present a dichotomous key to identify fish orders. Orders that include a single family or single species, have their respective names given in parentheses. Separate keys are presented for families and genera which have more than one species present in the area.

The extinction risk of each species of fish was obtained from the Brazilian Red List and IUCN Red List of Threatened species (MMA 2014; MMA 2018; ICMBIO 2018; IUCN 2021). The distribution map of the examined material (Supplementary file 1) was generated with QGIS software (http://qgis.org) following Calegari et al. (2016), and using river traces obtained manually from Google Earth satellite images.

Results

The 13.692 examined fish specimens (857 lots) belong to 54 species, 16 families, 9 orders of freshwater fishes (Table 3). Siluriformes (Figure 2) was the most diverse order (18 species), followed by Characiformes

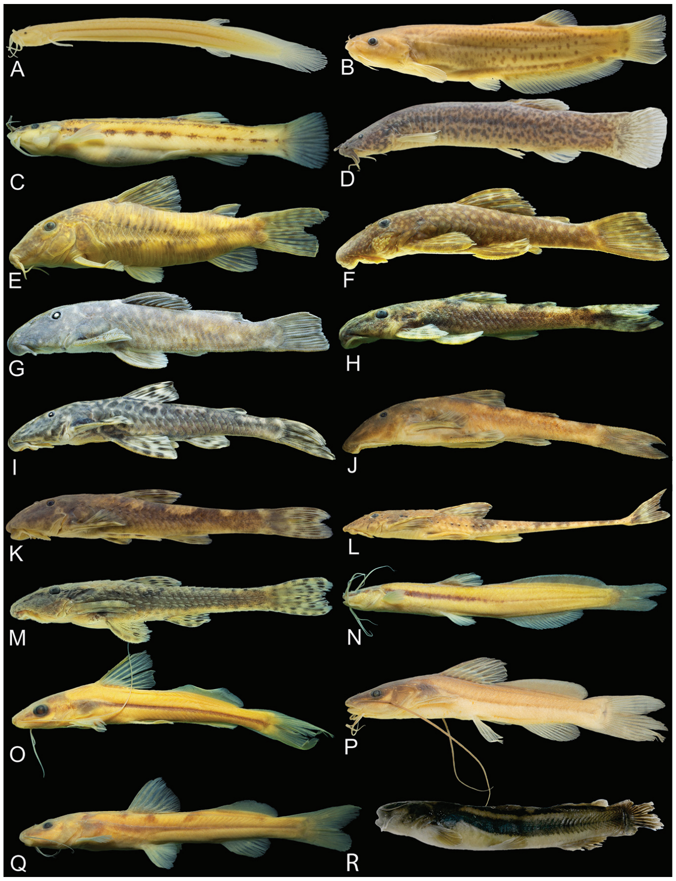

Figure 2. Species of Siluriformes from Costa Verde Fluminense region, southeastern, Brazil. A. *Listrura costai*, MNRJ 31917, 31.3 mm SL. B. *Trichogenes longipinnis*, MNRJ 11722, 62.3 mm SL. C. *Trichomycterus jacupiranga*, MNRJ 43846, 28.3 mm SL. D. *Trichomycterus potschi*, MNRJ 52215, 45.1 mm SL. E. *Scleromystax barbatus*, MNRJ 46672, 58.2 mm SL. F. *Ancistrus multispinis*, MNRJ 38081, 64.0 mm SL. G. *Hemipsilichthys nimius*, MNRJ 50595, 79.7 mm SL. H. *Kronichthys heylandi*, MNRJ 43848, 36.8 mm SL. I. *Neoplecostomus microps*, MNRJ 51835, 75.9 mm SL. J. *Neoplecostomus paraty*, MNRJ 41727, 50.9 mm SL. K. *Pareiorhina rudolphi*, MNRJ 24917, 46.0 mm SL. L. *Rineloricaria zawadzkii*, MNRJ 17185, 106.7 mm SL. M. *Schizolecis guentheri*, MNRJ 38080, 36.7 mm SL. N. *Acentronichthys leptos*, MNRJ 17182, 68.08 mm SL. O. *Pimelodella lateristriga*, MNRJ 46676, 54.1 mm SL. P. *Rhamdia quelen*, MNRJ 30539, 65.5 mm SL. Q. *Rhamdioglanis frenatus*, MNRJ 17184, 86.50 mm SL. R. *Taunayia bifasciata*, UFRN 5592, 74.9 mm SL.

Table 3. Freshwater fishes found in the Costa Verde Fluminense region. Drainages are numbered from east to west according to the position of their outlet into the sea (see Figure 1 and Table 2). One asterisk (*) indicates non-native species. Two asterisks (**) indicate record based solely on Medeiros et al. (2022).

Taxa	**Drainages**																																
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**
CHARACIFORMES																																	
Crenuchidae																																	
Characidium grajahuense Travassos 1944					X																												
Characidium japuhybense Travassos 1949									X		X	X		X				X	X					X		X			X		X	X	
Characidium sp.																										X							
Erythrinidae																																	
Hoplias malabaricus (Bloch 1794)																	X									X							
Characidae																																	
Astyanax keronolepis Silva, Malabarba & Malabarba 2019									X	X	X	X	X	X			X	X					X			X							
Astyanax lacustris (Lütken 1875)														X																			
Bryconamericus ornaticeps Bizerril & Perez-Neto 1995							X				X			X				X						X		X						X	
Deuterodon hastatus (Myers 1928)	X																						X										
Deuterodon intermedius (Eigenmann 1908)					X									X																			
Deuterodon sp.																								X									
Hollandichthys multifasciatus (Eigenmann & Norris 1900)				X		X			X			X		X				X	X					X		X			X				
Mimagoniates microlepis (Steindachner 1877)	X								X	X	X	X		X								X		X									
Oligosarcus hepsetus (Cuvier 1829)										X								X															
Psalidodon scabripinnis (Jenyns 1842)																								X									
SILURIFORMES																																	
Trichomycteridae																																	
Listrura costai Villa-Verde, Lazzarotto & Lima 2012											X																						
Trichogenes longipinnis Britski & Ortega 1983																								X		X							
Trichomycterus jacupiranga Wosiacki & Oyakawa							X		X	X	X	X		X				X						X		X			X				
Trichomycterus potschi Barbosa & Costa 2003					X									X																			
Callichthyidae																																	
Scleromystax barbatus (Quoy & Gaimard 1824)									X	X	X	X		X				X															
Loricariidae																																	
Ancistrus multispinis (Regan 1912)									X		X	X		X				X						X									
Hemipsilichthys nimius Pereira, Reis, Souza & Lazzarotto 2003																								X									
Kronichthys heylandi (Boulenger 1900)							X		X		X	X		X				X						X	X	X							
Neoplecostomus microps (Steindachner 1877)					X																												
Neoplecostomus paraty Cherobim, Lazzarotto & Langeani 2017																								X	X								
Pareiorhina rudolphi (Miranda Ribeiro 1911)																								X									
Rineloricaria zawadzkii Silva, Costa e Silva, Oliveira 2022					X						X	X		X				X															
Schizolecis guentheri (Miranda Ribeiro 1918)					X		X		X	X	X	X		X	X			X			X		X	X		X			X				

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...Continuation

Taxa	Drainages																																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Heptapteridae																																	
Acentronichthys leptos Eigenmann & Eigenmann 1889							X		X	X	X	X		X										X		X						X	
Pimelodella lateristriga (Lichtenstein 1823)									X	X	X	X		X			X	X						X									
Rhamdia quelen (Quoy & Gaimard 1824)					X				X		X	X		X		X	X	X						X		X							X
Rhamdioglanis frenatus Ihering 1907		X					X		X	X	X	X		X				X				X		X					X			X	
Taunayia bifasciata (Eigenmann & Norris 1900)**																		X															
GYMNOTIFORMES																																	
Gymnotidae																																	
Gymnotus pantherinus (Steindachner 1908)											X	X					X				X	X		X		X						X	
SALMONIFORMES																																	
Salmonidae																																	
Oncorhynchus mykiss (Walbaum 1792)*														X				X															
GOBIIFORMES																																	
Eleotridae																																	
Dormitator maculatus (Bloch 1792)				X													X						X										X
Eleotris pisonis (Gmelin 1789)				X			X							X				X						X		X							X
Gobiidae																																	
Awaous tajasica (Lichtenstein 1822)	X		X				X		X	X	X	X		X		X		X			X			X		X		X					X
CICHLIFORMES																																	
Cichlidae																																	
Coptodon rendalli (Boulenger 1897)*																										X							
Crenicichla lepidota Heckel 1840	X																																
Geophagus brasiliensis (Quoy & Gaimard 1824)					X			X	X	X	X	X		X	X		X	X	X		X			X		X			X				
Oreochromis niloticus (Linnaeus 1758)*																										X							
CYPRINODONTIFORMES																																	
Rivulidae																																	
Atlantirivulus lazzarotoi (Costa 2007)									X																								
Atlantirivulus simplicis (Costa 2004)																											X						
Kryptolebias brasiliensis (Valenciennes 1821)		X		X																													
Kryptolebias ocellatus (Hensel 1868)		X																															
Poeciliidae																																	
Phalloceros anisophallos Lucinda 2008	X	X		X	X		X	X	X	X	X	X		X	X	X	X	X		X	X	X	X	X	X	X						X	X
Phalloceros enneaktinos Lucinda 2008																											X		X	X			
Phalloceros harpagos Lucinda 2008										X				X			X	X						X									
Phalloceros leptokeras Lucinda 2008		X			X				X																	X							
Poecilia reticulata Peters 1859*	X	X			X		X	X	X								X																
Poecilia vivipara Bloch & Schneider 1801		X		X				X	X								X	X				X				X					X	X	X
SYNBRANCHIFORMES																																	
Synbranchidae																																	
Synbranchus marmoratus Bloch 1795									X																								X
SYNGNATHIFORMES																																	
Syngnathidae																																	
Microphis lineatus (Kaup 1856)				X											X			X					X			X							X
Pseudophallus brasiliensis Dawson 1974														X	X																		

(Figure 3, 14 species), Cyprinodontiformes (Figure 4 and Figure 5, 10 species), Cichliformes (Figure 6, four species), Gobiiformes (Figure 6, three species), Syngnathiformes (Figure 6, two species), and Gymnotiformes, Salmoniformes and Synbranchiformes (Figure 6, one species each). The most diverse family was Characidae (10 species), followed by Loricariidae (eight species), Poeciliidae (six species), Heptapteriade (five species), Trichomycteridae, Cichlidae and Rivuliidae (four species each), Crenuchidae (three species), Eleotridae and Syngnathidae (two species each), and Callichthyidae, Erythrinidae, Gobiidae, Gymnotidae, Salmonidae and Synbranchidae (one species each). *Phalloceros anisophallos* Lucinda 2008 was the most common species in Costa Verde (found in 24 drainages), followed by *Awaous tajasica* (Lichtenstein 1822) and *Geophagus brasiliensis* (Quoy & Gaimard 1824) (found in 15 drainages), and by *Schizolecis guentheri* (Miranda Ribeiro 1918) (found in 14 drainages). Some species were found only in a single drainage: *Crenicichla lepidota* Heckel 1840 in the Itinguçu drainage; *Kryptolebias ocellatus* (Hensel 1868) in the Muriqui drainage; *Characidium grajahuense* Travassos 1944 and *Neoplecostomus microps* (Steindachner 1877) in the Saco drainage (in the municipality of Mangaratiba); *Atlantirivulus lazzarotoi* (Costa 2007) in the Japuíba drainage; *Listrura costai* Villa-Verde, Lazzarotto & Lima 2012 in the Jurumirim drainage; *Astyanax lacustris* (Lütken 1875) the Bracuí drainage; *Deuterodon* sp., *Psalidodon scabripinnis* (Jenyns 1842), *Hemipsilichthys nimius* Pereira, Reis, Souza & Lazzarotto 2003, and *Pareiorhina rudolphi* (Miranda Ribeiro 1911) in the Perequê-Açu drainage; *Characidium* sp., *Coptodon rendalli* (Boulenger 1897) and

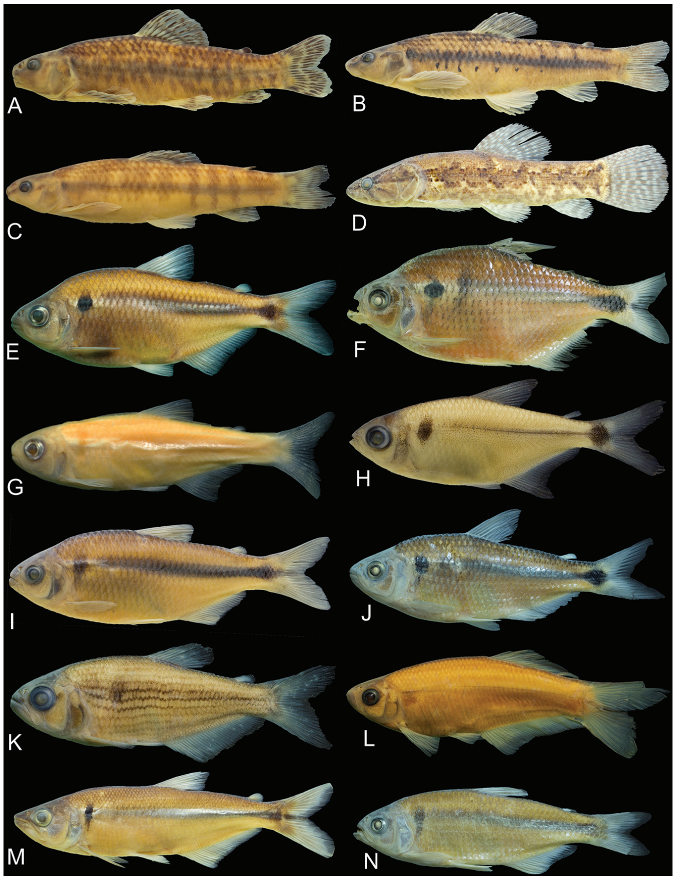

Figure 3. Species of Characiformes from Costa Verde Fluminense region, southeastern, Brazil. A. *Characidium grajahuense*, MNRJ 20866, 70.7 mm SL. B. *Characidium japuhybense*, MNRJ 43512, 58.6 mm SL. C. *Characidium* sp., MNRJ 15447, 57.8 mm SL. D. *Hoplias malabaricus*, MNRJ 43893, 120.7 mm SL E. *Astyanax keronolepis*, MNRJ 43492, 87.7 mm SL. F. *Astyanax lacustris*, MNRJ 52222, 68.30 mm SL. G. *Bryconamericus ornaticeps*, MNRJ 17181, 52.7 mm SL. H. *Deuterodon hastatus*, MNRJ 51734, 25.1 mm SL. I. *Deuterodon intermedius*, MNRJ 22795, 76.2 mm SL. J. *Deuterodon* sp., MNRJ 51718, 74.2 mm SL. K. *Hollandichthys multifasciatus*, MNRJ 43242, 46.2 mm SL. L. *Mimagoniates microlepis*, MNRJ 46673, 48.98 mm SL. M. *Oligosarcus hepsetus*, MNRJ 43495, 131.3 mm SL. N. *Psalidodon scabripinnis*, MNRJ 50607, 72.4 mm SL.

Figure 4. Females (left) and males (right) of species of Poeciliidae (Cyprinodontiformes) from Costa Verde Fluminense region, southeastern Brazil. A. *Phalloceros anisophallos*, MNRJ 43253, ♀ 34.8 mm SL, ♂ 26.0 mm SL. B. *Phalloceros enneaktinos*, MNRJ 43245, ♀ 24.9 mm SL, ♂ 22.9 mm SL. C. *Phalloceros harpagos*, MNRJ 43508, ♀ 36.2 mm SL, ♂ 19.5 mm SL. D. *Phalloceros leptokeras,* MNRJ 43505, ♀ 31.3 mm SL, MNRJ 4226, ♂ 21.2 mm SL. E. *Poecilia reticulata*, MNRJ 43892, ♀ 27.6 mm SL, ♂ 15.2 mm SL. F. *Poecilia vivipara*, MNRJ 43891, ♀ 45.1 mm SL, ♂ 31.2 mm SL.

Figure 5. Females (left), males (right), and hermaphrodite (center) of species of Rivulidae (Cyprinodontiformes) from Costa Verde Fluminense region, southeastern Brazil. A. *Atlantirivulus lazzarotoi*, MNRJ 5997, ♀ 30.2 mm SL, ♂ 35.2 mm SL. B. *Atlantirivulus simplicis*, MNRJ 20249, ♀ 12.5 mm SL, ♂ 19.8 mm SL. C. *Kryptolebias brasiliensis*, MNRJ 26460, ♀ 20.8 mm SL, ♂ 25.2 mm SL. D. *Kryptolebias ocellatus*, MNRJ 11397, hermaphrodite, 48.9 mm SL.

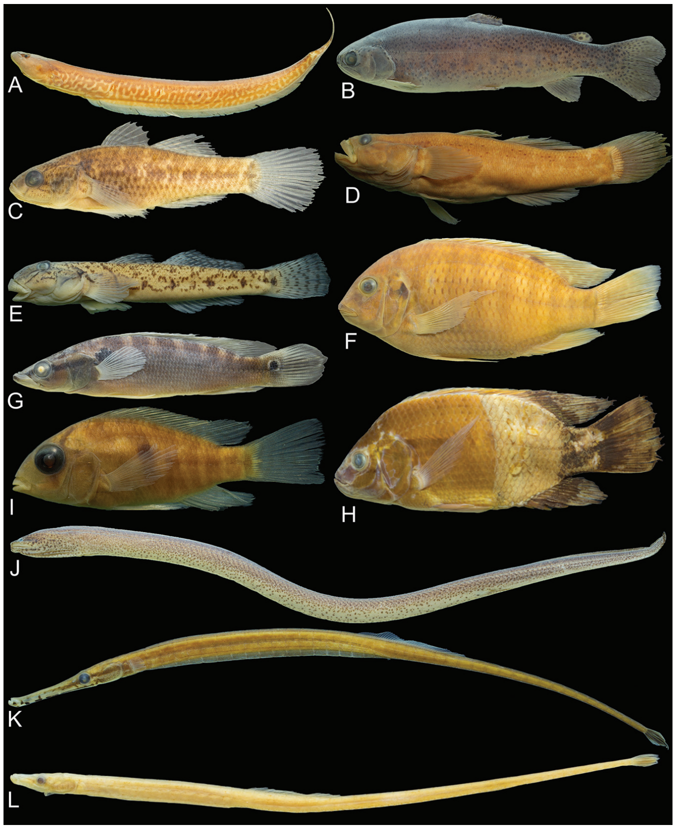

Figure 6. Fish species from Costa Verde Fluminense, southeastern Brazil. A. Gymnotiformes (*Gymnotus pantherinus*, MNRJ 28731, 88.5 mm SL). B. Salmoniformes (*Oncorhynchus mykiss*, MNRJ 22796, 181.8 mm SL). C. Gobiiformes (*Dormitator maculatus*, MNRJ 30631, 38.2 mm SL). D. Gobiiformes (*Eleotris pisonis*, MNRJ 22137, 99.02 mm SL). E. Gobiiformes (*Awaous tajasica*, MNRJ 43852, 79.6 mm SL). F. Cichliformes (*Coptodon rendalli*, MNRJ 11733, 159.1 mm SL). G. Cichliformes (*Crenicichla lepidota*, MNRJ 51738, 82.0 mm SL). H. Cichliformes (*Oreochromis niloticus*, MNRJ 11737, 157.5 mm SL). I. Cichliformes (*Geophagus brasiliensis*, MNRJ 46677, 31.8 mm SL). J. Synbranchiformes (*Synbranchus marmoratus*, MNRJ 30676, 219.0 mm SL). K. Syngnathiformes (*Microphis lineatus*, MNRJ 30930, 148.0 mm SL). L. Syngnathiformes (*Pseudophallus brasiliensis*, MNRJ 19178, 84.7 mm SL).

Oreochromis niloticus (Linnaeus 1758) in the Parati-Mirim drainage; and *Atlantirivulus simplicis* (Costa 2004) in Saco do Mamanguá drainage. Two possibly undescribed species were found (*Characidium* sp. and *Deuterodon* sp.). Four non-native species were recorded in the region: *Coptodon rendalli* (Boulenger 1897), *Oncorhynchus mykiss* (Walbaum 1792), *Oreochromis niloticus* (Linnaeus 1758), and *Poecilia reticulata* Peters 1859.

The ranking of species richness among the basins is as follows: Bracuí (25 species), Perequê-Açu (24 species), Mambucaba (23 species), Parati-Mirim (22 species), Japuíba (21 species), Jurumirim (19 species), Ariró (18 species), Caputera (13 species), Saco (Mangaratiba) and Ambrósio (11 species each), Jacuecanga (10 species), Sistema Lagunar do Sul e do Leste (eight species), Sahy, Muriqui, Andorinha and Toca do Boi (seven species each), Itinguçu and Pequeno (six species each), Saco (Angra dos Reis), São Roque and Barra Grande (five species each), Praia do Retiro (four species), Grataú, Praia Tarituba and Mateus Nunes (three species each), Saco do Mamanguá and Barra Pequena (two species each), and Praia Grande, Monsuaba, Floresta, Taquari, Praia Grande de Cajaíba and Lopes Mendes (one species each).

Identification keys

Identification Key to Orders

1\. a. Dorsal fin absent..2

1\. b. Dorsal fin present...3

2\. a. Anal fin absent..
....SYNBRANCHIFORMES
(Family Synbranchidae: *Synbranchus marmoratus*)

2\. b. Anal fin present ....
GYMNOTIFORMES (Family Gymnotidae: *Gymnotus pantherinus*)

3\. a. A single dorsal fin with rays..4

3\. b. Two dorsal fins with rays ....GOBIIFORMES

4\. a. Sensory lateral line divided on the flank into two sections.........
.... CICHLIFORMES (Family Cichlidae)

4\. b. Sensory lateral line continuous, without division....................5

5\. a. Pelvic fin absent ....
.... SYNGNATHIFORMES (Family Syngnathidae)

5\. b. Pelvic fin present...6

6\. a. Body covered with scales...7

6\. b. Body covered by skin or bone plates ....
.... SILURIFORMES

7\. a. Adipose fin usually present, except in *Hoplias malabaricus*
....8

7\. b. Adipose fin absent........................CYPRINODONTIFORMES

8\. a. Opercular membrane with 4-5 branchiostegal rays ....
....CHARACIFORMES

8\. b. Opercular membrane with more than 10 branchiostegal rays
....
SALMONIFORMES (Family Salmonidae: *Oncorhynchus mykiss*)

CHARACIFORMES

Identification Key to Families

1\. a. Posterior margin of caudal fin rounded ....
....Erythrinidae (*Hoplias malabaricus*)

1\. b. Posterior margin of caudal fin emarginated or forked 2

2\. a. Anal fin with less than 9 branched rays......................................
....Crenuchidae

2\. b. Anal fin with more than 15 branched rays ....
....Characidae

Family Characidae

Identification Key to Species

1\. a. Dentary with unicuspid teeth ....
....*Oligosarcus hepsetus*

1\. b. Dentary with multicuspid teeth...2

2. a. Seven to nine longitudinal black lines on the flank. Maxilla with more than 10 teeth....................... *Hollandichthys multifasciatus*

2. b. Flank with one or no longitudinal black line. Maxilla with up to 9 teeth..3

3. a. Inner premaxillary dental series with 4 teeth 4

3. b. Inner premaxillary dental series with 5 teeth 5

4. a. Base of first dorsal-fin ray anterior to first anal-fin ray .... *Bryconamericus ornaticeps*

4. b. Base of first dorsal-fin ray posterior to first anal-fin ray .... *Mimagoniates microlepis*

5. a. Humeral spot horizontally oval, without ventral extension. Posthumeral spot present. Maxilla toothless.............................. ....*Astyanax lacustris*

5. b. Humeral spot rounded, with ventral extension. Posthumeral spot absent. Maxilla with one or more teeth....................................6

6. a. No significant size difference in size between the fourth and fifth dentary teeth 7

6. b. Fifth dentary tooth conspicuously smaller than fourth tooth ....*Psalidodon scabripinnis*

7. a. Dark spot at the posterior tip of the caudal peduncle with a rhombus shape ....*Deuterodon hastatus*

7. b. Dark spot at the tip of the caudal peduncle with an oval shape or continuous with the dark longitudinal stripe on the flank 8

8. a. Spot on caudal peduncle continuous with the dark longitudinal stripe. Anterior half of longitudinal dark band with pigmentation similar to humeral spot ....*Deuterodon intermedius*

8. b. Spot on the posterior region of the caudal peduncle conspicuously distinct from longitudinal stripe. Anterior half of longitudinal dark band less pigmented than humeral spot............................9

9. a. Predorsal area tapered dorsally ....*Astyanax keronolepis*

9. b. Predorsal area rounded...................................... *Deuterodon* sp.

Family Crenuchidae

Identification Key to Species

1. a. Longitudinal maculae predominantly round darker ventral to the lateral longitudinal band.. ....*Characidium japuhybense*

1. b. Absence of round longitudinal maculae ventral to the lateral longitudinal band...2

2. a. Three or four conspicuous vertical bars on flank posterior to dorsal fin. Dorsal fin with two conspicuous horizontal stripes. Postorbital region with a macula .... *Characidium* sp.

2. b. More than four diffuse vertical bars in flank posterior to dorsal fin. Dorsal fin with variegated pigmented, with concentration of chromatophores in the rays. Postorbital region without macula ....*Characidium grajahuense*

SILURIFORMES

Identification Key to Families

1. a. Body extensively covered with bony plates 2

1. b. Body skin devoid of bony plates...3

2. a. Two series of plates ....Callichthyidae (*Scleromystax barbatus*)

2. b. Three or more series of plates .... Loricariidae

3. a. Adipose fin present; odontodes absent ....Heptapteridae

3. b. Adipose fin absent; patch of odontodes present in preopercle and opercle ....Trichomycteridae

Family Heptapteridae

Identification Key to Species

1. a. Maxillary barbel is half the length of the head .... *Taunayia bifasciata*

1. b. Maxillary barbel is longer than the length of the head 2

2. a. Adipose fin continuous with procurrent rays of caudal fin ....*Acentronichthys leptos*

2. b. Adipose and caudal fins separated from each other 3

3. a. Dorsum with transverse dark bands. Maxillary barbel short, not extending beyond the tip of the pectoral fin............................... ....*Rhamdioglanis frenatus*

3. b. Dorsum without dark bands. Maxillary barbel long, extending beyond the tip of the pectoral fin 4

4. a. Supraoccipital process narrow and long, reaching predorsal plate. First ray of dorsal fin stiff and pointed ....*Pimelodella lateristriga*

4. b. Supraoccipital process wide and triangular, not reaching predorsal plate. First ray of dorsal fin flexible ....*Rhamdia quelen*

Family Loricariidae

Identification Key to Species

1. a. Adipose fin absent 2

1. b. Adipose fin present..3

2. a. Caudal peduncle dorsoventrally depressed, forming lateral keels ....*Rineloricaria zawadzkii*

2. b. Caudal peduncle round in cross section...................................3

3. a. Teeth bicuspid. Pectoral girdle partly exposed ventrally, with visible odontodes near the pectoral-fin insertion ....*Schizolecis guentheri*

3. b. Teeth unicuspid. Pectoral girdle not exposed ventrally, without odontodes near pectoral fin insertion ....*Pareiorhina rudolphi*

4. a. Dorsal surface of snout without plates, with tentacles (in males). Interopercular spines evertible and hypertrophed .... *Ancistrus multispinnis*

4. b. Dorsal surface of snout covered with plates. Absence of evertible interopercular spines 5

5. a. Teeth with symmetric cusps. Presence of preadipose keel ....*Hemipsilichthys nimius*

5. b. Teeth with asymmetric cusps. Absence of preadipose keel 6

6. a. Odontodes of the first pelvic fin ray pointing medially. Area between pectoral and pelvic fins without plates.......................... ....*Kronichthys heylandi*

6. b. Odontodes of the first pelvic fin ray pointing distally. Area between pectoral and pelvic fins with plates.............................7

7. a. Light, horseshoe shaped area posterior to supraoccipital, with a central dark area, posterior to supraoccipital .... *Neoplecostomus paraty*

7. b. Post supraoccipital region with pigmentation similar to the rest of the body ....*Neoplecostomus microps*

Family Trichomycteridae

Identification Key to Species

1. a. First dorsal-fin ray posterior to first anal-fin ray .... *Trichogenes longipinnis*

1. b. First dorsal-fin ray anterior to first anal-fin ray.........................2

2. a. Pectoral fin consisting of a single filamentous ray...................... .... *Listrura costai*

2. b. Pectoral fin with more than 7 rays 3

3. a. Evenly variegated body color; conical jaw teeth ....*Trichomycterus potschi*

3. b. Rectangular or rounded sequential dark maculae laterally in the midline of the body, sometimes fused and with a vermicular pattern; incisiform jaw teeth ....*Trichomycterus jacupiranga*

GOBIIFORMES

Identification Key to Families

1. a. Six branchiostegal rays; separate pelvic fins............................... ....Eleotridae

1. b. Five branchiostegal rays; pelvic fins completely united ....Gobiidae (*Awaous tajasica*)

Family Eleotridae

Identification Key to Species

1. a. Anteroventral portion of preopercle with spine .... *Eleotris pisonis*

1. b. Preopercle without spine......................... *Dormitator maculatus*

CICHLIFORMES (Family Cichlidae)

Identification Key to Species

1. a. Upper branch of the first gill arch with fleshy lobe.................... .... *Geophagus brasiliensis*

1. b. Upper branch of the first gill arch without fleshy lobe 2

2. a. Presence of a humeral blotch .... *Crenicichla lepidota*

2. b. Region above tip the pectoral fin without a blotch 3

3. a. First ceratobranchial with up to gill 12 rakers ....*Coptodon rendalli*

3. b. First ceratobranchial with more than 20 gill rakers .... *Oreochromis niloticus*

CYPRINODONTIFORMES

Identification Key to Families

1. a. Tip of dorsal fin not reaching the beginning of the caudal fin; males with anal-fin rays 3, 4 and 5 extended, forming a copulatory organ (gonopodium) .... Poeciliidae

1. b. Tip of dorsal fin reaching the origin of the caudal fin; male anal fin not forming a gonopodium .... Rivulidae

Family Rivulidae

Identification Key to Species

1. a. Males and females without a spot on the upper posterior margin of the caudal peduncle. Males with vertical bars on the caudal peduncle ....*Kryptolebias brasiliensis*

1. b. Rounded spot on the upper margin of the caudal peduncle in females or hermaphrodites...2

2. a. Humeral spot present..............................*Kryptolebias ocellatus*

2. b. Humeral spot absent..3

3. a. Origin of dorsal fin on vertical line through 11th or 12th anal fin-ray base; tip of pelvic fin not reaching anus in males ....*Atlantirivulus lazzarotoi*

3. b. Origin of dorsal fin above base of 9th or 10th anal fin-ray; tip of fin reaching anus in males ....*Atlantirivulis simplicis*

Family Poeciliidae

Identification Key to Species

1. a. Lateral spot located anterior to the first dorsal-fin ray in males and females .... *Poecilia vivipara*

1. b. Lateral spot absent or located posterior to the first dorsal-fin ray 2

2. a. Males with ventral fleshy palp at the tip of ray 3 of the gonopodium. Females without fleshy process (urogenital papilla) between the anus and the first anal-fin ray .... *Poecilia reticulata*

2. b. Males with a pair of ventral bone appendix at the tip of ray 3 of the gonopodium. Females with fleshy palp (urogenital papilla) between the anus and the first anal-fin ray............................... 3

3. a. Urogenital papilla of females turned to the right. Males with asymmetrical gonopodium tip, left appendix of ray 3 with a hook and thinner than right appendix (hookless .... *Phalloceros anisophallos*

3. b. Urogenital papilla of females turned to left or straight ventrally. Males with symmetrical gonopodium tip, both appendices of ray 3 with a hook... 4

4. a. Urogenital papilla of females straight, pointing ventrally. In males, hook positioned in distal portion of both gonopodial appendix .... *Phalloceros enneaktinos* + *P. harpagos*

4. b. Urogenital papilla of females turned to the left. In males, hook positioned in medial portion of both gonopodial appendices .... *Phalloceros leptokeras*

SYNGNATHIFORMES (Family Syngnathidae)

Identification Key to Species

1. a. Anal fin present .... *Microphis lineatus*

1. b. Anal fin absent................................. *Pseudophallus brasiliensis*

Discussion

Although the Costa Verde Fluminense region is located between the two largest metropolitan areas (Rio de Janeiro and São Paulo) in Brazil, this study is the first comprehensive inventory of freshwater fishes of this region based on material deposited in a permanent collection. A previous broad ichthyological inventory of the region did not provide catalog numbers nor pictures of the material examined (Bizerril & Primo 2001), which limits identification and distribution discussions. Other publications provide reliable records, but focused on restricted taxa (Costa 2004; Medeiros et al. 2022; Souto-Santos et al. 2019) or restricted drainages (Guimarães et al. 2021).

Notable differences in species richness (number of species) were found among the drainages. Continental drainages of Ilha Grande Bay (drainages 6–28) are more diverse than those of Sepetiba Bay (drainages 1–5) and Ilha Grande island (drainages 30–33). The highest species richness was registered at Bracuí, Perequê-Açu, Parati-Mirim e Mambucaba, which are the basins with the largest area.

As expected for the Serra do Mar mountain range, several endemic coastal species were found. Eleven species have their type-locality within the study area (Table 1). Species of exclusively coastal distribution (52 %, excluding non native species from Table 3) along the Serra do Mar are *Characidium grajahuense, Characidium japuhybense, Characidium* sp., *Astyanax keronolepis, Deuterodon* sp., *Hollandichthys multifasciatus, Mimagoniates microlepis, Listrura costai, Trichogenes longipinnis, Trichomycterus potschi, Ancistrus multispinis, Hemipsilichthys nimius, Kronichthys heylandi, Neoplecostomus paraty, Acentronichthys leptos, Gymnotus pantherinus, Dormitator maculatus, Eleotris pisonis, Awaous tajasica, Atlantirivulus lazzarotoi, Atlantirivulus simplicis, Kryptolebias brasiliensis, Kryptolebias ocellatus, Phalloceros enneaktinos, Microphis lineatus*, and *Pseudophallus brasiliensis.* This coastal diversity demonstrates the importance of Serra do Mar as a biogeographical barrier for freshwater fishes.

Eleven species are listed in the Brazilian red list as "Critically Endangered" (*Characidium grajahuense*, *Listrura costai*, *Atlantirivulus lazzarotoi,* and *Kryptolebias brasiliensis*), as "Endangered" (*Atlantirivulus simplicis*)*,* as "Near Threatened" (*Trichogenes longipinnis*, *Hemipsilichthys nimius*, *Pareiorhina rudolphi*, *Dormitator maculatus,* and *Kryptolebias ocellatus*), and as "Vulnerable" (*Taunayia bifasciata*) (ICMBIO, 2018). Unlike most species recorded in Costa Verde Fluminense streams, *T. bifasciata* does not occur in lowland streams. A call for conservation of highland areas of the Costa Verde region was made by Medeiros et al. (2022), but our results highlight the strong need for conservation actions in lowland areas where these species are found.

Specific identifications of characids in faunal surveys of Atlantic Forest fishes are often inaccurate (Oyakawa et al. 2006). Identifying these species became an even more challenging task after the understanding that there are no clear morphological characters that diagnose some genera (Terán et al. 2020).

Previous ecological studies listed *Bryconamericus microcephalus* in rivers of the Ilha Grande (e.g. Mazzoni & Silva 2006). More recently the species of *Bryconamericus* from the Perequê-Açu drainage was identified as *B. ornaticeps* (Guimarães et al*.* 2021). However, based on our evaluation of morphological and molecular data from drainages associated with type localities we identify the species of *Bryconamericus* from Costa Verde Fluminense as *B. ornaticeps* Bizerril & Perez-Neto (1995). DNA sequences of the COI mitochondrial gene of *Bryconamericus* from Costa Verde Fluminense clusters with topotypes of *B. ornaticeps*, and are not related to topotypes of *B. microcephalus* (Buckup et al., in prep).

Guimarães et al. (2021) provided a list of 23 species of freshwater fishes from the Perequê-Açu drainage. Our sampling from the Perequê-Açu revealed an additional species, *Characidium japuhybense*. Additionally, according to our reexamination of voucher specimens, their identifications of "*Deuterodon intermedius"* and "*D. hastatus"* correspond, respectively, to *Psalidodon scabripinnis* and an undescribed species of *Deuterodon* morphologically similar to *Astyanax keronolepis*. Based on DNA barcode sequences of samples MNRJ 50603 and MNRJ 50607, the former species is a member of Barcode Index Number (BIN) BOLD:AAC5910. According to data available in the Bold Systems database (https://www.boldsystems.org/index.php/Public_BINSearch), BIN BOLD:AAC5910 this BIN includes 456 specimens from an extensive area in southeastern South America. These specimens have been identified by over two dozen taxonomic names. Among those names, *Psalidodon bockmanni* (83 occurrences), *Psalidodon paranae* (62 occurrences), *Psalidodon rivularis* (42 occurrences); and *Psalidodon scabripinnis* (32 occurrences) are the most frequent ones. The majority of these identifications suggest that BOLD:AAC5910 corresponds to the so-called *P. scabripinnis* species complex. Here we use the name *P. scabripinnis* for this widespread species, following Limeira et al. (2022). The extensive geographic distribution of this species and future reexamination of type specimens may eventually require synonymizing several nominal species that are currently regarded as valid (e.g., *P. paranae, P. rivularis*).

The family Trichomycteridae harbors the greatest diversity of species among Siluriformes (Nelson et al. 2016). The genus *Trichomycterus* comprises approximately 170 valid species (Katz et al. 2018), and is the most complex taxon in the family due to its non-monophyletic status and confusing taxonomy (Reis & de Pinna 2022). Despite the great diversity of this genus, we recognized only two species in the Costa Verde Fluminense region: *Trichomycterus potschi*, and *Trichomycterus jacupiranga*. *Trichomycterus potschi* belongs to the *T. brasiliensis* species complex (Barbosa & Costa 2003), and was recorded only in its type-locality in the Saco (municipality of Mangaratiba, Table 1), and Bracuí drainages. The second species belongs to the *T. jacupiranga* species complex (Costa et al. 2022) and occurs along the entire Costa Verde Fluminense region (Table 3). This species is remarkable for its great intraspecific variation in pigmentation pattern.

The single specimen of *Crenicichla* examined from the Costa Verde region fits the redescription of *C. lepidota* provided by Kullander (1982). This record is noteworthy because the known distribution of the species extends from Guaporé River (Amazonas basin) to coastal drainages in the State of Rio Grande do Sul (Kullander 1982). The occurrence in coastal rivers of southeastern Brazil raises three possibilities: *Crenicichla lepidota* is (1) native from Costa Verde or (2) an introduced species, or (3) the new record represents an undescribed species very similar to *C. lepidota*. However, testing these hypotheses requires additional studies that are beyond the scope of the present contribution.

We provided identification keys for species, but, in the identification key for Poeciliidae, *Phalloceros enneaktinos* and *P. harpagos* are morphologically indistinguishable. Morphological characters originally used by Lucinda (2008) to distinguish *P. enneaktinos* from *P. harpagos* are variable, and there is overlap in the number of dorsal-fin rays of the two species. These species were recognized through DNA barcodes (Souto-Santos et al. 2019).

According to a model of coastal paleodrainages for southeastern Brazil (Thomaz et al. 2015; Thomaz & Knowles 2018), the freshwater drainages from Ilha Grande and Sepetiba Bays, including those of the main island (Ilha Grande), were interconnected by a single paleodrainage during the Last Glacial Maximum (26,000-19,000 years before present). Such interconnection would allow for the presence of conspecific populations of fishes in currently isolated drainages along the Costa Verde Fluminense region. A test of phylogeographic hypotheses in the region corroborated low genetic divergence in currently isolated populations of *Phalloceros leptokeras* (Souto-Santos et al. 2022). It is likely that phylogeographic analyzes including other widely distributed species in the region will find this same pattern.

In conclusion our study demonstrates that the rivers that drain the Costa Verde slope of the Serra do Mar have 54 species of freshwater fishes reliably registered, including four introduced species, 11 species under threat of extinction, and two probably undescribed species. This ichthyological inventory fills an important gap in the knowledge about fish communities of coastal streams of the Atlantic Forest of southeastern Brazil.

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Conflict of Interest

The authors declare they have no conflict of interest.

Data availability

Supporting data are available at <https://data.scielo.org/dataset.xhtml?persistentId=doi:10.48331/scielodata.1WHG2P>

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The neglected tropical grasslands: first record of *campo com murundus* and its plant communities in the state of São Paulo, Brazil

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Abstract: Tropical grasslands have been systematically neglected worldwide in maps, conservation policies, and ecological studies. After eradicating invasive pine trees from a Cerrado reserve in southeastern Brazil, an unprecedented grassy ecosystem arose in recent satellite images. In the field, we confirmed the first record of wet grasslands with termite mounds – locally named *campo com murundus* - beyond 21°S in the São Paulo state. Besides reporting this occurrence, we sampled the two plant communities forming this peculiar vegetation type (the mounds and the waterlogged matrix around them) to investigate if they are floristically and functionally distinct. We also explored how these two communities relate to those of the surrounding open vegetation types (savanna, dry and wet grassland). Woody plants were recorded on the mounds but not in the matrix, although the two communities share some ground layer species. Compared to the adjacent vegetation types, the mounds were floristically distinct and functionally more balanced in growth forms, dispersal syndrome, and tolerance to waterlogging. We hope this borderline record of *campo com murundus* can stimulate the search for other unnoticed remnants out of their known occurrence region, triggering efforts for their conservation and studies to improve comprehension of these iconic ecosystems.

Keywords: *Earth mounds; termite savanna; wet grassland; wetland; Cerrado; floristic similarity.*

Campos tropicais negligenciados: primeiro registro de campo com murundus e suas comunidades vegetais no estado de São Paulo, Brasil

Resumo: Os campos naturais tropicais têm sido sistematicamente negligenciados em todo o planeta, seja nos mapas, nas políticas de conservação ou em estudos ecológicos. Após controle da invasão por *Pinus* em unidade de conservação do Cerrado no sudeste do Brasil, um ecossistema graminoso sem registro regional surgiu nas imagens de satélite recentes. Observação em campo resultou no primeiro registro de campo com murundus em latitude superior a 21°S, no estado de São Paulo. Além de relatar essa ocorrência, amostramos as duas comunidades vegetais que formam esse tipo de vegetação peculiar (ocorrendo sobre os murundus e na matriz alagadiça ao redor deles) para investigar se são florística e funcionalmente distintas. Também exploramos como essas duas comunidades estão relacionadas com os tipos de vegetação aberta circundantes (savana, campo seco e campo úmido). Plantas lenhosas foram registradas nos murundus, mas não na matriz, embora as duas comunidades compartilhem algumas espécies do estrato rasteiro. Em comparação com os outros tipos de vegetação adjacentes, os murundus se mostraram floristicamente distintos e funcionalmente mais equilibrados em relação às formas de crescimento, síndrome de dispersão e tolerância ao encharcamento. Esperamos que esse registro limítrofe de campo com murundus possa estimular a busca por outros remanescentes despercebidos fora da região de ocorrência já conhecida, desencadeando esforços para sua conservação e estudos que possam melhorar a compreensão desses ecossistemas icônicos.

Palavras-chave: *Murundu; covoal; campo úmido; área úmida; Cerrado; similaridade florística.*

Introduction

The knowledge about the structure and functioning of tropical grasslands and savannas is scarce compared to forests (Parr et al. 2014). Besides that, these open ecosystems have been highly threatened by land conversion, biological invasions, suppression of natural disturbances (*e.g.* fire and herbivory), and afforestation (Veldman *et al*. 2015a, b, Durigan & Ratter 2016). Although grasslands and savannas are neglected when compared to forest vegetation (Silveira et al. 2021), they are considered of significant environmental, economic, and cultural importance once they are responsible for essential ecosystem services such as water provisioning, carbon storage, and shelter for pollinators and wildlife animals (Scholes & Archer 1997, Van Der Werf et al. 2010, Bardgett et al. 2021).

Among the wide variety of tropical grassland types worldwide (Dixon et al. 2014), vast portions of land are dominated by intriguing earth mounds, primarily associated with termites, thus named termite savannas. The dotted-like landscape of termite savannas is widely distributed, with records in North America (Mima-mounds) and Africa (*heuweltjies*), with similar appearance and ecological drivers (Hlongwane 2009, Midgley 2010). In Brazil, this vegetation type is represented by the so-called *campo com murundus*, one of the many phytophysiognomic types of the Cerrado (Furley 1986, Oliveira-Filho 1992, Overbeck et al. 2022), also known as *parque de cerrado* (Ribeiro & Walter 2008), *savana parque* (IBGE 2012), termite savanna (Ratter et al. 1973), or hyperseasonal termite savanna (Eiten 1983). Apparently, *campo com murundus* is ecologically equivalent to the thicket clumps found in the Kagera savanna landscape, which occupy a large portion of East Africa, as observed by Bloesch (2008).

Cerrado – the Brazilian savanna – is a vast region dominated by savannas forming a landscape mosaic with distinct vegetation types conditioned by complex relationships between environmental and disturbance factors. The *campo com murundus* are characterised by the occurrence of earth mounds covered by woody plants, sometimes inconspicuous, but often regularly spread over large tracts of the landscape, invariably associated with termites and seasonally waterlogged grasslands, being included among the Brazilian wetlands (Junk et al. 2014; Durigan et al. 2022). In Brazil, this vegetation type has been recorded so far in several states: Amazonas, Bahia, Distrito Federal, Goiás, Mato Grosso, Minas Gerais, Rondônia, Roraima (Eiten 1975, Araujo Neto et al. 1986, Barbosa et al. 2005, Cianciaruso et al. 2005, Antunes et al. 2012, Marimon et al. 2012, Paêlo 2013, Morais et al. 2014, Oliveira et al. 2014, Maricato et al. 2018, Souza et al. 2020).

The earth mounds function as well-drained islands, harbouring endemic Cerrado species which are not flood-tolerant (Araújo Neto et al. 1986, Oliveira-Filho & Martins 1991, Oliveira-Filho 1992). The plant species found on top of the *murundus* and those found in the matrix around are reported to belong to different guilds (Ribeiro & Walter 2008), whose floristic and structural differences and relationships with other vegetation types in the landscape have rarely been explored. Compared to other vegetation types, grasslands have been poorly studied in the Cerrado (Walter et al. 2015). Those in wetlands are practically unknown, likely due to the difficulty of performing samplings in flooded areas. Marimon et al. (2012, 2015) found waterlogging as the main factor influencing the occurrence of both woody and non-woody species on top of the *murundus.* Cianciaruso et al. (2005) investigated the influence of hyperseasonality on plant communities in the Cerrado and demonstrated waterlogging as a significant environmental filter, restricting plant diversity of hyperseasonal *cerrado*.

The origin of termite mounds is still controversial (Hlongwane 2009, Midgley 2010, Silva et al. 2010), and two main hypotheses have been considered. The first hypothesis states that termite nests raised the microtopography above the grassland vegetation (Mathews 1977, Eiten 1984, 1990, Prance & Schaller 1982, Oliveira-Filho 1992, Ponce & Cunha 1993, Hlongwane 2009). The relationship between thicket clumps on earth mounds and termites in seasonally waterlogged flat land is well known (Walter 1973, Pomeroy 1976, Barbosa et al. 2005). Despite that, there is a second hypothesis proposing that the microtopography of the termite savannas is a consequence of differential erosion, suggesting that the earth mounds are remnants from a previous relief that were just occupied by termites and not formed by them (Araujo Neto et al. 1986, Furley 1986, Silva et al. 2010). Either way, the ecological importance of the *campo com murundus* in promoting habitat diversification and faunal refugia is undeniable.

The occurrence of termite savannas in South America has been mostly recorded in tropical regions, in latitudes smaller than 15 degrees. We here report the existence of a patch of *campo com murundus* at 22°47'22" S, which is the first record of this vegetation type beyond 21° S, in the state of São Paulo, Brazil. In addition to reporting this first occurrence, we aimed to investigate to which extent the plant communities of the termite savanna are floristically and functionally related to the plant communities occupying the surrounding open vegetation types. We expected the well-drained mounds to resemble savanna plant communities in well-drained soils (savanna and dry grassland) and the surrounding waterlogged matrix resembling the composition of a wet grassland without mounds due to the species filtering imposed by soil water saturation (Ribeiro et al. 2021). Although we primarily aimed at floristically describing the *campo com murundus* and their relationships with other vegetation types to increase basic knowledge, we considered that applying this knowledge is crucial to support biodiversity conservation and the species selection for ecological restoration of these ecosystems.

Material and Methods

1. *Study area*

Santa Bárbara Ecological Station (SBES) hosts a mosaic of vegetation types, including forests, savannas, and grasslands (dry and wet) near the southern edge of the Cerrado region in the state of São Paulo. The patch of *campo com murundus* studied occupies an area of 3.5 ha within SBES, located by the central coordinates 22°47'22"S to 49°14'40"W (Figure 1). The regional climate is classified as Köppen Cwa-type, with rainy summers and dry winters lasting for five months (Alvares et al. 2013). The mean annual precipitation is 1332 mm, the average daily minimum temperature is 10.1 °C in July, and the average daily maximum reaches 28.7 °C in January. Despite being almost flat, the altitude is 634 m in the centre of the studied patch and 635 m in its border, creating a long-lasting waterlogged condition during the rainy season. Being flooded in the summer and overdried in the winter, the fluctuation of the groundwater level allowed the formation of plinthosols, often associated with *campos com murundus* (Curi et al. 2017). Monitoring the groundwater level close

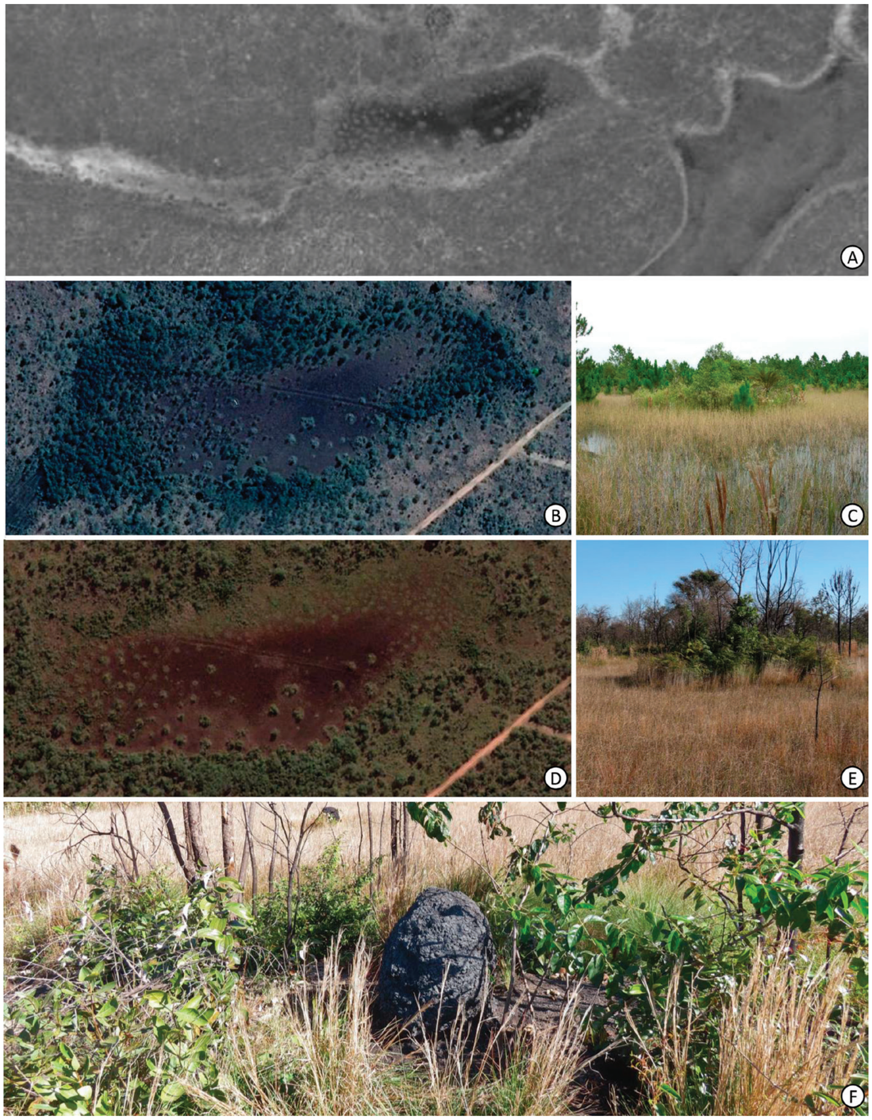

Figure 1. Views of the termite savanna studied at Santa Bárbara Ecological Station (SBES, Águas de Santa Bárbara, state of São Paulo, Brazil). A) The termite savanna patch in 1962, before pine invasion and without roads around (aerial photograph). B) In 2013, after the invasion by *Pinus elliottii* and before the invasion control (Google Earth image). C) A termite mound surrounded by *Pinus elliottii* (2010). D) In 2017, after clearcutting pines and burning, exposing the termite mounds (Google Earth image). E) A termite mound after pine eradication (2020). F) A termite nest surrounded by woody species on top of the mound (2020).

to the studied patch showed it ranging over the year from +10 cm to –210 cm (Manzione 2018), evidencing the hyperseasonal environment expected for *campo com murundus* (Eiten 1983).

The small patch of *campo com murundus* studied was already shown by aerial photographs taken in 1962 (Figure 1a), before the cattle farm became a governmental reserve (1964) and pine plantations replaced native grasslands around. For more than five decades, however, the peculiar feature of that vegetation was never noticed as a distinct ecosystem by the managers of SBES. *Pinus elliottii* Engelm slowly invaded this termite savanna, with some sparse founders arriving from the plantations around in 1994, massively colonising the whole patch and completely mischaracterising the landscape 19 years later (Brandes et al. 2020). The invasion process made it impossible to observe the earth mounds over a long period (Figure 1b-c). In 2013, there was an intervention to control the invasion by clearcutting the adult trees and applying a prescribed fire (2016) to burn pine needles and kill young invaders. The restoration intervention was successful, and the woody plants on top of the *murundus* and the grassy ground cover around them were quickly recovered, re-establishing the dotted landscape (Figure 1d-e). Not even a single pine individual was observed in the *campo com murundus* by the sampling occasion. When sampling, we observed at least one termite nest per mound (Figure 1f). The average height of the *murundus* (measured from the ground level of the wet grassland around to the top of the mound) was 93.8 cm (ranging from 73 cm to 113 cm).

2. *Experimental design and data collection*

To characterise the two plant communities of this termite savanna, in August 2020, we assessed 10 pairs of sampling units, each formed by a *murundu* (from now on referred to as mound) and a paired area of equivalent size in the wet grassland around the mound (from now on referred to as surrounding matrix), systematically positioned in the west from the termite mound. In the analyses, all plots on top of the mounds represented one plant community that is predominantly woody and associated with the well-drained condition. Those plots in the matrix represented another plant community, exclusively herbaceous, associated with seasonally waterlogged soils.

On top of each mound and in its paired area in the surrounding matrix, we sampled five circular 1-m² subplots in quincunx, totalling 100 1-m² subplots (50 on top of the mounds and 50 in the surrounding matrix). In each subplot we assessed plant richness and species composition. All individuals from the seedling stage were identified at the species level. When the identification was not possible in the field, we collected botanical material for later identification based on the literature (Durigan et al. 2004, 2018) or by comparison with material deposited in herbaria.

We investigated whether the plant community on top of the mounds and that in the surrounding matrix were floristically or functionally similar to the plant communities occupying three open vegetation types in the neighbourhood, according to the nomenclature proposed by Ribeiro & Walter (2008): savanna (*cerrado sentido restrito*), dry grassland (*campo limpo seco*), and wet grassland (*campo limpo úmido* without mounds, the groundwater close but never above the surface). Distance from the termite savanna was 1,400 m to the savanna, 400 m to the dry grassland, and 900 m to the wet grassland. We used the species composition sampled in randomly distributed 1-m² circular plots in patches of savanna (40 plots), dry grassland (30 plots), and wet grassland (10 plots). To explore the functional composition (relative abundance of functional guilds) of the five plant communities being compared, we categorised each species in functional guilds as follows: growth form (woody, forb, grass or sedge, following Durigan et al. 2004; 2018); dispersal syndrome (zoochory, anemochory or barochory, according to Peres 2016); and tolerance to waterlogging (yes or no, based upon Tannus & Assis 2004, and Pilon et al. 2017, 2018). In this case, tolerance to waterlogging refers to plants being able to survive and grow in habitats where the soil is fully water-saturated, at least in the rainy season, no matter if the groundwater rises above the surface. We expected differences related to waterlogging since it limits tree establishment (Ribeiro et al. 2021) and favours sedges (Pilon et al. 2017). We also explored the dispersal syndrome because the termite savannas resemble well-drained islands isolated by a waterlogged matrix. Therefore, their colonisation could depend on long-distance dispersal agents (volant animals or wind able to cross the waterlogged matrix) to bring diaspores of species able to survive in dry environments (the mounds).

3. *Data analysis*

To verify if plant species richness (number of species in 1 m²) differs between the community on the mounds and the other four communities sampled, we calculated the mean effect size using the log response ratio approach by mean values per plot of each community (Hedges et al. 1999). We constructed 95% confidence intervals for each community to determine whether the mean effect size differed from zero. Thus, we considered that the richness of each community differed from the mounds if 95% confidence intervals did not include zero (Zar 1999).

Differences in species composition (presence/absence) between sampled communities were explored using non-metric multidimensional scaling (NMDS), based upon a Bray-Curtis dissimilarity matrix, and calculating 95% confidence ellipses to check for overlapping of the confidence intervals. At first, we explored the floristic composition between the mounds and the matrix within the termite savanna. In the second step, besides the mound and the matrix, we included the plant communities representing each of the surrounding open vegetation types – dry grassland, savanna, and wet grassland – in the NMDS (all plant species and communities are presented in Table S1).

To verify a possible functional bias in the assembly of the studied communities, we adopted a guild proportionality approach, as recommended by Götzenberger et al. (2012). We used chi-square analysis ($\alpha = 0.05$). We applied Yates correction for $n < 5$ to investigate if the frequency of each functional guild within the group of species of each community differed from the expected. We considered as the expected values the proportion of each functional guild within the whole set of species sampled in all communities together (representative of the global species pool). If there was no difference between the observed value in a particular community and the regional pool, that attribute was not decisive for the composition of that community.

Results

A total of 64 plant species were recorded in the termite savanna, 59 on top of the mounds, and 22 in paired areas of the surrounding matrix. In the dry grassland, savanna, and wet grassland, 131, 121, and 27 species were recorded, respectively. Richness per square meter was distinct between communities (Figure 2). It was higher in dry grassland (19 species) and savanna (13 species) patches than on the mounds (7 species), and lower in the matrix (5 species) than on the mounds. The wet grassland without mounds did not differ from the mounds (both with 7 species). Of the 64 species sampled in the termite savanna, 17 species were common to

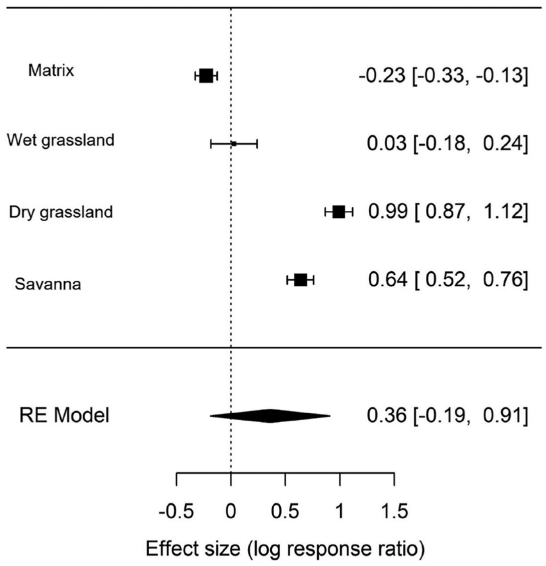

Figure 2. Effect size (distance from zero along the bar) of different plant communities in plant species richness related to that recorded on top of the mounds. Boxplots represent the mean effect size with 95% confidence interval. The dashed vertical line represents the mean richness recorded on top of the mounds. Values following each boxplot represent the mean and [confidence interval] in a logarithmic scale for each community. Richness of each community differs from the mounds if 95% confidence interval does not include zero.

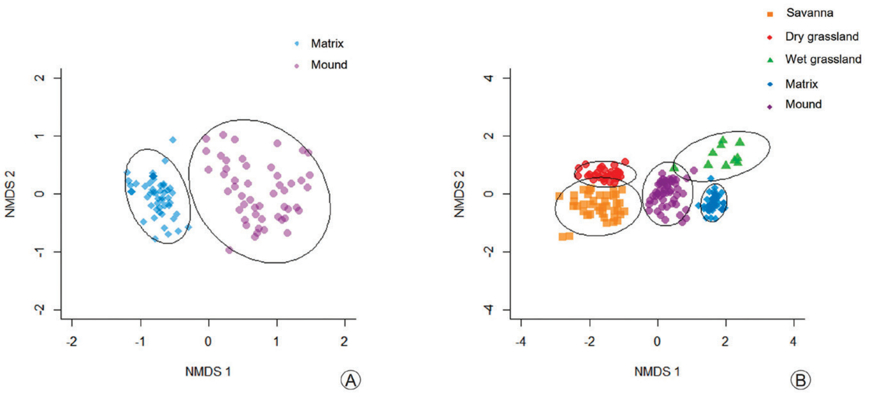

Figure 3. Nonmetric multidimensional scaling (NMDS) ordination across plots and community types based on Bray-Curtis distances. A) Floristic composition of mounds and matrix (wet grassland around the mounds). The best ordination solution was two-dimensional with final stress of 0,15. B) Floristic composition of different communities: on the mounds (purple), waterlogged matrix (blue), wet grassland without mounds (green), dry grassland (red), and savanna (orange). The best ordination solution was two-dimensional with final stress of 0,09. Ellipses represent 95% confidence intervals for the standard deviation.

mound and matrix, 42 species occurred only on top of the mounds, and 4 were exclusive of the matrix. When all communities were considered, the mounds shared 10 species with the wet, 15 with the dry grassland, and 19 with the savanna (Table S1).

Regarding the floristic composition, the NMDS ordination analysis showed a clear separation of the mound and the matrix (Figure 3a). When the species composition of the mounds and matrix of the termite savanna were compared to savanna, dry grassland, and wet grassland without termite mounds, neither the mound nor the matrix matched the other communities around (Figure 3b).

We found associations between functional guilds and plant communities, with differences related to tolerance to waterlogging (Figure 4a), growth form (Figure 4b), and dispersal syndrome (Figure 4c). Functional relationships between communities generally follow the taxonomic relationships, with the termite mounds occupying an intermediate position between dry (grassland and savanna) and waterlogged (wet grasslands and matrix) environments. The frequency of tolerant or intolerant species to waterlogging differed from the expected in all communities (Figure 4a, Table S2). The proportion of forbs was higher than expected only in the wet grassland (Figure 4b, Table S2). Dominant plants in the wet matrix around the mounds were grasses, followed by sedges, and both growth forms occurred in higher proportions than expected (Figure 4b). Compared to the regional pool, woody species were less frequent in the wet environments, not differing between dry grassland and the mounds. Regarding dispersal syndrome, the frequency of anemochory in all five communities did not differ from the regional pool (Figure 4c). Seed dispersal by gravity was more frequent than expected in both wet environments, while seed dispersal by animals was more frequent in the savanna.

Discussion

Termite savannas are peculiar ecosystems recorded in tropical regions worldwide, still not fully understood (Davies et al. 2014). Their microtopography creates a mosaic of two distinct habitats due to soil conditions (Hlongwane 2009), increasing patchiness, and heterogeneity of savanna vegetation (Moe et al. 2009). Our study indicated a bimodal floristic composition, resulting in distinct plant communities on the well-drained mounds and the waterlogged matrix, corroborating previous studies from Brazilian and African termite savannas showing distinct communities occupying the mounds and the surrounding matrix (Erpenbach et al. 2013, 2017, Van der Plas et al. 2013, Seymour et al. 2016, Muvengwi et al. 2017). This bimodality has important implications for the conservation and ecological restoration of these ecosystems. These permanently-dry 'islands' – the *murundus*, merged in seasonally flooded grasslands, are extremely important as refuges for terrestrial organisms and play relevant roles in maintaining biodiversity cycles, functions, and processes (Junk et al. 2014). By sampling only the woody plants on the mounds, which are mainly intolerant to waterlogging (Araujo Neto et al. 1986, Oliveira-Filho & Martins 1991), the biodiversity of the whole ecosystem will be underestimated for plants and likely also for animals and microorganisms (Leitner et al. 2020). If mounds and matrix have distinct biota, restoring the native vegetation of termite savannas will require separate sets of species to reintroduce in each microhabitat (Moe et al. 2009, Cuma Mushagalusa et al. 2018).

Besides creating well-drained islands, termites act as "ecosystem engineers" by promoting soil transformations (Dangerfield et al. 1998). Organic matter and mineral particles can be collected and deposited in the mounds by termites, increasing the content of organic C, clay, and nutrients (Sarcinelli et al. 2009). As in the hyperseasonal cerrado (Cianciaruso et al. 2005, Cianciaruso & Batalha 2009), seedlings of woody species are likely unable to survive the seasonal flooded conditions around the mounds. In our study areas, we expected the plant community on the well-drained mounds to resemble that of open Cerrado physiognomies on dry land. However, this was true only for woody plants, a subset of the surrounding dry areas. Since the herbaceous layer on the mounds is predominantly composed of a subset of species that occur in both the seasonally flooded matrix and the wet grasslands without mounds, the whole plant community on the mounds is floristically distinct from all other communities, being a mixture of the flora of humid and dry environments, as also observed by Sileshi et al. (2010) and Joseph et al. (2013). Despite the low species richness, the mounds presented a more balanced distribution among

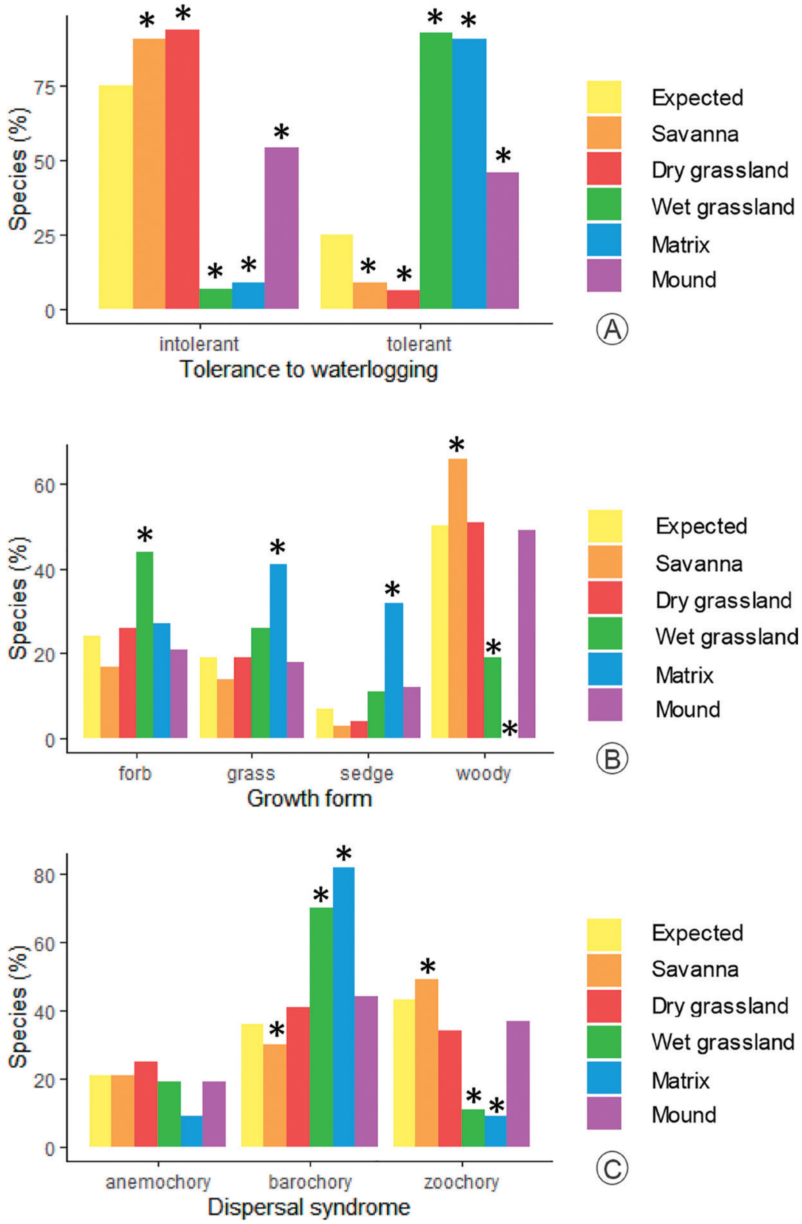

Figure 4. Proportion of functional guilds in the total species pool (Expected frequencies) and within each of the five community types (Observed frequencies): savanna, dry grassland, wet grassland without mounds, matrix (around the mounds), and on the mounds, at Santa Bárbara Ecological Station (SBES, Águas de Santa Bárbara, state of São Paulo, Brazil). A) Tolerance to waterlogging (tolerant or intolerant); B) Growth form (forb, grass, sedge, woody); C) Dispersal syndrome (anemochory, barochory, zoochory). Asterisks (*) mean the frequency of that guild in that community significantly differs from the expected frequency on the basis of the total species pool (α = 0.05).

functional guilds, either for tolerance to waterlogging, growth forms, or dispersal syndrome, in comparison with the matrix or even with the other communities compared. This functional redundancy may make the mound plant communities more resilient than the others analysed to abiotic or biotic changes, which cause species loss (Biggs et al. 2020). Even without exclusive flora, the plant community of the grassy and humid matrix around the mounds differed from all other communities, including the wet grassland, moreover due to the absence of species which are frequent in the other communities. In addition to the absence of woody plants, the forbs and part of the grasses and sedges recorded in the wet grasslands without mounds seem vulnerable to the long dry period that characterises the hyperseasonal environment around the mounds. On the other hand, some common grasses of dry land (*e.g., Andropogon leucostachyus* Kunth) take advantage of drought periods and colonise the matrix around the mounds.

The double environmental filtering (flooding and drought) likely resulted in the matrix around the mounds having the lowest richness (average number of species per square metre) among the five communities compared. We do not disregard that the legacy effects of about two decades of pine invasion can have contributed to the low richness in the matrix around the termite mounds. These plant communities can have suffered more intensively the negative effects of the needles layer and changes in the hydrological regime (Abreu & Durigan 2011). However, the mounds were also under pine invasion and presented higher richness. Batalha et al. (2005) also found lower richness in hyperseasonal savanna when compared to seasonal savanna, probably because most woody species are unable to survive this alternating double environmental filter, which enhances the anaerobic activity during the wet season, and then plants quickly dry after ceasing the waterlogging (Sarmiento & Monasterio 1975). Low species richness has been observed in *campos com murundus* in other regions, such as Roraima (Barbosa et al. 2005).

In addition to environmental filters, limitations on seed dispersal may explain the absence, on the mounds, of many species from the surrounding dry environments since barochoric species or even species whose seeds are windblown close to the ground (like many Poaceae) may have difficulties in transposing the seasonally flooded matrix. The influence of hyperseasonality on the efficiency of dispersal syndromes and the phenology of cerrado plants has been previously reported by Silva et al. (2009).

There are previous records of termite savannas throughout the tropical regions in Brazil, in the states of Goiás (Cianciaruso et al. 2005, Maricato et al. 2018), Mato Grosso (Eiten 1975, Marimon et al. 2012, Morais et al. 2014), Bahia (Oliveira et al. 2014, Souza et al. 2020), Distrito Federal (Araujo Neto et al. 1986), Roraima (Barbosa et al. 2005), and northern Minas Gerais (Antunes et al. 2012). However, none of these records was beyond 21°S, indicating a clear association with warm climates. The record of a remnant of *campo com murundus* in the state of São Paulo, at 22°47’22” S, considerably distant from the known records of this vegetation type in Brazil, demonstrates the climatic, hydrological, and edaphic conditions that allow their existence are broader than previously thought. Thus, it is possible that other patches still exist in the state of São Paulo or marginal regions elsewhere without having been noticed. It is also possible that they existed in the past, but the termite mounds were destroyed by the widespread perception of landowners that termites are an agricultural pest to be combated, besides blocking mechanisation.

Despite their great importance in maintaining biodiversity cycles, functions, and processes (Junk et al. 2014), the *campos com murundus*, like other vegetation types that cover Cerrado wetlands, have not been properly protected by law in Brazil (Durigan et al. 2022), being not even mentioned in Federal Law # 12651. The state of Goiás has a specific law declaring *campos com murundus* as Permanently Preservation Areas (State Law # 16153), but that is an isolated solution. Their protection depends, therefore, on a broad interpretation of the term ‘vereda’ as it is the federal law: “savanna vegetation occurring in hydromorphic soils, usually with sparse palms (*buritis*) over an herb-shrub layer” (Law # 12651, Art. 4°, XI). Alternatively, *campos com murundus* can be understood as wetlands and thus treated as restricted use areas (Law # 12651, Art. 10). Ideally, to effectively protect these iconic ecosystems, they should be one of the many different vegetation types internationally recognised as wetlands and subjected to a single legal treatment, as proposed by Junk et al. (2014).

The *campos com murundus* and most natural grasslands in Brazil appear on the maps of the remaining natural vegetation only when they occupy large extensions. That makes it even more difficult to preserve these ecosystems since they usually occupy small areas, such as the 3.5-ha patch of *campo com murundus* recorded in this study. Absent in the maps and neglected by conservation policies, these ecosystems have also been forgotten by scientists and thus misunderstood or unknown.

Supplementary Material

The following online material is available for this article:

Table S1 - List of species sampled in the study, with their growth form, dispersal syndrome, waterlogging tolerance, the vegetation type where each species was sampled, and the frequency of each species in the matrix and in the mound. Disp. Syn.: Dispersal syndrome; Wat. Tol.: water tolerance; Ane = anemochory; Bar = barochory; Zoo = zoochory. Veg. type = vegetation type; Dry grass. = Dry grassland; Wet grass. = Wet grassland. Freq. Matrix = frequency of the species in the matrix; Freq. mound = frequency of the species in the mound.

Table S2 - Chi-square analysis of the frequency of functional traits among six groups of species: Expected (all species recorded in the five vegetation types), Savanna, Dry grassland, Wet grassland, matrix and mound. The species attributes were tolerance to waterlogging (yes or no), growth form (forb, grass, sedge or woody) and dispersal syndrome (anemochory, barochory or zoochory). χ^2: chi-square values, df: degrees of freedom; *p*: p-value; ns: p-value non-significant (α = 0.05).

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Bruna Helena Campos: contributed to data collection, data analysis and interpretation, and manuscript preparation.

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Natalia Macedo Ivanauskas: contributed to manuscript preparation.

Giselda Durigan: was responsible for conceptualizing and designing the study; contributed to data collection, data analysis and interpretation, and manuscript preparation.

Conflicts of Interest

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

Ethics

This study did not involve human beings and/or clinical trials that should be approved by one Institutional Committee.

Data Availability

Data is available from the Biota Neotropica Dataverse: <https://doi.org/10.48331/scielodata.2MFNQW>.

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Inventory

The herpetofauna of priority highland areas for conservation of the Caatinga in the state of Rio Grande do Norte, northeastern Brazil

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Abstract: The Brazilian Caatinga has already lost extensive areas of original vegetation, thus it becomes imperative to perform fauna inventories within this region to fill geographical sampling gaps. Herein, we present a taxonomic list of the herpetofauna of a mountain chain located in the central zone of Rio Grande do Norte (RN) state whose region includes two priority areas for conservation of the Caatinga: "CA087 – Serra de Santana" in the west, and "CA078 – Nascente do Potengi" in the east. The sampling was carried out using methods of visual searching, pitfall traps with drift fences, specimens rescued during vegetation suppression activities in wind energy projects, occasional encounters, and third-party records. We recorded 19 amphibian species and 53 reptile species (23 lizards, 24 snakes, five amphisbaenians and one chelonian). About half of the recorded species have distributions entirely or mostly in the Caatinga. The mountain range sampled in this study harbors virtually all species found in nearby lowlands of the "sertaneja" depression of RN state, plus some relevant species with relictual distributions in the Caatinga, highlighting the importance of these highland areas for conservation of the Caatinga herpetofauna.
Keywords: *Amphibians; Nascente do Potengi; Reptiles; Serra de Santana; Wind farms.*

A herpetofauna de áreas serranas prioritárias para conservação da Caatinga no estado do Rio Grande do Norte, nordeste do Brasil

Resumo: A Caatinga brasileira já perdeu extensas áreas de vegetação original, por isso torna-se importante realizar inventários de fauna nesta região para preencher lacunas geográficas de amostragem. Aqui, apresentamos uma lista taxonômica da herpetofauna de uma cadeia serrana localizada na zona central do estado do Rio Grande do Norte (RN) e cuja região inclui duas áreas prioritárias para conservação da Caatinga: "CA087 – Serra de Santana" a oeste, e "CA078 – Nascente do Potengi" a leste. A amostragem foi realizada por meio de métodos de busca visual, armadilhas de interceptação e queda, espécimes resgatados durante atividades de supressão vegetal em projetos de energia eólica, encontros ocasionais e registros de terceiros. Registramos 19 espécies de anfíbios e 53 espécies de répteis (23 lagartos, 24 serpentes, cinco anfisbênias e um quelônio). Cerca de metade das espécies registradas tem distribuição inteiramente ou predominantemente na Caatinga. A cadeia serrana amostrada neste estudo abriga praticamente todas as espécies encontradas nas planícies próximas da depressão sertaneja do RN, além de algumas espécies relevantes com distribuição relictual na Caatinga, destacando a importância dessas áreas de altitude para a conservação da herpetofauna da Caatinga.
Palavras-chave: *Anfíbios; Nascente do Potengi; Parques Eólicos; Répteis; Serra de Santana.*

Introduction

The Caatinga is a well-recognized ecological region of about 900,000 km^2 and comprises a mosaic of deciduous and xerophytic thorny shrubs and seasonally dry forests that extend through most of semiarid northeastern Brazil (Leal et al. 2005), being the largest and most continuous expanse of seasonally dry tropical forest biome in the world (Queiroz et al. 2017). Most of the Caatinga covers lowlands up to 500 m above sea level, but isolated mountain ranges and high-altitude plateaus are scattered across the region, modifying the local climate, and acting as present-day refuges for species assemblages (Silva et al. 2017). This region constitutes a dynamic system whose characteristics are shaped by various ecological and evolutionary processes that interact at different spatial and temporal scales (Araújo et al. 2022).

Despite its importance, the Caatinga has already lost extensive areas of original vegetation (Antongiovanni et al. 2018), mostly due to the fast expansion of agriculture and livestock, and includes very large, disturbed areas, as well areas undergoing desertification processes, both of which have been given high priority for conservation (Albuquerque et al. 2012). In the last decade, the Caatinga has also harbored several renewable energy enterprises (Jong et al. 2017), mainly wind farms and photovoltaic solar plants, whose installation involves deforestation and soil removal for installation of wind turbines, solar modules, access roads and transmission lines.

With this continuous process of habitat loss in the Caatinga, it seems imperative to prioritize fauna inventories within this region to fill geographical sampling gaps, allowing more accurate decisions when licensing areas for construction by enterprises and defining priority areas for conservation (Dal Velchio et al. 2016, Pichorim et al. 2016). A recent evaluation conducted by the Brazilian Environment Ministry with large participation of federal agencies, environment state secretariats, universities, and other research bodies, as well as NGOs, has updated the priority areas for conservation of biodiversity in Brazil, originally established in 2004 (Fonseca et al. 2017, MMA 2018). Most of these defined priority areas still lack relevant information about biodiversity composition.

Rio Grande do Norte (RN) is the most northeastward state of Brazil, located between the latitudes 4.8317° S and 6.9828° S and longitudes 34.9686° W and 38.5822° W, and covering a total area of 52.811 km^2, which corresponds to 0.62% of Brazilian territory (IDEMA 2018). About 95% of the RN territory is within the Caatinga region, and its east coastal area comprises the north limit of the Atlantic Rainforest, with semi-deciduous forests, mangroves, and coastal vegetation (Tabarelli et al. 2005). The Caatinga of RN is in a relief composed by the lowland "sertaneja" depression and some mountain chains such as Serra de Martins, Serra de João do Vale, and Serra de Santana (Diniz et al. 2015).

Much of the biodiversity of RN is still unknown, but in recent years vertebrate lists for some sites were published regarding fish (Nascimento et al. 2014, Costa et al. 2017, Medeiros et al. 2019), amphibians (Magalhães et al. 2013, Caldas et al. 2016), reptiles (Freire et al. 2009, 2011, Sales et al. 2009, Caldas et al. 2016, Calixto & Morato 2017, Marques et al. 2021), birds (Silva et al. 2012, Pichorim et al. 2014, 2016, Sagot-Martin et al. 2020), terrestrial mammals (Marinho et al. 2018, Cherem et al. 2019), and bats (Vargas-Mena et al. 2018). With respect to the herpetofauna, only two sites in RN have published lists based on long-term standardized sampling effort: one in the Caatinga for amphibians and reptiles (Freire et al. 2009, Caldas et al. 2016), and the other in a transitional area between Caatinga and Atlantic Forest only for amphibians (Magalhães et al. 2013). Given the increase in threats to the biodiversity of the Caatinga in recent years, it is essential to expand the number of faunal inventories in RN, particularly within priority areas for conservation.

Considering that the main long-term study on the herpetofauna of the Caatinga of RN (Freire et al. 2009) was carried out in the Seridó sertaneja depression and that the species obtained were the most common that are widely distributed in the Caatinga, and additionally according to Rodrigues (2003), some species have relictual patterns of geographic distribution in the Caatinga, occurring only in areas with arboreal vegetation on sandy soils and/or in mountainous areas, increasing and expanding studies for these areas is essential. Herein, we combine data from two long-term studies with data from rescue and monitoring fauna programs of wind energy enterprises to present a taxonomic list of the herpetofauna of a mountain chain located in the central zone of RN whose area includes two priority areas for conservation of the Caatinga (MMA, 2018): "CA087 – Serra de Santana" in the west, and "CA078 – Nascente do Potengi" in the east.

Material and Methods

1. *Study sites*

The priority area for conservation of the Caatinga named "CA087 – Serra de Santana" (Figure 1) encompasses the western portion of a mountain range with an elongated shape in the east-west direction, featuring sedimentary geological formations which suffered weathering processes throughout geological history, and is characterized by plateau topography with ancient, eroded slopes covered by caatinga vegetation (RADAMBRASIL 1981). The Serra de Santana plateau fully or partially encompasses seven municipalities of RN (Lagoa Nova, Bodó, Santana

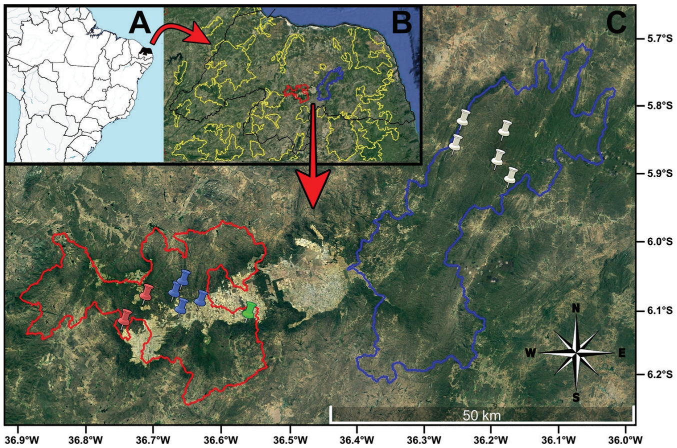

Figure 1. A = Location of Rio Grande do Norte state in northeastern Brazil. **B** = Location of CA087–Serra de Santana (red polygon) and CA078–Nascente do Potengi (blue polygon) priority areas for conservation of the Caatinga, in Rio Grande do Norte state (yellow polygons: other priority areas in the state). **C** = Sampled sites in each priority area; red pins correspond to Site 1 (municipality of Tenente Laurentino Cruz); green pin corresponds to Site 2 (municipality of Lagoa Nova); blue pins correspond to Site 3 (wind energy enterprise located in the rural zones of São Vicente, Santana do Matos, Tenente Laurentino Cruz and Lagoa Nova; and white pins correspond do Site 4 (wind energy enterprise located in the rural zones of Cerro Corá, Lajes and São Tomé municipalities).

do Matos, Florânia, Cerro Corá, São Vicente and Tenente Laurentino Cruz). Altitude in the plateau varies between 600 and 740 m, and the climate is semi-arid, with mean annual rainfall between 400 and 650 mm, and mean annual temperatures around 27 °C (Beltrão et al. 2005). Action conservation priority in CA087 – Serra de Santana is categorized as "very high", and the main proposed action is the creation of a protected area in the "integral protection" category of the National System of Conservation Units – SNUC (e.g., national park, biological reserve, ecological station; MMA 2018).

The second priority area for conservation of the Caatinga sampled in this study is "CA078 – Nascente do Potengi" (Figure 1), which partially includes the municipalities of Cerro Corá, São Tomé and Lajes. Action conservation priority in this area is also categorized as "very high", and the main proposed action is to create a protected area in the "integral protection" category (MMA 2018). This priority area encompasses the east portion of Serra de Santana plateau (Figure 1) and other mountain chains such as Serra do Feiticeiro in Lajes municipality. Altitude in the sampled area varies between 300 and 500 m, and climate conditions resemble the sampled areas of Serra de Santana.

The herpetofauna inventory of the two priority areas consisted of four distinct data sources (Figure 1). Two research projects coordinated by EMXF were conducted in Serra de Santana relatively well-preserved caatinga remnants in the municipalities of Tenente Laurentino Cruz (Site 1) and Lagoa Nova (Site 2). Plus, a third sampled site was a wind energy enterprise located in the rural zones of Santana do Matos, São Vicente, Tenente Laurentino Cruz and Lagoa Nova (Site 3). The sampled area in Nascente do Potengi was a wind energy enterprise located in the rural zones of Cerro Corá, Lajes and São Tomé municipalities (Site 4). Vegetation physiognomies are similar among study sites, characterized by arboreal-bushy stratum and abundance of rocky outcrops surrounded by vegetation (Figure 2A–D). Plus, habitat modification due to installation of wind farms and agriculture/livestock activities in the vicinities is present in all study sites (Figure 2E-F).

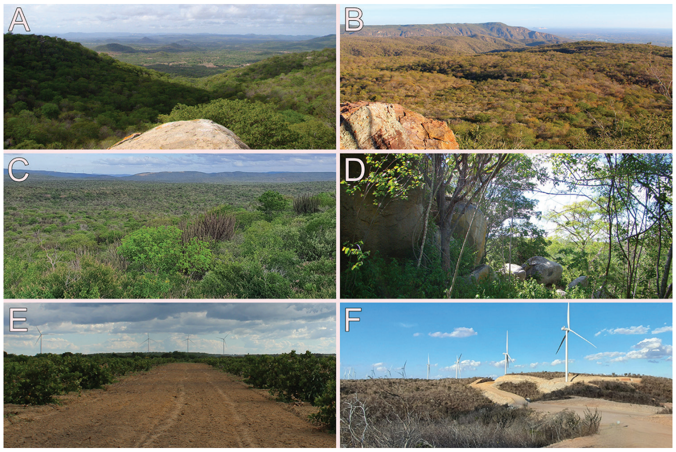

Figure 2. Panoramic view of the study sites and general aspect of the vegetation in Serra de Santana and Nascente do Potengi priority areas for conservation of the Caatinga in Rio Grande do Norte state, northeastern Brazil. **A -** Site 2; **B** - Site 3; **C** - Site 4; **D** - arboreal-bushy vegetation with rocky outcrops in Sites 2; **E** - land use for agriculture and wind farms in Site 3; **F -** wind farms installed in Site 4.

2. *Data collection*

The fieldwork in Site 1 (two sampling areas named Serra Nova – central coordinates: 06.0968° S, 36.7160° W, 704 m elev.; and Nascimento – central coordinates: 06.1337° S, 36.7481° W, 682 m elev.) consisted of 5-day monthly expeditions between September 2009 and August 2010 (except for February 2010), totaling 55 days of sampling effort. MG and MNCK collected the data in this site by two standardized methods: (1) time-constrained visual searches (Crump and Scott Jr 1994) at different times of the day (morning, afternoon, and night); and (2) pitfall traps with drift fences (Cechin and Martins 2000), installed in eight linear arrays, each one with 16 buckets of 38 L separated by 2.5 m. Additionally, occasional encounters outside the period dedicated to time-constrained visual search, and third-party records provided by local people were also considered for the list of species. Both amphibians and reptiles were sampled in Site 1, but the sampling of amphibians only occurred in September to November 2009, January and March 2010.

The fieldwork in Site 2 (one sampling area named Serro Alto – central coordinates: 06.1233° S, 36.5641° W, 682 m elev.) consisted of four 20-day expeditions in March and September 2014 (all reptiles), and March and September 2015 (only snakes and amphisbaenians), totaling 80 days of sampling effort. MFK, MMR, RFDS, MJMA and BPR collected the data from this site by two standardized methods: (1) time-constrained visual searches at different times of the day (morning, afternoon, and night); and (2) pitfall traps with drift fences, installed in six Y-shaped arrays, each one with 16 buckets of 38 L separated by 2.5 m. Additionally, occasional encounters outside the period dedicated to time-constrained visual search, and third-party records provided by local people were also considered for the list of species. Only reptiles were sampled at Site 2.

Data from Site 3 (four sampling areas; central coordinates: 06.0748° S, 36.6613° W, 627 m elev.; 06.0921° S, 36.6740° W, 648 m elev.; 06.1168° S, 36.6651° W, 711 m elev.; 06.1057° S, 36.6358° W, 704 m elev.) consisted of two sources: (a) the faunal monitoring environmental program and (b) the faunal rescue environmental program in the areas of influence of the wind energy enterprise (Acauã wind complex). Data from the faunal monitoring program was collected by RFDS along two 5-day expeditions in March and June 2021 by time-constrained visual searches in different times of the day (morning, afternoon, and night), totaling 10 days of sampling effort. Data from the faunal rescue program was collected by third parties (teams of biologists and veterinarians) during vegetation suppression activities for installing wind turbines and access roads of the enterprise, between March 2021 and February 2022, totaling 188 days of sampling effort. Data from the faunal rescue program was provided to us by the environmental consulting firm, together with voucher specimens. Both amphibians and reptiles were sampled at Site 3.

Similarly, data from Site 4 (five sampling areas; central coordinates: 05.8766° S, 36.2586° W, 347 m elev.; 05.8398° S, 36.2471° W, 420 m elev.; 05.8553° S, 36.1855° W, 511 m elev.; 05.8983° S, 36.1956° W, 261 m elev.; 05.9247° S, 36.1768° W, 249 m elev.) also consisted of two sources: (a) the faunal monitoring environmental program and (b) the faunal rescue environmental program in the areas of influence of the wind energy enterprise (Santa Rosa and Mundo Novo wind complex). Data from the faunal monitoring program was collected by VTCS along seven 4-day expeditions in August 2020, February, May, August and November 2021, and February and May 2022, totaling 28 days of standardized sampling effort. Sampling methods were time-constrained visual searches at different times of the day (morning, afternoon, and night), and pitfall traps with drift fences, installed in 5 Y-shaped arrays, each one with 3 marginal buckets of 20 L and separated by 3 m from a central bucket of 60 L. Data from the faunal rescue program was collected by third parties during vegetation suppression activities for installation of wind turbines and access roads of the enterprise between February 2020 and January 2021, totaling 194 days of sampling effort. Data from the faunal rescue program was provided to us by the environmental consulting firm, together with voucher specimens. Both amphibians and reptiles were sampled at this site.

Voucher specimens are housed at the Herpetological Collection of Universidade Federal do Rio Grande do Norte (UFRN-CH), and the voucher numbers are provided in the Supplementary Material (Appendix S1). Material identification was carried out using the current available literature and eventually by consulting other specialist colleagues. The taxonomic nomenclature follows Frost (2021) and Uetz et al. (2022).

3. *Data analysis*

The sampling effort in each priority area was evaluated by rarefaction curves generated in the EstimateS 9.1.0 program obtained by 1000 randomizations without replacement (Colwell 2013), considering each day of fieldwork as a sample unit, pooling all sampling methods developed in that day. We built separate curves for (a) amphibians, (b) lizards, and (c) snakes and amphisbaenians, considering the different degrees of rarity in sampling these animals. The expected richness was evaluated by the Jackknife 1 estimator, whose calculation emphasizes the number of species that occurs in only one sample unit (Santos 2003).

Results

We recorded 19 amphibian species and 53 reptile species in the two sampled priority areas for conservation of the Caatinga in RN state (Tables 1-2, Figures 3–5). Among these, 18 amphibian species and 49 reptile species were recorded in CA087–Serra de Santana, and

Table 1. List of amphibian species recorded at Serra de Santana and Nascente do Potengi priority areas for conservation of Caatinga in Rio Grande do Norte state, northeastern Brazil. Sampling methods: **AS** = active search; **PT** = pitfall traps; **FR** = fauna rescue activities during vegetation suppression in wind energy enterprises. Distribution: **M-CA** = mostly distributed in the Caatinga and marginally in Atlantic Forest and/or eastern Cerrado; **CA/AF**: distributed in Caatinga and Atlantic Forest; **W** = widespread (common in ≥ 3 biomes). Voucher: **UFRN-CH** = Coleção Herpetológica da Universidade Federal do Rio Grande do Norte (voucher numbers are in the Appendix S1); there is a photographic record (Figure 3) for species that do not have a voucher specimen in UFRN-CH.

Amphibian species	Number of records		Sampling methods	Distribution	Voucher
	Serra de Santana	Nascente do Potengi			
ANURA					
Bufonidae					
Rhinella diptycha (Cope, 1862)	10	27	AS, PT, FR	W	Figure 3A
Rhinella granulosa (Spix, 1824)	62	100	AS, PT, FR	M-CA	UFRN-CH
Hylidae					
Boana raniceps (Cope, 1862)	1	4	AS	W	Figure 3C
Corythomantis greeningi Boulenger, 1896	3	4	AS, FR	M-CA	UFRN-CH
Dendropsophus nanus (Boulenger, 1889)	1	–	AS	W	Figure 3E
Scinax x-signatus (Spix, 1824)	26	26	AS, FR	W	UFRN-CH
Leptodactylidae					
Leptodactylus fuscus (Schneider, 1799)	1	20	AS, FR	W	Figure 3G
Leptodactylus macrosternum Miranda-Ribeiro, 1926	30	24	AS, FR	W	UFRN-CH
Leptodactylus troglodytes Lutz, 1926	29	48	AS, PT, FR	M-CA	UFRN-CH
Leptodactylus vastus Lutz, 1930	2	2	AS, PT	M-CA	UFRN-CH
Physalaemus albifrons (Spix, 1824)	5	18	AS, PT, FR	M-CA	UFRN-CH
Physalaemus cicada Bokermann, 1966	8	5	AS, PT, FR	M-CA	UFRN-CH
Physalaemus cuvieri Fitzinger, 1826	–	1	PT	W	Figure 3M
Pleurodema diplolister (Peters, 1870)	2	23	AS, PT, FR	M-CA	UFRN-CH
Pseudopaludicola pocoto Magalhães, Loebmann, Kokubum, Haddad, and Garda, 2014	1	–	AS, PT	M-CA	Figure 3O
Microhylidae					
Dermatonotus muelleri (Boettger, 1885)	6	36	PT, FR	W	UFRN-CH
Odontophrynidae					
Proceratophrys cristiceps (Müller, 1883)	19	25	AS, PT, FR	M-CA	UFRN-CH
Pipidae					
Pipa carvalhoi (Miranda-Ribeiro, 1937)	1	–	PT	CA/AF	UFRN-CH
Phyllomedusidae					
Pithecopus gonzagai Andrade, Haga, Ferreira, Recco-Pimentel, Toledo, and Bruschi, 2020	30	44	AS, FR	CA/AF	UFRN-CH

Table 2. List of reptile species recorded at CA087–Serra de Santana and CA078–Nascente do Potengi priority areas for conservation of Caatinga, in Rio Grande do Norte state, northeastern Brazil. Sampling methods: **AS** = active search; **PT** = pitfall traps; **OE** = occasional encounters or third-party records by local people; **FR** = fauna rescue activities during vegetation suppression in wind energy enterprises. Distribution: **CA** = strictly distributed in the Caatinga; **M-CA** = mostly distributed in the Caatinga and marginally in Atlantic Forest and/or eastern Cerrado; **R-CA**: species with relictual distribution in the Caatinga; **CA/CA**: distributed in Caatinga and eastern Cerrado; **W** = widespread (common in ≥ 3 biomes). Voucher: **UFRN-CH** = Coleção Herpetológica da Universidade Federal do Rio Grande do Norte (voucher numbers are in the Appendix S1); there is a photographic record (Figures 4–5) for species that do not have a voucher in UFRN-CH.

Reptile species	**Number of records**		**Sampling methods**	**Distribution**	**Voucher**
	Serra de Santana	**Nascente do Potengi**			
SQUAMATA					
AMPHISBAENIA					
Amphisbaenidae					
Amphisbaena alba Linnaeus, 1758	5	12	AS, FR	W	UFRN-CH
Amphisbaena lumbricalis Vanzolini, 1996	682	–	AS, FR	CA	UFRN-CH
Amphisbaena pretrei Duméril & Bibron, 1839	18	–	AS, FR	W	UFRN-CH
Amphisbaena vermicularis Wagler, 1824	5	56	FR	W	UFRN-CH
Leposternon polystegum (Duméril, 1851)	1	12	FR	W	UFRN-CH
“LIZARDS”					
Diploglossidae					
Diploglossus lessonae Peracca, 1890	11	9	AS, PT, FR	R-CA	UFRN-CH
Gekkonidae			AS, PT		
Hemidactylus agrius Vanzolini, 1978	39	136	AS, FR	CA	UFRN-CH
Hemidactylus brasilianus (Amaral, 1935)	25	15	AS, FR	W	UFRN-CH
Hemidactylus mabouia (Moreau de Jonnés, 1818)	16	1	AS	W	UFRN-CH
Lygodactylus klugei (Smith, Martin & Swain, 1977)	78	82	AS, FR	M-CA	UFRN-CH
Gymnophthalmidae					
Acratosaura mentalis (Amaral, 1933)	31	9	AS, PT, FR	R-CA	UFRN-CH
Anotosaura vanzolinia Dixon, 1974	85	–	AS, PT, FR	R-CA	UFRN-CH
Micrablepharus maximiliani (Reinhardt & Luetken, 1862)	99	19	AS, PT, FR	W	UFRN-CH
Vanzosaura multiscutata (Amaral, 1933)	232	29	AS, PT, FR	M-CA	UFRN-CH
Iguanidae					
Iguana iguana (Linnaeus, 1758)	21	17	AS, FR	W	UFRN-CH
Leiosauridae					
Enyalius bibronii Boulenger, 1885	21	–	AS, PT, FR	R-CA	UFRN-CH
Mabuyidae			AS, PT		
Brasiliscincus heathi (Schmidt & Inger, 1951)	93	37	AS, PT, FR	W	UFRN-CH
Psychosaura agmosticha (Rodrigues, 2000)	–	42	FR	M-CA	Figure 4M
Phyllodactylidae					
Gymnodactylus geckoides Spix, 1825	240	130	AS, PT, FR	W	UFRN-CH
Phyllopezus periosus Rodrigues, 1986	27	33	AS, FR	CA	UFRN-CH
Phyllopezus pollicaris (Spix, 1825)	24	69	AS, FR	W	UFRN-CH
Polychrotidae					
Polychrus acutirostris Spix, 1825	122	70	AS, FR	W	UFRN-CH
Sphaerodactylidae					
Coleodactylus meridionalis (Boulenger, 1888)	23	1	AS, PT, FR	R-CA	UFRN-CH
Teiidae					
Ameiva ameiva (Linnaeus, 1758)	52	36	AS, PT, FR	W	UFRN-CH
Ameivula ocellifera (Spix, 1825)	1251	324	AS, PT, FR	W	UFRN-CH
Salvator merianae Duméril & Bibron, 1839	21	21	AS, PT, FR	W	UFRN-CH
Tropiduridae					
Tropidurus hispidus (Spix, 1825)	462	368	AS, PT, FR	W	UFRN-CH
Tropidurus semitaeniatus (Spix, 1825)	413	147	AS, PT, FR	M-CA	UFRN-CH

Continue...

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Reptile species	**Number of records**		**Sampling methods**	**Distribution**	**Voucher**
	Serra de Santana	**Nascente do Potengi**			
SERPENTES					
Boidae					
Boa constrictor Linnaeus, 1758	1	17	AS, OE, FR	W	UFRN-CH
Corallus hortulana (Linnaeus, 1758)	–	2	FR	W	Figure 5B
Epicrates assisi Machado, 1945	3	4	AS, FR	M-CA	UFRN-CH
Colubridae					
Leptophis dibernardoi Albuquerque, Santos, Borjes-Nojosa & Ávila, 2022	1	7	AS, FR	M-CA	UFRN-CH
Oxybelis aeneus (Wagler, 1824)	20	7	AS, OE, FR	W	UFRN-CH
Tantilla melanocephala (Linnaeus, 1758)	–	12	FR	W	Figure 5F
Dipsadidae					
Apostolepis cearensis Gomes, 1915	8	28	AS, PT, FR	M-CA	UFRN-CH
Apostolepis longicaudata Gomes, 1921	10	–	PT, FR	CA/CE	UFRN-CH
Boiruna sertaneja Zaher, 1996	3	5	FR	M-CA	Figure 5I
Erythrolamprus poecilogyrus (Wied-Neuwied, 1824)	7	6	AS, PT, FR	W	UFRN-CH
Erythrolamprus viridis (Günther, 1862)	1	9	FR	M-CA	UFRN-CH
Leptodeira tarairiu Costa, Graboski, Grazziotin, Zaher, Rodrigues & Prudente, 2022	4	9	AS, FR	W	UFRN-CH
Lygophis paucidens Hoge, 1952	–	3	FR	W	UFRN-CH
Oxyrhopus trigeminus Duméril, Bibron & Duméril, 1854	48	74	AS, PT, FR	W	UFRN-CH
Philodryas nattereri Steindachner, 1870	38	29	AS, FR	W	UFRN-CH
Philodryas olfersii (Lichtenstein, 1823)	26	3	AS, FR	W	UFRN-CH
Pseudoboa nigra (Duméril, Bibron & Duméril, 1854)	6	32	AS, FR	W	UFRN-CH
Dryophylax almae (Franco & Ferreira, 2002)	6	–	AS	M-CA	UFRN-CH
Dryophylax phoenix (Franco, Trevine, Montingelli & Zaher, 2017)	20	39	AS, FR	M-CA	UFRN-CH
Xenodon merremii (Wagler, 1824)	1	–	AS	W	UFRN-CH
Elapidae					
Micrurus aff. *ibiboboca*	15	18	AS, PT, FR	M-CA	UFRN-CH
Leptotyphlopidae					
Epictia borapeliotes (Vanzolini, 1996)	30	5	AS, PT, OE, FR	M-CA	UFRN-CH
Viperidae					
Bothrops erythromelas Amaral, 1923	14	29	AS, FR	M-CA	UFRN-CH
Crotalus durissus Linnaeus, 1758	1	3	OE, FR	W	UFRN-CH
TESTUDINATA					
Chelidae					
Mesoclemmys tuberculata (Luederwaldt, 1926)	1	–	OE	M-CA	Figure 4X

16 amphibian species and 45 reptile species in CA078–Nascente do Potengi. Rarefaction curves for Serra de Santana showed an increasing profile for amphibians and snakes/amphisbaenians and were asymptotic for lizards (Figure 6A–C). Rarefaction curves for Nascente do Potengi were very close to asymptotes for amphibians and lizards, and asymptotic for snakes/amphisbaenians (Figure 6D–F). The Jackknife 1 estimator predicted five additional amphibian species and six additional snake/amphisbaenian species for Serra de Santana, and three additional amphibian species and two additional lizard species for Nascente do Potengi (Figure 6).

The most common amphibian in the study sites was the toad *Rhinella granulosa*, followed by the frogs *Leptodactylus troglodytes* and *L. macrosternum*, and the treefrogs *Pithecopus gonzagai* and *Scinax x-signatus* (Table 1). The most common lizards were *Ameivula ocellifera*, *Tropidurus hispidus*, *T. semitaeniatus* and *Gymnodactylus geckoides*, and the most common snakes were *Oxyrhopus trigeminus*, *Philodryas nattereri* and *Dryophylax phoenix* (Table 2). Finally, *Amphisbaena lumbricalis* stood out as the most common amphisbaenian in Serra de Santana, while *A. vermicularis* was the most common one in Nascente do Potengi (Table 2).

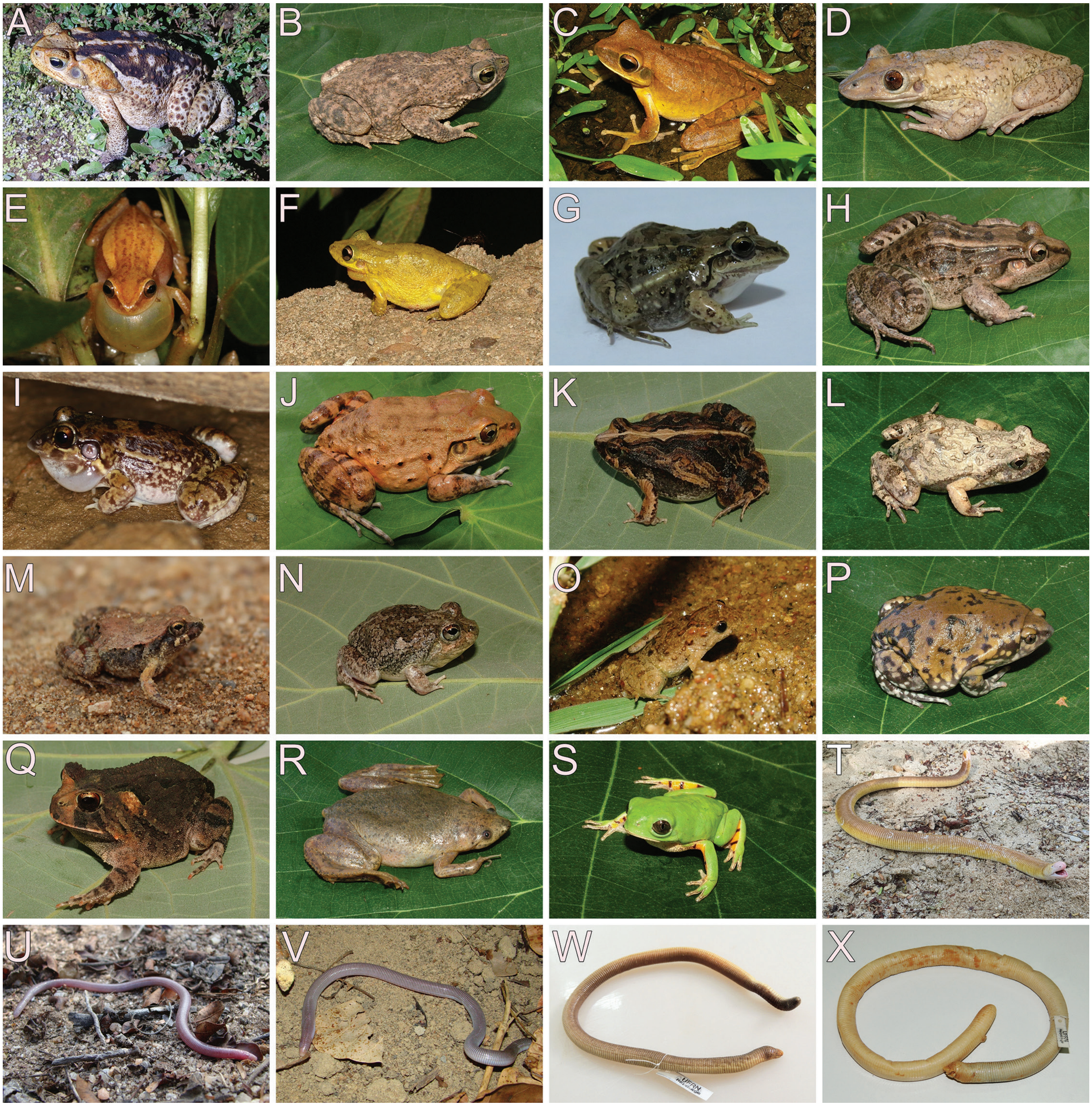

Figure 3. Herpetofauna recorded at Serra de Santana and Nascente do Potengi priority areas for conservation of the Caatinga in Rio Grande do Norte state, northeastern Brazil. **A** - *Rhinella diptycha*; **B** - *Rhinella granulosa*; **C** - *Boana raniceps*; **D** - *Corythomantis greeningi*; **E** - *Dendropsophus nanus*; **F** - *Scinax x-signatus*; **G** - *Leptodactylus fuscus*; **H** - *Leptodactylus macrosternum*; **I** - *Leptodactylus troglodytes*; **J** - *Leptodactylus vastus*; **K** - *Physalaemus albifrons*; **L** - *Physalaemus cicada*; **M** - *Physalaemus cuvieri*; **N** - *Pleurodema diplolister*; **O** - *Pseudopaludicola pocoto*; **P** - *Dermatonotus muelleri*; **Q** - *Proceratophrys cristiceps*; **R** - *Pipa carvalhoi*; **S** - *Pithecopus gonzagai*; **T** - *Amphisbaena alba*; **U** - *Amphisbaena lumbricalis*; **V** - *Amphisbaena pretrei*; **W** - *Amphisbaena vermicularis*; **X** - *Leposternon polystegum*.

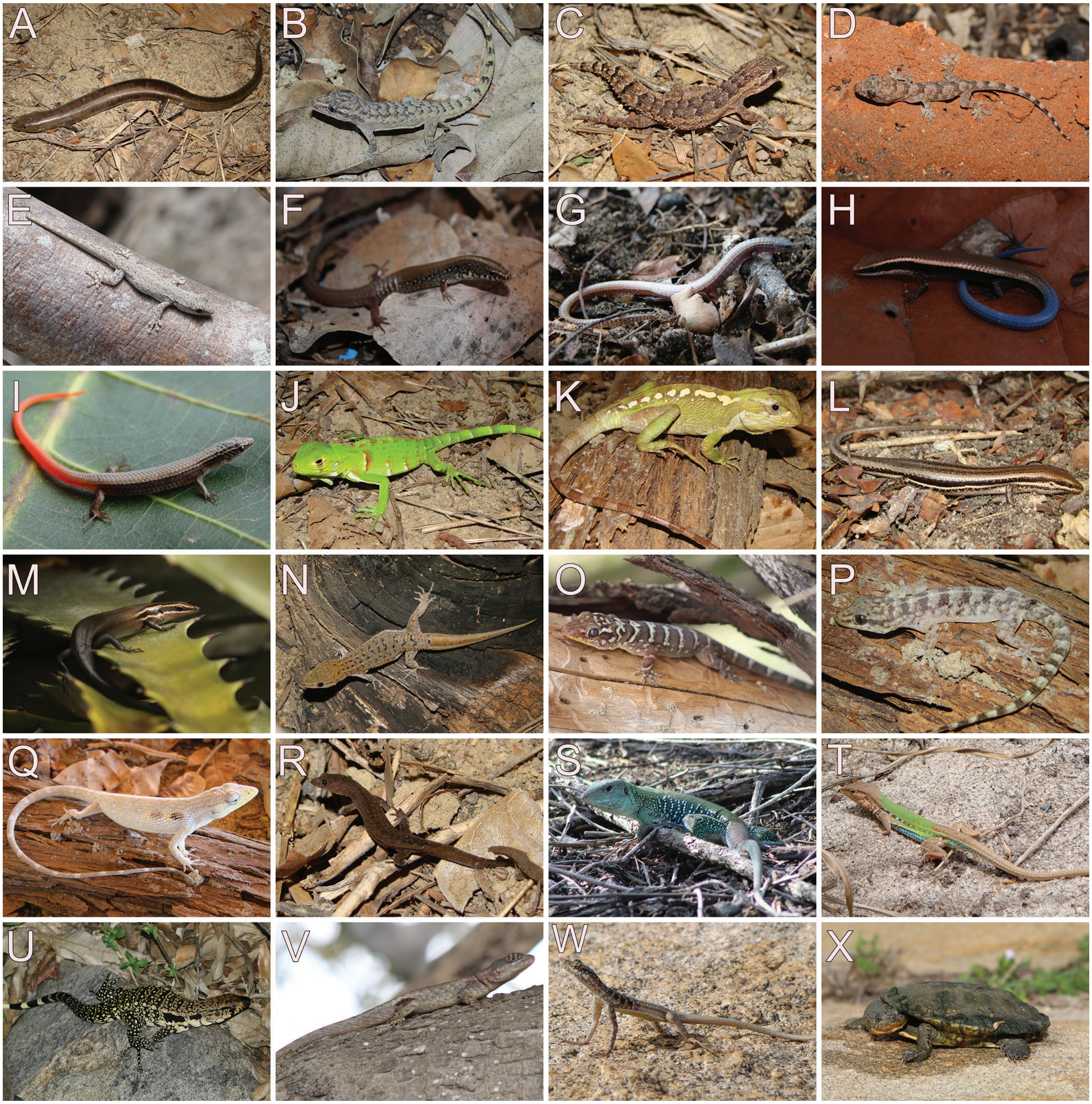

Figure 4. Herpetofauna recorded at Serra de Santana and Nascente do Potengi priority areas for conservation of the Caatinga in Rio Grande do Norte state, northeastern Brazil. **A** - *Diploglossus lessonae*; **B** - *Hemidactylus agrius*; **C** - *Hemidactylus brasilianus*; **D** - *Hemidactylus mabouia*; **E** - *Lygodactylus klugei*; **F** - *Acratosaura mentalis*; **G** - *Anotosaura vanzolinia*; **H** - *Micrablepharus maximiliani*; **I** - *Vanzosaura multiscutata*; **J** - *Iguana iguana*; **K** - *Enyalius bibronii*; **L** - *Brasiliscincus heathi*; **M** - *Psychosaura agmosticha*; **N** - *Gymnodactylus geckoides*; **O** - *Phyllopezus periosus*; **P** - *Phyllopezus pollicaris*; **Q** - *Polychrus acutirostris*; **R** - *Coleodactylus meridionalis*; **S** - *Ameiva ameiva*; **T** - *Ameivula ocellifera*; **U** - *Salvator merianae*; **V** - *Tropidurus hispidus*; **W** - *Tropidurus semitaeniatus*; **X** - *Mesoclemmys tuberculata*.

Figure 5. Herpetofauna recorded at Serra de Santana and Nascente do Potengi priority areas for conservation of the Caatinga in Rio Grande do Norte state, northeastern Brazil. **A** - *Boa constrictor*; **B** - *Corallus hortulana*; **C** - *Epicrates assisi*; **D** - *Leptophis dibernardoi*; **E** - *Oxybelis aeneus*; **F** - *Tantilla melanocephala*; **G** - *Apostolepis cearensis*; **H** - *Apostolepis longicaudata*; **I** - *Boiruna sertaneja*; **J** - *Erythrolamprus poecilogyrus*; **K** - *Erythrolamprus viridis*; **L** - *Leptodeira tarairiu*; **M** - *Lygophis paucidens*; **N** - *Oxyrhopus trigeminus*; **O** - *Philodryas nattereri*; **P** - *Philodryas olfersii*; **Q** - *Pseudoboa nigra*; **R** - *Dryophylax almae*; **S** - *Dryophylax phoenix*; **T** - *Xenodon merremii*; **U** - *Micrurus aff. ibiboboca*; **V** - *Epictia borapeliotes*; **W** - *Bothrops erythromelas*; **X** - *Crotalus durissus*.

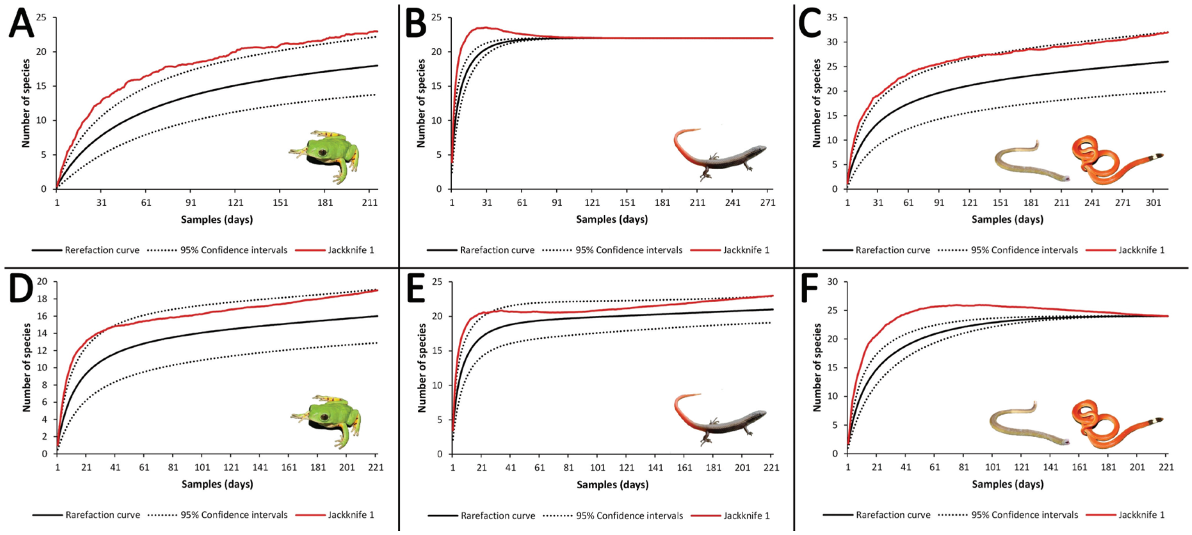

Figure 6. Rarefaction curves (black lines) with 95% confidence intervals (dotted lines) and Jackknife 1 richness estimators (red lines) for anurans, lizards, snakes and amphisbaenians in Serra de Santana (**A, B, C**) and Nascente do Potengi (**D, E, F**) priority areas for conservation of the Caatinga in Rio Grande do Norte state, northeastern Brazil.

Discussion

1. *Species richness, composition, and distribution patterns*

The richness of amphibians (19 species), lizards (23 species), snakes (24 species) and amphisbaenians (five species) found in Serra de Santana and Nascente do Potengi priority areas correspond, respectively, to 18.4%, 29.1%, 21.4% and 21.7% of current known richness for the Caatinga (Guedes et al. 2014, Garda et al. 2017, Mesquita et al. 2017, Ribeiro et al. 2018). These two priority areas harbor 71.9% of lizards, 50.0% of snakes, and 71.4% of amphisbaenians known for RN state (Costa et al. 2021, Marques et al. 2021). The rarefaction curve pattern indicates that our sampling is close to representing the total diversity of the herpetofauna present in the areas. Nonetheless, given the geographic proximity and climatic and biotic similarities among the sampled sites, we suggest that at least some of the species recorded solely at one of the two priority areas (e.g., *Dendropsophus nanus*, *Pseudopaludicola pocoto*, *Psychosaura agmosticha*, *Corallus hortulana*) may also occur in the other area but were not recorded due to sampling biases.

Regarding the composition and distribution patterns, most amphibian species recorded in Serra de Santana and Nascente do Potengi priority areas (N = 11, 57.9%, Table 1) have their distributions predominantly in the Caatinga, with marginal records in Atlantic Forest and/or eastern Cerrado (Narvaes & Rodrigues 2009, Linares & Melo 2011, Palmeira et al. 2011, Silva et al. 2014, Lantyer-Silva et al. 2016, Alves da Silva et al. 2020, Dubeux et al. 2020, Mângia et al. 2020, Vaz-Silva et al. 2020, Thomé et al. 2021), or are common in both the Caatinga and Atlantic Forest (Andrade et al. 2020, Lima et al. 2020). The remaining amphibian species recorded in the sampled areas (N = 8, 42.1%, Table 1) have wider geographic distributions in South America, being common in ≥ 3 biomes; most of them are widespread in the diagonal of open formations composed of Chaco, Cerrado and Caatinga biomes, also entering adjacent areas of Amazonia and Atlantic Forest (Oliveira et al. 2018, Barrio-Amorós et al. 2019, Araujo-Vieira et al. 2020, Camurugi et al. 2020, Magalhães et al. 2020, Pereyra et al. 2021).

With respect to reptiles, 45.3% of recorded species (N = 24, Table 2) have distributions entirely in the Caatinga biome or are mostly distributed in the Caatinga, but also marginally occur in adjacent biomes (Rodrigues 2003, Guedes et al. 2014, Mesquita et al. 2017, Recoder et al. 2014, Sales et al. 2015, Mesquita et al. 2017, Tavares et al. 2017, 2021, Nogueira et al. 2019, Albuquerque et al. 2022). A highlight regarding the species composition of the sampled mountainous areas is the occurrence of species with a relictual distribution pattern in mesic environments of the Caatinga, such as areas with arboreal vegetation on sandy soils, coastal areas, and/or in mountainous areas (Rodrigues 2003). This is the case for the lizards *Enyalius bibronii*, *Coleodactylus meridionalis*, *Diploglossus lessonae*, *Acratosaura mentalis* and *Anotosaura vanzolinia*; in addition to the relictual distribution in the Caatinga, some of them also occur in neighboring areas in northeastern Atlantic Forest and/or eastern Cerrado (Rodrigues 2003, Borges-Leite et al. 2014, Mesquita et al. 2017).

The remaining reptile species (N = 29, 54.7%, Table 2) have wider geographic distributions in South America; some are widespread in Atlantic Forest, Caatinga and Cerrado biomes (Vitt et al. 1996, Garda et al. 2012, Mesquita et al. 2017, Nogueira et al. 2019, Costa et al. 2021, Costa et al. 2022). The lizard *Hemidactylus mabouia* is an exotic (African) species which has been introduced and is successfully established in the New World, having colonized many countries in South America (Rocha et al. 2011).

2. *New records for Rio Grande do Norte state*

Two species are recorded for the first time in RN state: *Amphisbaena lumbricalis* (Figure 3U) and *Lygophis paucidens* (Figure 5M). The new records of *A. lumbricalis* presented here (several specimens from all four sampled areas of Site 3) extend its geographic distribution 100 km North from the nearest previously known locality (São Mamede, Paraíba state; Tavares et al. 2021), and increases the number of amphisbaenian species known for RN state to seven (the other species species are *A. alba*, *A. heathi*, *A. littoralis*, *A. pretrei*, *A. vermicularis*, and *Leposternon polystegum*; Costa et al. 2021). Morphometric and meristic characters of the specimens of *A. lumbricalis* from Serra de Santana match the species diagnosis presented by Vanzolini (1996); the examined species (UFRN-CH 4711, 6351-6432) have snout-vent length ranging from 106.2 to 168.3 mm, tail length 12.2 to 18.1 mm, head width 2.4 to 3.3 mm, body width 3.6 to 4.6 mm, body annuli 223 to 239, tail annuli 19 to 22, pre-cloacal pores 4, dorsal and ventral segments per midbody annulus 12–14 and 18, respectively.

The new record of *L. paucidens* extends its geographic distribution 444 km Southeast from the nearest previously known locality (Trairi, Ceará state; Serrano et al. 2020). The individual of *L. paucidens* from Nascente do Potengi (UFRN-CH 5980, coordinates: 05.8867° S, 36.2177° W) has dorsal scales in 17-17-15 rows, ventral scales 174, subcaudal scales 70, divided anal plate, eight supralabials, nine infralabials, dorsum with three dark lines from head to tail, 10 maxillary teeth, snout-vent length 323 mm, and tail length 106 mm; these characteristics match the species diagnosis presented by Hoge (1952a, b). The specimen was also successfully identified as *L. paucidens* by using the "key to species of *Liophis*" presented by Dixon (1989). This new record increases the number of snake species known for RN state to 48 (Marques et al. 2021). The only species of the genus *Lygophis* previously reported for RN state is *L. dilepis*, which differs morphologically from *L. paucidens* mainly for having 19 rows of dorsal scales (Hoge 1952a, b, Dixon 1989).

3. *Final considerations and conservation suggestions*

The Caatinga undergoes strong anthropic pressures throughout its extension. Habitat destruction, mainly through deforestation and fires, selective logging for domestic use and charcoal production, illegal hunting, mining, and more recently, renewable energy projects, have devastated the territory and biodiversity of this biome (Silva et al. 2017). In this context, the lowlands and plateaus of the Caatinga stand out as the most historically impacted areas, as they are easier to access by humans, housing the main urban centers in the region. These degrading processes made the highland regions of the Caatinga, known as "*serras*", become the most conserved areas of the biome (Pereira-Filho et al. 2017). Practices such as agriculture and livestock are not favored in these "*serras*", especially in the slopes, contributing to a landscape of still conserved vegetation. For instance, Pichorim et al. (2016) demonstrated that the highest richness values for birds in Serra de Santana remain in the slopes, followed by the plateaus and the lowlands, which are more impacted by human disturbances.

With respect to the herpetofauna, the mountain range present in the two priority areas sampled in this study harbors virtually all species found in nearby lowlands of the "sertaneja" depression of Rio Grande do Norte (e.g., Freire et al. 2009, Caldas et al. 2016), plus some relevant species because they are exclusively found in mesic areas of the Caatinga. This higher richness in the "*serras*" is due to a combination of more preserved habitats and milder climatic conditions due to altitude, which favors the occurrence of some species usually not found in nearby lowlands, such as the lizards *Anotosaura vanzolinia*, *Acratosaura mentalis*, *Enyalius bibronii* and *Diploglossus lessonae*.

Despite being one of the smallest states in Brazil, Rio Grande do Norte is the national leader in onshore wind energy, currently with about 6 gigawatts of installed power (source: *Agência Nacional de Energia Elétrica – ANEEL*). Accelerated action on modern renewable energy is a current global priority in the perspective of the Sustainable Development Goals of the United Nations 2030 Agenda (https://sdgs.un.org/2030agenda). However, the expansion of wind energy in northeastern Brazil has raised several socio-environmental issues (Gorayeb et al. 2019). Regarding biodiversity protection, the licensing of wind farms by state environmental agencies does not seem to be considering the national priority areas for conservation of biodiversity, as several projects are being licensed within these areas, which is the case of the Sites 3 and 4 sampled in this study.

Our results highlight the mountain range present in Serra de Santana and Nascente do Potengi priority areas for conservation of the Caatinga as a region with elevated herpetofauna richness. Considering that the "*serras*" are being chosen as preferred areas for installing wind projects, we reinforce the need for territorial planning in RN state to define sensitive areas from a natural and social point of view, define regions with the possibility of economic development, and define new protected areas, especially in the mountain ranges. Fortunately, a new protected area within Nascente do Potengi is being discussed by the environmental agency of Rio Grande do Norte state ("*Refúgio de Vida Silvestre Serra das Araras*"; IDEMA, *Portaria-SEI* No. 447/2022).

Supplementary Material

The following online material is available for this article:

Appendix S1 **-** List of voucher specimens from the sampled localities of this study housed at the Herpetological Collection of Universidade Federal do Rio Grande do Norte (UFRN-CH).

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Conflicts of Interest

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

Data Availability

The raw data of this study is available at <https://doi.org/10.48331/scielodata.B3WOXT>.

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Inventory

Entomogenous galls and their associated fauna in deciduous dry forest and woodland vegetation remnants (Caatinga) in the Northern *Depressão Sertaneja*, Brazil

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MARINHO, R.A., MAIA, V.C., BARBOSA, M.R.V. **Entomogenous galls and their associated fauna in deciduous dry forest and woodland vegetation remnants (Caatinga) in the Northern *Depressão Sertaneja*, Brazil**. Biota Neotropica 23(1): e20221428. https://doi.org/10.1590/1676-0611-BN-2022-1428.

Abstract: A survey and characterization of entomogenous galls and their associated fauna were carried out in six remnants of Caatinga in the Northern *Depressão Sertaneja*, in the states of Paraíba, Rio Grande do Norte and Ceará. We identified 41 gall morphotypes in 24 plant species, belonging to 12 botanical families. Fabaceae had 29.2% (n = 12) of the total number of gall morphotypes found. Leaves (61%) and stems (25%) were the most attacked organs. Most morphotypes are glabrous (75.6%), while only 24.4% exhibit trichomes. Most galls were induced by insects of the Cecidomyiidae family. The associated fauna comprised successors, cecidophages, tenants, and parasitoids. Sucessors were found in four morphotypes of galls and included spiders and four orders of insects: Hemiptera, Coleoptera, Lepidoptera, and Hymenoptera (Formicidae). The tenants were represented by *Tanaostigmoides* (Tanaostigmatidae). The parasitoids, found in 18 morphotypes (43.9%), were represented by six families of Hymenoptera. We recorded the occurrence of new types of galls in 12 species of host plants. These gall records are new references for the Northern *Depressão Sertaneja* in the studied states.
Keywords: *Caatinga; Cecidomyiidae; semi-arid; galls; morphotype; parasitoids.*

Galhas entomógenas e sua fauna associada em remanescentes de floresta seca e vegetação lenhosa decídua (Caatinga) na Depressão Sertaneja Setentrional, Brasil

Resumo: Realizou-se um levantamento e caracterização de galhas entomógenas e sua fauna associada em seis remanescentes de Caatinga presentes na Depressão Sertaneja Setentrional nos estados da Paraíba, Rio Grande do Norte e Ceará. Identificamos 41 morfotipos de galhas em 24 espécies de plantas, pertencentes a 12 famílias botânicas. Fabaceae abrigou 29,2% (n = 12) do total de morfotipos de galhas encontrados. As folhas (61%) e os caules (25%) foram os órgãos mais atacados. A maioria dos morfotipos é glabra (75,6%), enquanto apenas 24,4% exibiram tricomas. As galhas, em sua maioria, foram induzidas por insetos da família Cecidomyiidae. A fauna associada compreendeu sucessores, fungívoros, inquilinos e parasitoides. Os primeiros foram encontrados em quatro morfotipos de galhas, estando representados por aranhas e quatro ordens de insetos: Hemiptera, Coleoptera, Lepidoptera e Hymenoptera (Formicidae). Os inquilinos foram representados por *Tanaostigmoides* Ashmead, 1896 (Tanaostigmatidae). Já os parasitoides, encontrados em 18 morfotipos de galhas (43,9%), foram representados por seis famílias de Hymenoptera. Registramos a ocorrência de novos tipos de galhas em 12 espécies de plantas hospedeiras. Os registros de galhas também são novas referências para a Depressão Sertaneja Setentrional nos estados estudados.
Palavras-chave: *Caatinga; Cecidomyiidae; semiárido; galhas, morfotipo; parasitoides.*

Introduction

Some plants can undergo alterations in plant tissues, caused by parasitic insects, causing the formation of structures known as galls (Hartley 1998). Any organ of the host plant, regardless of its architecture, can have its tissue modified into a gall by a parasitic agent, which makes this association one of the most complex in the natural world (Shorthouse et al. 2005).

The emergence of galls is one of the most immediate responses of plants to the actions of gall-inducers and, therefore, it is a model capable of revealing important and quantifiable ecological patterns (Fonseca & Fleck 2007). Inside the gall, the immature forms of the insects receive protection against the effect of several abiotic factors, which vary in intensity according to the biome where they occur (Stone & Schönrogge 2003, Raman et al. 2005).

Among galling insects, the Cecidomyiidae (Diptera) present the highest radiation within the endophytic habit. They constitute a very diverse family, with ca. 6,500 described species (Gagné & Jaschhof, 2021), most of which are gall-inducing. Cecidomyiids establish complex trophic interactions with plants, symbiotic fungi, predators of larvae and parasitoids of their immature stages, making them important sources of ecological information (Stireman et al. 2010, Maia 2022).

The Cecidomyiidae appeared in the Cretaceous and intensely diversified in the Cenozoic (Gagné, 1989). Analyses of the feeding behavior in the Cecidomyiinae tribe suggest that the transition from ancestral fungus feeding to plant feeding occurred once or twice in its evolution (Dorchin et al. 2019). The colonization of plant tissues, galls, and leaf mines, dates from the Cretaceous, when fossil records of Cecidomyid bodies and insect-mediated damaged leaves were found (Srivastava et al. 2000).

Galls in the Caatinga biome began to be investigated only recently, with the first survey dating from 2011 (Santos et al. 2011). Currently there are data for the states of Ceará, Pernambuco, Alagoas, and Bahia (Carvalho-Fernandes et al. 2012, Costa et al. 2014b, Nogueira et al. 2016, Alcantara et al. 2017, Brito et al. 2018). However, the aspect that stands out about the occurrence of galls in this biome is the limited knowledge and the low number of inventories as compared to other Brazilian biomes such as the Atlantic Forest and Cerrado (Mendonça et al. 2008, Stehmann et al. 2009, Araújo et al. 2019). However, the Caatinga may have a galling fauna as relevant ecologically as have already been detected in the Cerrado (Gonçalves-Alvim & Fernandes. 2001, Araújo et al. 2013, Costa 2016) and in the Caatinga-Cerrado transition zones (Costa et al. 2014a, Nogueira et al. 2016).

The Brazilian Caatinga biome is considered one of the largest areas of the seasonally dry tropical forest and woodland biome (Pennington et al. 2001, Fernandes et al. 2020). It is composed of a mosaic of deciduous dry forests and woodland vegetation with thorns in Northeast Brazil. Veloso et al. (2002) divided the Caatinga into eight ecoregions reflecting differences in climatic seasonality, water availability (in soil and rainfall), relief, and geomorphology. According to them, the most typical Caatinga vegetation is found in the *Depressão Sertaneja*, the core region of the biome. It is divided by the Borborema Plateau in two ecoregions, the Northern and the Southern *Depressão Sertaneja*. The severe abiotic conditions, inherent to the Northern *Depressão Sertaneja*, make this Caatinga ecoregion unique for studies with galling insects, to find out variations in the occurrence of galls or even patterns of diversity.

In the present study, the Northern *Depressão Sertaneja* was selected to inventory, and characterize the occurrence of galls and their associated fauna.

Materials and Methods

1. *Study area*

The study area is the northern part of the *Depressão Sertaneja* (Figure 1). According to Veloso et al (2002), in this ecoregion, with a hot and semi-arid climate, rainfall is more scarce and concentrated than in the rest of the biome, with an annual average of 500 to 800 mm, and extremes as low as 350 mm/year. The soil is shallow, stony, of crystalline origin, with medium to high fertility, and very susceptible to erosion. Temperatures are high, with annual averages between 25 and 30 °C with only a few degrees of difference between the averages in the coldest and warmest months (Sampaio 2003). The predominant

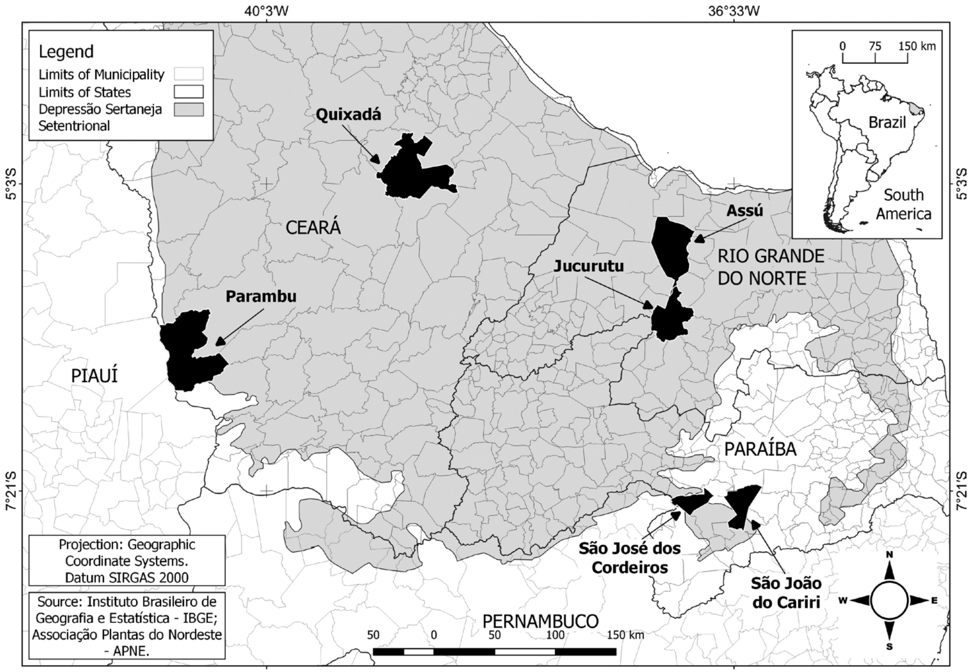

Figure 1. Location Map of the six study areas included in the Northern Depressão Sertaneja, Brazil. Map prepared by Maurício Oliveira dos Santos (2021).

vegetation physiognomy is shrub-tree, quite degraded, except in the few Conservation Units that still resist anthropic degradation.

In this region, six sites were selected: two in the state of Paraíba, both located in the Cariri Paraibano - The Experimental Station of the Federal University of Paraíba (EESJCariri), in the municipality of São João do Cariri, and the Private Natural Heritage Reserve (RPPN) Fazenda Almas (RPPN Almas), located in the municipality of São José dos Cordeiros; two in the state of Rio Grande do Norte - RPPN Stoessel de Brito (RPPN Stoessel), in the municipality of Jucurutu, and the National Forest of Açu (Flona), in the municipality of Açu; two in Ceará - the RPPN Olho d'água do Urucu, in the municipality of Parambu, and the RPPN Não me Deixes, in the municipality of Quixadá.

2. *Sampling*

The sampling of galls and host plants was conducted during two rainy seasons, from February to June 2019, and from February to May 2021, once per season at each site, totaling 9 months in the field. Due to the strong deciduousness of the vegetation during the dry season, the field work was conducted only in rainy seasons. In each area, 10 transects measuring 4 × 50 m, 100 meters apart from each other, were plotted. In each transect, for better orientation and surveying, a straight orientation line was plotted with the aid of a compass, and every 10 meters wooden stakes 1.20 m tall were inserted in the ground. Two people inspected the transects for at least one hour each seeking and collecting galls, for a total of 10 hours of minimum sampling effort per area. All trees, shrubs, and subshrubs inside the transect, with a minimum height of 1m and a maximum of 3 m, were inspected. All galls found were photographed in the field. The plants that had galls on leaves, or other visually identifiable organs, had their leaves and/or structures collected and stored in individual plastic bags with field identification. Subsequently, dried specimens of all species of plants collected were prepared and deposited at Herbarium JPB, at the Department of Systematics and Ecology of the Federal University of Paraíba (UFPB).

In the laboratory, the galls were separated by morphotype, and some samples of each morphotype were dissected under a stereomicroscope to verify the number of internal chambers, and obtain immature insect specimens, if present. These immatures were preserved in 70% ethanol and placed in labeled microtubes. The remaining samples were destined for the rearing of galling insects and possible associated fauna (parasitoids, predators, tenants, kleptoparasites, and successors). To this end, each gall morphotype was placed in labeled plastic pots lined with moistened paper (for species whose pupa matures in the gall) or containing soil from the area itself (for species whose pupa matures in the soil). The pots were inspected daily and each adult that emerged was captured using alcohol sprays with a plastic pipette. All specimens obtained from breeding in the laboratory were also preserved in 70% ethanol. The Cecidomyiidae (Diptera) were prepared and mounted on permanent microscopy slides (Gagné 1994) and identified at the Entomology Laboratory at the Rio de Janeiro National Museum (MNRJ). Gagné's keys (Gagné 1994) were used to identify the genera. For species identification, we used information from the host plant, gall morphotypes, and species descriptions. Micro-Hymenoptera were identified to the family and genus levels by Dr. Maria Antonieta Pereira de Azevedo (Collaborating Researcher, National Museum) using Gibson's key (Gibson 1997). Hymenoptera obtained only in the larval or pupal stage remained identified only to order. All insects were deposited in the Entomology collection of MNRJ.

The galls were characterized, in the laboratory, by color, shape, presence or absence of trichomes (hairy or glabrous), as well as the leaf surface on which they were found (adaxial, abaxial, both or intralaminar). To standardize the forms of the galls, we adopted the terminology of Isaias et al. (2013). Maximum specificity was considered in the separation of morphotypes so that similar galls on different plant species were classified as different morphotypes (Carneiro et al. 2009).

Results

A total of 2,796 plants, corresponding to 66 botanical species, were sampled in the six studied areas. Forty-one gall morphotypes were obtained on 24 plant species belonging to 12 botanical families (Table 1). Forty-two plant species (63,4%) did not present galls. Among the host plants, 23

Table 1. Characterization of insect galls in six areas of tropical dry forest **and woodland vegetation (Caatinga) in the Northern *Depressão Sertaneja*,** Northeastern Brazil. Legends: P = Parasitoid, S = Successor, T = Tenants, F = Fungivore; AL = RPPN Almas, FL = Flona de Açu, ND = RPPN Não me Deixes, OL = RPPN Olho do Urucu, SB = RPPN Stoessel de Brito, SC = EE São João do Cariri.

Family/ Species of host plants	**Galls**										
	Organ	**Leaf surface**	**Shape**	**Color**	**Trichomes**	**Occurrence**	**Chambers**	**Inductor Insect**	**Associated fauna**	**Site**	**Figure**
Anacardiaceae											
Spondias tuberosa Arruda	Stem	---	Fusiform	Gray	No	Isolated	various	Undetermined	Undetermined	AL	2-a
Bignoniaceae											
Handroanthus impetiginosus (Mart. ex DC.) Mattos	Stem	---	Fusiform	Gray	No	Grouped	various	Undetermined	Undetermined	ND	2-b
Handroanthus serratifolius (Vahl) S. Grose	Stem	---	Globoid	Green	No	Isolated	various	Cecidomyiidae	Tanaostigmatidae (T)/ Torymidae (P) (Hymenoptera)	FL	2-c

Continue...

...Continuation

Family/ Species of host plants	Galls										
	Organ	**Leaf surface**	**Shape**	**Color**	**Trichomes**	**Occurrence**	**Chambers**	**Inductor Insect**	**Associated fauna**	**Site**	**Figure**
Boraginaceae											
Cordia glazioviana (Taub.) Gottschling & J.S.Mill.	Leaf fold	Adaxial	Lenticular	Green	No	Isolated	one	Cecidomyiidae	Undetermined	OL	2-d
Varronia leucocephala (Moric.) J.S.Mill.	Leaf fold	Abaxial	Fusiform	Green	No	Isolated	one	Cecidomyiidae	Undetermined	AL	2-e
Burseraceae											
Commiphora leptophloeos (Mart.) J.B.Gillett	Bud	---	Fusiform	Green	Yes	Grouped	one	Undetermined	Hymenoptera (P)	AL	2-f
Capparaceae											
Cynophalla flexuosa (L.) J.Presl	Leaf fold	Adaxial	Lenticular	Green	No	Grouped	One	Undetermined	Undetermined	SB	2-g
Combretaceae											
Combretum leprosum Mart.	Stem	---	Fusiform	Green	No	Isolated	various	Clinodiplosini (Cecidomyiidae)	Galeopsomyia sp (P) Pteromalidae (P) Scelionidae (P) (Hymenoptera)	AL, ND	2-h
	Leaf fold	Adaxial	Globoid	Green	No	Isolated	one	Cecidomyiidae	Undetermined	AL	2-i
	Leaf fold	Intralaminar	Lenticular	Green	No	Isolated	one	Cecidomyiidae	Undetermined	ND	2-j
Euphorbiaceae											
Croton blanchetianus Baill.	Leaf fold	Adaxial	Globoid	Green	Yes	Isolated	one	Clinodiplosini (Cecidomyiidae)	Aranae (S)/ Hemiptera (S)/ Eulophidae (P)/ Galeopsomyia sp (P)/ Torymidae (P)/ Eurytomidae (P)/Scelionidae (P) (Hymenoptera)	AL, SJ, SB, FL, ND, OL	2-k
	Leaf fold	Adaxial	Globoid	Green	No	Isolated	one	Cecidomyiidae	Undetermined	AL	2-l
Croton adenocalyx Baill.	Stem	---	Fusiform	Yellow	No	Isolated	one	Undetermined	Undetermined	ND	2-m
Croton echioides Baill.	Leaf fold	Adaxial/ abaxial	Globoid	Green	Yes	Isolated	one	Cecidomyiidae	*Stomatosema sp* (F) Eulophidae (P)/ Eupelmidae (P) (Hymenoptera)	AL, OL	2-n
	Leaf fold	Intralaminar	Lenticular	Green	Yes	Isolated	one	Cecidomyiidae	Eulophidae (P) (Hymenoptera)	AL	2-o
	Stem	---	Fusiform	Green	No	Isolated	one	Cecidomyiidae	Hymenoptera (P)	AL	2-p
Manihot carthagenensis (Jacq.) Müll. Arg.	Leaf fold	Adaxial	Globoid	Green	No	Grouped	various	Cecidomyiidae	Eulophidae (P) (Hymenoptera)	AL	2-q
	Leaf fold	Adaxial	Clavate	Green	No	Isolated	one	Cecidomyiidae	Eulophidae (P) (Hymenoptera)	AL	2-r

Continue...

...Continuation

Family/ Species of host plants	Galls										
	Organ	Leaf surface	Shape	Color	Trichomes	Occurrence	Chambers	Inductor Insect	Associated fauna	Site	Figure
Manihot dichotoma Ule	Leaf fold	Adaxial	Clavate	Green	No	Isolated	one	Cecidomyiidae	Undetermined	SB, ND	2-s
Fabaceae											
Bauhinia cheilantha (Bong.) Steud.	Leaf Fold	Adaxial	Globoid	Green	Yes	Isolated	one	Undetermined	Undetermined	AL	2-t
	Leaf Fold	Adaxial	Globoid	Green	No	Isolated	one	Undetermined	Undetermined	SB	2-u
	Leaf Fold	Adaxial	Fusiform	Green	No	Isolated	one	Cecidomyiidae	*Eurytoma sp* (P)/ Hymenoptera (P)	AL, SB	2-v
	Vein	Abaxial	Globoid	Green	Yes	Isolated	one	Undetermined	Undetermined	SB	2-w
	Leaf Fold	Intralaminar	Lenticular	Green	No	Isolated	one	Undetermined	Undetermined	SB	2-x
Cenostigma pyramidale (Tul.) Gagnon & G.P. Lewis	Leaf fold	Adaxial	Lenticular	Green	No	Isolated	one	Undetermined	Undetermined	ND	3-a
	Stem	---	Globoid	Gray	No	Isolated	various	Undetermined	Formicidae (S)/ Hymenoptera (P)	AL, SJ, ND, OL, FL, SB	3-b
	Leaf fold	Intralaminar	Lenticular	Green	Yes	Isolated	one	Undetermined	Undetermined	AL	3-c
Desmodium tortuosum (Sw.) DC.	Leaf fold	---	Marginal roll	Green	No	Grouped	one	Contarinia sp (Cecidomyiidae)	Eulophidae (P)	SB	3-d
Geoffroea spinosa Jacq.	Leaf fold	adaxial	Globoid	Green	No	Isolated	one	Undetermined	Undetermined	SB	3-e
Mimosa tenuiflora (Willd.) Poir.	Peciole	---	Fusiform	Brown	No	Isolated	one	Undetermined	Undetermined	SB	3-f
	Stem	---	Fusiform	Black	No	Isolada	one	Undetermined	Undetermined	SB	3-g
Sapindaceae											
Allophylus quercifolius (Mart.) Radlk.	Stem	---	Fusiform	Green	Yes	Isolated	one	Undetermined	Undetermined	AL	3-h
Serjania glabrata Kunth	Stem	---	Fusiform	Green	No	Isolated	one	Undetermined	Undetermined	OL	3-i
	Leaf fold	Adaxial	Lenticular	Green	No	Isolated	one	Undetermined	Undetermined	OL	3-j
Solanaceae											
Capsicum parvifolium Sendtn.	Stem	---	Fusiform	Green	No	Isolado	various	Clinodiplosis sp (Cecidomyiidae)	Eulophidae (P)	AL	3-k
Verbenaceae											
Lantana camara L.	Leaf fold	Adaxial	Globoid	Green	Yes	Isolated	one	Schismatodiplosis lantanae (Cecidomyiidae)	Eulophidae (P) Hymenoptera / Hemiptera (S)	AL, ND	3-l
	Leaf fold	Intralaminar	Lenticular	Green	No	Isolada	one	(Clinodiplosini) Cecidomyiidae	Hymenoptera (P)	AL	3-m
	Stem	---	Fusiform	Green	No	Isolated	various	Clinodiplosini (Cecidomyiidae)_	Hymenoptera (P)	AL	3-n
	Leaf fold	adaxial	Conical	Green	No	Isolada	one	Undetermined	Undetermined	AL	3-o
Vitaceae											
Cissus decidua Lombardi	Stem	---	Globoid	Gray	No	Isolated	various	Undetermined	Coleoptera (S)/ Lepidoptera (S)/ Eulophidade (P)	AL	3-q

***New record**

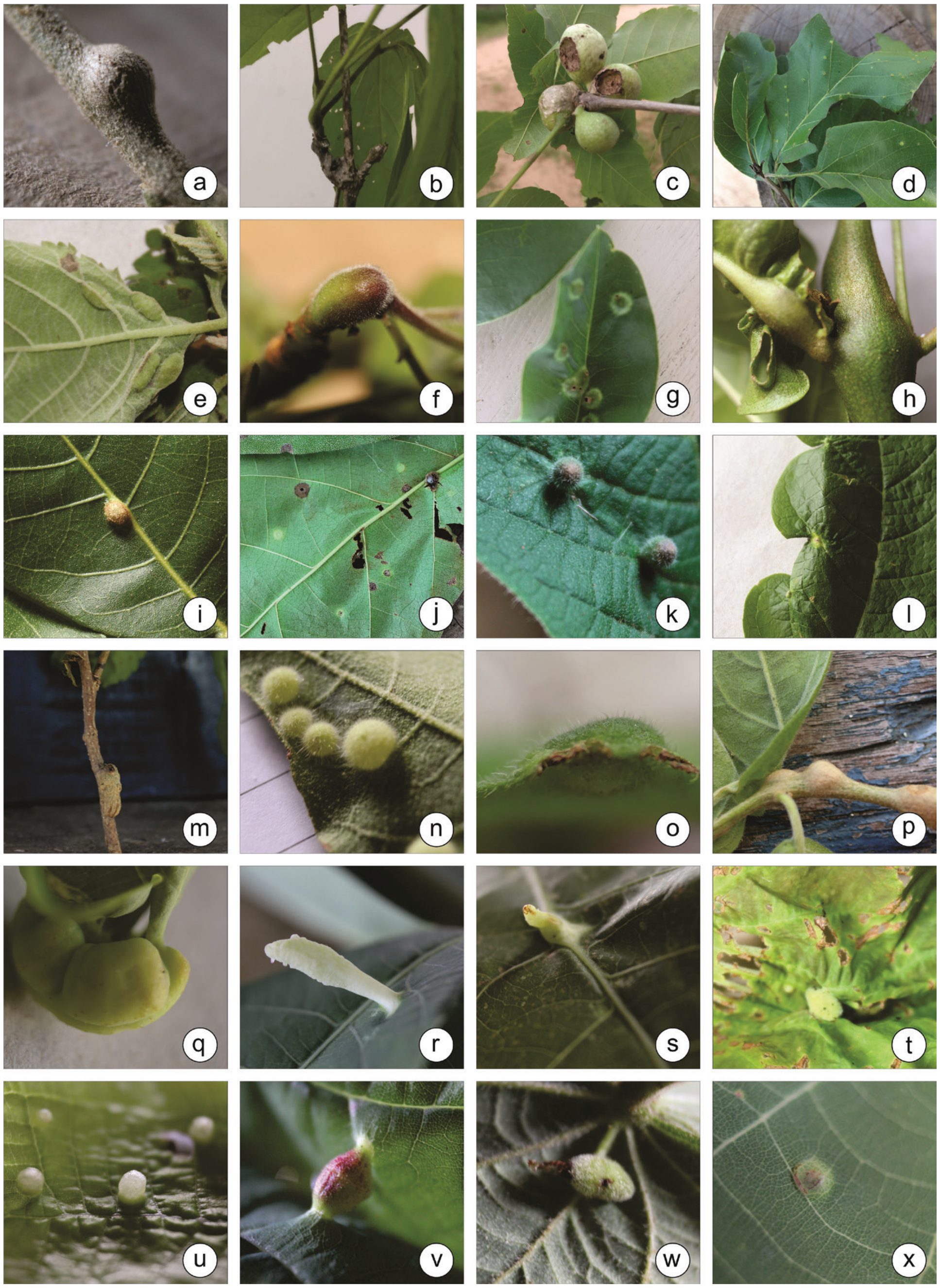

Figure 2. Galls found in six areas of Caatinga in the states of Ceará, Paraíba and Rio Grande do Norte, Brazil. a. In *Spondias tuberosa* - fusiform; b. In *Handroanthus impetiginosus* - fusiform; c. In *Handroanthus serratifolius* - globoid; d. In *Cordia glazioviana* - lenticular; e. In *Varronia leucocephala* - fusiform; f. In *Commiphora leptophloeos* - fusiform; g. In *Cynophala flexuosa* - lenticular; h-j. In *Combretum leprosum*: h. Fusiform, i. Globoid; j. lenticular; k-l. In *Croton blanchetianus*: k. globoid, l. globoid; m. In *Croton adenocalyx* - fusiform; n-p. In *Croton echioides*: n. Globoid, o. Lenticular, p. Fusiform; q-r. In *Manihot carthagenensis*, q. globoid, r. clavada; s. In *M. dichotoma* - clavate; t-x. In *Bauhinia cheilantha*: t. globoid, u. globoid, v. fusiform, w. globoid, x. lenticular. Sources: From the author (2019–2021).

are native and only *Lantana camara* L. is naturalized. Among the native species, six are endemic to the Caatinga: *Cenostigma pyramidale* (Tul.) Gagnon & G.P.Lewis; *Croton adenocalyx* Baill.; *C. blanchetianus* Baill.; *Manihot dichotoma* Ule; *Varronia leucocephala* (Moric.) J.S.Mill.; and *Spondias tuberosa* Arr. Others, endemic to Brazil but not to restricted to the Caatinga, also occur in the Cerrado, such as *Allophylus quercifolius* (Mart.) Radlk. and *Croton echioides* Baill. *Capsicum parvifolium* Sendtn. occurs in both the Caatinga and the Atlantic Forest.

The greatest richness of host plants was recorded in RPPN Almas, with 14 species distributed in 10 families. In the RPPN Olho do Urucu seven host species, belonging to five families, were identified. The EESJ Cariri presented the lowest richness, with only two species of host plants, in two botanical families (Table 1).

Fabaceae, Euphorbiaceae, and Verbenaceae had the greatest richness of host plants species, with Fabaceae harboring 29.2% (n = 12) of the total gall morphotypes found. *Bauhinia cheilantha* (Bong.) Steud.

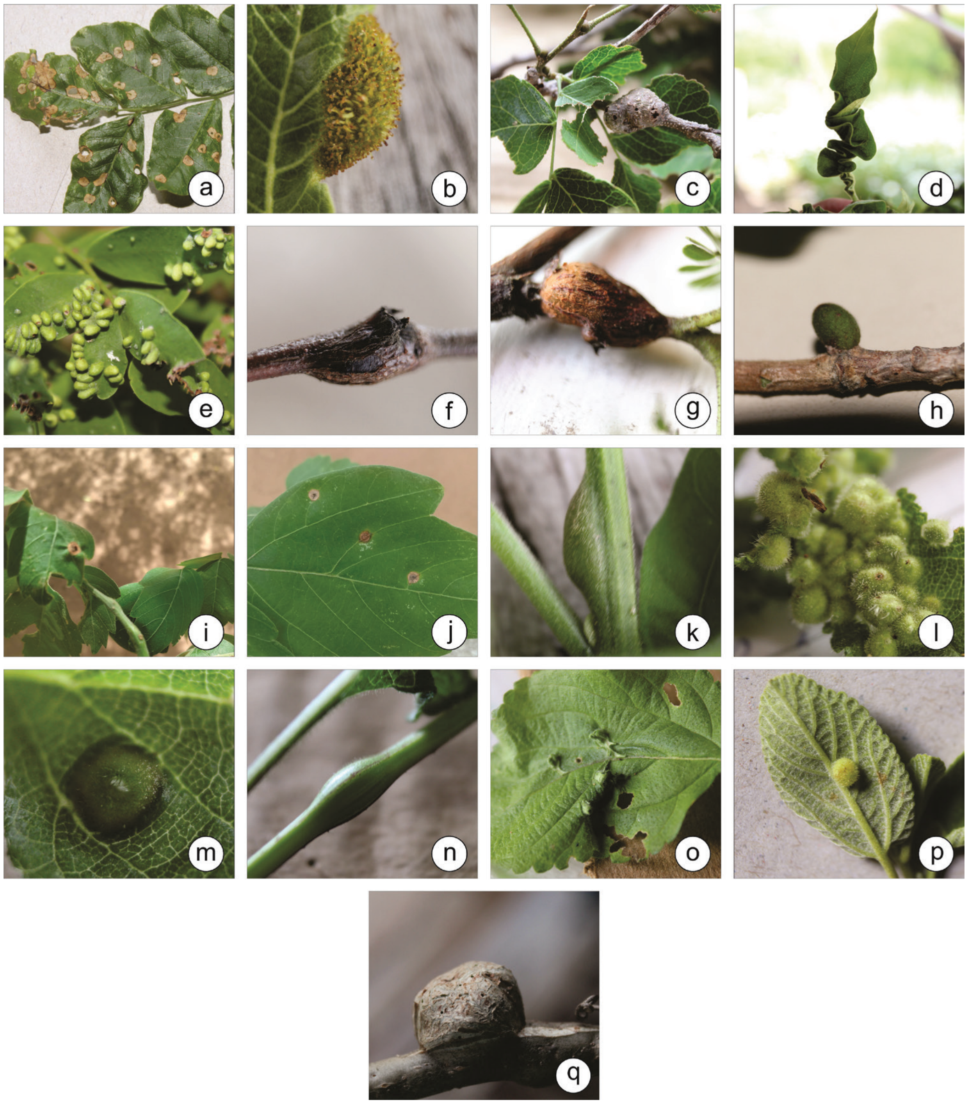

Figure 3. Galls found in six areas of Caatinga in the states of Ceará, Paraíba and Rio Grande do Norte, Brazil. a-c. In *Cenostigma pyramidale*: a. lenticular, b. Globoid, c. lenticular; d. In *Desmodium tortuosum* - marginal roll; e. In *Geoffroea spinosa* - globoid; f-g. In *Mimosa tenuiflora*; f. fusiform, g. fusiform; h. In *Allophylus quercifolius* - fusiform. i-j. In *Serjania glabrata*: i. Fusiform, j. fenticular; k. In *Capsicum parvifolium* - fusiform; l-o. In *Lantana camara*: l. globoid, m. lenticular, n. fusiform, o. conical; p. In *Lippia origanoides* - globoid; q. In *Cissus decidua* - globoid. Sources: From the author (2019–2021).

(Fabaceae) was the species with the highest gall richness, with five associated morphotypes, followed by *Lantana camara* (Verbenaceae) with four morphotypes. Therefore, these two species are indicated as super hosts. *Cenostigma pyramidale* and *Croton blanchetianus* were the only host species that occurred in all the six areas investigated. Leaves (61%) and stems (25%) were the most attacked organs.

Globoid and fusiform galls were the most frequent, each representing 34.1% of the total. Lenticular galls corresponded to 22%. Most morphotypes were glabrous (75.6%), while only 24.4% exhibited trichomes. The colors green (58.5%) and gray (9.7%) prevailed. However, we observed that the color of two morphotypes varied over time. The globoid morphotype present on the leaves of *Croton blanchetianus* varied from light green in the young stage to dark green or brown in its final stage. The clavate morphotype present on the leaves of *Manihot carthagenensis* (Jacq.) Müll.Arg., initially light green, later became red. Regarding the number of internal chambers, 32 morphotypes (78%) had a single chamber while only 9 (22%) had more than one.

Inducers of 21 morphotypes (51.21%) were identified at family level. The others were not identified, either because the galls were empty, or with parasitoids, or even with some immature whose life habits were not determined. Of four morphotypes (Figures 2h, 2k, 3m, 3n), only larvae of the tribe Clinodiplosini were obtained. Adult gallers were obtained from only three morphotypes, all belonging to Cecidomyiidae (Diptera). They were identified as: *Contarinia* sp. in *Desmodium tortuosum* (Sw.) DC. (Figure 3d); *Clinodiplosis* sp. in *Capsicum parvifolium* (Figure 3k); and *Schismatodiplosis lantanae* (Rübsaamen, 1916) in *Lantana camara* (Figure 3i). In addition to these, adults of *Stomatosema* emerged from galls on *Croton echioides* (Figure 2n), but that genus does not include galling species (Table 1) and they were considered as fungivores.

The associated fauna comprised successors, fungivores, tenants, and parasitoids. Successors, represented by spiders and four orders of insects - Hemiptera (one morphospecies), Coleoptera (one morphospecies), Lepidoptera (one morphospecies), and Hymenoptera (Formicidae - two morphospecies), were found in four morphotypes of galls. The tenants were represented by *Tanaostigmoides* Ashmead, 1896 (one morphospecies) (Tanaostigmatidae). The parasitoids, found in 18 morphotypes of galls (43.9%), were represented by six families of Hymenoptera: Eulophidae (five morphospecies), Scelionidae (one), Eupelmidae (one), Eurytomidae (one), Torymidae (one) and Pteromalidae (one).

Parasitoids were found in globoid, fusiform, lenticular, and leaf fold galls, and were more frequent in globoid (57.1%) and fusiform (42.8%) galls. Eight families of plants hosted parasitoids and, among them, Fabaceae, Euphorbiaceae, and Verbenaceae together represented 37.5% of the records. Other parasitoids were found in other gall morphotypes but, as only larvae were obtained, they could not be separated into morphospecies. The successors were found only in globoid galls, in hosts representing four botanical families, Euphorbiaceae, Fabaceae, Verbenaceae, and Vitaceae, and were more diverse in Euphorbiaceae and Vitaceae.

Parasitoids were mainly obtained from galls on leaves (55.5%) and stems (38.9%). Of the total number of leaf galls, 37.5% of them were parasitized. Likewise, 53.8% of galls on the stems were parasitized. Successors were obtained from two morphotypes of leaf galls and two morphotypes of stem galls, at frequencies below 9% of the total number of galls on these organs.

Of the total number of unilocular galls (32), 11 had parasitoids (34.4%) and two harbored successors (6.25%). Regarding the total number of multilocular galls (9), 7 galls contained parasitoids (77.8%), and 2 exhibited successors (22.2%). The occurrence of parasitoids was observed in all the six areas investigated. RPPN Almas had the highest number of parasitized galls (66.7%).

Intense occurrence of multiparasitism was observed in globoid leaf galls of *Croton blanchetianus* and *Lantana camara*, both with two wasp morphospecies. On the other hand, the presence of more than one inquiline taxon was recorded in globoid leaf galls of *Croton blanchetianus* and globoid stem galls of *Cissus decidua* Lombardi.

Since this is the first inventory of galls and their host plants carried out in areas of the *Depressão Sertaneja* in the states of Paraíba and Rio Grande do Norte, all records are new for these states. For the state of Ceará, all records are new, except the morphotypes that occur in *Croton blanchetianus* (Figure 2k and 2i) and *Combretum leprosum* Mart. (Figure 2h), already registered in a previous study (see Alcantara et al. 2017). We also registered the occurrence of new types of galls in 12 species of host plants, represented in the following illustrations: (Figures 2 - 2a, 2b, 2c, 2d, 2f, 2j, 2q) and (Figures 3 - 3d, 3e, 3h, 3j, and 3q).

Discussion

When comparing our results with the first gall inventory carried out in the Caatinga (Santos et al. 2011), we can observe differences in the richness of gall morphotypes, the composition of host plants, and the associated fauna. However, regarding the presence of parasitism in certain plant families, the results are similar. Santos et al (2011) inventoried eight areas in the state of Pernambuco, included in both the Southern *Depressão Sertaneja* and Borborema Plateau ecoregions, including Vale do Catimbau National Park and two state parks. They found 64 morphologically distinct types of insect galls in 48 species of host plants, belonging to 31 genera and 17 families. In our research, we found 41 gall morphotypes in 24 plant species, and 12 host families. The variation in morphotype richness may be partially associated with differences in floristic composition in the Northern and Southern *Depressão Sertaneja* ecoregions. In addition, Santos et al. (2011) adopted the random walk method (Fernandes & Negreiros 2006; Coelho et al. 2009, Silva et al. 2015), while we established systematically distributed transects as a way of minimizing interference of walking through more accessible or already open places.

According to Araujo et al. (2019) the total richness of gall-inducing insects differs among sampling sites of different Brazilian regions and biomes. For Fernandes and Price (1988), factors such as latitude, elevation, temperature, and humidity strongly influence the diversity and distribution of galling species in the world. Therefore, variations in morphotypes and gall-inducing insects' richness among ecoregions should be expected.

Within a single ecoregion, Carvalho-Fernandes et al. (2012) found 25 morphotypes of galls distributed in 18 host species in areas in the Southern Depressão Sertaneja, in the state of Alagoas. Their results revealed patterns like ours and those found by Santos et al. (2011). Fabaceae, the family with the greatest richness in our study, was also the richest in theirs, with eleven morphotypes. In another study in the same ecoregion, Alcântara et al. (2017) recorded only three host plants and 12 gall morphotypes. In that case, the low number of morphotypes may have been a consequence of the authors having established only three random plots of 10 m².

Our data indicated Fabaceae as the family with the most galled species, which allows us to say that it constitutes a super host taxon for galling insects (Santos-Silva, & Araújo, 2020). Carvalho-Fernandes et al. (2012) and Alcântara et al. (2017) presented a similar result to ours, indicating Fabaceae as the main host family. Fabaceae is the most species-rich family in the Caatinga, occupying the second position in the Atlantic Forest, Cerrado, and Pantanal (Brazil Flora Group 2015). This high diversity and its prominence in relation to the number of gall host species and morphotypes were also recorded in other biomes such as the Cerrado (Gonçalves-Alvim and Fernandes 2001), Pantanal (Ascendino and Maia, 2018), Atlantic Forest and Chaco (Urso-Guimarães et al. 2017). According to Gagné (1994), Fabaceae stands out as the family with the greatest richness of galls related to Cecidomyiidae in the Neotropical region. Since Fabaceae is the most species-rich family in the semi-arid region of Brazil (Queiroz et al. 2006, BFG 2015, Fernandes et al. 2020), the present study adds evidence in favor of the taxon size hypothesis, which predicts that the richness of gall morphotypes is greater in plant families with a greater number of species (Veldtman & McGeoch, 2003; Mendonça Júnior 2007).

Our data also reveals a higher colonization in Euphorbiaceae. The occurrence of galled individuals of *Croton blanchetianus* in all studied areas indicates oviposition preference on this species. *C. blanchetianus* is considered a pioneer, frequent in places that are recovering after environmental changes, with a great capacity of regrowth during the rainy season, even after being cut by man (Maia, 2004). The relationship between oviposition preference and performance of immature forms ingalling tissues can help understanding the evolution of interactions between herbivorous insects and their host plants (Thompson & Pellmyr 1991). Most plant families with non-galled species may suggest the presence of intrinsic mechanisms of herbivory resistance in them. Also, the presence of more tolerant plant species in the environment may induce changes in the target plant by galling insects, influencing the distribution and concentration of consumer species within habitats (Gaillard et al., 2010).

The prevalence in our study of gall induction on leaves confirms the worldwide pattern observed since Felt (1940) and Mani (1964), and reinforced in previous inventories carried out in the Caatinga (Santos et al, 2011; Costa et al, 2014; Brito et al, 2018). As a general pattern, the globoid and fusiform morphotypes stood out as the most frequent. According to Isaias et al (2013), gall inventories in the Neotropical region pointed to globoid galls as the predominant morphotype.

Cecidomyiidae (Diptera) were the most frequent inducers in our study, as verified in previous surveys carried out in Brazil (Julião et al. 2002; Urso-Guimarães & Scareli-Santos, 2006; Luz et al. 2012, Maia & Siqueira, 2020). Thus, our results reinforce previous results and corroborate the hypothesis of Gagné and Jaschhof (2021), which points out Cecidomyiidae as the family with the greatest diversity of galling insects in the world.

In our study area, 78% of the galls did not present trichomes on their external surface. This result can be attributed to particular characteristics of semi-arid regions, where the urgent need of the galling insect to defend itself from the action of parasitoids may have led to evolutionary pressures reinforcing the gall structure to the detriment of the presence of external trichomes. Although we did not assess this defensive role, the reported defense strategy may be applied, since a more intense attack by multiple parasitoids was verified in globoid leaf galls with trichomes. According to László et al (2014), larvae of inducers in smaller galls, with thinner walls, face the action of parasitoids more frequently, as they are closer to their ovipositors, thus becoming less secure. The presence of trichomes in the gall would have a better function in maintaining temperature and humidity, fundamental factors for the establishment and development of galls (Woodman & Fernandes 1991; Fernandes, 1994; Oliveira et al. 2006).

Almost all morphotypes in our study were one-chambered, which is also in line with previous results on gall diversity in the Caatinga (Brito et al. 2018) and other biomes in Brazil, such as the Cerrado (Gonçalves-Alvim & Fernandes, 2001) and the Atlantic Forest (Fernandes et al., 2009). Regarding color, most galls were similar in color to the organ of the attacked plant, with a predominance of green on the leaves, as already observed by several authors (Bregonci et al., 2010; Santos et al., 2011, Bergamini et al. 2017, Ascendino & Maia 2018).

As for the associated fauna, Eulophidae, Eurytomidae, Braconidae, Eupelmidae, and Pteromalidae have already been recorded as parasitoids of galling insects in Brazil (Maia & Tavares 2000, Maia & Azevedo 2009, Bergamini et al 2017). In this sense, our data reinforce that the parasitoid guild is more frequent and diverse than the tenant and successor guilds (Maia & Siqueira, 2020). However, in *Cissus decidua* Lombardi, three orders were found (Coleoptera, Lepidoptera, and Hymenoptera), forming three new associations of successors in the Caatinga. Eulophidae was the most frequent parasitoid family in our study, as previously verified by Maia and Azevedo (2009) in the restinga.

The occurrence of Micro-Hymenoptera in several galls evidences the formation of a "plant-galler-parasitoid" tritrophic system (Araujo & Maia, 2021). However, there is a need for further investigation on the status of the Micro-Hymenoptera collected, since these organisms constitute a diverse taxon, of great importance for studies of interaction with galling insects. Many galling insects, originating from hosts with less galls, could not be identified due to the intense attack of micro-Hymenoptera, which prevented the emergence of adults from the galls. This fact is recognized in the literature as one of the biggest obstacles to the success of taxonomic identification of galls (Maia et al. 2008).

According to Maia (2001), galls represent an important micro-habitat, where several trophic relationships are established. In the restinga areas of Rio de Janeiro, Maia and Azevedo (2009) found that the vast majority of microhymenopterans were parasitoids, but some of them, for example, the Tanaostigmatidae and some species of Torymidae and Eulophidae were gall tenants. According to Carvalho-Fernandes et al (2016), some species of Micro-Hymenoptera are found, as parasitoids, in galls induced by Cecidomyiidae, or even as phytophagous tenants, capable of altering the physical structure of galls. These results reinforce the need to elucidate and separate the role of parasitism and inquilinism in the plant-galler interaction observed in our results.

Price (2005) reported that many invertebrate organisms may be associated with galls. These organisms include predators, tenants, or successors, and are represented by many taxa, such as Acari, Collembola, Hymenoptera, Coleoptera, Lepidoptera, Thysanoptera, Diptera, Hemiptera, and Psocoptera (Bregonci et al., 2010).

In addition to the presence of parasitoids, many gall inducers in our work could not be identified, at the genus or species level, due to the absence of the male or female adult, as well as the stages of a complete series (larva, pupa, or pupal exuvia and adults), necessary for their identification. We point out the removal of leaves from the host plants, for gall sampling and insect rearing, as a factor that makes it difficult to obtain these individuals, since cutting off the flow of nutrients to the gall can make the development of the insect unfeasible.

Conclusions

There is a moderate occurrence of gall morphotypes in the Northern *Depressão Sertaneja* Ecoregion. Results from previous studies, which recorded the Cecidomyiidae family as the main gall-inducing group in the Caatinga, were confirmed, as well as the high rate of parasitism by Hymenoptera.

Fabaceae was confirmed as the family with the highest number of galled species, an already recognized pattern. However, we recorded new associations between host plant species, their galls, and successors, expanding the knowledge about galls in the caatinga.

The presence in the RPPNs of several plant species endemic to the Caatinga, for which new gall records were registered in our study, indicates the importance of preserving these areas for the galling insect community. The new associations registered here highlight the importance of inventories to provide information about the richness and diversity of galls in Brazil.

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Conflicts of Interest

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

Ethics

This study did not involve human beings and/or clinical trials that should be approved by one Institutional Committee.

Data Availability

The datasets generated during and/or analyzed during the current study are available at: https://doi.org/10.48331/scielodata.IREBGF.

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Article

Ichthyofauna of the Nascentes do Rio Parnaíba National Park: watershed divide in the main agricultural encroachment area in the Brazilian Cerrado

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Abstract: The Nascentes do Rio Parnaíba National Park (NPNP), located in Brazilian Cerrado, protects portions of three river basins: headwaters of Parnaíba, a small portion in upper Tocantins-Araguaia, and tributaries of the middle section of the São Francisco. This protected area is in the boundaries of the states of Maranhão, Tocantins, Piauí, and Bahia, also known as MATOPIBA, a region that has established rapid agricultural expansion associated to land conflicts between corporate agriculture, family agriculture, protected areas, indigenous territories, and quilombola communities. The knowledge of the ichthyofauna in this region is scarce while the impacts on the aquatic environments are increasing. We made a survey of fishes in the NPNP and its surroundings areas, estimating richness, endemics, introduced and shared species between river basins. During 2014, 54 sampling sites were visited, 19 in the NPNP and 35 in the surrounding area. Ninety-five species, 51 genera, 22 families, and six orders were recorded, of which 38 (40%) are in the NPNP. One introduced species were recorded in the Parnaíba River basin and no endangered species were registered. Our data corroborate the importance of the network of protected areas for the preservation of Cerrado fishes, including some possibly undescribed and restricted-range species that may be threatened due to intense agricultural encroachment in the MATOPIBA region.

Keywords: *MATOPIBA; Tocantins-Araguaia River; headwaters, Cerrado fishes; conservation unit.*

Ictiofauna do Parque Nacional Nascentes do Rio Parnaíba: um divisor de bacias hidrográficas na principal área de expansão agrícola do Cerrado Brasileiro

Resumo: O Parque Nacional Nascentes do Rio Parnaíba (PNNP), localizado no Cerrado brasileiro, protege diferentes porções de três bacias hidrográficas, as cabeceiras do Parnaíba, uma pequena porção do alto rio Tocantins e tributários do trecho médio do São Francisco. Esta área protegida está localizada nos limites dos estados do Maranhão, Tocantins, Piauí e Bahia, também conhecida como MATOPIBA, região que tem apresentado rápida expansão agrícola associada a conflitos fundiários do agronegócio com agricultura familiar, áreas protegidas, territórios indígenas e comunidades quilombolas. O conhecimento da ictiofauna nessas regiões é escasso, embora os impactos sobre os ecossistemas aquáticos sejam crescentes. Assim, elaboramos um levantamento de peixes do PNNP e em seu entorno, identificando a riqueza, espécies endêmicas, introduzidas e compartilhadas entre bacias hidrográficas. Durante o ano de 2014 foram visitados 54 locais de amostragem, 19 no PNNP e 35 no entorno. Foram coletadas 95 espécies, 51 gêneros, 22 famílias e seis ordens, das quais 38 espécies (40%) estão no PNNP. Uma espécie introduzida foi registrada na bacia do rio Parnaíba e nenhuma espécie ameaçada de extinção foi registrada. Os dados aqui apresentados corroboram a importância da rede de áreas protegidas para a preservação dos peixes do Cerrado, com espécies potencialmente novas e de distribuição restrita, que podem estar ameaçadas devido à intensa expansão agrícola na região do MATOPIBA.

Palavras-chave: *MATOPIBA; rio Tocantins-Araguaia; cabeceiras; peixes do Cerrado; unidade de conservação.*

Introduction

The Cerrado is a tropical woodland-savannah in central Brazil under intense anthropogenic pressure, with land conflicts and high deforestation rates, which have been increasing since the 1990s. It possesses a high level of endemism and is considered a global hotspot for biodiversity conservation (Myers et al. 2000, Strassburg et al. 2017). Thenceforth, approximately 50% of its area was transformed into agricultural areas or pastures (Beuchle et al. 2015), with the loss of natural landscapes approximately 47% larger than in the Amazon rainforest in the same period (Carvalho et al. 2019). Among the most intensely impacted areas is the MATOPIBA, an acronym formed by the initials of the Brazilian states of Maranhão, Tocantins, Piauí and Bahia, one of the main areas of agricultural expansion in Brazil, based on high technology productivity of vast soybean and corn plantations (Miranda et al. 2014, Lopes et al. 2020).

Despite the biological importance and the historical deforestation, when compared with other Brazilian biomes, few conservation units are in the Cerrado, protecting less than 10% of its original area. Among the federal protected areas, are the Ecological Station Serra Geral do Tocantins (7,163 km²), Araguaia National Park (5,577 km²), Chapada dos Veadeiros National Park (2,406 km²), Serra das Confusões National Park (8,234 km²), and Nascentes do Rio Parnaíba National Park (NPNP) (7,498 km²). This latter is located on the boundaries of the MATOPIBA states, encompassing three hydrographic basins and freshwater ecoregions, the Parnaíba, Tocantins-Araguaia, and São Francisco rivers (sensu Abell et al. 2008, Brasil 2019) (Figure 1). The NPNP and surrounding areas are considered of great importance for the conservation of Cerrado's biodiversity, given the advance of deforestation due to cash crops and cattle raising (Carvalho et al. 2019).

The Cerrado contributes to 43% of Brazil's surface water, outside the Amazon region (Strassburg et al. 2017), comprising headwaters from at least five hydrographic basins: Amazon, Tocantins-Araguaia, São Francisco, Paraná-Paraguay, and Parnaíba rivers (Lima & Silva 2005, Abell et al. 2008). The knowledge of fish diversity in these drainages is heterogeneous, varying among them and along different stretches of the same basin, usually reflecting the distance from research institutions (Langeani et al. 2009, Dagosta & de Pinna 2019). The richness of fish species in the Cerrado drainages is estimated in approximately 1,200 species (Klink & Machado 2005).

Recent fish surveys in the Parnaíba, São Francisco, and Tocantins-Araguaia river basins were carried out by Lima & Caires (2011), Ramos et al. (2014), Lima et al. (2017), Bartolette et al. (2017), Silva et al. (2020a, b), and Chamon et al. (2022). However, the ichthyofauna of the headwaters of the upper Parnaíba and middle São Francisco basins were not fully explored (Ramos et al. 2014, Melo et al. 2016, Lima et al. 2017, Barbosa et al. 2017, Silva et al. 2020a, b). Among the studies encompassing the upper Parnaíba, Silva et al. (2015) recorded 90 species in the Gurgueia River (about 60% of the drainages' richness), with 34 endemic and six new records in the basin, including localities in the vicinity of the NPNP.

Few ichthyological studies focused on the Tocantins and São Francisco River basins in the MATOPIBA region. The most important was conducted by Lima & Caires (2011) at the Serra Geral do Tocantins Ecological Station and surrounding areas, encompassing headwaters of both drainages, including a shared one (known in Portuguese as 'águas emendadas'). As evidence of the exchange of fish species through this natural connection, Lima & Caires (2011) reported the presence of two species that have unequivocally traversed this common headwater, the characin *Astyanax novae* Eigenmann 1911 and the cichlid *Cichlasoma sanctifranciscense* Kullander 1983.

As many Cerrado drainages from the region, the MATOPIBA rivers are threatened by the deforestation of riparian vegetation, the input of fertilizers and pesticides from nearby agriculture areas, and the construction of dams (ICMBio 2018, Latrubesse et al. 2019, Chamon et al. 2022). A mosaic of federal and private Protected Areas (PAs) in MATOPIBA encompass several tributaries of one of the largest and least known PAs of the Cerrado (Nogueira et al. 2011, ISA 2015). Thus, this study aimed to inventory the ichthyofauna in the drainages that are protected by the NPNP and its surroundings areas. With this, we intend to expand the knowledge of the fish diversity of the headwaters of the upper Parnaíba and Tocantins drainages and middle São Francisco River basins in the MATOPIBA region that is a knowledge gap presenting high vulnerability due to the intense agricultural expansion.

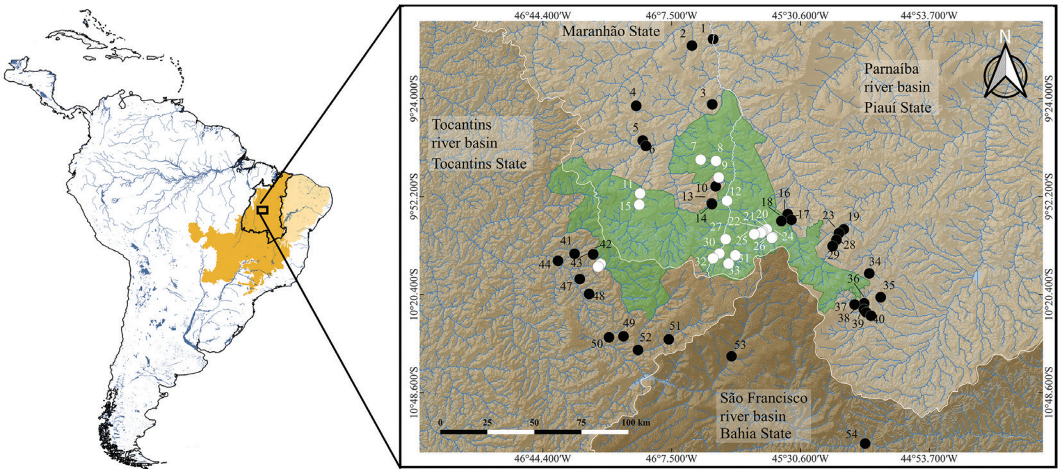

Figure 1. Sampling sites in the Nascentes do Rio Parnaíba National Park (NPNP) and surroundings in MATOPIBA (black line) in the Brazilian Cerrado (orange). White dots, sampling sites in the NPNP; black dots, sampling sites outside of the NPNP. The sites in Maranhão (MA) e Piauí (PI) states flow to Parnaíba River basin, those in Tocantins (TO) to Tocantins River basin and, those in Bahia (BA) to São Francisco River basin.

Material and Methods

1. *Study area*

The studied area encompasses the headwaters of the upper Parnaíba River, and tributaries of the upper Tocantins (sensu Dagosta & de Pinna 2019) and middle of the São Francisco river basins located in the NPNP and vicinities (Figure 1). The park has an extension of 7,497.74 km^2, and is situated in the boundaries of Maranhão (MA), Piauí (PI), Tocantins (TO), and Bahia (BA) states and nine municipalities, Alto Parnaíba (MA), Lizarda (TO), Mateiros (TO), São Félix do Tocantins (TO), Barreiras do Piauí (PI), Corrente (PI), Gilbués (PI), São Gonçalo do Gurgueia (PI) and Formosa do Rio Preto (BA).

Entirely inserted in the Cerrado biome, temperatures in the NPNP region vary between 20 °C and 32 °C, with rainfall concentrated from October to March (MMA 2019, Macena et al. 2008). The relief presents the Chapada das Mangabeiras as its main geological formation, which interconnects with the Urucuia Formation, known for its sandstone composition and high soil permeability. These characteristics enable the formation of headwaters in the foothills, in addition to waterfalls and rapids which make up watercourses that later consolidate the drainages in the region (Brasil 2019).

The Parnaíba River headwaters are situated at the foothills of the Chapada das Mangabeiras, which is formed from numerous springs of the Água Quente (between PI and MA), Curriola, and Lontra rivers (PI). To the south of the Chapada das Mangabeiras, at the northern limit of NPNP, are the headwaters of the Sono River, a tributary of the upper Tocantins river basin. The southeast portion of the NPNP (BA) drains the São Francisco river basin, forming the Sapão River, one of the headwaters of the Preto River. However, the headwaters of the Sapão River (São Francisco) and the Galheiros River (Novo River, tributary of the Tocantins River), the region of 'águas emendadas', is situated outside the NPNP according to the shapefiles of the Agência Nacional de Águas e Saneamento Básico (ANA 2021) and federal conservation units by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio 2018).

2. *Collection and identification*

The collections were carried out in June 2014 at 54 sampling sites distributed in the São Francisco (2), Parnaíba (40), and Tocantins (12) river basins (Table 1, Figure 2), under permits n° 20088/2014 and 30532/2011 issued by the ICMBio/SISBIO. The effort for the collection followed the AquaRAP approach (Rapid Assessment

Table 1. Sampling sites in Nascentes do Rio Parnaíba National Park (NPNP) and surroundings. (P) sampling in the Park. BA, Bahia; MA, Maranhão; PI, Piauí; TO, Tocantins.

ID	River basin	Sampling sites	Geographic coordinates
1	Parnaíba	Parnaíba River, Alto Parnaíba, MA	09°06'54.3"S 45°55'37.8"W
2	Parnaíba	Brejinho Stream, road between Alto Parnaíba and Morrinhos, Alto Parnaíba, MA	09°08'46.4"S 46°01'41.8"W
3	Parnaíba	Unnamed stream between Taboca and Alto Parnaíba, Alto Parnaíba, MA	09°25'40.1"S 45°55'53.4"W
4	Parnaíba	Unnamed stream near Morrinhos, Alto Parnaíba, MA	09°26'05.8"S 46°17'39.7"W
5	Parnaíba	Unnamed stream between Morrinhos and Bonfim, Alto Parnaíba, MA	09°36'04.5"S 46°15'47.6"W
6	Parnaíba	Parnaibinha River, road between Morrinhos and Bonfim, Alto Parnaíba, MA	09°37'37.0"S 46°14'54.3"W
7	Parnaíba $^{(P)}$	Parnaíba River, Taboca rapids, Alto Parnaíba, MA	09°41'34.2"S 45°59'12.5"W
8	Parnaíba $^{(P)}$	Unnamed stream between Castelo and Taboca, Alto Parnaíba, MA	09°41'57.2"S 45°54'48.3"W
9	Parnaíba	Unnamed stream, Castelo village, Alto Parnaíba, MA	09°46'41.3"S 45°54'01.7"W
10	Parnaíba	Unnamed stream between Curupá and Castelo, Alto Parnaíba, MA	09°49'16.2"S 45°54'53.7"W
11	Parnaíba $^{(P)}$	Unnamed stream tributary of Riozinho river, Alto Parnaíba, MA	09°51'18.2"S 46°16'32.8"W
12	Parnaíba $^{(P)}$	Parnaíba River, near bridge in NPNP, Alto Parnaíba, MA	09°53'24.3"S 45°51'37.6"W
13	Parnaíba	Angico Stream (Curupá marsh), Alto Parnaíba, MA	09°54'08.4"S 45°56'03.5"W
14	Parnaíba	Stream in Curupá (Sumidor marsh), Alto Parnaíba, MA	09°54'21.6"S 45°55'57.9"W
15	Parnaíba $^{(P)}$	Unnamed stream tributarty of Riozinho river, Alto Parnaíba, MA	09°54'31.5"S 46°16'47.4"W
16	Parnaíba	Uruçuí-vermelho River, Prata village, Barreiras do Piauí, PI	09°57'14.7"S 45°34'15.2"W
17	Parnaíba	Uruçuí Vermelho River, near Alto Alegre (Quebra-Bunda), Barreiras do Piauí, PI	09°58'53.0"S 45°33'11.7"W
18	Parnaíba $^{(P)}$	Temporary pond in Curicaca, near Prata village, Barreiras do Piauí, PI	09°59'13.5"S 45°36'04.6"W
19	Parnaíba	Gurgueia River, under bridge on highway BR-135, São Gonçalo do Gurgueia, PI	10°01'37.1"S 45°18'12.4"W
20	Parnaíba $^{(P)}$	Atoleiro marsh, Barreiras do Piauí, PI	10°01'37.4"S 45°40'16.0"W
21	Parnaíba $^{(P)}$	Porto marsh, Barreiras do Piauí, PI	10°02'17.1"S 45°41'30.6"W
22	Parnaíba $^{(P)}$	Lontras River in NPNP, Barreiras do Piauí, PI	10°02'36.2"S 45°41'56.1"W
23	Parnaíba	Gurgueia River, Corrente, PI	10°02'41.6"S 45°19'33.6"W
24	Parnaíba $^{(P)}$	Fortaleza marsh, Barreiras do Piauí, PI	10°03'52.2"S 45°38'35.1"W
25	Parnaíba $^{(P)}$	Madeiro marsh, Barreiras do Piauí, PI	10°03'00.3"S 45°43'51.2"W
26	Parnaíba $^{(P)}$	Fortaleza lagoon, Barreiras do Piauí, PI	10°04'04.4"S 45°38'47.4"W
27	Parnaíba $^{(P)}$	Marsh, upstream confluence of Corriola and Água Quente rivers, Barreiras do Piauí, PI	10°04'27.0"S 45°52'01.7"W
28	Parnaíba	Headwaters of Gurgueia River, São Gonçalo do Gurguéia, PI	10°04'38.8"S 45°20'18.2"W
29	Parnaíba	Gurgueia River, Araras Park, Corrente, PI	10°06'27.0"S 45°21'24.0"W
30	Parnaíba $^{(P)}$	Parnaíba River, downstream confluence of Pintado and Água Quente rivers, Barreiras do Piauí, PI	10°08'35.4"S 45°53'50.7"W

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ID	River basin	Sampling sites	Geographic coordinates
31	Parnaíba (P)	Curriola River, under bridge, Barreiras do Piauí, PI	10°09'06.4"S 45°49'15.0"W
32	Parnaíba (P)	SussuaparaWaterfall, Sussuapara River, tributary of Água Quente River, Barreiras do Piauí, PI	10°09'56.7"S 45°55'39.1"W
33	Parnaíba (P)	Pintado Waterfall, tributary of Água Quente River, Barreiras do Piauí, PI	10°11'28.9"S 45°51'12.9"W
34	Parnaíba	Pond at the margins of highway BR-135, Corrente, PI	10°14'19.4"S 45°10'53.9"W
35	Parnaíba	Corrente River, Corrente, PI	10°21'09.4"S 45°07'38.2"W
36	Parnaíba	Tají River, Corrente, PI	10°22'54.9"S 45°12'21.4"W
37	Parnaíba	Corrente River, Corrente, PI	10°23'14.9"S 45°15'05.9"W
38	Parnaíba	Unnamed stream, tributary of Corrente River, Corrente, PI	10°24'39.4"S 45°12'25.0"W
39	Parnaíba	Corrente River under bridge at highway BR-135, Corrente, PI	10°25'30.6"S 45°11'47.4"W
40	Parnaíba	Corrente River under bridge at highway BR-135, Corrente, PI	10°26'29.4"S 45°10'24.3"W
41	Tocantins	Unnamed stream tributary of Prata River, São Felix do Tocantins, TO	10°08'39.6"S 46°35'19.6"W
42	Tocantins	Prata Stream, Prata Village, São Felix do Tocantins, TO	10°08'45.0"S 46°29'55.4"W
43	Tocantins	Porcos Stream, Prata Village, São Felix do Tocantins, TO	10°08'48.1"S 46°30'00.4"W
44	Tocantins	Soninho River, São Felix do Tocantins, TO	10°10'40.8"S 46°40'04.4"W
45	Tocantins (P)	Vereda in Prata River, between Cachoeira and Mateiros, São Felix do Tocantins, TO	10°11'33.5"S 46°27'52.0"W
46	Tocantins (P)	Prata Waterfall, São Felix do Tocantins, TO	10°12'21.6"S 46°28'35.4"W
47	Tocantins	Unnamed stream under bridge between Prata and Mateiros Village, Mateiros, TO	10°15'55.1"S 46°33'49.9"W
48	Tocantins	Formiga River under bridge between Prata and Mateiros, Mateiros, TO	10°20'13.3"S 46°31'10.1"W
49	Tocantins	Unnamed stream under bridge between Mateiros and Coaceral, Mateiros, TO	10°32'23.4"S 46°21'18.9"W
50	Tocantins	Unnamed stream under bridge, Mateiros, TO	10°32'42.4"S 46°25'27.7"W
51	Tocantins	Raízes Stream, under bridge between Mateiros and Coaceral, Mateiros, TO	10°33'16.3"S 46°08'20.5"W
52	Tocantins	Come Assado Stream, Mateiros, TO	10°36'20.9"S 46°17'08.2"W
53	São Francisco	Sassafrás River, tributary of Sapão River, Formosa do Rio Preto, BA	10°38'08.5"S 45°50'21.2"W
54	São Francisco	Preto River, Formosa do Rio Preto, BA	11°03'14.3"S 45°12'04.8"W

Figure 2. Subset of sampling sites visited in Nascentes do Rio Parnaíba National Park and surroundings. A. Temporary pond Curicaca, Barreiras do Piauí – PI; B. Prata waterfall, São Felix do Tocantins – TO; C. Susuapara waterfall, Barreiras do Piauí – PI; D. Porcos stream, São Felix do Tocantins – TO; E. Unnamed stream, Mateiros – TO; F. Parnaíba River, Alto Parnaíba – MA; G. Soninho River, São Felix do Tocantins – TO; H. Atoleiro marsh, Barreiras do Piauí, PI ; I. Vereda tributary of Prata River, São Felix do Tocantins – TO; J. Parnaibinha River, road between Morrinhos and Bonfim, Alto Parnaíba – MA; K. Parnaíba River, Taboca rapids, Alto Parnaíba – MA; L. Area deforested by business agriculture in São Francisco River basin in Bahia. MA, Maranhão; PI, Piauí; TO, Tocantins.

Table 2. Systematic list of fish species collected in Nascentes do Rio Parnaíba National Park (NPNP) and surroundings. PAR, Parnaíba River basin; TOC, Tocantins River basin; SFR, São Francisco River basin. END = Endemic species.

ORDER/Family/*Species*	**NPNP**	**PAR**	**TOC**	**SFR**	**END**	**VOUCHER**
CHARACIFORMES						
Acestrorhynchidae						
Acestrorhynchus lacustris (Lütken, 1875)				X		UFRN 3746
Anostomidae						
Leporinus friderici (Bloch, 1794)	X	X				UFRN 2725
Leporinus piau Fowler, 1941		X		X		UFRN 2724 $^{(PAR)}$ UFRN 3651 $^{(SFR)}$
Megaleporinus obtusidens (Valenciennes, 1837)		X				UFRN 3094
Characidae						
Astyanax lacustris (Lütken, 1875)				X		UFRN 3739
Astyanax novae Eigenmann, 1911			X			UFRN 2816
Brachychalcinus parnaibae Reis, 1989	X	X			X	UFRN 3143
Bryconamericus sp.	X	X			X	UFRN 3034
Caiapobrycon tucurui Malabarba & Vari, 2000			X		X	UFRN 2814
Compsura heterura (Eigenmann, 1915)		X				UFRN 2715
Creagrutus sp.			X		X	UFRN 3597
Hasemania sp.		X			X	UFRN 2874
Hemigrammus brevis Ellis, 1911	X	X			X	UFRN 3039
Hemigrammus marginatus Ellis, 1911		X	X			UFRN 2840 $^{(PAR)}$ UFRN 3696 $^{(TOC)}$
Hemigrammus rodwayi Durbin, 1909		X				UFRN 2854
Hemigrammus sp. 1	X	X			X	UFRN 2829
Hemigrammus sp. 2	X		X		X	UFRN 3594
Hemigrammus sp. 3			X		X	UFRN 3738
Hyphessobrycon stegemanni Géry, 1961			X		X	UFRN 3596
Hyphessobrycon sp. 1		X			X	UFRN 2876
Hyphessobrycon sp. 2	X		X		X	UFRN 2788
Jupiaba polylepis (Günther, 1864)		X	X			UFRN 3084 $^{(PAR)}$ UFRN 3691 $^{(TOC)}$
Knodus chapadae (Fowler, 1906)			X			UFRN 3665
Knodus victoriae (Steindachner, 1907)	X	X			X	UFRN 3095
Knodus sp. 1			X		X	UFRN 2810
Knodus sp. 2				X	X	UFRN 3742
Moenkhausia collettii (Steindachner, 1882)			X			UFRN 3593
Moenkhausia costae (Steindachner, 1907)				X	X	UFRN 3722
Moenkhausia sanctaefilomenae (Steindachner, 1907)	X	X	X	X		UFRN 2706 $^{(PAR)}$ UFRN 2790 $^{(TOC)}$ UFRN 3374 $^{(SFR)}$
Orthospinus franciscensis (Eigenmann, 1914)				X	X	UFRN 339
Phenacogaster calverti (Fowler, 1941)		X				UFRN 2740
Psalidodon fasciatus (Cuvier, 1819)	X	X				UFRN 2707
Serrapinnus heterodon (Eigenmann, 1915)		X				UFRN 2714
Serrapinnus sp.		X			X	UFRN 2754
Chilodontidae						
Caenotropus labyrinthicus (Kner, 1858)	X	X				UFRN 3134
Crenuchidae						
Characidium aff. *bahiensis* Almeida, 1971			X		X	UFRN 3702
Characidium gr. *zebra* Eigenmann, 1915	X	X				UFRN 3044
Characidium tapuia Zanata, Ramos & Oliveira-Silva, 2018	X	X			X	UFRN 2784
Characidium sp.	X	X			X	UFRN 2871

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ORDER/Family/*Species*	**NPNP**	**PAR**	**TOC**	**SFR**	**END**	**VOUCHER**
Curimatidae						
Curimatella immaculata (Fernández-Yépez, 1948)	X	X				UFRN 3140
Cyphocharax cf. *spilurus* (Günther, 1864)			X			UFRN 3676
Steindachnerina notonota (Miranda Ribeiro, 1937)	X	X				UFRN 2759
Erythrinidae						
Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)	X	X	X	X		UFRN 2830 $^{(PAR)}$ UFRN 3185 $^{(TOC)}$ UFRN 3375 $^{(SFR)}$
Hoplias malabaricus (Bloch, 1794)	X	X	X	X		UFRN 2739 $^{(PAR)}$ UFRN 3338 $^{(TOC)}$ UFRN 3373 $^{(SFR)}$
Hemiodontidae						
Hemiodus parnaguae Eigenmann & Henn, 1916		X			X	UFRN 3079
Iguanodectidae						
Bryconops affinis (Günther, 1864)				X		UFRN 3719
Bryconops gr. *melanurus* (Bloch, 1794)	X	X	X			UFRN 2713 $^{(PAR)}$ UFRN 3674 $^{(TOC)}$
Bryconops sp. 1				X	X	UFRN 3750
Bryconops sp. 2			X		X	UFRN 2787
Bryconops sp. 3			X		X	UFRN 3704
Paradontidae						
Apareiodon sp. 1		X			X	UFRN 2774
Apareiodon sp. 2		X			X	UFRN 2746
Serrasalmidae						
Colossoma macropomum (Cuvier, 1816)		X				UFRN 3011
Metynnis lippincottianus (Cope, 1870)			X			UFRN 3692
Triportheidae						
Triportheus signatus (Garman, 1890)		X				UFRN 3081
CICHLIFORMES						
Cichlidae						
Aequidens tetramerus (Heckel, 1840)	X	X	X			UFRN 2827 $^{(PAR)}$ UFRN 2818 $^{(TOC)}$
Cichlasoma orientale Kullander, 1983	X	X				UFRN 3009
Cichlasoma sanctifranciscense Kullander, 1983	X	X	X			UFRN 3016 $^{(PAR)}$ UFRN 3255 $^{(TOC)}$
Crenicichla brasiliensis (Bloch, 1792)	X	X				UFRN 2712 $^{(PAR)}$ UFRN 3255 $^{(TOC)}$
Crenicichla sp. 1	X		X		X	UFRN 3763
Crenicichla sp. 2	X	X			X	UFRN 2859
Geophagus parnaibae Staeck & Schindler, 2006	X	X			X	UFRN 2796
CYPRINODONTIFORMES						
Rivulidae						
Melanorivulus jalapensis (Costa, 2010)	X		X		X	UFRN 3065
Melanorivulus parnaibensis (Costa, 2003)	X	X			X	UFRN 3061
Melanorivulus sp.	X		X	X		UFRN 3187 $^{(TOC)}$ UFRN 3376 $^{(SFR)}$
GYMNOTIFORMES						
Gymnotidae						
Gymnotus aff. *carapo* Linnaeus, 1758	X	X	X			UFRN 3058 $^{(PAR)}$ UFRN 3673 $^{(TOC)}$
Sternopygidae						
Eigenmannia besouro Peixoto & Wosiacki, 2016			X	X		UFRN 3705 $^{(TOC)}$ UFRN 3740 $^{(SFR)}$

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ORDER/Family/*Species*	**NPNP**	**PAR**	**TOC**	**SFR**	**END**	**VOUCHER**
Sternopygus macrurus (Bloch & Schneider, 1801)			X			UFRN 3652
Sternopygus sp.				X	X	UFRN 3743
SILURIFORMES						
Auchenipteridae						
Tatia bockmanni (Sarmento-Soares & Buckup, 2005)				X	X	UFRN 3730
Centromochlus sp.				X	X	UFRN 3413
Callichthyidae						
Aspidoras raimundi (Steindachner, 1907)	X	X			X	UFRN 2795
Aspidoras sp.	X	X			X	UFRN 3069
Callichthys callichthys (Linnaeus, 1758)		X				UFRN 3377
Corydoras sp.	X	X			X	UFRN 3028
Heptapteridae						
Cetopsorhamdia sp.		X			X	UFRN 3356
Imparfinis sp.		X			X	UFRN 2716
Phenacorhamdia cabocla Rocha, Ramos & Ramos, 2018		X			X	UFRN 2768
Phenacorhamdia sp.			X		X	UFRN 2815
Pimelodella parnahybae Fowler, 1941	X	X			X	UFRN 2733
Pimelodella sp.				X	X	UFRN 3598
Rhamdia quelen (Quoy & Gaimard, 1824)	X	X				UFRN 3057
Loricariidae						
Ancistrus damasceni (Steindachner, 1907)		X			X	UFRN 2719
Hypostomus gr. *plecostomus* (Linnaeus, 1758)			X		X	UFRN 3590
Hypostomus johnii (Steindachner, 1877)			X			UFRN 2705
Hypostomus velhomonge Lustosa-Costa, Ramos, Zawadzki & Lima 2022		X			X	UFRN 2720
Hypostomus sp. 1		X			X	UFRN 2718
Hypostomus sp. 3			X		X	UFRN 2811
Hypostomus sp. 4			X		X	UFRN 2812
Hypostomus sp. 5	X	X			X	UFRN 3043
Loricaria parnahybae Steindachner, 1907	X	X			X	UFRN 3112
Parotocinclus cabessadecuia Ramos, Lima & Ramos, 2017		X			X	UFRN 2846
Pimelodidae						
Pimelodus maculatus Lacepède, 1803		X				UFRN 3023
Pimelodus sp.		X			X	UFRN 3025
SYNBRANCHIFORMES						
Synbranchidae						
Synbranchus gr. *madeirae* Rosen & Rumney, 1972	X	X				UFRN 2837

Protocol in Aquatic Systems) (Alonso & Willink 2011), and in order to avoid selectivity in captures, active collection gear, such as a short seine net (4 m × 1.5 m high and 5 mm mesh), sieves (0.8 m × 0.5 mm) and trawl nets (10 m × 4 m and 5.0 mm), and passive, as gill nets (25 mm × 35 m and 45 mm) and traps, were used (Sabino 1999).

To record the natural live coloration, some specimens were photographed in aquarium during collections. The specimens were anesthetized in eugenol alcoholic solution (9:1 dilution of ethanol 92° GL and eugenol) (Lucena et al. 2013) and fixed in formalin aqueous solution (9:1 dilution of water and a solution of formalin containing a minimum of 37% formaldehyde). Tissue samples or entire specimens were fixed in ethanol P.A. (99.9%) for molecular studies. In laboratory, they were transferred to an ethanol 70% solution, and separated into lots.

The specimens were sorted and identified using the ichthyological literature available for the Parnaíba, São Francisco, and Tocantins river basins (Fowler 1941, Menezes 1969, Nijssen & Isbrücker 1976, Kullander 1983, Britski et al. 1984, Ploeg 1991, Lima & Gerhard 2001, Staeck & Schindler 2006, Costa 2016, Melo & Espindola 2016, Ramos et al. 2017a, b, Ramirez et al. 2017, Rocha et al. 2018, Varella et al. 2018, Zanata et al. 2018, Lustosa-Costa et al. 2022). Whenever necessary, the taxonomic term ‘aff.’ was used for a taxon that has an affinity with another species but that can be recognized as distinct, ‘cf.’ when additional studies are necessary to confirm the identification, ‘gr.’

Figure 3. Subset of species collected in Nascentes do Rio Parnaíba National Park and surroundings. A. *Astyanax novae*; B. *Hyphessobrycon* sp.; C. *Knodus victoriae*; D. *Hoplerythrinus unitaeniatus*; E. *Characidium tapuia*; F. *Hemigrammus* sp. 1; G. *Aspidoras* sp.; H. *Ancistrus damasceni*; I. *Hypostomus* sp. 3; J. *Phenacorhamdia cabocla*; K. *Aequidens tetramerus*; L. *Crenicichla brasiliensis*; M. *Melanorivulus jalapensis*; N. *Melanorivulus* sp.; O. *Melanorivulus parnaibensis*; P. *Tatia bockmanni*; Q. *Cetopsorhamdia* sp.; R. *Gymnotus* aff. *carapo*.

for taxa with affinities to, but which must be distinct from the nominal taxon to which it was assigned, and 'sp.' indicating possibly undescribed species or simply specimens that could not be identified at the specific level (Winston 1999). The collected material was deposited in the ichthyological collection of the Universidade Federal do Rio Grande do Norte (UFRN) (Table 2).

The systematic classification and nomenclature of the species followed Fricke et al. (2023). Endemism was attributed to species restricted to a single hydrographic ecoregion as proposed by Albert et al. (2011). The geographic distribution of species was verified in Reis et al. (2003), Buckup et al. (2007), Ramos et al. (2014), and Lima et al. (2017). To ascertain the conservation status, the official national lists of endangered fish species from Brazil were used (MMA 2014, 2022).

Results

In total, 411 specimens were sampled among the 54 locations, representing 95 species in 56 genera, 22 families, and six orders (Table 2, Figure 3, Figure 4a–b). The order Characiformes had the highest richness, with 55 species (58%), 32 genera, and 12 families, followed by Siluriformes with 25 species (26%), 15 genera and five families, and Cichliformes with seven species (8%), four genera and a single family. Some orders were represented by a few species, such as Gymnotiformes with two families and four species (4%), Cyprinodontiformes with one family and three species (3%), and Synbranchiformes with one family and species (1.5%). The family Characidae was the most representative, with 30 species (32%), followed by Loricariidae with ten (11%), and Heptapteridae and Cichlidae with seven (7%), each. The families Gymnotidae (Gymnotiformes), Triportheidae, Hemiodontidae, Chilodontidae, and Acestrorhynchidae (Characiformes) were represented by a single species.

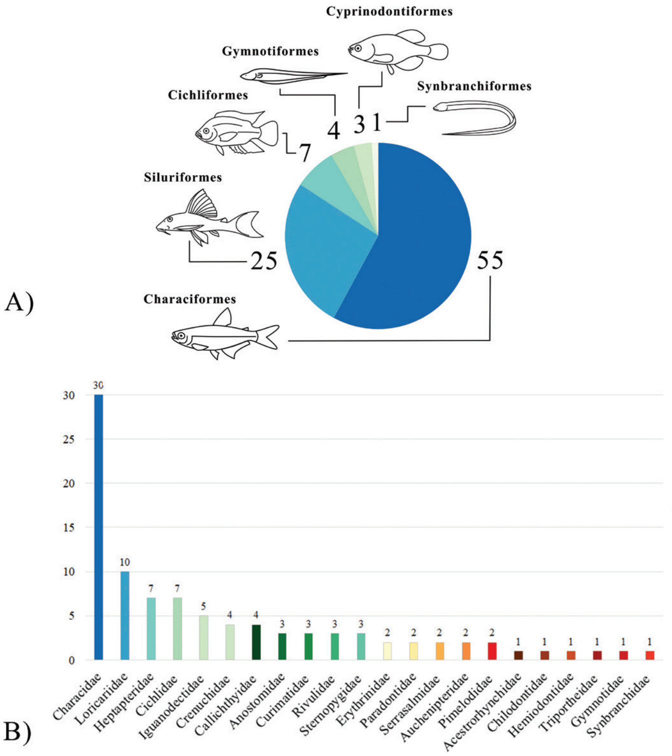

Figure 4. Taxonomic composition of the fishes from the Nascentes do Rio Parnaíba National Park and surroundings. A. Sampled orders; B. Sampled families.

Of the 95 species recorded, 58 (61%) occurred in only one of the three hydrographic ecoregions that compose the NPNP and its surroundings area. Thirty-three species (34.7%) were identified at the generic level and may represent species belonging to a complex or represent potential undescribed species. *Colossoma macropomum* (Cuvier 1816) was recorded near the NPNP in the Parnaíba river basin and was the only introduced species recorded in the survey. No recorded species is currently classified in any threatened IUCN category.

In the Parnaíba River basin, 59 species (62%) were recorded in 40 sampling sites, while in the Tocantins River basin 34 species (36%) in 12 localities, and in the São Francisco River basin, 17 species (18%) in two sampling sites (Tables 1–2, Figure 3c). Nineteen localities were sampled in the NPNP, 17 in the Parnaíba, and two in the Tocantins river basins, with 38 species (40%) belonging to 28 genera, 14 families, and six orders (Tables 1–2). In the NPNP, the order Characiformes was the most representative, with 19 species representing 50% of those recorded in the PA, followed by Siluriformes and Cichliformes, with seven species (18%), each. The Characidae family was the richest in the NPNP, with nine species (24%), followed by Cichlidae, with seven (18%) (Table 2).

The comparison of fish fauna between river basins tends to be superficial because sampling effort and access to water bodies were quite heterogeneous between each one. However, four species (4%) were recorded in Parnaíba and São Francisco drainages (*Hoplerythrinus unitaeniatus* (Spix & Agassiz, 1829), *Hoplias* aff. *malabaricus* (Bloch 1794), *Moenkhausia sanctaefilomenae* (Steindachner, 1907), and *Leporinus piau* Fowler, 1941) (Figure 3d). Nine species (9%) are shared between the Parnaíba and Tocantins rivers basins (*Aequidens tetramerus* (Heckel 1840), *Bryconops* gr. *melanurus* (Bloch, 1794), *Cichlasoma sanctifranciscense*, *H. unitaeniatus*, *H.* aff. *malabaricus*, *Jupiaba polylepis* (Günther 1864), *Gymnotus* aff. *carapo* Linnaeus 1758, *Hemigrammus marginatus* Ellis 1911, and *M. sanctaefilomenae*) (Figure 3d). And five species (5%) shared between the Tocantins and São Francisco basins (*Eigenmannia besouro* Peixoto & Wosiacki 2016, *Melanorivulus* sp., *H. unitaeniatus*, *H.* aff. *malabaricus* and *M. sanctaefilomenae*) (Figure 3d). The species *H.* aff. *malabaricus*, *H. unitaeniatus*, and *M. sanctaefilomenae* were recorded in the three drainages. In the region of the shared headwaters between Tocantins and São Francisco river basins, *Eigenmannia besouro* was recorded, and may indicate a potential use of the natural connection as a passage.

Discussion

The knowledge of fish diversity in the Parnaíba, São Francisco and Tocantins river basins has advanced considerably in recent decades (e.g., Lima & Caires 2011, Ramos et al. 2014, Lima et al. 2017, Chamon et al. 2022), although the headwaters of these drainages, part of which are located in the NPNP, remain relatively unexplored. As other Brazilian protected areas, the NPNP does not have a management plan and this fish survey can support future environmental policies, in addition to taxonomic, systematics, ecological, biogeographic, and conservation studies of the aquatic biota in the Cerrado. Although Brazil is responsible for the majority of new PAs in the world (approximately

75%) established since 2003 (Jenkins & Joppa 2009), the freshwater fauna has generally not been considered for demarcation strategies (Agostinho et al. 2005). For example, at the Tocantins River basin the number of threatened fish species is greater than of other vertebrates (ICMBio 2018).

No endangered species was recorded in the NPNP drainages and surroundings area. However, it is noteworthy that in the Tocantins basin there are at least 51 threatened species, 42 in the São Francisco, and one in the Parnaíba River basin (Chamon et al. 2022, Lima et al. 2017, MMA 2014, 2022). Additionally, the impacts resulting from agricultural expansion can adversely affect species that inhabit the 'veredas' (i.e., palm swamps dominated by the *Mauritia flexuosa* L.f) (Figure 2h). In these habitats, three species of non-annual rivulids were found. This family includes the largest number of threatened freshwater fish species in Brazil (MMA 2014, 2022), mainly due to the loss of their shallow and lentic habitats (Costa 2002). *Melanorivulus* sp. is possibly an undescribed species recorded in some 'veredas' of the NPNP in the Parnaíba and Tocantins drainages (Figure 3n, Table 2). *Melanorivulus jalapensis* has not been recorded since its original description and was only known from its type locality (Costa 2010). The new records expands its distribution by 55 km to the northeast (Figure 1). Anteriorly known only from two localities (Costa 2016), *Melanorivulus parnaibensis* were collected in several 'veredas' sampling sites, expanding the range of the species in about 240 km to the south. In the middle and lower Parnaíba, Tocantins and São Francisco River basins, previous studies recorded several introduced species (Ramos et al. 2014, Silva et al. 2015, Garavello et al. 2010, Bartolette et al. 2017, Barbosa et al. 2017). In the NPNP no exotic species was recorded, however, in the surrounding region, juveniles of 'tambaqui' (*Colossoma macropomum*) were collected. It is a well-known species that has a native range encompassing the western and central Amazon basins, and the Llanos portion of the Orinoco basin (Araújo-Lima & Goulding 1997, Jégu & Keith 1999). Its occurrence out of its native range, as in the rivers of northeastern Brazil, are the result of escapes from aquaculture facilities, since it is one of the most cultivated freshwater fishes in South America.

Thirty-three species were identified only at the generic level as they have diagnostic characters different from the known species in the sampled basins, requiring further taxonomic studies. Some of these were previously identified by Ramos et al. (2014), Silva et al. (2015), and Melo et al. (2016) in the Parnaíba River basin, and by Lima & Caires (2011) in the Tocantins River basin. Recent taxonomic revisions using material of the NPNP expedition from the Parnaíba River basin resulted in the description of four new species, the cascudinho *Parotocinclus cabessadecuia* (Ramos et al. 2017), the characid *Characidium tapuia* (Zanata et al. 2018), the small heptapterid *Phenacorhamdia cabocla* (Rocha et al. 2018), and the armored catfish *Hypostomus velhomonge* (Lustosa-Costa et al. 2022).

It is estimated that the Parnaíba River harbor approximately 155 species (Ramos et al. 2014, Lima et al. 2017). In the portion of the NPNP that protects the headwaters of this drainage, 20% (32 species) of the basin were recorded. According to Chamon et al. (2022), in the Tocantins-Araguaia River basin there are 751 species. Although the number of species recorded in the Tocantins River basin in the NPNP is relatively low (13 species), this area protects the headwaters, small environments characterized by low diversity and high endemism (Richardson 2019). Finally, the São Francisco River basin, with 304 fish species, and approximately 60% of these are endemic (Barbosa et al. 2017), does not have its headwaters protected by the NPNP. However, it presented a distinct and diverse ichthyofauna, with 17 species recorded in just two localities.

The headwaters and tributaries of the São Francisco River that cross Bahia State remain little studied (Langeani et al. 2009, Silva et al. 2020b). However, some stretches of the São Francisco River in northwestern Bahia harbor one of the largest and best-preserved areas of Cerrado, including streams and 'veredas' (Nogueira et al. 2011), which should be integrated in the mosaic of PAs, known as the Jalapão Region Ecological Corridor Project (ICMBio 2023), in the MATOPIBA region. During collections, the area apparently most impacted by agricultural expansion was in the São Francisco River basin, with vast landscape completely deforested for soybean and cotton plantations (Figure 2l), with some croplands close to the rivers.

While there is no standardization in our sampling effort to support more accurate comparisons across watersheds, the shared species may indicate some evidence. Four shared species were recorded between the Parnaíba and São Francisco River basins (Table 2), possibly evidencing a recent hydrological connection (about 400,000 years) as suggested by Costa et al. (2018) between these drainages (Coutinho-Abreu et al. 2008). Five species were shared between the São Francisco and Tocantins River basins (Table 2). Although some of these species are widely distributed and the taxonomy poorly understood (e.g. *Gymnotus* aff. *carapo*, *Hoplias* aff. *malabaricus*, and *Rhamdia* aff. *quelen*), the occurrence of some species may be due to the natural connection between these basins. Among the species that occur in the upper Tocantins and middle São Francisco River basins are *Astyanax novae*, *Cichlasoma sanctifranciscense, Eigenmannia besouro*, *Hyphessobrycon diastatos* Dagosta, Marinho & Camelier 2014 and *Pristella crinogi* Lima, Caires, Conde-Saldaña, Mirande & Carvalho 2021 (Garutti & Venere 2009, Lima & Caires 2011, Dagosta et al. 2014, Birindelli et al. 2015, Lima et al. 2021). Lima & Caires (2011) and Dagosta et al. (2014) discussed the connections between the headwaters of the three drainages and the possible routes for the exchange of freshwater organisms, including those between the Novo River (Tocantins basin) and the Sapão river (São Francisco River basin), and between the São Domingos River (Tocantins basin) and the Grande River (São Francisco River basin). Since this is a region with unique hydrographic aspects (preserved 'veredas', clear water rivers used for tourism, and shared headwaters between drainages) and inhabited by many possibly undescribed species, we suggest that additional studies be carried out in the region to assess the possibility of expanding the NPNP encompassing portions of the Sapão River, thereby also protecting part of the fish fauna from the headwaters of the middle São Francisco River drainage.

While some headwaters of the Parnaíba and Tocantins river basins are protected in the NPNP, the intense agricultural expansion, as well as the construction of hydroelectric dams and water diversion projects (Daga et al. 2020, Chamon et al. 2022) may compromise the downstream habitats in the tributaries that drain the MATOPIBA region. To ensure the conservation of the fish species of this watershed divide, the freshwater environments must be included in the creation or expansion of the protected areas (Azevedo-Santos et al. 2019).

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Conflicts of Interest

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

Ethics

This study did not involve human beings and/or clinical trials that should be approved by one Institutional Committee.

Data Availability

The datasets generated during and/or analyzed during the current study are available at: https://ipt.sibbr.gov.br/sibbr/resource?r=ufrn_ciufrn_pnnp01

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