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Inventory

Fishes from affluents of Rio Branco, Municipality of Caracaraí, Roraima State, northern Brazil

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Abstract: The Amazon has the richest freshwater ichthyofauna of the planet, with tens of new species being described annually. Although studies on Amazonian fish in the literature are increasingly common recently, there are still significant gaps concerning primary data on the ichthyofauna. One such gap is the state of Roraima and its main drainage, Rio Branco. There is a single book published in 2007 on fishes of Rio Branco, and although it presents a rather complete list of over 580 species known until then, the information is now a little outdated and many species found in some of its affluents are not listed in the book. Due to the scarcity of published data on the fish diversity of Roraima and taking into account that ichthyofaunal surveys are important tools towards freshwater conservation, we carried out an inventory of the ichthyofauna in the region of Caracaraí (RR) in 18 sampling sites including seven affluents of both left and right margins of Rio Branco. We recorded a total of 64 species of 41 genera and 18 families of five orders that occur in the Neotropical region, representing more than 11% of the species previously registered in the book for the entire Rio Branco basin. Twelve species were added to the list presented in the book, with four representing first records for the basin, one of them a new record for Brazil. Two of the 64 species are putative new taxa in need of further taxonomic studies. The order with the highest diversity was Characiformes (40 species), with highlights for the family Characidae (24 of these species), followed by Cichliformes (11 species) and Siluriformes (9 species). The richest collecting sites had 23 species, and the least rich site had only two species. *Hyphessobrycon bentosi* and *Nannostomus marginatus* occurred in more than 60% of the sites. There has been a significant difference in the exclusive ichthyofauna from affluents of both margins of Rio Branco, with the number of exclusive species in left margin tributaries approximately five times higher. Results presented herein complement data from the literature regarding the still poorly known ichthyofauna from Roraima.
Keywords: *Amazon; Guiana Shield; ichthyofauna.*

Peixes de afluentes do Rio Branco, Município de Caracaraí, Estado de Roraima, norte do Brasil

Resumo: A Amazônia possui a mais rica ictiofauna de água doce do planeta, com dezenas de novas espécies sendo descrita anualmente. Apesar de estudos sobre os peixes amazônicos serem cada vez mais comuns na literatura, ainda existem lacunas importantes com relação aos dados primários da ictiofauna. Uma dessas lacunas é o estado de Roraima e sua principal bacia hidrográfica, o Rio Branco. Até hoje, há apenas um livro publicado em 2007 sobre os peixes do Rio Branco, e apesar de apresentar uma lista bastante completa com pouco mais de 580 espécies conhecidas até então, atualmente as informações estão um pouco desatualizadas e diversas espécies de peixes encontradas em alguns de seus afluentes não constam do livro. Devido a escassez de dados publicados sobre a diversidade de peixes de Roraima e levando em consideração que levantamentos de ictiofauna são ferramentas importantes para mensurar o potencial de conservação dos corpos d'água, nós fizemos um levantamento da ictiofauna da região de Caracaraí (RR) em 18 pontos incluindo sete afluentes das margens esquerda e direita do Rio Branco. Foram registradas ao todo 64 espécies de 41 gêneros e 18 famílias de peixes de cinco ordens que ocorrem na região Neotropical, representando pouco mais de 11% das espécies registradas no livro para toda a bacia do Rio Branco. Doze espécies foram adicionadas à lista apresentada no livro, sendo quatro registradas pela primeira vez neste estudo, uma delas registrada pela primeira vez no Brasil. Duas das 64 espécies representam possíveis espécies ainda não descritas, necessitando de estudos taxonômicos mais aprofundados. A ordem com maior diversidade foi Characiformes (40 espécies), com destaque para a família Characidae (24 destas espécies), seguida de Cichliformes (11 espécies) e Siluriformes (9 espécies). Os pontos com maior riqueza apresentaram 23 espécies e o com menor riqueza apresentou apenas duas espécies. *Hyphessobrycon bentosi* e *Nannostomus marginatus* ocorreram em mais de 60% dos pontos. Houve diferença significativa na ictiofauna exclusiva entre os afluentes das duas margens do Rio Branco, com o número de espécies exclusivas da margem esquerda sendo aproximadamente cinco vezes maior. Os resultados apresentados aqui complementam os dados presentes na literatura a respeito da ainda pouco estudada ictiofauna de Roraima.

Palavras-chave: *Amazônia; Escudo das Guianas; ictiofauna.*

Introduction

The Actinopterygii comprises the largest group of vertebrates, with more than 36.000 valid species and many more currently being described (Fricke et al. 2022). The Amazon basin includes the largest freshwater ichthyofauna on the planet, with recent estimates of more than 3.000 species and dozens of others described annually (Van der Sleen & Albert 2018). This vast diversity is mostly included in four orders (Characiformes, Siluriformes, Cichliformes and Cyprinodontiformes) which together comprise more than 90% of the freshwater fish species in the Amazon (Van der Sleen & Albert 2018).

Although the Amazonian ichthyofauna has been studied for more than two centuries (Böhlke et al. 1978, Vanzolini, 1996; Ceríaco, 2021), many gaps still exist nowadays concerning primary information on certain regions and the distribution of many species (e.g., Albert & Reis 2011, Dagosta & de Pinna 2019). One such gap is the Rio Branco basin, Roraima State, Brazil. Until now, there is a single book published on its ichthyofauna (Ferreira et al. 2007) that presents a little more than 580 species for the entire basin, with approximately 150 of these species consolidated two years later (Vari & Ferraris Jr., 2009). Nevertheless, some species have been described in the past 16 years since its publication, and there are many species ranges that have been broadened, so the information presented by this seminal work is a little outdated.

Rio Branco is the main affluent of the Rio Negro and it crosses the State of Roraima from North to South through different environments such as eroded highlands, tropical forests and savannahs (Ferreira et al. 2007, Lemos et al. 2017). Its main tributaries are Rios Uraricoera and Tacutu which drain the Southwestern margin of the Guyana Shield between the Brazilian and Guyana borders. It is in the center of the Amazonas-Orinoco-Guyana (AOG) core, and it is included in the ecoregion 315 (Amazonas Guyana Shield) of Abell et al. (2008). Interestingly, although the Rio Branco directly empties into the Rio Negro, these two drainages have very distinct water features and the ichthyofauna of Rio Branco is more related to the Essequibo River in Guyana with which it shares many rivers captures and flood connections through the Rupununni Portal (Souza et al. 2012, Dagosta & de Pinna 2019).

Recently, one of us organized an expedition to the region of Caracaraí, Roraima, to sample miniature species. We brought back samples of most species caught in that expedition and present herein an inventory of the fish fauna aiming to complement the knowledge of the ichthyofauna of Rio Branco basin.

Material and Methods

1. Study area

Caracaraí is one of the largest municipalities of Roraima and the city of Caracaraí is situated approximately 200km South of the state capital Boa Vista. It is covered by tropical forest, campinarana (i.e., a vegetation ranging between forest and savannah that grows on white sand soils in the Amazon according to Anderson, 1981) and savannah (“cerrado” or “lavrado”), with wide ranges of land transformed into rice, soy, and cattle farms. Nevertheless, some of the Caracaraí territory is still protected by a mosaic of Federal Conservation Units (Ferreira et al. 2007). Along the water bodies, buriti palm groves (*Mauritia flexuosa* Mart.) were common, as well as vast flooded savannahs covered by water plants such as *Nymphaea* spp., *Montrichardia arborescens* (L.) Schott, 1854, piperaceans, among others.

2. Fish sampling

This study was the result of a single expedition to the municipality of Caracaraí conducted between December 11th–15th, 2019, during the dry season. All the collection were realized during daylight. Eighteen sampling sites representing seven tributaries of Rio Branco (Igarapé Água Viva, Igarapé das Pedras, Rio Ajarani, Rio Anauá, Rio Barauana, Rio Itã and Rio Viruá) were surveyed for small to middle-sized fishes using hand nets (Table 1, Figures 1 and 2). Twelve of the sampling sites were on the left side of the Rio Branco and six were on the right side. Fish caught were handled with care, put in buckets and trays and at least one specimen for most species promptly recognized in the field was photographed live in a photography tank using a Nikon D3100 camera and Mikkro Lenses (Figures 3, 4 and 5). Fish were then anesthetized using an overdose of eugenol (clove oil) and fixed in buffered formalin for 48 hours. After that period, fishes were rinsed in water and preserved in 70% alcohol. Tissue samples were also preserved in 100% alcohol. All fish and tissue samples are deposited in the Laboratório de Ictiologia de Sorocaba (LISO). The collecting permit was issued by Ministério do Meio Ambiente (MMA/SISBIO 45429-3). In the lab, fishes were sorted and identified to the lowest taxonomic level possible using the keys to families and genera in Van der Sleen & Albert (2018) with additional keys to species published in different journals coupled with photographs available in Ferreira et al. (2007). A simple comparison between the ichthyofauna of tributaries of left and right margins was done including two samples *t*-student test and rarefaction curves.

Table 1. Geographic information of sampling sites, all in the municipality of Caracaraí, Roraima, northern Brazil. All references to roads (distance, side of the road) refers to the center of the municipality of Caracaraí. Side refers to the side of Rio Branco (L = left; R = right).

Site	Locality	Micro-basin	Latitude	Longitude	Side
1	Rio Barauana	Rio Barauana	01º28'55.70" N	60º51'8.40" W	L
2	Igarapé Seco	Rio Barauana	01º29'0.22" N	60º49'38.00" W	L
3	Igarapé Tamandaré	Igarapé das Pedras	01º18'31.30" N	60º34'12.30" W	L
4	Flooded area next to Rio Dias	Igarapé das Pedras	01º16'43.20" N	60º30'47.80" W	L
5	Marginal lake, Igarapé Tamandaré	Igarapé das Pedras	01º18'28.40" N	60º34'10.50" W	L
6	Marginal lake, Igarapé Caleffi	Rio Itã	01º23'4.95" N	60º38'6.16" W	L
7	Flooded area with Buriti trees, left side of BR-174 road	Rio Viruá	01º39'0.47 N	60º03'19.80" W	L
8	Igarapé Água Viva	Igarapé Água Viva	01º57'0.70" N	61º14'7.13" W	R
9	Flooded area, left side of BR-210 road	Rio Ajarani	01º59'0.49" N	61º20'9.41" W	R
10	Flooded area, right side of BR-210 road	Rio Ajarani	01º57'9.28" N	61º17'2.26" W	R
11	Flooded igarapé, left side of BR-210 road	Rio Ajarani	01º56'7.43" N	61º14'5.25" W	R
12	Igarapé, left side of BR-210 road	Rio Ajarani	01º55'23.15" N	61º08'6.82" W	R
13	Igarapé, both sides of BR-210 road	Rio Ajarani	01º55'0.77" N	61º07'9.95" W	R
14	Igarapé Viruá	Rio Viruá	01º36'8.64" N	61º01'13.80" W	L
15	Igarapé under BR-174 road, km 333	Rio Viruá	01º35'20.40" N	61º00'17.90" W	L
16	Stream bordering right side of Perdida Road	Rio Anauá	01º25'25.20" N	60º59'15.60" W	L
17	Unnamed igarapé affluent of Rio Viruá	Rio Viruá	01º32'8.53" N	60º59'00.60" W	L
18	Igarapé under bridge, Nova Petrolina Village	Rio Viruá	01º33'52.70" N	60º59'6.68" W	L

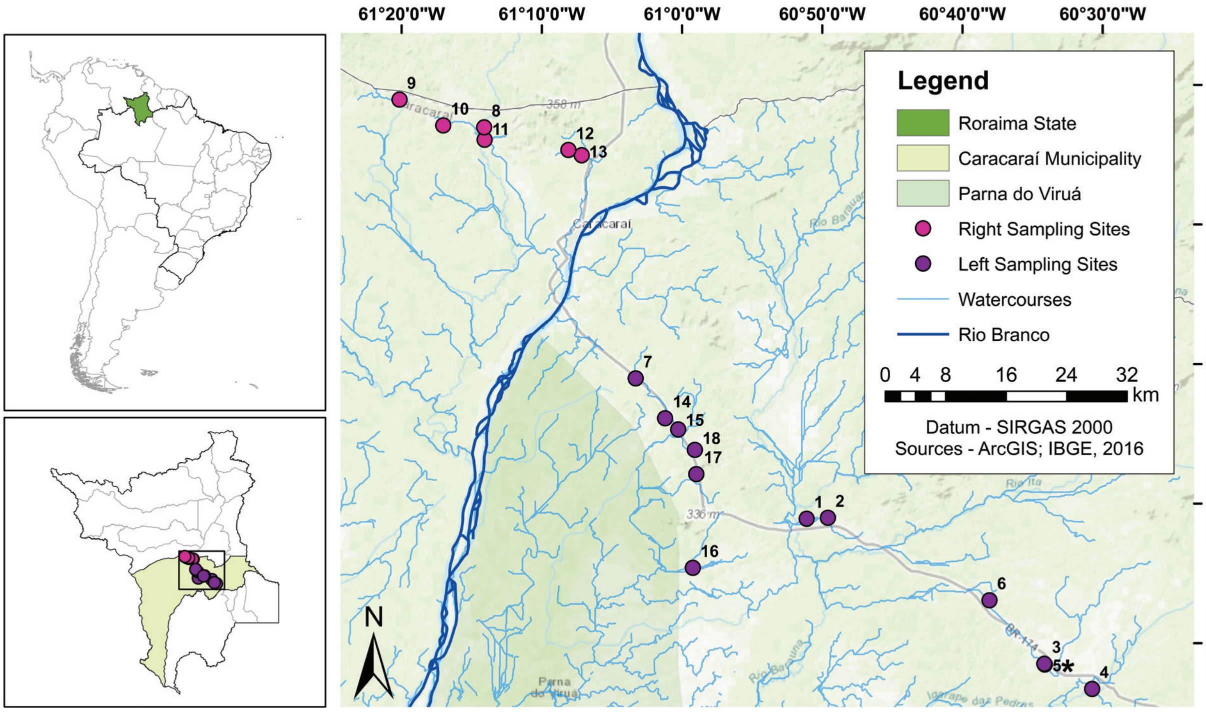

Figure 1. Map of the study area showing the location of the municipality of Caracaraí, Roraima State, northern Brazil and sampling sites in the tributaries of Rio Branco. Twelve of the sampling sites were on the left side (purple dots) of the Rio Branco and six were on the right side (pink dots). *Two nearby sampling sites (Igarapé Tamandaré and marginal lake, Igarapé Tamandaré).

Results and Discussion

We sampled 1.055 specimens, representing 64 species belonging to 41 genera and 18 families of five orders usually found in Neotropical freshwater ecosystems (Table 2). The most diverse order was Characiformes (40 species), with 24 species in the Characidae and 5 in the Lebiasinidae, followed by Cichliformes (11 species of cichlids) and Siluriformes (9 species, 4 of which in the Loricariidae) (Figure 6). Two species were common, occurring in more than 60% of the sampling sites: the characid *Hyphessobrycon bentosi* and the lebiasinid *Nannostomus marginatus*. Two other species were not as common but locally abundant: *Hemigrammus* aff. *rodwayi* and *Hyphessobrycon saizi*.

Figure 2. Photographs of sampling sites in the municipality of Caracaraí, Roraima State, northern Brazil. A) Rio Barauana; B) Igarapé Seco; C) Igarapé Tamandaré; D) Flooded area with Buriti trees, left side of BR-174 road; E) Flooded area, left side of BR-210 road; F) Flooded area, right side of BR-210 road; G) Igarapé Viruá; H) Stream bordering right side of Perdida Road. Sites A-D and G-H belong to tributaries of the left margin of Rio Branco, and sites E-F belong to tributaries of the right margin of Rio Branco.

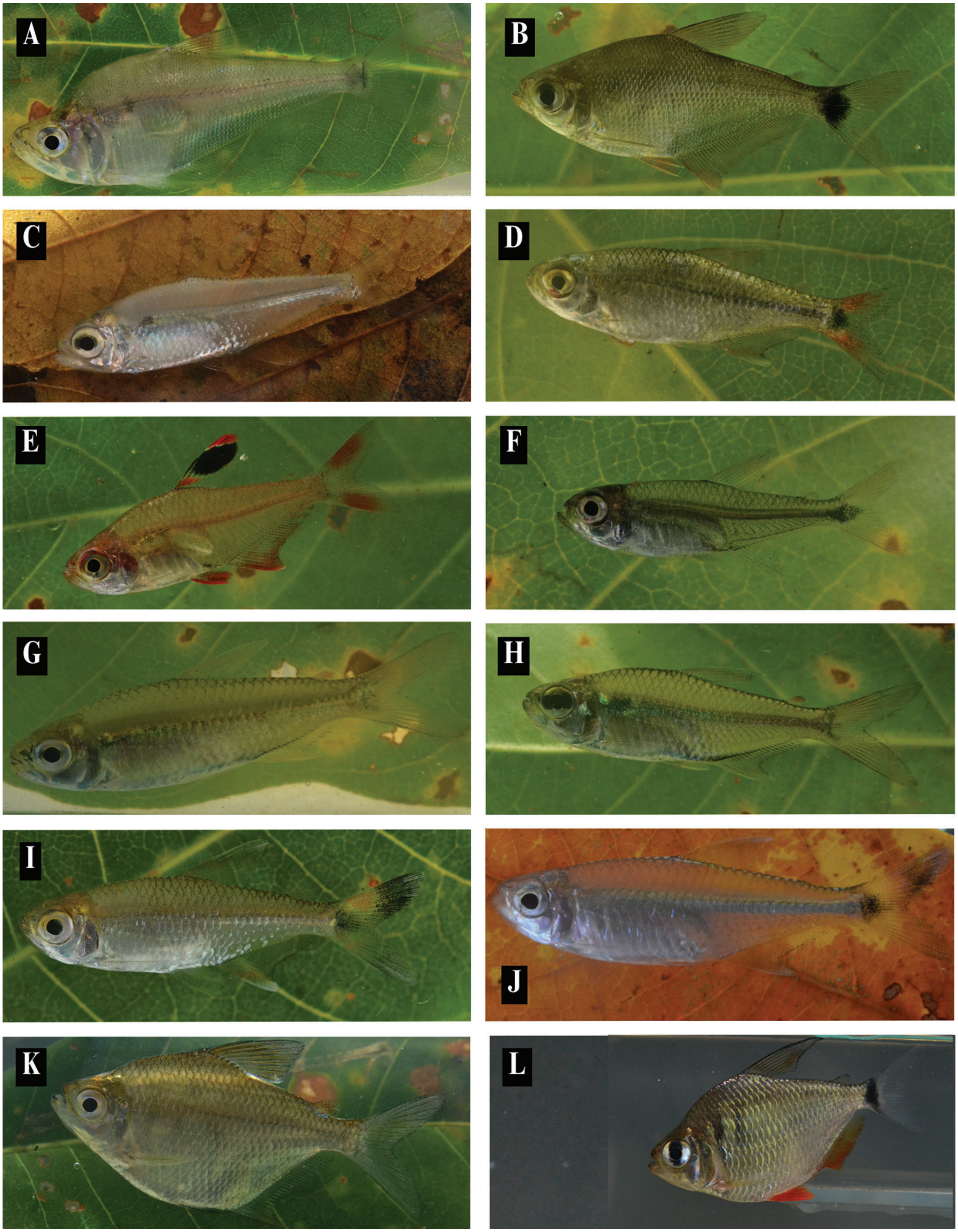

Figure 3. Photographs of some fish species from tributaries of Rio Branco in the municipality of Caracaraí, Roraima State, northern Brazil. A) *Charax gibbosus* B) *Ctenobrycon hauxwellianus* C) *Hemigrammus microstomus* D) *Hemigrammus* aff. *rodwayi* E) *Hyphessobrycon bentosi* F) *Hyphessobrycon saizi* G) *Microschemobrycon melanotus* H) *Moenkhausia collettii* I) *Moenkhausia* aff. *dichroura* J) *Moenkhausia lepidura* K) *Poptella brevispina* L) *Tetragonopterus argenteus.*

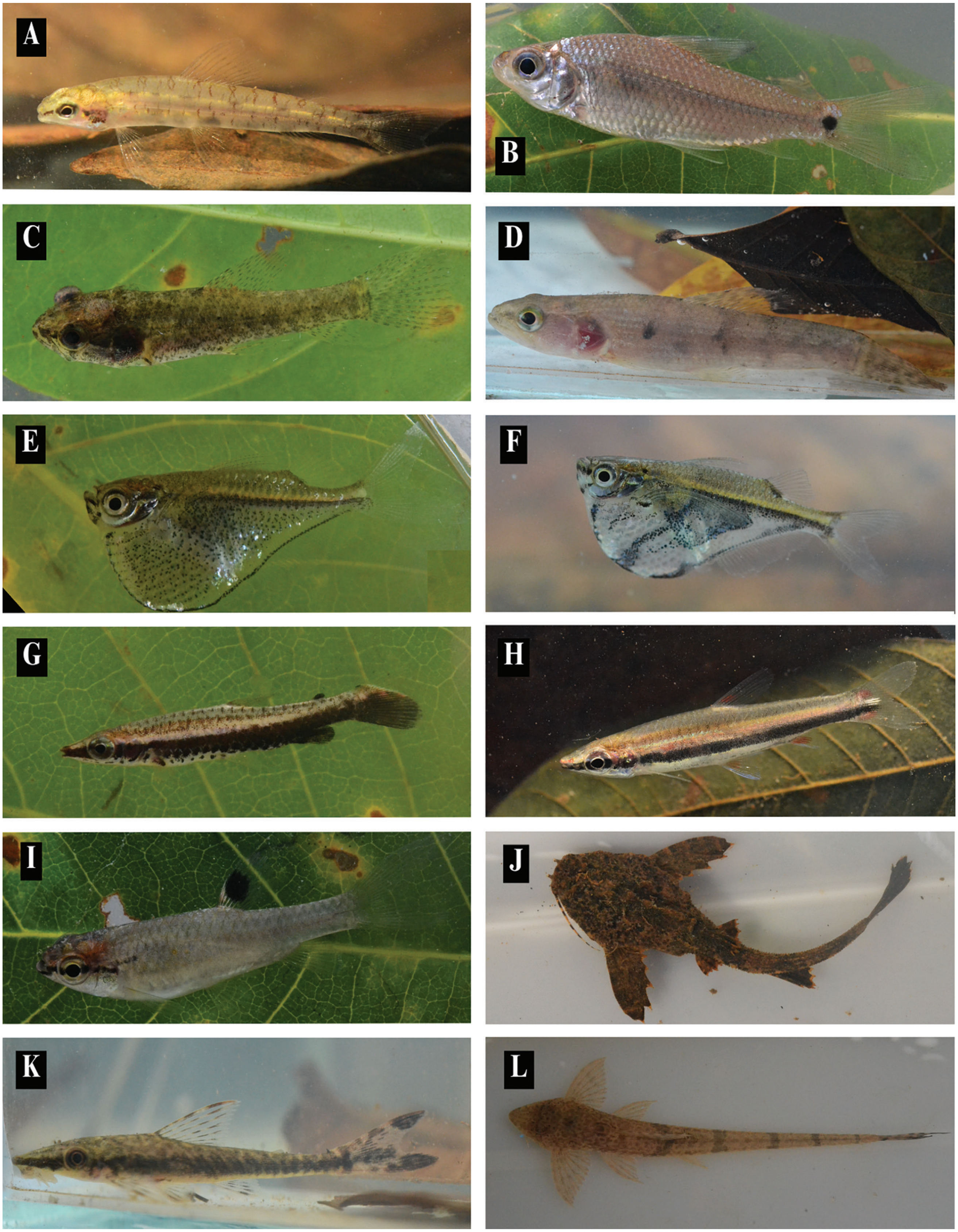

Figure 4. Photographs of some fish species from tributaries of Rio Branco in the municipality of Caracaraí, Roraima State, northern Brazil. A) *Characidium pellucidum* B) *Cyphocharax spilurus* C) *Hoplias curupira* D) *Hoplias malabaricus* E) *Carnegiella marthae* F) *Carnegiella strigata* G) *Nannostomus eques* H) *Nannostomus unifasciatus* I) *Pyrrhulina brevis* J) *Bunocephalus verrucosus* K) *Hypoptopoma guianense* L) *Rineloricaria fallax.*

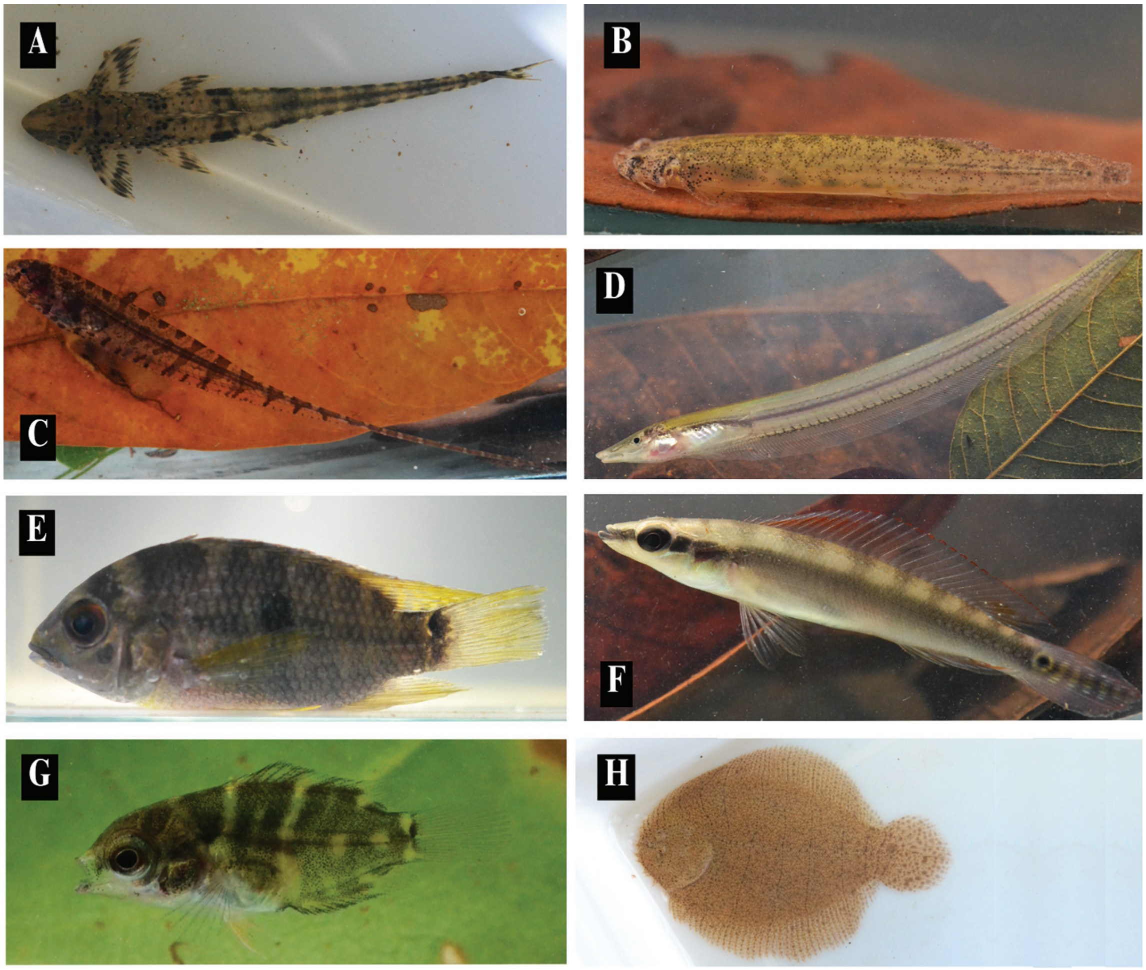

Figure 5. Photographs of some fish species from tributaries of Rio Branco in the municipality of Caracaraí, Roraima, northern Brazil. A) *Rineloricaria lanceolata* B) *Ochmacanthus alternus* C) *Hypopygus lepturus* D) *Gymnorhamphichthys rondoni* E) *Aequidens tetramerus* F) *Crenicichla* cf. *saxatilis* G) *Mesonauta insignis* H) *Hypoclinemus mentalis.*

Seventeen species were rare, each with a single specimen sampled. Two species were identified as miniature fish according to Toledo-Piza et al. (2014): *Hyphessobrycon saizi* and *Tyttobrycon xeruini.*

In terms of spatial distribution, two sampling sites were the richest with 23 species each (Rio Barauana and Igarapé Tamandaré), one presented only three species (Igarapé Seco, with *Tetragonopterus argenteus*, *Metynnis hypsauchen* and *Aequidens tetramerus*), and one presented only two species (flooded area with Buriti trees, with *Hyphessobrycon saizi* and *Nannostomus marginatus*). Twenty-two species were found in affluents of both margins of Rio Branco, 36 were found exclusively in affluents of the left margin and 6 were sampled only in affluents of the right margin of Rio Branco. Although the sampling effort was twice on the left side (12 sites) than on the right side (6 sites), the average number of exclusive species found on the left side (5.1, SD = 4.8) was five times higher than on the right side (1.0, SD = 1.3). This may be due to the diversity of meso-habitats available for sampling on the left side of Rio Branco, with sampling sites generally more homogeneous on affluents of the right margin (Fig. 2E-F) than of the left margin (Fig. 2A-D, G-H), in addition to the fact that more micro-basins were sampled on the left side (Table 1). A two samples *t*-student test confirmed the significance of this difference ($F = 13.12$; $t_{0.05;16} = 2.12$). Rarefaction sampling curves (Figure 7) demonstrate that our sampling effort is still far from reaching the estimated richness in the study area but comparing the rarefaction curves of the whole ichthyofauna (Figure 7A) with the one based on exclusive species only (Figure 7B) reveals a greater influence of species common to both sides of the Rio Branco in the right side ichthyofauna.

Species sampled herein represent a little more than 11% of the total number of species recorded for the entire Rio Branco basin by Ferreira et al. (2007). Still, we were able to sample twelve species that were not recorded by Ferreira et al. (2007), three of which were described concomitantly or after the publication of the book: *Apistogramma wapisana* (Römer et al. 2006), *Hoplias curupira* (Oyakawa & Mattox 2009) and *Potamoglanis wapixana* (Henschel 2016), and a fourth species, *Megalechis picta*, with a junior synonym described from the Rio Branco basin (Reis et al., 2005). Four species were not previously recorded in the Rio Branco basin (*Hemigrammus microstomus*, *Hemigrammus schmardae*, *Hyphessobrycon saizi* and *Serrapinnus micropterus*) despite three of them being widespread in the Amazonas and other basins according to Fricke et al. (2022). *Hyphessobrycon saizi*, whose distribution was restricted to the Orinoco River basin (Colombia) is recorded herein for the first time in Brazil.

Table 2. List of freshwater fish species in tributaries of Rio Branco in the municipality of Caracaraí, Roraima, northern Brazil. Orders organized systematically; lower categories organized alphabetically within each order. Classification follows Fricke et al. (2022). Occurrence refers to which margin of Rio Branco the species was recorded in the present study (B = both, L = left, R = right). NR = New record [Ferreira et al. (2007), Fricke et al. (2022)]. LISO = voucher specimens deposited in the collection of Laboratório de Ictiologia de Sorocaba, Universidade Federal de São Carlos (UFSCar).

Taxon	Occurrence	NR	LISO
CHARACIFORMES			
Acestrorhynchidae			
Acestrorhynchus microlepis (Jardine 1841)	R		503
Gnathocharax steindachneri Fowler 1913	B		494
Characidae			
Charax gibbosus (Linnaeus 1758)	L		513
Ctenobrycon hauxwellianus (Cope 1870)	B		497
Hemigrammus analis Durbin 1909	L		464
Hemigrammus bellottii (Steindachner 1882)	R		465
Hemigrammus aff. *lunatus* Durbin 1918	R		460
Hemigrammus microstomus Durbin 1918	B	X	466
Hemigrammus ocellifer (Steindachner 1882)	L		526
Hemigrammus aff. *rodwayi*	B		522
Hemigrammus schmardae (Steindachner 1882)	L	X	527
Hemigrammus vorderwinkleri Géry 1963	B		523
Hyphessobrycon bentosi Durbin 1908	B		488
Hyphessobrycon saizi Géry 1964	B	X	467
Makunaima guianensis (Eigenmann 1909)	B		499
Microschemobrycon melanotus (Eigenmann 1912)	R		469
Moenkhausia collettii (Steindachner 1882)	B		528
Moenkhausia aff. *dichroura*	L		529
Moenkhausia grandisquamis (Müller & Troschel 1845)	L		530
Moenkhausia hemigrammoides Géry 1965	B		531
Moenkhausia lepidura (Kner 1858)	L		463
Phenacogaster microsticta Eigenmann 1909	L		489
Poptella brevispina Reis 1989	L		500
Serrapinnus micropterus (Eigenmann 1907)	B	X	490
Tetragonopterus argenteus Cuvier 1816	L		507
Tyttobrycon xeruini Géry 1973	R		524
Crenuchidae			
Characidium pellucidum Eigenmann 1909	L		495
Curimatidae			
Curimatopsis cryptica Vari 1982	L		487
Cyphocharax spilurus (Günther 1864)	L		493
Erythrinidae			
Hoplias curupira Oyakawa & Mattox 2009	B		659
Hoplias malabaricus (Bloch 1794)	B		643
Gasteropelecidae			
Carnegiella marthae Myers 1927	R		646
Carnegiella strigata (Günther 1864)	B		642
Lebiasinidae			
Nannostomus digrammus (Fowler 1913)	L		611
Nannostomus eques Steindachner 1876	B		621
Nannostomus marginatus Eigenmann 1909	B		606
Nannostomus unifasciatus Steindachner 1876	B		615
Pyrrhulina brevis Steindachner 1876	B		675
Serrasalmidae			
Metynnis hypsauchen (Müller & Troschel 1844)	L		532
Serrasalmus elongatus Kner 1858	L		511

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Taxon	Occurrence	NR	LISO
SILURIFORMES			
Aspredinidae			
Bunocephalus verrucosus (Walbaum 1792)	L		635
Callichthyidae			
Megalechis picta (Müller & Troschel 1849)	L		609
Loricariidae			
Farlowella amazonum (Günther 1864)	L		610
Hypoptopoma guianense Boeseman 1974	L		639
Rineloricaria fallax (Steindachner 1915)	L		618
Rineloricaria lanceolata (Günther 1868)	L		673
Pseudopimelodidae			
Microglanis poecilus Eigenmann 1912	L		645
Trichomycteridae			
Ochmacanthus alternus Myers 1927	L		652
*Potamoglanis wapixan*a (Henschel 2016)	L		492
GYMNOTIFORMES			
Hypopomidae			
Hypopygus lepturus Hoedeman 1962	L		622
Rhamphichthyidae			
Gymnorhamphichthys rondoni (Miranda Ribeiro 1920)	L		690
Sternopygidae			
Eigenmannia trilineata López & Castello 1966	L		619
CICHLIFORMES			
Cichlidae			
Acaronia nassa (Heckel 1840)	L		624
Aequidens tetramerus (Heckel 1840)	L		638
Apistogramma pulchra Kullander 1980	L		630
Apistogramma regani Kullander 1980	L		687
Apistogramma steindachneri (Regan 1908)	B		656
Apistogramma wapisana Römer, Hahn & Conrad 2006	B		657
Crenicichla alta Eigenmann 1912	L		629
Crenicichla cf. *saxatilis*	L		486
Mesonauta insignis (Heckel 1840)	B		626
Satanoperca jurupari (Heckel 1840)	B		461
Satanoperca lilith Kullander & Ferreira 1988	R		462
PLEURONECTIFORMES			
Achiridae			
Hypoclinemus mentalis (Günther 1862)	L		672

Two putatively undescribed species (listed with the suffix “aff.”) were sampled. The first putative new species (*Hemigrammus* aff. *lunatus*) is very similar to *Hemigrammus lunatus* but differs from it by the lack of a broad dark longitudinal midlateral stripe across eye and of two humeral blotches typical of the species (Ota et al. 2014). Another putative underscribed species sampled herein, *Hemigrammus* aff. *rodwayi*, a species that resembles *H. rodwayi* but differs from it in the colour patter (specimens sampled here have a smaller caudal peduncle blotch and a more conspicuous lateral stripe than *H. rodwayi*). Whether these two species are indeed new depends on further and broader studies beyond the scope of this paper.

This ichthyofauna inventory resulted in the identification of 64 species while the work by Ferreira et al. (2007) presented a list of 584 fish species for the whole Rio Branco basin. This numerical difference can be explained by the sampling effort applied in each of the projects. Ferreira et al. (2007) carried out three collection expeditions between November 2004 and November 2005 sampling different stretches of the Rio Branco with the aim of collecting species from different ecological niches. In contrast, the present study was the result of a single 5-day expedition to the municipality of Caracaraí, which had as its main objective the collection of specimens of the genus *Priocharax*, having, therefore, a focus on the collection of small-sized fishes in a restricted part of the basin. Nevertheless, two putatively undescribed species and four new occurrence records were identified, demonstrating the importance of the present study.

The increase in the deforested area for agricultural production and the growth of mining activities in the Caracaraí region cause silting of rivers, destruction of important areas for fish reproduction, change in the flooding patterns and pollution of river water, directly

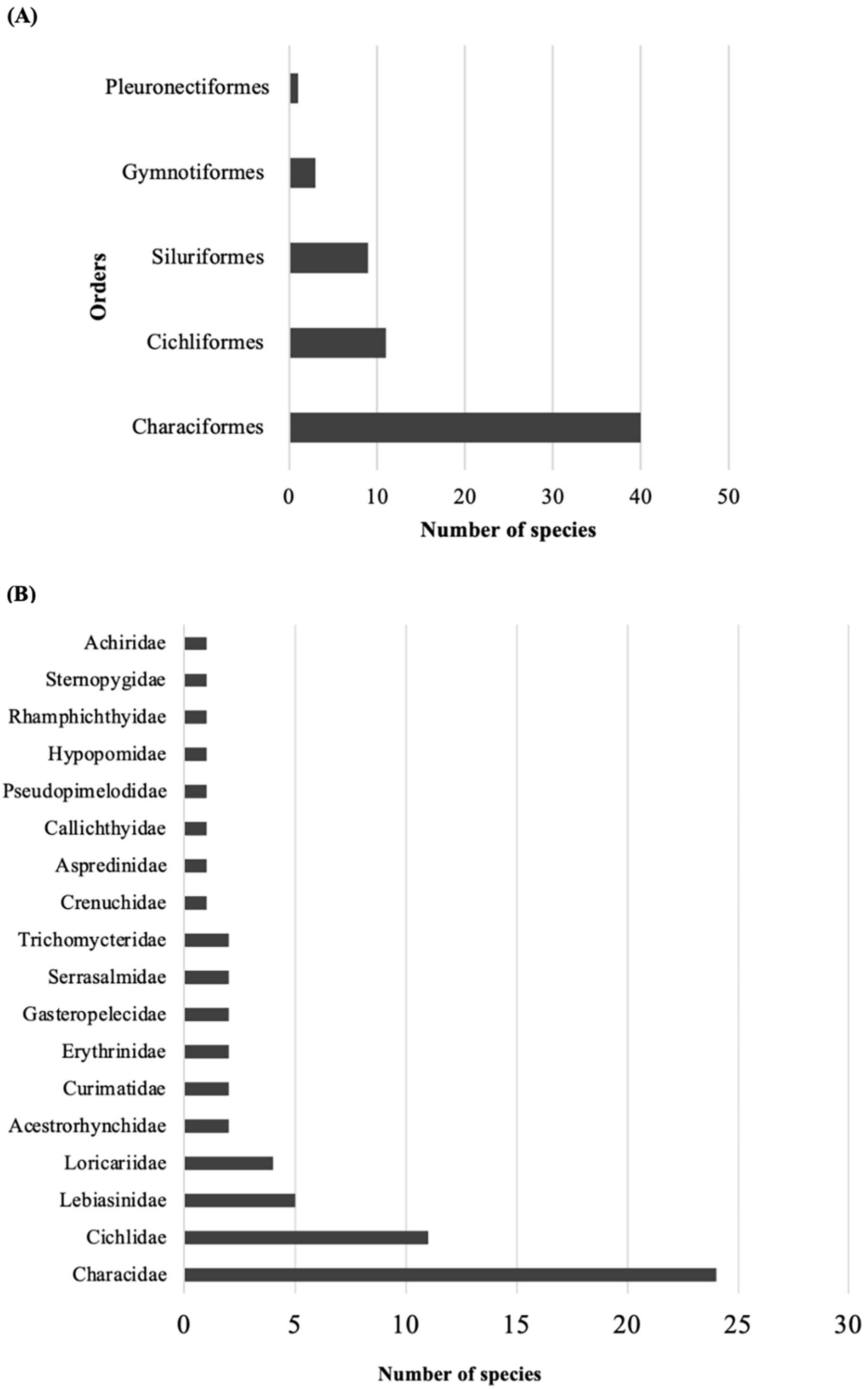

Figure 6. Distribution of number of fish species by orders (A) and families (B) in tributaries of Rio Branco in the municipality of Caracaraí, Roraima State, northern Brazil.

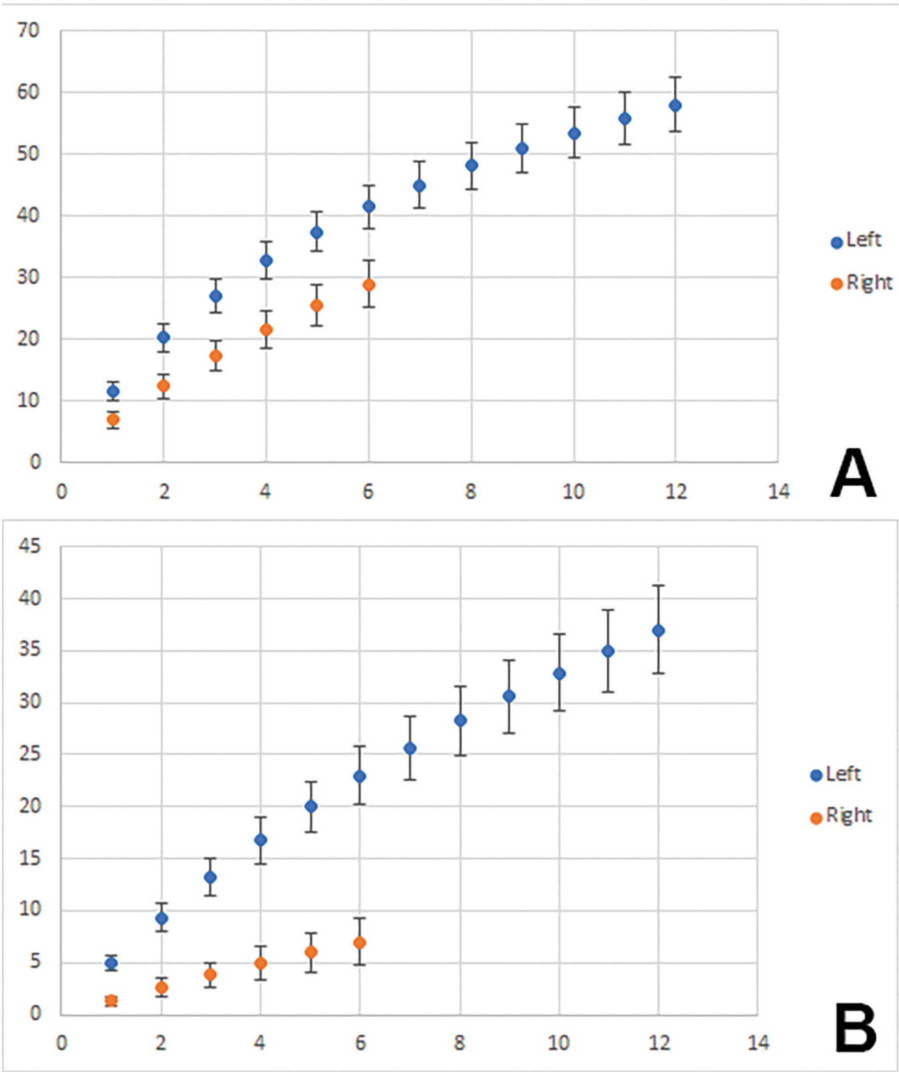

Figure 7. Sample size-based richness rarefaction sampling curves for affluents in the left (blue dots) and right (orange dots) margins of Rio Branco, Caracaraí municipality, Roraima State, northern Brazil with (A) all sampled species included and (B) only exclusive species included, and confidence intervals.

impacting the ichthyofauna of the Rio Branco (Ferreira et al. 2007). The data presented herein can be used in future research projects and conservation initiatives in the region.

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

Conflicts of Interest

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

Data Availability

Supporting data are available at <https://repositorio.ufscar.br/handle/ufscar/18166>.

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Short Communication

Fish attractors when resources abound: prevalence of juveniles and lack of assemblage structure in a field experiment in the Amazon floodplain

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Abstract: Floating structures, both natural and artificial, attract fish by providing shelter, feeding areas, and nesting sites. Occupancy can be either more permanent, leading to a gradual gathering of the assembly, or transient, occurring randomly. The ability of an attractor to hold a fish assemblage may depend on the availability of habitat resources in the environment. New artificial attractors are more valuable when natural ones are scarce. Additionally, fish characteristics play a role; young and small fishes may need new habitat for shelter more than adult fish. As aquatic herbaceous areas are abundant during high water, coinciding with the period of fish reproduction, they are particularly relevant for juveniles. We constructed fish attractors composed of natural materials to investigate the structure of fish assemblages during the flood of an Amazonian floodplain lake. Our aim was to test the hypothesis that assembly processes during the flood period would be random, with a predominance of juveniles in the attractors. We collected fish at intervals of 5, 15, and 30 days, resulting in 39 observations, and classified them as either adult or juvenile. Species composition was compared among treatments using Principal Coordinates Analysis (PCoA). The assembly process was tested through species co-occurrence patterns employing null models and the C-score index. The proportion of juveniles and adults was compared using a Chi-square test. Species composition remained consistent throughout the experiment. The assembly was random, with a prevalence of juveniles, possibly serving only as temporary shelter and feeding areas. Our study contributes to understanding the role of habitat availability for floodplain fishes during high waters. The results suggest that floating attractors and new habitats may be more valuable for the juveniles than adult fish and can be used as a management strategy for population recovery, especially when floating herbaceous habitats are scarce.

Keywords: *Artificial attractors; assembly of fish assemblage; field experiment; habitat use; seasonality.*

Atratores de peixes quando os recursos são abundantes: prevalência de juvenis e falta de estrutura da assembleia em um experimento de campo na planície de inundação amazônica

Resumo: As estruturas flutuantes, naturais ou artificiais, atraem os peixes, fornecendo abrigo, áreas de alimentação e locais de nidificação. A ocupação pode ser mais permanente, resultando em um recolhimento gradativo da assembleia, ou transitória, ocorrendo aleatoriamente. A capacidade de um atrator de manter uma assembleia de peixes pode depender da disponibilidade de recursos de habitat no ambiente. Novos atratores artificiais são mais valiosos quando os naturais são escassos. Além disso, as características dos peixes desempenham um papel, já que peixes jovens e pequenos podem necessitar de novos habitats como abrigo mais do que peixes adultos. Como as áreas com herbáceas aquáticas são abundantes durante as cheias, coincidindo com o período de reprodução dos peixes, elas são especialmente relevantes para peixes juvenis. Construímos atratores de peixes compostos de material natural para investigar a estrutura das assembleias de peixes durante a cheia de um lago de várzea amazônico, a fim de testar a hipótese de que durante o período de cheia, os processos de montagem seriam aleatórios e com predominância de juvenis nos atratores. Os peixes foram coletados em intervalos de 5, 15 e 30 dias, resultando em 39 observações, e classificados como adultos ou juvenis. A composição de espécies foi comparada entre os tratamentos usando uma Análise de Coordenadas Principais (PCoA). O processo de montagem foi testado por meio de padrões de coocorrência de espécies usando modelos nulos e o índice C-score. A proporção de jovens e adultos foi comparada usando um teste Qui-quadrado. A composição de espécies permaneceu a mesma ao longo do experimento. A montagem da assembleia foi aleatória com prevalência de juvenis nos atratores, que possivelmente serviam apenas como abrigo temporário e áreas de alimentação. Nosso estudo contribui para entender o papel da disponibilidade de novos habitats para peixes de várzea durante a cheia. Os resultados sugerem que atratores flutuantes e novos habitats podem ser mais valiosos para os peixes jovens do que para adultos e podem ser usados como estratégia de manejo para a recuperação populacional, especialmente quando habitats de herbáceas flutuantes são escassos.

Palavras-chave: *Atratores artificiais; experimento de campo; montagem da assembleia de peixes; sazonalidade; uso do habitat.*

Introduction

In an aquatic environment, floating habitats such as aquatic macrophytes and underwater structures like wood branches increase environmental complexity and heterogeneity, attracting fish fauna (Freitas et al. 2002, Freitas et al. 2005, Thomaz and Cunha 2010; Rossoni et al. 2014, Yamamoto et al. 2014). These floating and underwater structures attract fish by providing shelter, feeding, and nesting sites for reproduction (Junk and Piedade 1997, Esteves 1998, Agostinho et al. 2003). The observation that fish aggregate near natural structures, such as rocks, fallen trees, aquatic herbaceous, and floating detritus, prompted the use of artificial structures that mimic the natural ones to attract fish (Bolding et al. 2004, Rossoni et al. 2014). This technique was first implemented in Japan in the late 1700s, aiming to increase the efficiency of fishery activities and was later adopted worldwide (Meier 1989). Nowadays, this technique serves various purposes, including habitat restoration, recreational diving and snorkeling activities, and scientific research (Bohnsack et al. 1997).

These structures form an important substrate for the growth of periphyton (consisting of algae, bacteria and associated micro-invertebrates) and macroinvertebrates, representing a crucial food source for many fish species (Araújo-Lima et al. 1986, Forsberg et al. 1993, Benedito-Cecilio et al. 2000) and allowing an assemblage to assembly. The colonization by periphytivorous fish can attract piscivores, triggering a process of assembling the local fish community (Chase 2003, Meerhoff et al. 2003, Mazzeo et al. 2010, Thomaz and Cunha 2010). Predation and interspecific competition are local-scale factors that can determine the composition of fish fauna, influencing the distribution of species (Hoeinghaus et al. 2007), and the local fauna within the attractors (Arrington and Winemiller 2006). The occurrence of a local assembly structure depends on how fish use these structures and the environmental availability of habitat (Arrington and Winemiller 2006). Individuals may stay for long periods or might only temporarily visit such places, either seasonally or occasionally during a period of less than a day (Talbot et al. 1978). In seasonal environments, the temporal pattern in the use of attractors is highly dependent on the availability of food resources and habitat surrounding the attractors (Arrington and Winemiller 2006).

Colonization in attractors can occur quickly or slowly (Bohnsack et al. 1991). The moment of setting them can influence the initial colonization and the use of attractors, making them more or less attractive in comparison to the surrounding environment (Bohnsack et al. 1991, Arrington and Winemiller 2006). During the flood season, these structures may not be as attractive due to the immense availability of habitats (Arrington and Winemiller 2006). However, despite being abundant during high-water periods, the availability of floating habitat, mainly aquatic herbaceous banks, have been described as the most important factor for fish recruitment in river floodplains (Sánchez-Botero and Araújo-Lima 2001). The observed higher juvenile survival in years of large floods (Bayley et al. 2018, Castello et al. 2019) has suggested that the availability of habitats for growth and feeding may regulate density-dependent processes (Bayley et al. 2018) and determine the occupation and fish assemblage structure in these habitats. We do not yet fully understand the colonization ecology of natural habitats, such as aquatic herbaceous banks, so experimental studies using artificial habitats are important to understand successional processes, such as community building (Bohnsack et al. 1991). Such processes depend on the moment in which they occur, making them more easily observed in artificial habitats than in natural ones.

This study examines fish assembly over 30 days in the high-water period through a manipulative experiment using floating attractors. We tested the hypothesis that during the flood period, assembly processes would not occur due to the high variety of habitats and the abundance of available food resources, and fish occupation in floating attractors would be random. However, we would expect a predominance of juveniles throughout the experiment as new habitat would be more valuable for this set of individuals.

Material and Methods

Most natural habitats of floating aquatic macrophytes occur in floodplain lakes and the border of flooding forests (Junk and Piedade 1997), serving as areas for fish growth and reproduction (Neves dos Santos et al. 2008, Röpke et al. 2022). The study was carried out in Lago do Padre, a floodplain lake at Ponta do Catalão, a lowland area located near the confluence of the Solimões and Negro rivers, about 10 km from the city of Manaus, Amazonas, Brazil (Figure 1). This area has a high diversity of floating habitats (Bleich et al. 2014), most available during high water. When the water level increases, typically between December and May, the pelagic area expands, providing habitat for the growth of aquatic herbaceous plants, which form extensive banks next to the edges of the surrounding flooded forest, as well as floating banks that detach from the margins (Junk and Piedade 1997). In this region, the most frequent and abundant aquatic plants are the emerging *Paspalum repens* (Poaceae), and the floating *Salvinia auriculata* (Salviniaceae), *Pistia stratiotes* (Araceae), and *Lemna valdiviana* (Araceae) (Junk and Piedade 1993; Bleich et al. 2014). Additionally, this area has a scientific station belonging to the National Institute for Amazonian Research (INPA), providing logistic support for the study. Fish samplings in macrophyte stands have been conducted in this area (Catalão project - CPD data not published), allowing easy fish identification and addition to the monitoring dataset with future value.

To study fish colonization, we used artificial attractors aiming to simulate floating aquatic herbaceous banks. Each attractor consisted of a 1.0 m^2 square frame (Figure 2), constructed with 40 mm diameter PVC pipes, similar to the frame used by Santos et al. (2011). The pipes were connected by PVC connectors to prevent water from entering and allowing the structure to float. A black plastic screen was placed on this frame as a substrate to the root-like tufts made of sisal rope. Each tuft was composed of three pieces of sisal rope, each 60 cm long and 6 mm thick, in which the threads were untwined, forming bulky tufts to simulate the roots of floating plants (for instance, Eichhornia). Each attractor contained twenty-five tufts (Figure 2). Sisal rope was chosen because it is a natural product made from fibers of the species *Agave sisalana* (Agavaceae) that, when untwined, resembles the roots of aquatic herbs.

The attractors were placed in the water, close to the INPA research base, to initiate the initial colonization by periphyton for a substrate as close as possible to natural growth. Once the tufts were covered

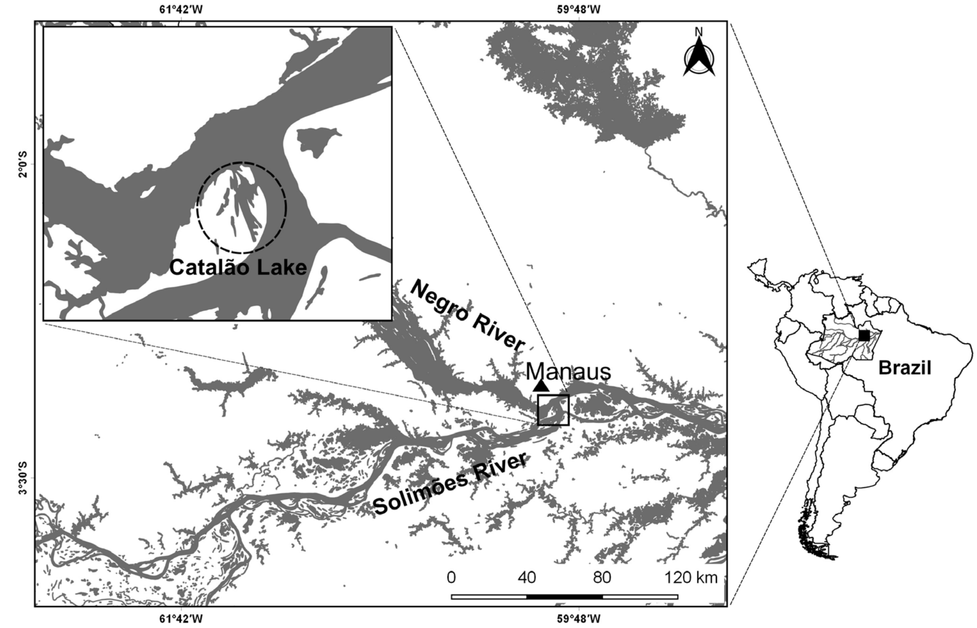

Figure 1. Map showing the Catalão area, Amazonas, Brasil.

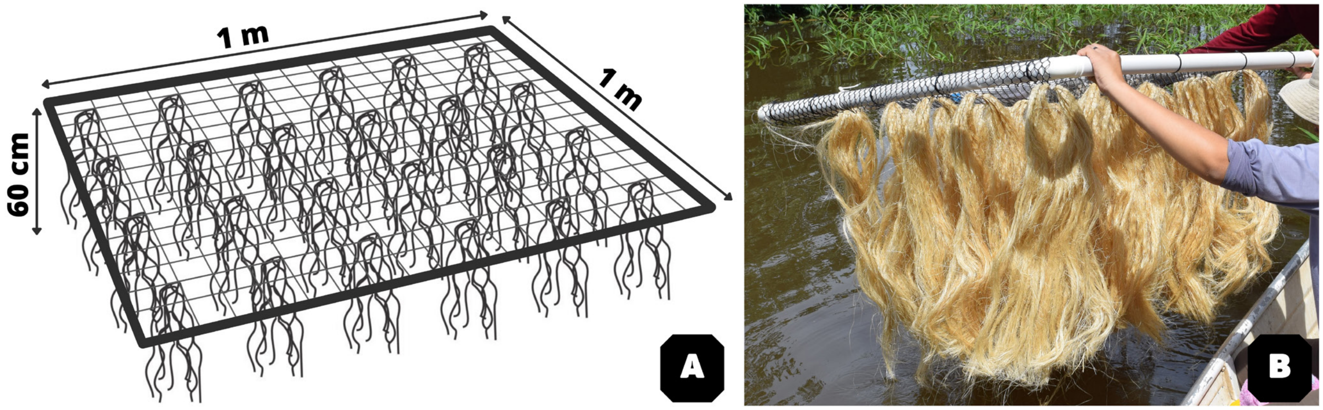

Figure 2. Illustration of the attractor with its respective dimensions (A) and the actual attractor being immersed in the water at the experiment site (B).

with periphyton, which could be observed with the naked eye (about 5–6 days), the attractors were removed from the water, checked for the presence of macroscopic organisms adhered to the tufts (which were then removed), and finally immersed in the water to begin the experiment. The attractors were placed close to the natural banks of aquatic herbaceous plants, anchored by rocks to prevent them from moving due to wind or water current.

The experiment was conducted over a period of 30 days, from June 9 to July 10, 2017, during a period of high water when the natural banks of aquatic herbaceous plants were already formed. The attractors were installed in the pelagic zone at standardized distances of at least 5 m from each other and 2.0 m from the border of the banks of herbaceous plants. To maintain the same distance from the marginal habitat, daily visits were made to the experiment site, adjusting the positions of the attractors when necessary.

The total number of attractors built and initially used in the experiment was 28. Several attractors were reused during the experiment and the removal of fish from the attractors after the intervals of 5, 15, and 30 days was carried out. Each time the attractors were removed for fish collection, the tufts of rope were meticulously inspected to ensure no fish were left adhered to the strings, so as not to interfere with the results of the next moment of colonization. The treatments were as follows:

1) Treatment 1 (5 days): five attractors were used. After 5 days of colonization, the attractors were removed from the water, the fish were collected, and the same attractors were returned to the water to restart the 5-day treatment. This procedure was repeated three times to obtain a total of 15 observations for the first treatment of 5 days;
2) Treatment 2 (15 days): eight attractors were used, which, at the end of 15 days, were reused for an equal period, totaling 16 observations for the second treatment of the 15 days;
3) Treatment 3 (30 days): 15 attractors were used, but two attractors were lost during the experiment, thus obtaining 13 observations for this third and last treatment.

To maintain the balance of the number of observations in the treatments, 2 and 3 observations from the first and second treatments, respectively, were excluded by drawing lots. Thus, in the end, each treatment had 13 observations (Table 1). The attractors were always inspected in the morning, and fish were collected using a 5 mm mesh net between opposite nodes and 1.5 meters high, tied to a 1.5 × 1.5 m square metal frame. The bottom of the seine net was closed to avoid fish escape. For collection, each attractor was carefully enveloped (from the bottom to the surface) with the adapted net and carefully removed from the water (Figure S1). Then, the fish were collected and immediately euthanized according to the CONCEA Euthanasia Practice Guidelines. Fish were immersed in a solution of clove oil (Eugenol) in the proportion of 1ml for each liter of water until the opercular movement ceased. After euthanized, the fish were fixed in a 10% formalin solution and deposited in containers containing information about the sample and the date of collection. Samples were then taken to the Fish Population Dynamics Laboratory at the National Institute for Amazonian Research (INPA) in Manaus, where each fish was identified at the species level by taxonomic specialists. Biometric data such as standard length (cm) and total weight (g) were registered for each specimen (data available at Rocha et al. 2023). The total number of fish and species in each sample was recorded (data available at Rocha et al. 2023). This study was authorized by IBAMA nº101932 e nº 74454-1and the Ethics Committee on the Use of Animals at INPA (CEUA Authorization 037/2017).

Principal coordinate analysis (PCoA) was used to explore the similarity in the composition of fish species among treatments, using a Bray-Curtis distance matrix, which considers the abundance of species in the samples. Species with only one occurrence in the dataset were excluded from this analysis (6 species). The statistical significance of the similarity among treatments was tested using the similarity analysis (ANOSIM), with 999 permutations (Legendre and Legendre 1998).

To identify possible effects of biotic interactions on how fish assembled on the attractors, species co-occurrence patterns were tested using null models, through the C-score index (Stone and Roberts 1990). For this, we created matrices of presence and absence of species for each treatment/time interval, in which the lines represented the species, and the columns represented the artificial attractors. Subsequently, the original matrices were randomized, and the C-scores were calculated, using the SIM9 algorithm, which maintains fixed sums of rows and columns (fixed-fixed model) (Connor and Simberloff 1979) and has good properties to avoid type I errors (Gotelli 2000). Therefore, the occurrence of each species among the attractors was simulated through randomizations, assuming the same probability of occurrence of the species. Then, the C-scores obtained from the original matrices were compared statistically with the values calculated from matrices generated through a null distribution based on 5000 Monte Carlo permutations, using the EcoSim program.

The average size of each species was compared to the maximum and/or L50 sizes available in the literature to identify the life stage of each fish occupying the attractors (Wolf 2014, Hernandes 2015, Röpke et al. 2017). The proportion of juveniles and adults were tested among treatments by a Chi-squared test based on pooled data. The expected proportion of juveniles was set at 29% and adults 71%, these proportions were estimated from 12 samplings in aquatic macrophytes between

Table 1. Number of samplings and total number of observations for each treatment.

Treatment	1ª sampling (5º day)	2ª sampling (10º day)	3ª sampling (15º day)	4ª sampling (30º day)	Initial number of observations	Number of observations after exclusion
1	5	5	5		15	–2* = **13**
2			8	8	16	–3* = **13**
3				15	15	–2** = **13**

*attractors withdrawn from analyses by drawing lots.
**attractors lost during the experiment.

May and August in 2009, 2011, and 2012 (Catalão project, unpublished data), to which collected fishes have the life stage determined. A krukall-wallis test was applied to test differences in the average fish size among treatments.

Results

A total of 208 specimens of 21 fish species, belonging to 9 families and 2 orders, were captured. Characiformes contributed with 16 species distributed among 7 families, being the predominant group in this study. Serrasalmidae (Characiformes) and Cichlidae (Cichliformes) were the families with the highest richness values, hosting 6 and 4 species, respectively. The most abundant species were *Mesonauta festivus* (Heckel 1840) and *Serrasalmus maculatus* Kner 1858, with 40 and 36 specimens, respectively, representing together 36.53% of the total abundance (Table 2).

Out of the 21 species captured, 11 occurred throughout the experiment (across all three treatments). These species are *Cichla monoculus* Agassiz, 1831, *Ctenobrycon spilurus* (Valenciennes, 1850), *Hemigrammus diagonicus* Mendonça & Wosiacki, 2011, *Heros notatus* (Jardine, 1843), *Hoplias malabaricus* (Bloch, 1794), *Mesonauta festivus* (Heckel, 1840), *Moenkhausia intermedia* Eigenmann, 1908,

Table 2. List of the species collected during the experiment at Catalão Lake with their respective abundances for each treatment (T).

ORDER/Family/*species*	**T1**	**T2**	**T3**	**Total**
	5 days	**15 days**	**30 days**	
CHARACIFORMES				
Anostomidae				
Leporinus fasciatus (Bloch, 1794)	1	0	3	4
Rhytiodus microlepis Kner, 1858	0	1	0	1
Characidae				
Ctenobrycon spilurus (Valenciennes, 1850)	1	1	1	3
Hemigrammus diagonicus Mendonça & Wosiacki, 2011	10	8	3	21
Moenkhausia intermedia Eigenmann, 1908	3	2	4	9
Curimatidae				
Cyphocharax plumbeus (Eigenmann & Eigenmann, 1889)	1	0	0	1
Erythrinidae				
Hoplias malabaricus (Bloch, 1794)	8	9	5	22
Lebiasinidae				
Copella nigrofasciata (Meinken, 1952)	0	1	0	1
Prochilodontidae				
Prochilodus nigricans Spix & Agassiz, 1829	1	0	0	1
Semaprochilodus taeniurus (Valenciennes, 1821)	0	0	1	1
Serrasalmidae				
Mylossoma albiscopum (Cuvier, 1818)	2	0	0	2
Pygocentrus nattereri Kner, 1858	2	1	0	3
Serrasalmus elongatus Kner, 1858	4	10	8	22
Serrasalmus maculatus Kner, 1858	7	20	9	36
Serrasalmus rhombeus (Linnaeus, 1766)	2	3	2	7
Serrasalmus sp “rob”	0	1	0	1
CICHLIFORMES				
Cichlidae				
Cichla monoculus Agassiz, 1831	3	1	3	7
Heros notatus (Jardine, 1843)	1	2	2	5
Mesonauta festivus (Heckel, 1840)	12	17	11	40
Pterophyllum scalare (Schultze, 1823)	4	11	5	20
Eleotridae				
Microphilypnus ternetzi Myers, 1927	0	1	0	1
TOTAL	**62**	**89**	**57**	**208**

Pterophyllum scalare (Schultze, 1823), *Serrasalmus elongatus* Kner, 1858, *Serrasalmus maculatus* Kner, 1858, and *Serrasalmus rhombeus* (Linnaeus, 1766). Two species appeared in two treatments: *Pterophyllum scalare* (Schultze, 1823) (T1 and T2) and *Leporinus fasciatus* (Bloch, 1794) (T1 and T3). Some species occurred only in one treatment, such as *Cyphocharax plumbeus* (Eigenmann & Eigenmann, 1889), *Prochilodus nigricans* Spix & Agassiz, 1829, and *Mylossoma albiscopum* (Cuvier, 1818), which appeared only in T1; *Semaprochilodus taeniurus* (Valenciennes, 1821), captured only in T3; *Rhytiodus microlepis* Kner, 1858, *Copella nigrofasciata* (Meinken, 1952), *Serrasalmus* sp. "rob", and *Microphilypnus ternetzi* Myers, 1927 that were present exclusively in T2 (Table 2).

PCoA analysis did not reveal different groups of species PCoA (Figure 3), and the similarity analysis (ANOSIM) showed that the composition of fish species remained similar in the three treatments (ANOSIM, R = –0.03579, p = 0.792).

Species co-occurrence analysis (C-score) indicated that the construction of fish assemblages during high-water occurred randomly over time. The observed C-score values were not significantly different from the expected values generated by null models for the time intervals (Table 3).

The attractors were mostly colonized by juveniles (Chi-squared = 198.41, df = 1, p < 0.001) for all treatments. No difference in fish body size was detected among treatments (Kruskal-Wallis = 3.7825, df = 2; 205, p = 0.1509), suggesting that fish were not resident and did not grow in the attractors.

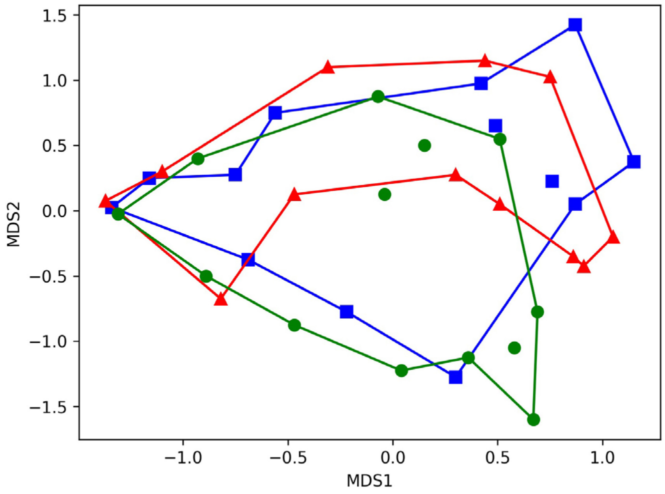

Figure 3. PCoA analysis for the treatments (time of colonization) using species taxonomic composition and respective abundances. Green dots indicate five-day treatment, red triangles a fifteen-day treatment and blue squares a thirty-day treatment (n = 13 for each treatment).

Table 3. Co-occurrence analysis (C-score) using randomized matrices of presence and absence of species, for each treatment. Obs. = observed value with co-occurrence index; Exp. = expected value from the randomized matrices; p (obs > exp) = probability of a value greater than the observed one, from the randomization process. Level of significance: p ≤ 0.05.

Index	Values	5 days	15 days	30 days
C-score	Obs.	2,85	3,19167	4,47436
	Exp.	2,94763	3,15484	4,52778
	p (obs > exp)	0,9098	0,3354	0,7096

Discussion

In this experimental study conducted in a lowland area of the Brazilian Amazon during the high-water season, the prevalence of young fish in the attractors was observed, and there was no evidence of structure in fish assemblages. Amazonian floodplains are dynamic environments and rich in fish species (Lowe-McConnell 1999). Given this scenario, we expected fish to assemble on the attractors through biotic interactions, resulting in interspecific competition (MacArthur 1972, Pianka 1974). Several studies suggest that biotic interactions are more influential in assemblages of tropical fish with high species richness (Willis et al. 2005, Arrington and Winemiller 2006, Montaña et al. 2014, Fitzgerald et al. 2017). However, such observations more frequently occurred during low-water periods when habitat availability decreases, and predation pressure overall increases (Hoeinghaus et al. 2003).

Notably, during the high-water period, our results demonstrated that the fish assemblages at the attractors did not exhibit a predictable organizational structure throughout the colonization time. This indicates that the occurrence of the species may have happened randomly, with no evidence of competitive forces acting in the assembly of these assemblages. Few studies carried out in the Amazonian floodplains have found that fish assemblages are stochastically built, such processes seem to be more likely in the high-water period (Goulding et al. 1988, Jepsen 1997, Saint-Paul et al. 2000, Santorelli et al. 2014). A general model of community building predicts that this process must be neutral, where both the effect of competition and habitat selection is weak (Weiher and Keddy 1995). In the high-water period, the flooded area expands, distributing the species over a larger area and reducing their competitive and/or predatory interactions. Under these conditions, in the floodplains, biological processes may have a weak influence, generating random patterns of colonization.

The period of the experiment (high waters) may have influenced this random pattern of colonization of the attractors, since the high connectivity between environments, provided by the flood, allows fish to disperse and colonize the newly available areas so that the occurrence of species is common in several habitats (Arrington et al. 2005, Freitas et al. 2010). Additionally, the habitat of aquatic herbaceous abounds, representing no limiting resource and reducing the environmental filtering effect. Thus, the high-water condition seems to have enabled similar opportunities for the colonizing species so that different combinations of species were possible, regardless of the time interval considered. The increased mobility of fish during this period may also increase the chances of fish only shortly visiting the experiment. Despite that juveniles were present for the entire month of the experiment. Although our results of the assembly process only represent the taxonomic pattern of species assembly and regarding the massive presence of juveniles as colonizers, the occupation may not be totally random if other functional aspects are considered. This result raises important insight that availability of floating habitat may be always limited for juveniles in the early life stage and corroborates the hypothesis that this is the limiting factor regulating fish recruitment for many Amazonian fish (Bayley et al. 2018, Castello et al. 2019).

In general, the fish assemblages in the attractors were characterized by the occurrence of young individuals by both, small-sized (*Mesonouta festivus*, *Pyterophylum scalare*) and larger or medium-sized species (*Hoplias malabaricus*, *Cichla monoculus*, *Serasalmus* spp.); many were sedentary species. Other experimental studies, using artificial aquatic herbaceous, have also registered specimens of small fish, such as the study by Teixeira-de-Melo et al. (2015), in which the specimens measured 4.6 cm ± 0.2 SE, and Santos et al. (2011), with fish measuring 10 cm on average. In natural aquatic macrophytes banks, Sánchez-Botero and Araújo-Lima (2001) and Röpke et al. (2014) found that the fish assemblages collected in aquatic herb banks were represented mainly by juveniles and small-sized species (90%). These results confirm the role that aquatic herbaceous play as shelter for young fish and small species, which use these environments mainly to prevent predation (Araújo-Lima et al. 1986).

In the Amazon, very few works used attractors (artificial microhabitats) to study fish assemblage (Yamamoto et al. 2014, Arrington and Winemiller 2006), usually using submerged reefs. The use of midwater attractors made by a large tangle of branches has been described as used by fishermen to capture the discus fish (*Symphysodon aequifasciatus*, Pellegrin 1904) during the low-water in the Piagaçu-Purus Sustainable Development Reserve (RDS-PP), lower Purus River, Amazonas (Rossoni et al. 2014). Attractors have been used and tested in different environments to improve and restore fishery by increasing fish abundance by enhancing recruitment (Schroeder 1987, Bolding et al. 2004). Our results support the use of floating artificial habitat to increase fish recruitment and support the restoration of fish population when habitat availability was reduced by natural (short flood pulses due to natural hydrological variation) or anthropogenic (flow control) causes.

It may be worth mentioning here that we tried to replicate this experiment during the low-water season (October 2017) following the same protocol implemented during the high-water period. Each attractor was about 5 meters distant from each other and 2 m distant from the marginal area once banks of aquatic herbaceous were absent. Five days after the period of periphyton colonization, during the first sampling, it was observed that tufts of sisal rope were present only as remains and no longer were present after the 5 days (Figure S2). No fish were captured, and the colonization process was not observed. One hypothesis is that sisal was consumed by the detritivorous, periphytivous fishes when foraging the periphyton and macroinvertebrates which colonize the tufts of sisal rope in the attractors. Despite the experiment failure, this observation raises important evidence for food limitation during low-water (Lowe-McConnell 1987) and may help to design new studies using attractors to understand the role of food and habitat availability for fish assemblages in low-water season when floating habitats are almost nonexistent.

Due to the advantages of the method, a discussion about the material used is also current, mainly regarding the use of plastic structures due to the problem of plastic residues (Wilbur 1978, Baumann et al. 2016). Despite the lower durability, researchers have argued that attractors made of natural material should be preferred (Baumann et al. 2016). Bright gray curly ribbon and green light sticks were used by Gentil et al. (2020) as floating attractors in the Araguaia River and could be a non-natural option during low-water season. As natural options, the use of midwater reefs made of wood and branches should be considered.

In this experiment, we tried to control many confounding factors that would weaken the interpretation of the results. However, some points may limit the experiment and should be improved in future study replications. The small size of the attractors may have contributed to these results, as fish would gather around the attractor in higher numbers than it would support. Larger attractor should be used in the future or different sizes tested. The number of days of experiment was too short, and treatments should regard longer periods than 30 days with larger períodos between samplings. Freitas et al. (2002) and Yamamoto et al. (2014) conducted experiments with artificial reefs for about one year, with at least two months between samplings. Arrington and Winemiller (2006) repeated the experiments with the attractors in low, falling, and rising waters, and sampling occurred always after 21–24 days. These authors identified a temporal effect, Yamamoto et al. (2014) and Arrington and Winemiller (2006) found seasonal differences in the species occupying the attractors. Linked to the length of the experiment, the period of the peak of high water may also limit the assembly processes and changes in species composition, and future studies may start earlier. As already mentioned, our experiment failed, having data for seasonality, and future studies would elucidate the effect of seasonality on the attractors use. Finally, performing experiments with attractors regarding interannual variation would elucidate the effect of habitat limitation in juveniles' colonization of attractors, as well as the value of using these structures for fish management and conservation.

Supplementary Material

The following online material is available for this article:

Figure S1 - Adapted fishing seine net used for fish collection during the experiment.

Figure S2 - The remains of sisal tufts were observed on the attractors during the first fish collection conducted in the low-water season (October 2017).

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Authors Contributions

Silvia I.B. da Rocha: Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

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

Sidinéia A. Amadio: Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

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Conflicts of Interest

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

Data Availability

The data collected and generated during this study are available in the Biota Neotropica Dataverse at https://doi.org/10.48331/scielodata.LEUSD8. The authors confirm that all data necessary for reproducing the study findings are available in the designated dataset.

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Inventory

Preliminary checklist of dragonflies (Insecta: Odonata) of the Santa Catarina State, Brazil

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Abstract: In this study, we provide a checklist of the species of Odonata (Insecta) from the state of Santa Catarina (southern Brazil), along with their location records in the municipalities across the state (whenever possible). We compiled 147 species from 60 genera and nine families, making Santa Catarina the second state with the most Odonata species recorded in southern Brazil. The families with the highest number of species were Libellulidae (54 species from 18 genera), followed by Coenagrionidae (36 species from 17 genera), Gomphidae (20 species from ten genera) and Aeshnidae (15 species from eight genera). Several regions of Santa Catarina are unexplored (mostly the westernmost and central regions of the state), whereas the knowledge in the southern coast and the subtropical highland grasslands remains restricted to sparse occurrence records. Moreover, the distribution records in the state show an enormous historical track associated with the establishment of late entomologists in the region. Our study highlights the role of Atlantic Forest biome in maintaining high levels of diversity of Odonata species richness in Brazil and also shows that many areas in subtropical forests in Brazil are not adequately sampled.

Keywords: *Anisoptera; aquatic insects; Atlantic Forest; Inventory; Zygoptera.*

Checklist preliminar de libélulas (Insecta: Odonata) do Estado de Santa Catarina, Brasil

Resumo: Neste estudo, fornecemos um checklist das espécies de Odonata (Insecta) do estado de Santa Catarina (sul do Brasil), juntamente com seus registros de localização nos municípios do estado (quando disponíveis na literatura). Compilamos 147 espécies distribuídas em 60 gêneros e nove famílias, tornando Santa Catarina o segundo estado com mais espécies de Odonata registradas na região Sul do Brasil. As famílias com maior número de espécies foram Libellulidae (54 espécies distribuídas em 18 gêneros), seguida por Coenagrionidae (36 espécies distribuídas em 17 gêneros), Gomphidae (20 espécies distribuídas em dez gêneros) e Aeshnidae (15 espécies distribuídas em oito gêneros). Diversas regiões de Santa Catarina seguem inexploradas (principalmente as regiões centrais e do extremo oeste do estado), enquanto conhecimento no litoral sul e campos de altitude subtropicais permanecem restritos a registros pontuais de ocorrência. Além disso, os registros de distribuição no estado mostram um enorme legado histórico associado à fixação de entomologistas tradicionalmente lotados na região. Nosso estudo destaca o papel do bioma Mata Atlântica na manutenção de altos níveis de diversidade da riqueza de espécies de Odonata no Brasil e também mostra que muitas áreas de florestas subtropicais no Brasil não são amostradas adequadamente.

Palavras-chave: *Anisoptera; Insetos aquáticos; Inventário; Mata Atlântica; Zygoptera.*

Introduction

Odonata (dragonflies and damselflies) constitute a medium order of insects whose adults show terrestrial habits, whereas the large majority of their larval stages have aquatic habit. Odonata play important roles in freshwater ecosystems (May 2019). Given their generalist predatory habit in both larval and adult stages, they are key to the regulation of pest populations and mediation of community-level processes such as trophic cascades (Arnaud et al. 2022). To date, more than 6400 species of Odonata are recorded globally (Paulson et al. 2024), and the majority of the species is found in the Neotropics (Kalkman et al. 2008). In Brazil, the largest country in South America, more than 900 species of Odonata are recorded (Pinto 2024a). However, the knowledge about the Odonata diversity is highly heterogeneous throughout the country (De Marco & Vianna 2005). Despite the increase of species descriptions and regional checklists (Costa et al. 2000, Rodrigues & Roque 2017, Costa & Oldrini 2005, Koroiva et al. 2021, 2020), the knowledge about the species occurrence and distribution is still unevenly distributed in Brazil, preventing accurate assessment of diversity as well as conservation policies (Cardoso et al. 2011).

In particular, the Southern region of Brazil (states of Paraná, Rio Grande do Sul and Santa Catarina) remains as one of the least studied in the country (Miguel et al. 2017), and the only state checklist of Odonata in the region is available for the state of Rio Grande do Sul (Dalzochio et al. 2018). The state of Santa Catarina is located in the Southern region of Brazil (Figure 1) has an area of 95,730.690 km², occupying 1.12%

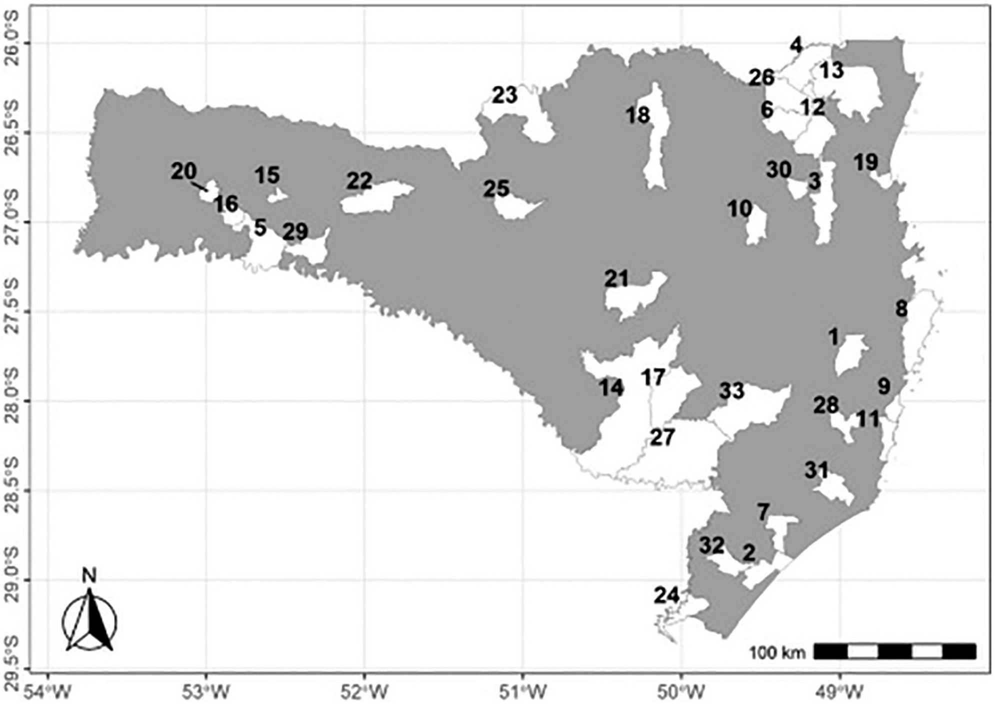

Figure 1. Municipalities in the state of Santa Catarina with known records of Odonata species. For code numbers, see Table S2.

of the Brazilian territory and the 19th position of territorial extension of Brazilian states; by 2022, the state population reached over 7.5 Mi people, currently among the ten states with highest population density in the country (IBGE 2022). The original vegetation type in the state is entirely situated within the range of the Atlantic Forest biome (IBGE 2019), a biome long considered a hotspot of biodiversity and as a priority for conservation (Brooks et al. 2006). Although Santa Catarina is the smallest state in the region, native forests cover 64% of the state territory, making SC the state with largest area of native vegetation in the Southern region of Brazil; nevertheless, trends of continuous loss of native vegetation are reported for the state over the 21st century (Projeto MapBiomas 2023).

With regards to the knowledge on the diversity of Odonata in Santa Catarina, the large majority of the studies focusing odonates in the state over the last 120 years encompass descriptions of new species, while the few ecological studies focused on larval stages of the order (Pires et al. 2020, Siegloch et al. 2018, Turra et al. 2018), preventing species-level assessments. In fact, as most of the available information on the known diversity of Odonata in SC is fragmentary and dispersed across taxonomic keys without reference to their known locations across the municipalities of the state (Lencioni 2005, 2006, Heckman 2006, 2008), or taxon-specific synopsis (Table S1). Considering such knowledge gap, the main goal of this study is to provide a preliminary checklist of the species of Odonata recorded for the state of Santa Catarina through searches in the bibliography.

Material and Methods

1. *Study area*

The state of Santa Catarina (SC; geographical coordinates: 25° 57’ 41” – 29° 23’ 55” S; 48° 19’ 37” – 53° 50’ 00” W), is bordered by the states of Rio Grande do Sul (south) and Paraná (north), and by the Province of Misiones (Argentina) to the west. The major relief units in SC include the lowlands in the coastal plain, the eastern (altitudes up to 400 m) and the western plateaus (mean altitudes ranging between 400–800 m covering fluvial depressions and plateaus, but also highland grassland plateaus located at altitudes >1,200 m) (Rocha 2016).

Across the state, annual precipitation ranges between 1,400–2,200 mm (Wrege et al. 2012). According to the Köppen classification system, the climate types in the state range from Cfa (humid subtropical with hot summers) in the coastal and plateaus areas (annual average temperatures ranging between 15–20 °C), while in the highland grassland plateaus, climate type is Cfb (humid subtropical with cool summers), with annual average temperature ranging between 12–15 °C (Alvares et al. 2013). Native vegetation typed in the state include Seasonal and Evergreen forests in the central and western regions, *restinga* in the Atlantic coast (Leão et al. 2014) and subtropical grasslands in the highland plateaus (Overbeck et al. 2024).

2. *Data sources and elaboration of the list*

To prepare the checklist, we compiled occurrence records of odonate species from a total number of 107 data sources. These data sources derived from a combination of procedures that included: screening of published and grey literature (items I and II); and consultation to databases of odonate species records (items III-V).

For literature screening, we assembled a list of (I) 101 publications (scientific articles, books and book sections) published between 1905 and 2023, after revising the reference list available in published catalogs of odonate species from Brazil (De Marco & Vianna 2005) and Neotropical region (Santos 1988) and regional checklists of odonate species for Brazilian states recently published in the journal (Dalzochio et al. 2018, Koroiva et al. 2021, 2020). (II) We also searched for

Table 1. List of odonate species recorded for the state of Santa Catarina, Brazil (and corresponding location). For references and municipalities codes, please check Tables S1 and S2. In cases the reference sources did not provide the location record, only the state is provided.

Suborder	Family	Species	Reference/location
Anisoptera	Aeshnidae	*Anax concolor* Brauer, 1865	R27: Corupá, São Bento do Sul; R73: State only;
		Castoraeschna decurvata Dunkle & Cook, 1984	R64: Blumenau; R67: Blumenau
		Castoraeschna januaria (Hagen, 1867)	R22: Seara; R73: State only; R102: State only;
		Coryphaeschna adnexa (Hagen, 1861)	R102: State only;
		Coryphaeschna perrensi (McLachlan, 1887)	R22: Seara; R45: Joinville; R73: State only;
		Coryphaeschna viriditas Calvert, 1952	R22: Seara
		Gynacantha bifida Rambur, 1842	R56: State only; R73: State only;
		Limnetron antarcticum Förster, 1907	R43: Seara; R104: Blumenau
		Limnetron debile (Karsch, 1891)	R43: Seara
		Remartinia luteipennis (Burmeister, 1839)	R17: Seara; R23: Seara; R64: Blumenau; R73: State only; R104: Morro dos Conventos, Seara
		Rhionaeschna bonariensis (Rambur, 1842)	R63: Seara; R73: State only; R104: Jaraguá do Sul, Seara
		Rhionaeschna confusa (Rambur, 1842)	R22: Seara; R63: Seara; R73: State only; R104: Seara
		Rhionaeschna planaltica (Calvert, 1952)	R1: State only; R21: Seara; R22: Seara; R59: Seara; R63: Seara; R73: State only; R104: Seara, Jaraguá do Sul, Joinville, Blumenau
		Rhionaeschna punctata (Martin, 1908)	R22: Jaraguá do Sul, Seara; R63: Seara; R73: State only; R85: São Joaquim, Urubici; R104: Seara, Jaraguá do Sul
		Triacanthagyna nympha (Navás, 1933)	R14: Blumenau; R62: Blumenau, Joinville; R104: Blumenau, Joinville
	Corduliidae	*Navicordulia aemulatrix* Pinto & Lamas, 2010	R82: São Bento do Sul; R83: Timbó; R102: State only;
		Navicordulia atlantica Machado & Costa, 1995	R52: Joinville; R73: State only; R100: Joinville; R104: Joinville
		Neocordulia androgynis (Selys, 1871)	R46: Painel; R73: State only; R102: State only;
		Neocordulia santacatarinensis Costa, Ravenello & Souza-Franco, 2008	R76: Ponte Serrada
	Gomphidae	*Aphylla producta* Selys, 1854	R48: Joinville; R102: State only;
		Archaeogomphus densus Belle, 1982	R36: Seara; R102: State only;
		Archaeogomphus globulus Belle, 1994	R50: Corupá; R73: State only; R102: State only;
		Cyanogomphus waltheri Selys, 1873	R16: Seara; R35: Seara; R70: Corupá; R73: State only; R94: Corupá; R102: State only; R104: Corupá
		Gomphoides praevia St. Quentin, 1967	R25: Seara; R28: Seara; R73: State only; R102: State only;
		Idiogomphoides demoulini (St. Quentin, 1967)	R41: Ibirama; R70: Ibirama; R73: State only; R102: State only;
		Phyllocycla pallida Belle, 1970	R28: Seara; R42: Seara; R73: State only; R102: State only; R104: Seara
		Phyllocycla propinqua Belle, 1972	R28: Seara; R42: Seara; R73: State only; R102: State only;
		Phyllocycla viridipleuris (Calvert, 1909)	R16: Seara; R28: Seara; R42: Seara; R73: State only; R102: State only;
		Phyllogomphoides annectens (Selys, 1869)	R28: Seara; R40: Seara; R104: Seara

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Suborder	Family	Species	Reference/location
Anisoptera	Gomphidae	*Phyllogomphoides regularis* (Selys, 1873)	R28: Seara; R40: Seara; R73: State only; R102: State only;
		Progomphus basistictus Ris, 1911	R32: Seara; R73: State only;
		Progomphus complicatus Selys, 1854	R32: State only; R91: State only
		Progomphus costalis Hagen in Selys, 1854	R32: Lages; R104: Lages
		Progomphus elegans Belle, 1973	R32: Águas Mornas
		Progomphus gracilis Hagen in Selys, 1854	R106: State only;
		Progomphus lepidus Ris, 1911	R32: Seara; R73: State only; R104: Seara
		Progomphus virginiae Belle, 1973	R32: Seara; R73: State only;
		Tibiagomphus uncatus (Fraser, 1947)	R30: Seara; R35: Seara; R73: State only; R94: Seara; R102: State only; R104: Seara
		Zonophora diversa Belle, 1983	R39: Seara; R73: State only; R102: State only; R104: Seara
	Libellulidae	*Brachymesia furcata* (Hagen, 1861)	R38: Florianópolis
		Brechmorhoga nubecula (Rambur, 1842)	R4: Águas Mornas; R9: Águas Mornas
		Dasythemis mincki (Karsch, 1890)	R6: Águas Mornas; R104: Seara
		Dasythemis venosa (Burmeister, 1839)	R9: Blumenau
		Dythemis nigra Martin, 1897	R9: State only; R12: State only
		Dythemis sterilis Hagen, 1861	R73: State only;
		Erythemis attala (Selys in Sagra, 1857)	R8: Águas Mornas; R88: São Bento do Sul; R102: State only;
		Erythemis peruviana (Rambur, 1842)	R103: Tubarão
		Erythemis plebeja (Burmeister, 1839)	R93: Blumenau; R103: Tubarão
		Erythemis vesiculosa (Fabricius, 1775)	R88: Itajaí; R93: Blumenau; R97: Florianópolis; R103: Joinville
		Erythrodiplax anomala (Brauer, 1865)	R18: State only; R38: Florianópolis
		Erythrodiplax atroterminata (Ris, 1911)	R18: State only; R29: State only; R102: State only; R104: Seara
		Erythrodiplax castanea (Burmeister, 1839)	R7: Águas Mornas; R18: Seara Águas Mornas; R73: State only;
		Erythrodiplax chromoptera Borror, 1942	R103: Imbituba
		Erythrodiplax corallina (Brauer, 1865)	R107: State only;
		Erythrodiplax diversa (Navás, 1916)	R11: State only; R73: State only; R104: State only
		Erythrodiplax fusca (Rambur, 1842)	R7: Águas Mornas; R18: Seara; R38: Florianópolis; R73: State only;
		Erythrodiplax hyalina Förster, 1907	R18: Seara Águas Mornas; R73: State only; R104: Seara
		Erythrodiplax juliana Ris, 1911	R7: Águas Mornas; R18: Águas Mornas; R104: Seara
		Erythrodiplax media Borror, 1942	R7: State only; R18: Blumenau, Seara, Águas Mornas; R29: State only; R73: State only; R103: Araranguá; R104: Seara
		Erythrodiplax melanorubra Borror, 1942	R18: Seara; R88: State only

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Suborder	Family	Species	Reference/location
Anisoptera	Libellulidae	*Erythrodiplax ochracea* (Burmeister, 1839)	R73: State only;
		Erythrodiplax paraguayensis (Förster, 1905)	R29: State only
		Libellula herculea Karsch, 1889	R2: Águas Mornas; R6: Águas Mornas; R88: Seara
		Macrothemis heteronycha (Calvert, 1909)	R70: Seara; R72: Seara; R104: Seara
		Macrothemis imitans Karsch, 1890	R9: Águas Mornas; R73: State only; R104: Seara
		Macrothemis marmorata Hagen, 1868	R9: Águas Mornas
		Macrothemis musiva Calvert, 1898	R9: Águas Mornas
		Miathyria marcella (Selys in Sagra, 1857)	R97: Florianópolis
		Micrathyria catenata Calvert, 1909	R61: Blumenau; R73: State only; R104: Blumenau
		Micrathyria didyma (Selys in Sagra, 1857)	R7: Águas Mornas
		Micrathyria eximia Kirby, 1897	R7: State only; R19: State only; R61: Ponte Alta do Sul
		Micrathyria hesperis Ris, 1911	R61: Ponte Alta do Sul; R73: State only;
		Micrathyria hypodidyma Calvert, 1906	R61: State only; R73: State only; R104: Seara
		Micrathyria ocellata Martin, 1897	R51: Blumenau; R61: State only; R73: State only; R103: Criciúma, Tubarão
		Micrathyria stawiarskii Santos, 1953	R51: Ponte Alta, Blumenau, Lages; R61: Lages, Ponte Alta; R73: State only; R104: Seara, Lages
		Micrathyria ungulata Förster, 1907	R7: Águas Mornas; R61: State only
		Nephepeltia flavirons (Karsch, 1889)	R104: Papanduva
		Nephepeltia phryne (Perty, 1834)	R3: State only; R7: State only; R9: Blumenau; R92: Blumenau; R104: Blumenau
		Orthemis ambinigra Calvert, 1909	R12: Blumenau; R20: Seara; R73: State only; R87: Blumenau, Seara; R104: Blumenau, Seara
		Orthemis discolor (Burmeister, 1839)	R38: Florianópolis; R83: Timbó; R103: Criciúma
		Orthemis schmidti Buchholz, 1950	R105: State only;
		Pantala flavescens (Fabricius, 1798)	R31: Balneário Piçarras; R102: State only; R103: Garopaba, Tubarão
		Perithemis domitia (Drury, 1773)	R6: State only; R9: Blumenau; R102: State only;
		Perithemis icteroptera (Selys in Sagra, 1857)	R9: Blumenau; R15: Blumenau; R73: State only; R102: State only; R103: Tubarão
		Perithemis tenera (Say, 1840)	R102: State only; R103: Tubarão
		Rhodopygia cardinalis (Erichson in Schomburgk, 1848)	R104: São Bento do Sul
		Tramea abdominalis (Rambur, 1842)	R10: State only; R102: State only;
		Tramea binotata (Rambur, 1842)	R37: Florianópolis
		Tramea cophysa Hagen, 1867	R37: Porto União, Corupá, Pinhal, Seara, São Bento do Sul; R102: State only; R103: Corupá, Florianópolis
		Tramea darwini Kirby, 1889	R37: Porto União, Corupá; R73: State only; R102: State only; R103: Corupá
		Uracis ovipositrix Calvert, 1909	R53: Rio das Antas; R73: State only;

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Suborder	Family	Species	Reference/location
Anisoptera	Libellulidae	*Zenithoptera anceps* Pujol-Luz, 1993	R47: São Francisco do Sul, Joinville; R54: São Francisco do Sul, Joinville
		Zenithoptera lanei Santos, 1941	R47: Rio das Antas; R54: Rio das Antas
Zygoptera	Calopterygidae	*Hetaerina cruentata* (Rambur, 1842)	R103: Joinville
		Hetaerina hebe Selys, 1853	R103: Joinville
		Hetaerina longipes Hagen in Selys, 1853	R5: State only; R44: São Bento do Sul; R65: State only; R79: State only; R81: Seara; R104: Seara, São Bento do Sul
		Hetaerina mendezi Jurzitza, 1982	R44: Seara; R65: State only; R79: State only; R103: Seara; R104: Seara
		Hetaerina proxima Selys, 1853	R103: Joinville
		Mnesarete borchgravii (Selys, 1869)	R65: State only; R69: Blumenau, Joinville, São Bento do Sul; R79: State only; R81: Seara; R102: State only; R103: Joinville; R104: Blumenau, Joinville, São Bento do Sul
		Mnesarete pruinosa (Hagen in Selys, 1853)	R65: State only; R69: Seara; R79: State only; R81: Seara; R102: State only; R103: Seara; R104: Seara
	Coenagrionidae	*Acanthagrion aepiolum* Tennessen, 2004	R26: Seara; R84: Seara
		Acanthagrion ascendens Calvert, 1906	R33: Seara; R79: State only; R84: Seara
		Acanthagrion gracile (Rambur, 1842)	R26: Seara; R84: Seara; R104: Blumenau, Seara
		Acanthagrion lancea Selys, 1873	R33: State only; R71: State only; R79: State only; R84: State only
		Aceratobasis macilenta (Rambur, 1842)	R72: Joinville; R75: Joinville; R81: Joinville; R102: State only; R103: Joinville; R104: Joinville
		Argentagrion ambiguum (Ris, 1904)	R77: Seara; R102: State only; R104: Seara
		Argia albistigma Hagen in Selys, 1865	R71: State only; R79: State only; R104: Seara, São Bento do Sul
		Argia collata Selys, 1865	R104: São Bento do Sul
		Argia croceipennis Selys, 1865	R78: Ponte Serrada; R79: State only; R104: Seara, São Bento do Sul, Águas Mornas
		Argia cyathigera Navás, 1934	R71: State only; R79: State only; R104: Seara
		Argia fumigata Hagen in Selys, 1865	R104: São Bento do Sul
		Argia lilacina Selys, 1865	R104: Seara
		Argia modesta Selys, 1865	R104: São Martinho, Campo Alegre
		Argia serva (Hagen in Selys, 1865)	R71: State only; R79: State only; R81: Seara; R104: São Martinho, Seara
		Forcepsioneura haerteli Machado, 2001	R60: Blumenau; R65: State only; R79: State only; R102: State only; R104: Blumenau
		Forcepsioneura sancta (Hagen in Selys, 1860)	R102: State only; R104: Seara
		Fredyagrion andromache (Hagen in Selys, 1876)	R104: Seara
		Homeoura chelifera (Selys, 1876)	R77: Seara; R102: State only; R104: Seara
		Ischnura capreolus (Hagen, 1861)	R102: State only
		Ischnura fluviatilis Selys, 1876	R104: Seara

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Suborder	Family	Species	Reference/location
Zygoptera	Coenagrionidae	*Leptagrion macrurum* (Burmeister, 1839)	R57: Joinville; R66: Joinville; R71: State only; R79: State only; R81: Joinville; R104: Joinville, São Bento do Sul
		Mecistogaster amalia (Burmeister, 1839)	R81: Seara; R86: Blumenau, Joinville, São Bento do Sul; R95: Blumenau, Joinville; R103: Joinville; R104: Seara
		Mecistogaster mielkei Lacerda & Machado, 2019	R95: Joinville, Campo Alegre, São Bento do Sul; R102: State only
		Minagrion mecistogastrum (Selys, 1976)	R71: State only; R79: State only; R96: Joinville
		Nathaliagrion perlongum (Calvert, 1909)	R57: Joinville; R71: State only; R79: State only; R99: State only; R103: Joinville
		Neoneura confundens Wasscher & Van't Bosch, 2013	R90: State only; R102: State only
		Neoneura jurzitzai Garrison, 1999	R55: Seara; R65: State only; R79: State only; R81: Seara; R104: Joinville
		Neoneura leonardoi Machado, 2005	R68: Seara; R71: State only; R79: State only; R102: State only; R104: Joinville
		Oxyagrion brevistigma Selys, 1876	R71: State only; R79: State only; R102: State only
		Oxyagrion hempeli Calvert, 1909	R24: Seara; R34: Seara; R71: State only; R102: State only; R104: Seara
		Oxyagrion simile Costa, 1978	R102: State only; R103: Ponte Alta
		Oxyagrion terminale Selys, 1876	R34: Seara; R71: State only; R79: State only; R102: State only; R104: Seara
		Peristicta aeneoviridis Calvert, 1909	R85: Turvo, Lages, Blumenau, Lajeado Grande; R104: Seara
		Telebasis carmesina Calvert, 1909	R80: Seara; R81: Seara; R104: Seara
		Telebasis filiola (Perty, 1834)	R86: Joinville, São Bento do Sul
		Telebasis theodori (Navás, 1934)	R80: Seara, São Bento do Sul; R81: Seara; R103: São Bento do Sul; R104: Seara, São Bento do Sul
	Heteragrionidae	*Heteragrion luizfelipei* Machado, 2006	R74: Joinville, Urubici; R81: Joinville, Seara; R89: Joinville, Seara; R101: Seara, Urubici; R103: Seara, Urubici; R104: Joinville, Seara, Urubici
		Heteragrion triangulare Hagen in Selys, 1862	R89: State only; R94: State only; R101: State only; R104: Seara
	Lestidae	*Archilestes exoletus* (Hagen in Selys, 1862)	R13: Águas Mornas; R79: State only; R104: Águas Mornas
		Lestes auritus Hagen in Selys, 1865	R65: State only; R79: State only; R98: Seara; R104: Seara
		Lestes bipupillatus Calvert, 1909	R49: Seara; R98: Seara; R103: Seara; R104: Seara
		Lestes paulistus Calvert, 1909	R49: Seara
		Lestes pictus Hagen in Selys, 1862	R49: Seara; R104: Seara
		Lestes spatula Fraser, 1946	R49: Seara
		Lestes tricolor Erichson, 1848	R65: State only; R79: State only; R98: State only; R104: Seara
	Megapodagrionidae	*Allopodagrion brachyurum* De Marmels, 2001	R58: Seara; R65: State only; R79: State only; R81: Seara; R104: Seara
		Allopodagrion contortum (Hagen in Selys, 1862)	R58: São Bento do Sul; R65: State only; R79: State only; R103: Florianópolis; R104: São Bento do Sul

records in doctoral thesis and master dissertations specifically targeted on systematic and taxonomy of Neotropical odonate taxa; in each bibliographic source, we investigated the location of species records to cross-examine the occurrence of each species for the state.

Furthermore, we consulted the following online public and personal databases, as follows: (III) The Brazilian Fauna Taxonomic Catalog ("Catálogo Taxonômico da Fauna do Brasil"; http://fauna.jbrj.gov.br) (Pinto 2024a); (IV) range distribution maps available at IUCN (International Union for Conservation of Nature) (IUCN 2023); and (V) personally updated versions of previously published databases (De Marco & Vianna 2005, Ellenrieder 2011) provided with the help of researchers and collaborators (see Acknowledgments) (Table S1).

We also gathered information about the municipalities where the species were collected, whenever available in the bibliographic records (Table S2; Figure 1). For the systematic classification, we followed the list all of the valid species of Odonata available in the World Odonata list website (Paulson et al. 2024).

We double-checked species records according to recent synopsis and reviews (Ellenrieder & Garrison 2003, Vilela et al. 2023, Lencioni 2022) and species synonymies for specific genera, as follows: for the genus *Navicordulia* Machado & Costa, 1995 (Corduliidae), *N. mielkei* and *N. miersi* are considered synonymies of *N. atlantica* Machado & Costa, 1995 (Pinto et al. 2022). For the genus *Perithemis* Hagen, 1861 (Libellulidae), we followed the synonymy proposed by Paulson (2020), which considers records of *P. mooma* Kirby, 1889 as *P. tenera* (Say, 1840). For the genus *Tramea* Hagen, 1861 (Libellulidae), *T. calverti* Muttkowski, 1910 is synonymized with *T. darwini* Kirby, 1889 (Lorenzo-Carballa et al. 2020). As for the genus *Orthemis* Hagen, 1861 (Libellulidae), we considered previous records of *O. ferruginea* (Fabricius, 1775) as *O. discolor* (Burmeister, 1839), as revised by recent cytogenetic studies (Mola et al. 2021) that attempt to solve the problematic status of species within this genus.

Results and Discussion

1. Species list

The total number of Odonata species recorded for the state of Santa Catarina is 147 (distributed in 60 genera and nine families; Table 1). The families with the highest number of species were Libellulidae (54 species from 18 genera) and Coenagrionidae (36 species from 17 genera), followed by Gomphidae (20 species from ten genera) and Aeshnidae (15 species from eight genera). The remaining families (Calopterygidae, Lestidae and Corduliidae) were represented by two genera each and nine, eight and four species, respectively; Heteragrionidae and Megapodagrionidae were represented by a single genus and two species each (Table 1). The species with the highest number of records in the state were *Rhionaeschna planaltica* (Calvert, 1952) and *R. punctata* (Martin, 1908) (Aeshnidae), Erythrodiplax media Borror, 1942, *Tramea cophysa* Hagen, 1867 (Libellulidae), *Mnesarete borchgravii* (Selys, 1869) (Calopterygidae), *Mecistogaster amalia* (Burmeister, 1839) and *Peristicta aeneoviridis* Calvert, 1909) (Coenagrionidae), recorded in four locations (Table 1).

Some species cited by Heckman (2006) were only known for other regions of South America or Brazil and were not added to the final checklist to avoid mistakes. In specific, *Erythrodiplax connata* (Burmeister, 1839) (Libellulidae) is thought to be confined Patagonia (western Argentina and Chile) (Paulson 2003), and records outside these countries are questionable (Lozano & Muzón 2020); *Micrathyria pseudhypodidyma* Costa, Lourenço & Viera, 2002 (Libellulidae) is known to central and southeastern Brazil (states of Goiás and Rio de Janeiro, and Distrito Federal) (Costa et al. 2002), and is reported as vulnerable species in those regions (Ellenrieder 2009); *Zonophora campanulata* (Burmeister, 1839) (Gomphidae) encompasses a group of subspecies with allopatric distribution in central and southeastern Brazil (as stated in the original review and further studies on Brazilian Gomphidae), while only records of the sister clade (*Z. diversa* Belle, 1983) are valid to the state so far (Belle 1983, Almeida et al. 2013). Checklists for states in the Brazilian Amazon and regional inventories in central Brazil mention the occurrence of *Aphylla distinguenda* (Campion, 1920) (Gomphidae) and *Perithemis cornelia* (Say, 1840) (Libellulidae) in SC (Miranda Filho et al. 2022, Barbosa et al. 2019). Both species are known to central and northern Brazil and their corresponding sources do not mention their occurrence in Santa Catarina, most likely constituting erroneous records. *Heteragrion beschkii* Hagen in Selys, 1862 (Heteragrionidae) is cited as occurring in Santa Catarina based on personal records (Vilela & Guillermo-Ferreira 2021). However, recent synopsis on the genus do not confirm the occurrence of *H. beschkii* in SC (Vilela et al. 2023), and this species was thus not added to the final checklist.

Discussion

The 147 species listed for the state of Santa Catarina represent 16% of the known species of Odonata in Brazil (918 spp. (Pinto 2024a)). With the results presented in this study, the diversity of Odonata recorded for state of Santa Catarina is the second in number of species in the Southern region of Brazil, behind Rio Grande do Sul (184 species) (Dalzochio et al. 2018, Pires et al. 2019, Muzón & Lozano 2020), although no checklist for the state of Paraná has been published to date.

The total number of species recorded for the state of Santa Catarina is also lower than the diversity recorded for other states of the country, such as Minas Gerais (344 spp.) (Vilela 2023), São Paulo, 251 spp. (Costa et al. 2000), Mato Grosso do Sul, 198 spp. (Rodrigues & Roque 2017), Amazonas, 335 spp. (Koroiva et al. 2020). However, this result conveys rather important information both under zoogeographical and conservation perspectives which should be taken into consideration. The observed diversity of Odonata in SC corresponds to 80% of the number of species recorded for the neighboring state of Rio Grande do Sul (Dalzochio et al. 2018, Pires et al. 2019, Muzón & Lozano 2020), despite the area of SC being less than half of the latter (IBGE 2022). In fact, the number of odonate species recorded in SC is similar to the state of Espírito Santo (a subtropical state of similar area entirely situated within the Atlantic Forest; 180 species (Costa & Oldrini 2005). Considering the small area of the state of, our study highlights the prominent role of Atlantic Forest biome in maintaining high levels of diversity of Odonata species richness in Brazil and the Neotropics (Paulson 2006).

More than 50% of the species recorded in SC fall under the 'LC category' of conservation by IUCN (i.e., species with widespread distribution). This is likely because more than 80% of the species recorded in SC are shared with preserved areas of the state of Paraná

(Araujo & Pinto 2021), and R io Grande do Sul (Dalzochio et al. 2018), as well as the Argentinian province of Misiones to the west (Lozano et al. 2020) also situated within the Atlantic Forest biome. So far, *Forcepsioneura haerteli* Machado, 2001 (Coenagrionidae) is the single species recorded in the state listed as 'Endangered under criteria', whereas nine species (Appendix 2) fall under the Data Deficient category (i.e., insufficient assessment). This includes the three species so far recorded only in the state (*Progomphus elegans* Belle, 1983 (Gomphidae), *Neocordulia santacarinensis* Costa, Ravanello & Souza-Franco, 2008 and *Navicordulia atlantica* Machado & Costa, 1995 (Corduliidae)). In relation to the latter, *N. atlantica* was recently reviewed to encompass synonymies (Pinto et al. 2022) and lacks a thorough assessment of its conservation status.

Considering the municipal limits of the state, Seara municipality (western SC) stands out by far as the location with the most species recorded, followed by Joinville and Blumenau (Table 1). This remarkable pattern is largely due to the outstanding legacy of the late entomologist Fritz Plaumann (1902–1994), settled in (former Nova Teutonia, currently Seara) in the early decades of the 20th century (Lubenow 2017). The continuous sampling effort and wide network of scientific collaboration by Mr. Plaumann throughout the 20th century resulted in a long-standing rate of description of new insect species for the region, which ensured a continuous increase in the knowledge of the regional diversity (Silva 1998). Several regions of the state remain unexplored, mostly the central and westernmost areas of the state, near the border with Argentina (Figure 1). In addition, although several records are reported for the southern and eastern coast, the richer and more densely populated areas of the state, including the surroundings of Joinville and Florianópolis (the largest city and the state capital, respectively), many of these areas are under-sampled. This is because almost the entirety of the knowledge in the state is represented by species descriptions, and studies using systematic sampling of adult Odonata are basically non existing in the state. In fact, the known diversity of several odonate groups covering forest specialist taxa (Anisoptera species from many genera of Gomphidae and Aeshnidae; Zygoptera species from families Coenagrionidae and Heteragrionidae) is lower than in other states. In this context, the loss of several specimens stored in scientific collection of the Museu Nacional (MNRJ; Rio de Janeiro, Brazil), likely represented an important impediment for a deeper understanding of the Odonata diversity in the state, considering that many holotypes of the fauna of SC were stored at MNRJ.

Conclusion

Finally, the checklist of species of Odonata presented here poses a significant advance considering the previously unsystematic available literature for the state (Pinto 2024b, Heckman 2006, 2008), this number increases the species records for the state by 40%.

However, considering the scientific nature of this research (full recollection of secondary data), our list is to be considered only preliminary. We specifically refrained ourselves from including species records available at online databases and unreviewed by taxonomists. On this matter, we strongly recommend further review of records available at institutional repositories (e.g., museums and university collections) and public (e.g., GBIF, Splink) to tackle the shortfalls of biodiversity of Odonata in southern South America.

Supplementary Material

Table S1 - Codes for the bibliographic sources consulted for elaboration of the checklist of Odonata species from Santa Catarina state, Brazil.

Table S2 - List and codes for the municipalities (and corresponding locality names, when available) in Santa Catarina state where occurrence of species was recorded, as extracted from the literature.

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Author Contributions

Mateus M. Pires: contributed to data collection, visualization and manuscript preparation.

Eduardo Périco: supervised and coordinated several aspects of the project and participated in the review and editing of the manuscript.

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

Data used in this work were deposited in a permanent repository in accordance with the instructions for authors: https://doi.org/10.48331/scielodata.YLYT3X.

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Inventory

An annotated list of plant viruses described in Paraguay (1920–2023)

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ESQUIVEL-FARIÑA, A., GONZÁLEZ-SEGNANA, L.R., KITAJIMA, W.E. **An annotated list of plant viruses described in Paraguay (1920–2023).** Biota Neotropica 24(1): e20231574. https://doi.org/10.1590/1676-0611-BN-2023-1574

Abstract: Despite an economy based mostly on agriculture, literature on viral diseases of plants is scarce in Paraguay. Only recently, researches on plant viruses took an impulse resulting in a precise identification of many of them affecting plants either cultivated or not. To provide reliable information regarding plant viruses present in Paraguay, an annotated list of them was prepared, covering descriptions from 1920 to present day. There have been some important outbreaks with severe yield losses in crops as cucurbits, citrus, sesame, bean, maize, peanuts and tomato. Many of older descriptions are included for their historical significance, but most identifications made require confirmation. On the other hand, recent descriptions have been completed, based on several assays, especially molecular characterization. This list is organized alphabetically following scientific names of the plant species found naturally infected by viruses, with comments about symptoms, geographical distribution, incidence, identification procedures, and other information, with due literature references. It is based on a compilation of publications made on plant virus diseases in Paraguay. Described virus species, in a total of 38 recognized by ICTV, belonging to 17 different genera (*Alphaendornavirus, Ampelovirus, Begomovirus, Benyvirus, Carlavirus, Cilevirus, Closterovirus, Comovirus, Cucumovirus, Dichorhavirus, Fabavirus, Luteovirus, Ophiovirus, Orthotospovirus, Potexvirus, Potyvirus* and *Tobamovirus*), besides two unclassified, and four unidentified. There is also a case of viroid described in *Citrus* spp. Infections caused by potyviruses are the most numerous. These viruses were described in more than 40 plant species, belonging to 18 botanical families. Because of crop diversity and richness in native flora, many more viruses must be present in Paraguay, which future works will certainly reveal, especially with the increase in manpower involving researches, especially cooperative with foreign centers, on plant viruses, which has been very limited until now. Also, knowledge on existing viruses may have relevance in understanding their epidemiology and provide the basis for their control strategies and quarantine measures, to avoid new variants of existing viruses or new viruses being introduced.

Keywords: *Plant virus identification; plant species; virus species.*

Una lista comentada de virus de plantas descritos en Paraguay (1920–2023)

Resumen: A pesar de una economía basada principalmente en la agricultura, la literatura sobre enfermedades virales de las plantas es escasa en Paraguay. Sólo recientemente se han impulsado las investigaciones sobre los virus de plantas, lo que ha permitido identificar con precisión muchos de ellos que afectan a plantas cultivadas o no. Para brindar información confiable sobre los virus de plantas presentes en el Paraguay, se elaboró una lista comentada de los mismos, abarcando descripciones desde 1920 hasta la actualidad. Se han producido algunos focos importantes con severas pérdidas de rendimiento en cultivos de cucurbitáceas, cítricos, sésamo, frijol, maíz, maní y tomate. Muchas de las descripciones más antiguas se incluyen por su importancia histórica, pero la mayoría de las identificaciones realizadas requieren confirmación. Por otro lado, las descripciones recientes han sido completadas, basadas en varios ensayos, especialmente de caracterización molecular. Esta lista está organizada alfabéticamente siguiendo los nombres científicos de las especies de plantas que se encontraron naturalmente infectadas por virus, con comentarios sobre síntomas, distribución geográfica, incidencia, procedimientos de identificación y otras informaciones, con las debidas referencias bibliográficas. Se basa en una recopilación de publicaciones realizadas sobre enfermedades virales de plantas en Paraguay. Especies de virus descritas, en un total de 38 reconocidas por el ICTV, pertenecientes a 17 géneros diferentes (*Alphaendornavirus, Ampelovirus, Begomovirus, Benyvirus, Carlavirus, Cilevirus, Closterovirus, Comovirus, Cucumovirus, Dichorhavirus, Fabavirus, Luteovirus, Ophiovirus, Orthotospovirus, Potexvirus, Potyvirus y Tobamovirus*), además de dos sin clasificar y cuatro sin identificar. También existe un caso de un viroide descrito en *Citrus* spp. Las infecciones causadas por potyvirus son las más numerosas. Estos virus fueron descritos en más de 40 especies de plantas, pertenecientes a 18 familias botánicas. Debido a la diversidad de cultivos y la riqueza de la flora nativa, muchos más virus deben estar presentes en Paraguay, lo que seguramente revelarán trabajos futuros, especialmente con el aumento de la mano de obra involucrada en investigaciones, en cooperación con centros extranjeros, sobre virus de plantas, que ha sido muy limitada hasta el momento. Además, el conocimiento sobre los virus existentes puede ser relevante para comprender su epidemiología y proporcionar una base para sus estrategias de control y medidas de cuarentena, para evitar la introducción de nuevas variantes de virus existentes o nuevos virus.

Palavras-chave: *Identificación de virus vegetales; especies de plantas; especies de virus.*

Introduction

1. Agriculture in Paraguay

The territorial area of Paraguay is roughly 406,000 km2, with an estimated population of 7.2 million (Hanratty & Meditz, 1988). The main agricultural products are soybean (planted area 3.4 million Ha), maize (800,000 Ha) and wheat (400,000 Ha), followed by crops as sugarcane, cassava, rice, citrus, sorghum, mate herb, and in smaller scale, tobacco, pineapple, oily seeds, sesame, etc. Agricultural inputs represent a market of approximately US$ 2 billion, with agrochemicals accounting for about 1/3 of this value (CAPECO, 2023).

The Paraguayan economy has been very favorable in the last decade, with an average gross domestic product (GDP) growth of approximately 5%, higher than the average for the continent. Export growth and favorable international prices for primary products led to this result (Brozón, G. R., & Nakayama, H. D., 2023). Paraguay's main export product is soybean, and its production directly influences the national GDP (Morínigo et al., 2018). In 2020, Paraguay was the fourth largest producer of soybeans in the world. In 2022, incomes of 2.8 Million dollars came from export of soybeans and derivatives (CAPECO, 2023). Soybean frontier expansion continues principally in the Paraguayan Chaco, where approximately 700.000 ha of land are considered suitable for soybean production (Henderson et al., 2021).

Crop production in 2021 in Paraguay was 10.5 million tons of soybean, 4.0 million tons of maize, 7.2 million tons of sugarcane, 3.3 million tons of cassava, 1.1 million tons of rice, 900 thousand tons of wheat, 116 thousand tons of mate herb and 29.8 thousand tons of cotton (MAG, 2023).

Concerning livestock, beef exports went from 82 million kilos in 2004 to 232 million kilos in 2013 according to the United Nations Comtrade Database - (UN Comtrade 2014). According to the Central Bank of Paraguay, the export of these agricultural commodities is currently representing almost 40% of the GDP. Interestingly, the logistics of these exports are mostly based on very efficient river transportation, with many portuary terminals installed along the rivers Paraguay and Paraná (BCP, 2017).

2. Current situation of the agricultural research in Paraguay

Historically, agricultural research in Paraguay started with Moisés Santiago Bertoni, a Swiss researcher, in his private research station in Yaraguarazapá in 1887, and produced more than 300 publications on Eastern Paraguayan agricultural themes until 1927 (Wilcox, 2020). Despite some modest governmental efforts, agricultural research has not made much progress in subsequent years. Most of agricultural expansion and increase in productivity was based on the import of foreign technology. Though in small scale, formal agricultural and livestock researches started in 1943, when the Inter-American Technical Service for Agricultural Cooperation (STICA), a US agency, organized the National Agronomic Institute (IAN) in Caacupé and the Experiment Station Barrerito (EEB) in Caapucú. IAN focused their efforts on crops like wheat, soybean, bean, corn, sorghum, citrus, cotton, tobacco, and pasture, while EEB operated an animal farm for cattle. STICA was restructured in 1966 by the Ministry of Agriculture and Livestock (MAG), being transferred to the newly created Agricultural Research and Rural Extension Directorate (DIAER), and ten experimental fields were organized in most important agroecological zones. Four emblematic programs on cotton, wheat, soybeans, and corn were established based on a multidisciplinary team with capable human resources trained at undergraduate and graduate levels abroad. These efforts led to the release of crop products that were adapted to Paraguay's agroclimatic conditions. In 1990, the MAG structure was simplified. The DIAER became the Directorate of Agricultural Research (DIA) and the Directorate of Agrarian Extension (DEAg), under the Subsecretary of Agriculture. The Subsecretariat for livestock became responsible for Animal Research and Production Directorate (DIPA) (Beintema et al., 2000). However, since then, there has been a progressive decrease in the efficiency of these structures due to budget decreases, resulting in lower salaries for researchers and technicians. To mend the situation, a new organization, the Paraguayan Institute of Agrarian Technology (IPTA) was created by the law (Ley de la Nación nº 3788, May 21st, 2010), fusing DIA and DIPA.

The Japanese community in Paraguay also played an important role in the development of agricultural research. Research and technical assistance centers were created in Pirapó, Yguazú and La Paz, which formed the so-called Agricultural Technology Center in Paraguay (CETAPAR), funded by the Japan International Cooperation Agency (JICA). With the help of Japanese specialists, soybean crop was introduced in these regions as well as the adaptation of vegetable crops and the creation of new varieties as the melon 'Luna Yguazú' and tomato 'Súper Cetapar'. More recently, the so-called National Institute of Biotechnology (INBIO), which is a non-profit civil association, has been funding research to promote the development of national biotechnology research (Beintema et al., 2000; IPTA, 2022).

Presently, the National Council for Science and Technology (CONACYT), created in 1997, became more active in recent years with increased budget, funding a large number of research projects

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and providing scholarships, including to agricultural sciences. (Ekboir et al., 2003).

The Agricultural College of the National University of Asuncion (UNA) in San Lorenzo was founded in mid-1950s to offer undergraduate courses in agronomy and veterinary science. Two decades later, these courses served as the basis of the Faculty of Agronomy and Veterinary Sciences. Research at UNA was limited due to limited budget. Although the Research Projects Directorate (DIPRI) has funded research for full-time faculties, it has been on a limited scale. In September 1974, the Superior University Council separated the Faculty of Agronomy and Veterinary Sciences into two independent faculties, and retained the Faculty of Agronomic Engineering. Finally, in 1994, the name of the Faculty of Agronomic Engineering was changed and it became the Faculty of Agrarian Sciences (FCA) (Ekboir et al., 2003).

3. *A brief history of plant virology in Paraguay*

The first mention of a plant viral disease in Paraguay goes back to 1920, when Spegazzini published a paper on citrus diseases. On inspections made in Paraguay in 1919, he described lesions on stems and trunk, but not on fruits, and designated the disease as 'lepra explosiva', attributing wrongly the causal agent as *Amylirosa aurantiorum*. Bitancourt (1955) commented that the symptoms observed by Spegazzini were caused by citrus psoriasis. Fawcett & Bitancourt (1940) toured several South American countries from April 17th to 22nd, 1937 to examine citrus diseases. Visits were made in the region of Asunción, Trinidad and San Lorenzo, where they found leprosis symptoms on sweet oranges, calling attention to differences in symptoms between leprosis symptoms in Florida and South America. In that same decade, Howard Porter, served with the Food supply division of the Institute of Inter-American Affair (U.S.) and worked with IAN from July 1946 to August 1947, and described what appears to be the first documented geminivirus symptoms in tomato crops in the country (Porter, 1947).

The study of plant viruses in Paraguay has begun with the collaborations of Japanese experts. During the period 1986 to 1988, Toshihiko Katusbe from the Japan International Research Center for Agricultural Sciences (JIRCAS) established the first partnerships. In surveys of 14 major crops, more than 50 kinds of diseases were identified, five of them, in strawberries, citrus, sugarcane and soybean, were attributed to a virus (Katusbe & Romero, 1991).

Starting July 1991, for three years, Dr. Kenichiro Shohara, a Japanese consultant at JICA, conducted a comprehensive survey on plant viral diseases in Paraguay. In FCA/UNA, he worked with local staff members from the Department of Agronomy and Phytopathology. The regions that were surveyed included Asunción and surrounding regions that produce agricultural products in the triangle of Asunción, Ciudad de Este, and Encarnación. A large number of viruses were found, and most of them were recognized using transmission assays, serology, and electron microscopy, while some were only recognized based on symptoms. These results were published in Spanish and Japanese (Shohara, 1995; Shohara et al., 1994).

From April 1997 to March 2002, the framework of the "Project for the Improvement of Vegetable Production Technology for Small-Scale Farmers in Paraguay", six JICA experts worked with IAN and DEAG to develop technology improvement activities, led by Dr. Takashi Ishijima (Ishijima & Okwara, 2002). Among those six experts, Dr. Yutaka Kimura investigated the chemical management of tospovirus and geminivirus vectors in tomato crops and the density of vector insect populations. In the same JICA Project, Dr. Tamito Sakurai (Department of Biology and Environmental Sciences, National Agricultural Research Center for Tohoku Region, Japan) studied the transmission of tospovirus by adults of *Frankliniella schultzei* collected in tomato fields in Paraguay in February of 2000, in collaboration with Dr. Yutaka Kimura and Dr. Takashi Ishijima (Sakurai, 2004).

Regarding local scientists, González-Segnana, from the Biology Department at FCA/UNA, was the first full-time plant virologist in Paraguay starting in September 1989. He earned his master's degree at the Universidade Federal de Viçosa and characterized an isolate of Orchid Ringspot Tobamovirus (ORSV) from Paraguay (González-Segnana, 1989). He also received additional training, especially on citrus viruses, at the Citrus Research and Educational Center (CREC) of the University of Florida, in Lake Alfred, and he devoted his initial works on surveying Citrus tristeza virus (CTV) in Paraguay.

Starting in 2005, a close cooperation program was developed between González-Segnana's group and the Departamento de Fitopatologia e Nematologia (LFN) from Escola Superior de Agricultura Luiz de Queiroz (ESALQ), Universidade de São Paulo (USP), Piracicaba campus. The beginning of cooperation occurred when E.W. Kitajima, a plant virologist from ESALQ, arrived in Paraguay to investigate citrus leprosis and first met González-Segnana. In the years that followed, Kitajima visited Paraguay several times, and along with González-Segnana and his team, visited several agricultural production areas in Paraguay. One important problem on sesame grown in San Pedro was identified as viral nature, caused by Cowpea aphid-borne mosaic virus (CABMV) (González-Segnana et al., 2011), and subsequent studies resulted in an efficient control. This cooperation extended also with Argentinian research groups of National Institute of Agricultural Technology (INTA) from Bella Vista and Concórdia, on citrus viruses (Cáceres et al., 2013). Because of this cooperation program, starting 2014, Esquivel-Fariña, a student of González-Segnana, did his graduate studies (MS 2014/2016; Ph.D 2017/2020), working with Tomato chlorosis virus (ToCV), supervised by J.A.M. Rezende, at the LFN/ESALQ (Esquivel-Fariña, 2016; 2019). He also received additional training as a visiting PhD student at the U.S. Agricultural Research Station in Salinas (CA) under the supervision of Dr. Willian Wintermantel. After returning to Paraguay, Esquivel-Fariña served successively as a researcher for the Ministry of Agriculture and a private company, surveying plant viruses in Paraguay, and recently joined the FCA/UNA.

Material and Methods

The present list was inspired on by a similar one, prepared for plant viruses and viroids described in Brazil (Kitajima, 2020), and it is based on a list of publications about plant viruses described in Paraguay beginning with the seminal paper by Spegazzini on citrus leprosis in 1920 to recent works in 2023. Such list was prepared by the authors, compiling publications made on plant viruses found in Paraguay, by local specialists or foreign visitors, and also of the viruses detected in samples collected in Paraguay and analyzed elsewhere. Following the model used by former listings (Sastry et al., 2019; Kitajima, 2020), this list was prepared by the scientific name of hosts, in alphabetical order, and within each species, viruses found naturally infecting them, with details about site of occurrence, incidence, symptoms and procedures for their identification, and the pertinent reference. In addition, a complementary, reverse list, by viruses and host plants they found infecting was prepared, relaying on the most recent listing organized by ICTV-ICTV_Master_Species_List_2021_v2.xlsx (ICTV, 2022). In older papers, identification of viruses was made by symptoms, serology and in a few cases, by electron microscopy. Only in recent descriptions, more reliable molecular detection and identification were used.

Results and Discussion

The literature search resulted in finding a total of 38 virus species, belonging to 17 genera, presently recognized by ICTV, besides two still unclassified and two, unidentified, and one classified viroid species. The pathogens were infecting more than 40 plant species, belonging to 18 botanical families. *Potyvirus* was, by far, the genus with the most representatives described in Paraguay, comprising 16 species and two unidentified members, followed by *Potexvirus*, with four species, and *Begomovirus, Tobamovirus* and *Orthotospovirus*, with two species each. On the host side, The *Fabaceae* family had the highest number of virus-infected species, with eight, followed by *Solanaceae*, with seven. Cucumber mosaic virus and Cowpea aphid-borne virus were viruses found infecting more plant species, each with seven [see list of plant species and the reverse list of viruses (Table 1) below].

Since the territory of Paraguay faces strongly agricultures regions of Brazil (states of Paraná and Mato Grosso do Sul) and Argentina (provinces of Formosa, Corrientes and Misiones), it is likely that many viruses, present in these areas may already occur in Paraguay. Indeed, recently epidemy of "huanglongbing" (HLB), caused by the phloem bacterium *Candidatus* Liberibacter, and transmitted by the psyllid *Diaphorina citri*, a serious problem for citrus crops in Brazil, reached Paraguay in 2013 (Mora-Aguilera et al., 2013), seven years after first detection in the state of São Paulo, Brazil (Sanches et al., 2018).

Recent impulse in scientific research in Paraguay, including in agricultural sciences, with a new generation of specialists, it is expected that an exponential increase in knowledge on viral diseases will occur, with an ever growing number of plant viruses being discovered in Paraguay.

Table 1. List of plant viruses and viroids described in Paraguay, with the plant species found infected by them, in the nature.

Realm: ***Monodnavira***	
Kingdom: *Shotokuvirae*	
Phylum: *Cressdnaviricota*	
Class: *Repensiviricetes*	
Order: *Geplafuvirales*	
Family: *Geminiviridae*	
Genus: *Begomovirus*	
Species: *Sweet potato leaf curl virus*	*Ipomea batatas*
Tomato yellowspot virus	*Leonurus sibiricus*
Realm: ***Ribovira***	
Kingdom: *Orthornavirae*	
Phylum: *Kitrinoviricota*	
Class: *Alsuviricetes*	
Order: *Hepelivirales*	
Family: *Benyviridae*	
Genus: *Benyvirus*	
Species (unc.): Wheat stripe mosaic virus	*Triticum aestivum*
Order: *Martellivirales*	
Family: *Bomoviridae*	
Genus: *Cucumovirus*	
Species: *Cucumber mosaic virus*	*Brassica rapa*
	Citrullus lanatus
	Cucumis melo
	Cucumis sativus
	Cucurbita maxima
	Nicotiana tabacum
	Zea mays
Family: *Closteroviridae*	
Genus: *Ampelovirus*	
Species: *Pineapple mealybug wilt-associated virus***	*Ananas comosus*
Genus: *Closterovirus*	
Species: *Citrus tristeza virus*	*Citrus spp*

Continue...

Continuation

Family: *Endornaviridae*	
Genus: *Alphaendornavirus*	
Unclass. species: *Capsicum frutescens* endornavirus	*Capsicum baccatum* var. pendulum
Family: *Kitaviridae*	
Genus: *Cilevirus*	
Species: Citrus leprosis virus C	*Citrus spp*
Unidentified	*Hibiscus rosa-sinensis*
Family: *Virgaviridae*	
Genus: *Tobamovirus*	
Species: *Odontoglossum ringspot virus*	Several orchid genera
Species: *Tobacco mosaic virus*	*Nicotiana tabacum* *Solanum lycopersicum*
Order; *Tymovirales*	
Family: *Alphaflexiviridae*	
Genus: *Potexvirus*	
Species: *Cassava common mosaic virus*	*Manihot esculenta*
Cymbidium mosaic virus	Several orchid genera
*Potato virus X***	*Solanum tuberosum*
Strawberry mild yellow edge virus	*Fragaria x ananassa*
Family: *Betaflexividae*	
Subfamily: *Quinvirinae*	
Genus: *Carlavirus*	
Species: *Chrysantem virus B***	*Chrysanthemum sp*
Unidentified	*Solanum tuberosum*
Class: *Tolucaviricetes*	
Order: *Tolivirales*	
Family: *Tombusviridae*	
Genus: *Luteovirus*	
Species: *Barley yellow dwarf virus*	*Triticum aestivum*
Phylum: *Negarnaviricota*	
Subphyum: *Haploviricotina*	
Class: *Mineviricetes*	
Order: *Serpentovirales*	
Family: *Aspivirale*	
Genus: *Ophiovirus* (1)	
Species: *Ophiovirus citri***	*Citrus spp.*
Class: *Monjiviricetes*	
Order: *Mononegavirales*	
Family: *Rhabdoviridae*	
Subfamily: *Betarhabdovirinae*	
Genus: *Dichorhavirus*	
Species: Orchid *fleck virus*	Several orchid genera
Subphylum: *Polyploviricotina*	
Class: *Elliotviricetes*	
Order: *Bunavirales*	
Family: *Tospoviridae*	
Genus: *Orthotospovirus*	
Species: *Groundnut ringspot orthotospsovirus*	*Arachis hypogaea* *Petunia x hybrida* *Solanum lycopersicum*
Tomato spotted wilt orthotospovirus	*Acanthospermum hispidum* *Nicotiana longiflora* *Physalis sp.* *Solanum lycopersicum*

Continue...

Continuation

Phylum: *Pisuviricota*	
Class: *Pisoniviricetes*	
Order: *Picornavirales*	
Family: *Secoviridae*	
Subfamily: *Comovirinae*	
Genus: *Comovirus*	
Species: *Cowpea severe mosaic virus*	*Vigna unguiculata*
Genus: *Fabavirus*	
Species: *Broad bean wilt virus***	*Pisum sativum*
Class: *Stelpaviricetes*	
Order: *Patatavirales*	
Family: *Potyviridae*	
Genus*: Potyvirus*	
Species: *Bean common mosaic virus***	*Phaseolus vugaris*
*Bean common mosaic necrosis virus***	*Phaseolus vugaris*
*Bean yellow mosaic virus***	*Phaseolus vugaris*
Cowpea aphid-borne mosaic virus	*Amaranthus hybridus* *Arachis hypogaea* *Crotalaria incana* *C. juncea* *C. spectabilis* *Sesamum indicum* *Vigna unguiculata*
*Dasheen mosaic vírus***	*Colocasia sp.*
Papaya ringspot virus	*Carica papaya* *Cucurbita maxima*
*Peanut mottle vírus***	*Arachis hypogaea*
Potato virus Y	*Nicotiana tabacum*
Sorghum mosaic virus	*Saccharum officinarum*
*Soybean mosaic vírus***	*Glycine max*
Sugarcane mosaic virus	*Saccharum officinarum* *Sorghum bicolor* *Zea mays*
Sweet potato feathery mottle virus	*Ipomea batatas*
Sweet potato virus G	*Ipomea batatas*
*Turnip mosaic virus***	*Brassica rapa*
*Watermelon mosaic vírus***	*Cucurbita maxima*
Zucchini yellow mosaic virus	*Citrullus lanatus* *Cucumis sativus* *Cucurbita maxima*
Unidentified	*Allium schoenoprasum* *Manihot esculenta*
Family: *Pospiviroidae*	
Genus: *Pospiviroid*	
Species: *Citrus exocortis viroid***	*Citrus* spp.
Other viruslike cases:	
Isometric particles, unidentified	*Manihot esculenta* *Stevia* sp.

*Based on ICTV Master Species List 2021 v.2.

**Pending confirmation by serological or molecular detection.

List of plant species infected by viruses and viroids, described in Paraguay (1920–2023)

A

***Acanthospermum hispidum DC (Bristlly starbur) Asteraceae**
Orthotospovirus
***Tomato spotted wilt orthotospovirus* (TSWV)**

A. hispidium, locally known as Toro-rati, is a common wild plant with antifungal activity with potential use in medicine (1). ELISA made on samples of bristly starbur plants with leafroll and yellows symptoms showed a positive reaction against TSWV antibodies (2).
Ref.: (1) Portillo et al. Journal of Ethnopharmacology 76(1): 93. 2001; (2) Shohara, K. Shokubutsu boeki 49(2): 32. 1995.

***Allium schoenoprasum L. (Chives) Amaryllidaceae**
Potyvirus
Potyvirus unidentified

A still unidentified presumed potyvirus causing mosaic symptoms on chives was observed by electron microscopy analysis, as deduced by the detection of elongated particles ca. 760 nm long in leaf extracts of symptomatic onion plants (1).
Ref.: (1) Shohara K Shokubutsu boeki 49(2): 32. 1995.

***Amaranthus hybridus* L. (Amaranth) Amaranthaceae**
Potyvirus
***Cowpea aphid-borne mosaic virus* (CABMV)**

Amaranth plants displaying chlorotic spots and mosaic were found in Choré, San Pedro, next to a bean plantation with high incidence of virus-like symptoms. Mechanical inoculation in indicator plants, serology and molecular (RT-PCR) assays confirmed CABMV infection in plants of *A. hybridus*. (1).
Ref.: (1) González-Segnana, L. R. et al., Tropical Plant Pathology 38(6): 539. 2013.

****Ananas comosus* (L.) Merr. (Pineapple) Bromeliaceae**
Closterovirus
***Pineapple mealybug wilt-associated virus* (PMWaV)**

Plant samples collected from Paraguay and maintained at the USDA-A RS National Clonal Germplasm Repository in Hilo, Hawaii, were tested positive for PMWaV by ELISA test (1). The natural infection has not been confirmed since then, and its actual presence in the country is unknown.
Ref.: (1) Hu, J. S. et al. Plant Pathology 45(5): 829. 1996.

****Arachis hypogaea* L. (Groundnut, peanut) Fabaceae**
Potyvirus
***Peanut mottle virus* (PMoV)**

Natural infections of peanut plants showing mosaic and mottle symptoms were reported in the Central Department. The presence of 740 nm viral particles was confirmed by electron microscopy analysis of infected tissue. Mechanical inoculation produced local lesions in *Chenopodium quinoa.* The causal virus was tentatively identified as Peanut mottle virus (PMoV), but it needs to be confirmed.
Ref.: (1) Shohara, K. Shokubutsu boeki 49(1): 32. 1995.

***Cowpea aphid-borne mosaic virus* (CABMV)**

CABMV was found infecting peanut plants causing mosaic symptoms in the Deptarment of San Pedro during a survey made in the period of 2010 to 2012. Serological (ELISA) and molecular (RT-PCR) assays confirmed CABMV-infections in peanut plants surrounding CABMV-infected sesame plantations. Thus, peanut plants are suggested as part of the epidemiology of dispersion of CABMV in sesame culture (1).
Ref.: (1) González-Segnana, L. R. et al., Tropical Plant Pathology 38(6): 539. 2013.

Orthotospovirus
***Groundnut ringspot orthotospovirus* (GRSV)**

Peanut plants displaying symptoms of tospovirus, including ringspots, mosaic, yellowing, and reduced leaf size, were found in an experimental area at FCA/UNA. Serology confirmed the infection of these peanut plants with GRSV.
Ref.: (1) Macchi-Leite, G., et al. Res. V Congreso Nacional de Ciencias Agrarias. 2021.

B

****Brassica rapa* (Turnip) Brassicaceae**
Cucumovirus
***Cucumber mosaic virus* (CMV)**
Potyvirus
***Turnip mosaic virus* (TuMV)**

Transmission assays and serology were used to detect CMV in turnip samples with mosaic symptoms found in Colonia Iguazú. On the other hand, flexuous and elongated particles ca. 750 nm long were found in leaf extracts of the same sample, by electron microscopy, suggesting potyvirus infection, possibly by TuMV, indicating a case of double infection (1). TuMV infection has not been confirmed by serological or molecular assays since then, and its actual presence in the country is unknown.
Ref.: (1) Shohara, K. Shokubutsu boeki 49 (1): 32. 1995.

C

****Capsicum baccatum* L. var. *pendulum* (Chili pepper) Solanaceae**
Endornavirus unclassified
***Capsicum frutescens endornavirus** 1* **(CFEV1)**

During a study on the evolution of endornaviruses in pepper and related species, CFEV1 was detected in *C. bacatum* seeds collected in Paraguay, by molecular means (1).
Ref.: (1) Safari, M. & Roossinck, M. J. Molecular Plant-Microbe Interactions 31(7): 766. 2018.

****Carica papaya* L. (Papaya) Caricaceae**
Potyvirus
***Papaya ringspot virus-P* (PRSV-P)**

Leaf extracts of papaya plants showing mosaic symptoms revealed the presence of elongated, ca. 740 nm particles by electron microscopy. Cucumber was able to be infected mechanically. The causal virus was tentatively identified as PRSV-P (1). In November 2020, papaya trees showing symptoms of leaf size reduction, yellow and severe mosaic, and

ringspots on the fruits were found in the Asunción Central department. PRSV-P infection was confirmed by RT-PCR and serologic assays.
Ref.: (1) Shohara, K. Shokubutsu boeki 49 (1): 32. 1995; (2) Esquivel-Fariña, A. et al., Journal of Plant Pathology 104(1), 451. 2022.

***Chrysanthemum sp.* Asteraceae**

Carlavirus

***Chrysantemum virus B* (CVB)**

Elongated particles, ca. 670 nm long, possibly a carlavirus, were detected by electron microscopy, in leaf extracts of asymptomatic chrysanthemum plants, and tentatively identified as CVB, pending confirmation (1).
Ref.: (1) Shohara, K. Shokubutsu boeki 49 (1): 32. 1995.

***Citrullus lanatus* Thumb. Matsui & Nakai (Watermelon) Cucurbitaceae**

Cucumovirus

***Cucumber mosaic virus* (CMV)**

CMV was detected using electron microscopy, transmission assays, and serology in mosaic-bearing watermelon plants (1).
Ref.: (1) Shohara, K. Shokubutsu boeki 49 (1): 32. 1995

Potyvirus

***Zucchini yellow mosaic virus* (ZYMV)**

The presence of 750 nm particles in extracts of watermelon leaves with mosaic symptoms was detected by electron microscopy analysis. Based on mechanical transmission tests and serology this potyvirus was identified as ZYMV (1).
Ref.: (1) Shohara, K. Shokubutsu boeki 49 (1): 32. 1995.

***Citrus spp*. Rutaceae**

Closterovirus

***Citrus tristeza virus* (CTV)**

Surveys conducted between 1986 and 1988 on major crops in Paraguay revealed several viral diseases on citrus crops, including CTV (1). Shohara in 1991-1993 also identified CTV in citrus plant samples showing leaf curling symptoms based on the presence of 1800 nm particles in leaf extracts by electron microscopy, and confirmed by serology (2). Using a technique combining serology and electron microscopy (MEIAD), CTV was detected in samples from Paraguay (3). By the end of the nineties, CTV had infected 96% of the citrus trees in the eastern regions of Paraguay. Interestingly, no CTV was detected in citrus plants grown in the Dept. Boquerón. The initial plants were imported into Texas by German colonizers in 1930. It is likely that the hot and dry conditions of the region do not favor the aphid vectors, thus avoiding incoming of CTV, since no citrus plants were introduced from other regions (4). In 2007, CTV was detected in selected grapefruit clones through a biological test using subtle lemon (*C. aurantifolia*) as an indicator plant, in the Depts. of San Pedro and Concepción (5).
Ref.: (1) Katusbe, T., & Romero, M. I. JARQ-japan agricultural research quarterly, 25(3), 172. 1991; (2) Shohara, K. Shokubutsu boeki 49 (1): 32. 1995; (3) Vega, J. et al. Fitopatologia Brasileira 16: XXVI. 1991; (4) González-Segnana, L.R. et al., Proceedings Florida State Horticultural Society 110: 43. 1997. (5) Perez, J. A., & González-Segnana, L.R. Investigación Agraria 9(2): 5. 2013.

Ophiovirus

***Ophiovirus citri* [*Citrus psorosis virus* (CPsV)]**

During the limited inspection made in 1937, Fawcett & Bitancourt observed mild cases of psorosis, based on symptoms, in citrus plants nearby Asunción (1). The presence of CPSV in Paraguay was confirmed during surveys conducted between 1986 and 1988 on major crops. More recently, the presence of CPsV in symptomatic citrus trees was reported in the city of Carlos A. López at Itapúa department (3).
Ref.: (1) Fawcett, C.H. & Bitancourt, A.A. O Biológico 6: 289. 1940; (2) Katusbe, T., & Romero, M. I. JARQ-Japan agricultural research quarterly 25(3): 172. 1991. (3) Godoy, G. M. et al. Investigación Agraria 6 (1): 15. 2013.

Cilevirus

***Citrus leprosis virus C* (CiLV-C)**

Just a few years after the disease was described in Florida, citrus leprosis was reported in Paraguay, in Asunción and named as "lepra explosiva" in 1920, by Spegazzini. At the time, he wrongly attributed the causal agent as a fungus *Amylirosa aurantiorum* (1). In 1937 Fawcett & Bitancourt visited Asunción and surroundings (Trinidad, San Lorenzo) as part of a long journey throughout several South American countries observing citrus diseases, and confirmed the presence of leprosis based on symptoms (2, 3). Further inspections revealed that citrus leprosis is widespread on orange and/or mandarin orchards in Paraguay (Boquerón, Concepción, San Pedro, Cordillera, Alto Paraná and Itapúa departments), the identification confirmed by electron microscopy and molecular assays (4). An extensive molecular survey on samples collected from several sites on the American continent, confirmed that Citrus leprosis virus C (CiLV-C) is the prevalent virus causing the citrus leprosis syndrome in Southern South America, including Paraguay (5). CiLV-C vector in Paraguay, as elsewhere, is identified as *Brevipalpus yothersi* (6).
Ref.: (1) Spegazzini, C. Annales de la Sociedad Científica 90:155. 1922. (2) Fawcett, H.S. & Bitancourt, A.A. O Biológico 6: 209. 1940; (3) Bitancourt, A.A. Arquivos do Instituto Biológico 22: 161. 1955; (4) Cáceres, S. et al. Tropical Plant Pathology 38(4): 282. 2013; (5) Chabi-Jesus, C. et al. Frontiers in Microbiology 12: 641. 2021; (6) Tassi, A.D. Tese Doutorado, ESALQ/USP. 2018.

Pospiviroid

Citrus exocortis viroid (CEVd)

The possible presence of CEVd in Paraguay, affecting citrus plants, was suggested based on symptoms observed in surveys during 1986 to 1988. The identification is still pending confirmation (1).
Ref.: (1) Katusbe, T., & Romero, M. I. JARQ-J agricultural research quarterly 25(3): 172. 1991.

***Colocasia sp.* (Yam) Araceae**

Potyvirus

***Dasheen mosaic virus* (DsMV)**

Electron microscopic analysis detected 750 nm particles in leaf extracts of yam plants showing mosaic symptoms, which were tentatively identified as being of DsMV (1).
Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

***Crotalaria incana* L. Fabaceae**
***Crotalaria juncea* L. Fabacea**
***Crotalaria spectabilis* L. Fabaceae**
Potyvirus
***Cowpea aphid-borne mosaic virus* (CABMV)**

Sesame crops have been found commonly infected by CABMV, occasionally resulting in significant losses. As part of studies to understand the epidemiology of this virus, surveys have been conducted to assess its presence in cultivated or spontaneous plants nearby sesame fields. Assays to detect CABMV included mechanical transmission to certain indicators (*Chenopodium quinoa, Vigna unguiculata, Sesamum indicum*) and ELISA using specific antiserum. During such inspections, three species of *Crotalaria* (*C. incana, C. juncea,* and *C. spectabilis*) showing mosaic symptoms were confirmed to be CABMV-infected (1). During the early survey made by Shohara in 1990's (2), he found mosaic bearing *Crotalaria* sp. associated with the presence of potyvirus-like particles, and suggested infection by BYMV. It is likely that the virus that caused the infection was CABMV.

Ref.: (1) González-Segnana, L. R. et al., Tropical Plant Pathology 38(6): 539. 2013; (2) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

***Cucumis melo* L. (Melon) Cucurbitaceae**
Cucumovirus
***Cucumber mosaic virus* (CMV)**

Samples of melon plants, exhibiting mosaic symptoms, were used in mechanical transmission assays, which resulted in the infection of NN tobacco (mosaic) and cowpea (local lesions). Electron microscopy detected isometric particles with a diameter of around 30 nm, and a serology test was positive for CMV (1).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

***Cucumis sativus* L. (Cucumber) Cucurbitaceae**
Cucumovirus
***Cucumber mosaic virus* (CMV)**

Similar results to those reported above for cucumber were obtained with samples of cucumber with mosaic symptoms, indicating a case of infection by CMV (1).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

Potyvirus
***Zucchini yellow mosaic virus* (ZYMV)**

The presence of 750 nm particles was found in leaf extracts of mosaic bearing cucumber when examined by electron microscopy. The causal virus was determined to be ZYMV because of a positive serological reaction against ZYMV antiserum (1).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

***Cucurbita maxima* Duch. (Pumpkin) Cucurbitaceae**
Cucumovirus
***Cucumber mosaic virus* (CMV)**

Isometric particles of approximately 30 nm were found in leaf extracts of field pumpkin plants with mosaic symptoms, by electron microscopy. Mechanical transmission assays resulted in infection of tobacco (mosaic) and cowpea (local lesions), while a serological test was positive for CMV antigen, confirming infection by this virus (1).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

Potyvirus
***Watermelon mosaic virus* (WMV)**

Leaf extracts of *C. maxima* plants showing mosaic symptoms were analyzed by electron microscopy, revealing the presence of potyvirus-like, elongated particles. ZYMV antigen was found to be negative in the serological test. The identity of this potyvirus has been tentatively suggested to be watermelon mosaic virus (WMV), but it has not yet been confirmed (1).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

***Papaya ringspot virus-W* (PRSV-W)**
***Zucchini yellow mosaic virus* (ZYMV)**

Potyviruses infection of cucurbits has been considered a common occurrence in Paraguay. Shohara (1) reported a case that was tentatively determined to be caused by WMV. In 2017, during a routine survey, leaf deformation, chlorosis and stunting were observed in plants of *C. maxima* var. Zapallito in an experimental area located in the campus of the National University of Asuncion. A mixed infection with PRSV-W and ZYMV (2) was confirmed by both molecular and serologic detection.

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995; (2) Esquivel-Fariña, A. et al., Journal of Plant Pathology 102(1): 231. 2020.

F

***Fragaria x ananassa* Duch. (Strawberry) Rosaceae**
Potexvirus
***Strawberry mild yellow edge virus* (SMYEV)**

According to the European and Mediterranean Plant Protection Organization (EPPO), SMYEV has a localized presence in some regions of Paraguay (1). However, there are no research studies confirming the actual presence of the virus in the country.

Ref.: (1) CABI, EPPO, 2004. Map 937. doi:10.1079/DMPD/20066500937.

G

***Glycine max* (L.) Merr. (Soybean) Fabaceae**
Potyvirus
***Soybean mosaic virus* (SMV)**

Potyvirus-like particles were found by electron microscopy in leaf extracts of soybean plants with mosaic symptoms, and this case was tentatively considered to be caused by SMV infection (1).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

H

***Hibiscus rosa-sinensis* L. (Hibiscus) Malvaceae**
Cilevirus
Unidentified cilevirus

H. rosa-sinensis plants collected in Asunción were naturally found infected by the *Brevipalpus* mite-transmitted virus, tentatively identified as HGSV, still uncharacterized (1).

Ref.: (1) Kitajima, E. W. et al. Scientia Agricola, 67(3): 348. 2010.

I

***Ipomea batatas* (L.) Lam. (Sweet potato) Convulvulaceae**

Potyvirus

***Sweet potato feathery mottle virus* (SPFMV)**

***Sweet potato* virus *G* (SPVG)**

Begomovirus

***Sweet potato leaf curl virus* (SPLCV)**

During an investigation on synergistic interactions of begomoviruses and the crinivirus Sweet potato chlorotic stunt virus (SPCSV), at the International Potato Center in Peru. SPFMV and SPLCV were detected in mixed infection with sweet potato virus G (SPVG) in samples originated from Paraguay, maintained in the collection of sweet potato accessions. Detection was based on grafting onto the indicator plant *I. setosa,* followed by PCR (1).

Ref.: (1) Cuellar, W. J. et al. Molecular Plant Pathology 16(5), 459. 2015.

L

***Leonurus sibiricus* L. (Chinese motherwort, Honeyweed) Lamiaceae**

Begomovirus

***Tomato yellow spot virus* (ToYSV)**

ToYSV was identified, based on molecular assays, infecting two *L. sibiricus* plants displaying viral symptoms within citrus orchards in Major Otaño, Itapúa, Paraguay (1).

Ref.: (1) Fernandes-Acioli, N. A. N., et al. Plant Disease 98(10): 1445. 2014.

M

***Manihot esculenta* Kranz (Cassava) Euphorbiaceae**

Potexvirus

***Cassava common mosaic virus* (CsCMV)**

Symptomatic cassava leaf samples were collected in the early 1990s during a virus disease survey in Paraguay, and leaf extracts were loaded onto ELISA plates and dried. ELISA reactions were later carried out at CIAT, Colombia, and CsCMV was detected in cassava samples collected in Paraguay (1). Molecular characterization studies carried out on Brazilian, Colombian and Paraguayan isolates of CsCMV indicated that they were essentially similar (2).

Ref.: (1) Nolt, B.L. et al. Annals of Applied Biology 118(1): 105. 1991; (2) Calvert, L. et al., Journal of General Virology 77(3): 525. 1996.

Potyvirus

Potyvirus unidentified

Leaf extracts of cassava plants showing viral symptoms were analyzed by electron microscopy, revealing the presence of particles with 760 nm in in length, which were interpreted as being of potyviral nature. Further confirmation is needed for this finding (1).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

Unidentified isometric virus

Isometric particles measuring 28 nm in diameter were observed in leaf extracts of cassava plants showing viral symptoms using transmission electron microscopy. No further confirmation of their viral nature is available.

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

N

***Nicotiana longiflora* Cav. (Longflower tobacco) Solanaceae**

Orthotospovirus

***Tomato spotted wilt orthotospovirus* (TSWV)**

TSWV was detected infecting *N. longiflora* plants by serology (1).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49(1): 32. 1995.

***Nicotiana tabacum* L. (Tobacco) Solanaceae**

Cucumovirus

***Cucumber mosaic virus* (CMV)**

Potyvirus

***Potato virus Y* (PVY)**

Tobamovirus

***Tobacco mosaic virus* (TMV)**

Tobacco plants with mosaic symptoms were examined using electron microscopy and serology. Presence of rod-like and flexuous particles, as well as of isometric particles ca. 30 nm diameter was observed in leaf extracts by electron microscopy. Serological analysis confirmed the presence of TMV, PVY and CMV in these samples (1).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

O

***Orchids* (several genera) Orchidaceae**

Dichorhabdovirus

***Dichorhavirus orchidacea* [*Orchid fleck virus* (OFV)]**

Orchid fleck virus (OFV) was first reported to infect plants of *Dendrobium moschatum* in 2013. Plants exhibiting chlorotic and necrotic lesions on the leaves were observed in the municipalities of Asunción and Caacupé (1). Leaf samples showing virus-like symptoms were found in plants grown in commercial greenhouses in the Paraguayan municipalities of Asunción and Caacupé during 2014 and 2015. Mixed infections with *Cymbidium mosaic virus* (CymMV) and *Odontoglossum ringspot virus* (ORSV) were reported (2).

Ref.: (1) Ramos-González, P.L. et al. Journal of Phytopathology 164(5): 342. 2016; (2) Esquivel-Fariña, A. et al. New Disease Reports 37(1): 3. 2018.

Potexvirus

***Cymbidium mosaic virus* (CymMV)**

During surveys carried out by Shohara in the 1990', *Cattleya* and *Dendrobium* plants showing viral symptoms were analyzed by electron microscopy, which detected elongated particles 460–480 nm long and tentatively identified as CymMV (1). Further surveys carried out on commercial and private collection of orchids, during 2014 and 2015, virus-like symptoms were observed in plants of five orchid genera (*Cattleya, Dendrobium, Miltonia, Oncidium* and *Phalaenopsis*) grown in commercial greenhouses in the Paraguayan municipalities of Asunción and Caacupé. Presence of CymMV was confirmed in samples of all these genera by electron microscopy and RT-PCR assays (2).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995; (2) Esquivel-Fariña, A. et al. New Disease Reports 37(1): 3. 2018.

Tobamovirus

***Odontoglossum ringspot virus* (ORSV)**

ORSV is believed to be the first virus formally studied in Paraguay. It was characterized during González-Segnana's master's dissertation in

1989 (1, 2), which analyzed ORSV isolates from Minas Gerais, Brazil, and Paraguay by biological analysis and electron microscopy. During surveys made by Shohara in the 1990's, ORSV was found in *Cattleya* and *Oncidium* orchids also by biological tests and electron microscopy (3). Recent surveys confirmed the presence of ORSV, in mixed infection with CymMV in plants of several orchid genera, as shown by electron microscopy and molecular assays (4).

Ref.: (1) González-Segnana L.R., Universidade Federal de Viçosa, MSc Dissertation, 1989; (2) González-Segnana, L.R. et al. Fitopatologia Brasileira 15: 152. 1990; (3) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995; (4) Esquivel-Fariña, A. et al. New Disease Reports 37(1), 3. 2018.

P

******Petunia x hybrida*** (Petunia) Solanaceae**

Orthotospovirus

***Groundnut ringspot orthotospovirus* (GRSV)**

In 2018, flower growers in Luque County, Central Department, were forced to eliminate entire sets of GRSV-infected petunias due to a high incidence of necrotic ringspot symptoms on their leaves. Identification of the causal agent as an isolate of GRSV was made by serology and RT-PCR (1).

Ref.: (1) Esquivel-Fariña, A. et al. Australasian Plant Disease Notes 14(1): 5. 2019.

******Phaseolus vugaris*** L. (Common bean) Fabaceae**

Potyvirus

***Bean yellow mosaic virus* (BYMV)**

Flexible, elongated particles were found in leaf extracts of bean plants exhibiting mosaic symptoms. These particles were tentatively identified as Bean yellow mosaic virus (BYMV). Further confirmation is required by serological or molecular assays (1).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

***Bean common mosaic virus* (BCMV), *Bean common mosaic necrosis virus* (BCMNV)**

Worrall et al., in their review on BCMV and BCMNV, they mention the presence of these viruses in Paraguay (p.16), possibly affecting bean plants, without details (1).

Ref.: (1) Worrall, E.A., et al. Advances in Virus Research 93: 1–46. 2015.

******Physalis sp.*** Solanaceae**

Orthotospovirus

***Tomato spotted wilt orthotospovirus* (TSWV)**

Physalis spp. plants with virus-like symptoms were collected by Shohara during surveys carried out in the 1990's. The biological assays were negative, but serology confirmed TSWV infection (1).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

******Pisum sativum*** L. Fabaceae**

Fabavirus

***Broad bean wilt virus* (BBWV)**

Isometric particles, ca. 25 nm, were detected by electron microscopy of leaf extracts from symptomatic pea plants during a survey of plant viruses in the 1990's, and tentatively identified as Broad bean wilt virus (BBWV), pending confirmation (1).

Ref.: (1) Shohara, K. et al. *Shokubutsu boeki* 49 (1): 32. 1995.

S

****Saccharum officinarum L.* (Sugar cane) Poaceae**

Potyvirus

***Sorghum mosaic virus* (SrMV)**

During studies developing a large-scale rapid identification of viruses causing sugarcane mosaic by direct sequencing of RT-PCR products from crude extracts made at Chacra Experimental Agricola, Argentina, SrMV were detected in samples collected at Guairá department (1). The exact presence and/or distribution in the country is not known.

Ref.: (1) Gómez, M. et al. Journal of Virological Methods 157(2): 188. 2009.

***Sugarcane mosaic virus* (SCMV)**

In the extensive review made by ISSCT, the presence of SCMV in Paraguay was registered, but without details (1).

Ref.: (1) International Society of Sugar Cane Technologists (ISSCT). Elsevier. 341. 1989.

******Sesamum indicum*** L. (Sesamum) Pedaliaceae**

Potyvirus

***Cowpea aphid-borne mosaic virus* (CABMV)**

A sesame's disease, observed in the Department of San Pedro, characterized by yellowing and curling down of leaves, was coined locally as "ka'are", for the resemblance of affected plants with *Chenopodium ambrosioides,* known by this name. Until 2005, it was of marginal importance, but since then it has become widespread, causing significant losses. An intensive cooperative study was carried out by researchers of FCA/UNA and ESALQ/USP, to determine the causal agent and its epidemiology, as well as of control measures. As a result, CABMV was identified as the etiological agent by biological tests, electron microscopy, aphid transmission, serology and RT-PCR (1,2). Further studies identified many legume plants as alternative hosts for CABMV (3). The transmission of CABMV by cowpea (*Vigna unguiculata*) suggests that seeds may be involved in the epidemiology of sesame 'ka'are' disease (4).

Ref.: (1) González-Segnana, L. R. et al., Plant Disease 95(5): 613. 2011; (2) González-Segnana, L. R. et al., Identificación, detección y transmission de la enfermidad del Ka'are del sésamo. FCA-UNA/INBIO. 2011; (3) González-Segnana, L.R. et al. Tropical Plant Pathology 38(6): 539. 2013; (4) Delgado-Godoy, M.L. et al. Investigación Agraria 16(2): 93. 2014.

******Solanum lycopersicum*** L. (Tomato) Solanaceae**

Tobamovirus

***Tobacco mosaic virus* (TMV)**

TMV was detected on tomato plants with mosaic symptoms during Shohara's survey. Identification was based on biological assays, electron microscopy and serology (1).

Ref: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

Orthotospovirus

***Tomato spotted wilt orthotospovirus* (TSWV)**

Tospovirus-like symptoms (necrosis and ringspots on the leaves) have frequently been observed in tomato fields. In the 90s, TSWV was serologically detected infecting tomato plants, which showed necrosis (1). TSWV is quoted as causing "vira-cabeza" in Ishijima's manual on fruit vegetable crops, and considered to be transmitted by the dark form of *Frankliniella schultzei* (2), which was confirmed experimentally by Sakurai (3).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995; (2) Ishijima, T. (Ed.) Manual de técnicas de cultivo de hortalizas de frutas (tomate, melón, frutilla). Inst.Nac.Agric., Caacupé. 240p. 2002; (3) Sakurai, T. Applied Entomology and Zoology, 39(1), 189. 2004.

***Groundnut ringspot orthotospovirus* (GRSV)**

In 2018, tomato plants (cv. 'Santa Clara') showing typical tospovirus-like symptoms including chlorotic spots, concentric and necrotic rings on the leaves and stunting were found in high incidence (ca 50%), at the experimental field of FCA/UNA in San Lorenzo. The infection of GRSV on these tomato plants was confirmed by both serology and molecular assays.

Ref.: (1) Esquivel-Fariña, A. et al. Australasian Plant Disease Notes 14(1): 5. 2019.

***Solanum tuberosum* L. (Potato) Solanaceae**

Potexvirus

***Potato virus X* (PVX)**

Electron microscopy and serology were used to detect PVX in samples from symptomatic potato leaves (1). The actual presence and distribution in the country is unknown.

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

Potyvirus

***Potato virus Y* (PVY)**

Potato plants showing mosaic, dwarfism, vein necrosis and leaf rolling were analyzed by electron microscopy, resulting in the detection of flexible particles ca. 750 nm long. The causal agent was tentatively identified as PVY, but this requires confirmation (1).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

Carlavirus

Unidentified carlavirus

Potato plants showing mosaic, dwarfism, vein necrosis and leaf rolling were sampled during a Shohara's survey in 1990's. Electron microscopy examination of leaf extracts revealed the presence of carlavirus-like particles, which was considered evidence for the presence of Potato Virus S or Potato Virus M, not yet confirmed (1).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

***Sorghum bicolor* L. (Sorghum) Poaceae**

***Sugarcane mosaic virus* (SCMV)**

Teyssandier in his review on sorghum diseases in Paraguay mentions the presence of the sugarcane mosaic virus in sorghum, but without providing any details. The actual presence and/or distribution of the in the country is unknown.

Ref.: (1) Teyssandier, E. In Millano, W.A.J. et al. Sorghum diseases: a second world review. ICRISTAT. p.63. 1992.

***Stevia* sp. Asteraceae**

Fabavirus

***Broad bean wilt virus* (BBWV)**

Leaf extracts from *Stevia* plants with yellow symptoms were examined by electron microscopy revealing the presence of isometric virus-like particles ca. 25 nm. The virus has been tentatively identified as *Broad bean wilt virus* (BBWV), but it is still awaiting confirmation (1).

Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

T

***Triticum aestivum* L. (Wheat) Poaceae**

Benyvirus

***Wheat stripe mosaic virus* (WhSMV)**

WhSMV is the only virus associated with a soil-borne wheat mosaic disease in Paraguay. It is transmitted by the soil-borne plasmodiophorid *Polymyxa graminis*. In June 2016, randomly irregular patches of wheat plants (cv. 'Itapúa 65') exhibiting streaking mosaic on the leaves and stunting were observed in an experimental field at IPTA, located in the district of Capitán Miranda, Itapúa Department, Southeast of Paraguay. Based on electron microscopy observations of virus particles in symptomatic leaf and molecular assays, the virus was identified as WhSMV, which was recently described in Brazil (1).

Ref.: (1) Esquivel-Fariña, A. et al. Australasian Plant Disease Notes 14(1): 24. 2019.

Luteovirus

***Barley yellows dwarf virus* PAV and MAV types (BYDV)**

BYDV is a virus widely distributed in the world affecting various Poaceaeas. It has a persistent relationship in their aphid vectors. The presence of BYDV in Paraguay was reported since 1987 (1), and during the nineties (2, 3), and more recently during the agricultural periods 2013 and 2014 in wheat crops in the Southern region of Paraguay. In the analyzed samples, serology revealed a broad prevalence of BYDV-PAV, with only one positive case for BYDV-MAV (4).

Ref.: (1) de Viedma et al., (No. CIS-1090. CIMMYT.) 1987. (2) Ramirez Araya, I. C1990, (91-061795. CIMMYT.) 1990. (3) Webby, G.N. et al. Annals of Applied Biolology 123: 63. 1993; (4) Gonzáles-Segnana, L.R. et al., Investigación Agraria 17(1), 60. 2015.

V

***Vigna unguiculata* (L.) Walp. (Cowpea) Fabaceae**

Comovirus

***Cowpea severe mosaic virus* (CPSMV)**

CPSMV was first reported in Paraguay in cowpea, during investigations on seed-borne viruses of cowpea in Paraguay, related to the epidemiology of "ka-are" of sesame. Cowpea seeds were collected from cowpea plants that were experiencing symptoms at the IPTA experimental site in Choré, Department of San Pedro. ELISA was used to detect CPSMV on germinated plants. CPSMV was detected only in cultivars 'Negro' and 'Moteado' (1). More recently, a screening program for cowpea genotypes for resistance to CABMV and CPSMV identified resistant genotypes/cultivars that can be used in breeding programs (2).

Ref.: (1) Delgado-Godoy, M.L., et al., Investigación Agraria, 16(2): 93. 2014; (2) Alonso, G., et al., Agric. Sci. Dig, 43(5), 593-597. 2023.

Potyvirus

***Cowpea aphid-borne mosaic virus* (CABMV)**

CABMV was first described in Paraguay infecting sesame plants (*Sesamum indicum*). Simultaneously, several cowpea fields and nearby sesame diseased crops also contained plants exhibiting mosaic symptoms, which revealed that they were also infected with CABMV (1). Subsequent surveys conducted to identify alternative hosts of CABMV have detected this virus in cowpea plants in several regions of the country. *Aphis crassivora* proved to be vector of CABMV in

Paraguay (3). This virus may have been what Shohara (4) detected by electron microscopy during his survey in the 1990's. Seed transmission of CABMV occurs in most of the cowpea cultivars studied (5).
Ref.: (1) González-Segnana, L. G. et al., Plant Disease 95(5): 613. 2011; (2) González-Segnana, L.R. et al., Tropical Plant Pathology 38(6): 539. 2013; (3) Zelada-Cardozo, N.J.J. et al., Investigación Agraria 12(2): 85. 2010. (4) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995; (5) Delgado-Godoy, M.L., et al., Investigación Agraria, 16(2): 93. 2014.

Z

***Zea mays L.* (Maize) Poaceae**

Cucumovirus

***Cucumber mosaic virus* (CMV)**

Serology detected CMV in maize samples that displayed mosaic symptoms. The presence of isometric particles was confirmed by electron microscopy of leaf extracts.
Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32. 1995.

Potyvirus

***Sugarcane mosaic virus* (SCMV)**

Maize plants displayed mosaic and yellowing symptoms, as observed by Shohara. The presence of particles 750 nm long in symptomatic plants was detected by electron microscopy analysis of leaf extracts, resulting in the tentative identification of the causal agent SCMV (1). This information still is pending by further confirmation.
Ref.: (1) Shohara, K. et al. Shokubutsu boeki 49 (1): 32.

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Author Contributions

Arnaldo Esquivel-Fariña: writing the original draft, data collection, manuscript preparation, and critical revision, adding intellectual content.

Luis R. Segnana-González: data analysis and results interpretation, and critical revision, adding intellectual content.

Elliot W. Kitajima: concept and design, data collection, substantial contribution in critical revision, data analysis and results interpretation, adding intellectual content.

Conflicts of Interest

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

Ethics

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

Data Availability

The data collected and generated during this study includes the available literature on plant virus description in Paraguay used in the analysis and can be accessed at https://zenodo.org/records/8387860. The authors confirm that all data necessary for reproducing the study findings are available in the designated dataset.

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Inventory

Inventory of red algae (Rhodophyta) from the Sian Ka'an Biosphere Reserve, Mexican Caribbean

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Abstract: Studies of marine and estuarine red algae (Rhodophyta) are in the early stages in the littoral of the Sian Ka'an Biosphere Reserve, Mexico. The inventory of these organisms was made based on samples obtained from ten sampling during 2009 to 2015 in 22 localities, eight of them in marine and fourteen in estuarine environments. We found 182 species and subspecific taxa of Rhodophyta. The Rhodomelaceae family was the best represented with 65 taxa, followed by Ceramiaceae 13 and Delesseriaceae 12. Of the 182 taxa, 25 are new records Sian Ka'an Biosphere Reserve with *Harveylithon rupestre, Spongites fruticulosus, Acrochaetium barbadense, Dasya harveyi, Chondria pumila, Spermothamnion repens, Metapeyssonnelia milleporoides* and *M. tangerina* being new records for the Mexican Caribbean. Of the 182 species, 119 of them are epiphytes, most of them, 54, grew exclusively on other macroalgae, 29 on mangrove roots and 8 on *Thalassia* leaves. The floristic list is accompanied by data on seasonality, reproduction, habitat, and environment. Species diversity was compared between the winter rains, dry and rainy seasons during the period study. The Rhodophyta of the Sian Ka'an Biosphere Reserve is tropical, and the greatest diversity was found in the marine environment with 83 taxa and during the winter rains with 132.

Keywords: *Seaweed; marine; estuarine.*

Inventário de algas vermelhas da Reserva da Biosfera Sian Ka'an, Caribe Mexicano

Resumo: Os estudos de algas vermelhas marinhas e estuarinas (Rhodophyta) estão em fase inicial no litoral da Reserva da Biosfera de Sian Ka'na, México. O inventário desses organismos foi feito com base em amostras obtidas em oito amostragens no período do 2009 a 2015 em 22 localidades, sendo oito em ambientes marinhos e quatorze em ambientes estuarinos. Neste levantamento, foram identificadas um total de 182 espécies e táxons subespecíficos de Rhodophyta. A família Rhodomelaceae foi a mais representativa com 65 táxons, seguida por Ceramiaceae com 13 e Delesseriaceae com 12. Dos 182 táxons, 25 são referidos pela primeira vez para a Reserva da Biosfera Sian Ka'an, sendo *Harveylithon rupestre*, *Spongites fruticulosus*, *Acrochaetium barbadense*, *Dasya harveyi*, *Chondria pumila*, *Spermothamnion repens*, *Metapeyssonnelia milleporoides* e *M. tangerina* também novos registros para o Caribe mexicano. Das 182 espécies, 119 são epífitas, sendo a maioria, 54, aderidas exclusivamente em outras macroalgas, 29 em raízes de mangue e 8 em folhas de *Thalassia*. A lista florística apresentada é acompanhada de dados sobre sazonalidade, reprodução, habitat e ambiente. A diversidade de espécies foi comparada entre as temporadas de chuvas de inverno, seca e chuvas de verão durante o período estudado. Rhodophyta da Reserva da Biosfera Sian Ka'an são tropicais, e a diversidade mais representativa foi encontrada no ambiente marinho com 83 táxons e durante as chuvas de inverno com um total de 132 táxons.

Palavras-chave: *Algas; marinhas; estuarinas.*

Introduction

Most of the marine benthic macroalgae are Rhodophyta and there are 7,475 species, which constitutes the highest diversity of all the large groups of macroalgae (Guiry & Guiry 2023). Red algae develop at all latitudes and are found in greater numbers in temperate and tropical, far surpassing the remaining macroalgae groups (García-García et al. 2020, Guiry & Guiry 2023). In addition to their specific richness, the Rhodophyta are primary producers and participate in ecological processes such as recruitment niches, fish and invertebrate nurseries, coralline red algae also are important components of coral reefs (Ceballos-Corona et al. 2019). Mexican Caribbean is one of the shoreline areas having the greatest red seaweeds diversity in Mexico (García-García et al. 2020); however, the area has not been well explored, suggesting that species diversity is not entirely known. The red seaweeds around the Sian Ka'an Biosphere Reserve (RBSK) had been investigated mainly during 1989–1992 and the last contribution was eight years ago. Currently, 168 species of red marine and estuarine algae are reported (Taylor 1972, Aguilar-Rosas et al. 1989, 1992, 1998, Aguilar-Rosas 1990, Keeney 1999, Mendoza-González & Mateo-Cid 2007, Valadez-Cruz et al. 2014, Mateo-Cid et al. 2014, García-García et al. 2020). Now, the marine life of RBSK is threatened due to the overexploitation of natural resources, urbanization, and the other anthropogenic activities (Espejel-Montes 1983, Convención RAMSAR 2003). In this context, the use of marine algae as ecological indicators is essential in monitoring the reserve. However, its application is still not possible due to the absence of a reliable and updated list (Cepeda-González et al. 2007). Therefore, this study complements the knowledge of the three groups of seaweeds (green, brown, and red algae) that inhabit the RBSK, and the goal of this study is to update red algae list with new records and to revise the information of this group in the RBSK, with additional information as distribution, seasonality, environment, reproduction, habitat, epiphytism, and observations.

Material and Methods

Materials, methods, and description of the study area in this work are those described by Acosta-Calderón et al. (2016). Red algae were collected in 22 locations along the RBSK coastline (Figure 1) from March 2009 to April 2015, through ten samplings in three climatic seasons. The specimens were obtained from different substrates that Rhodophyta require for their fixation and development, such as rocks, pebbles, seagrass meadows, mainly *Thalassia testudinum* Banks ex König, mangrove roots, coral skeletons and mollusk remains. The plants were collected by hand with the help of spatulas and field knives at the intertidal level and at the subtidal level by free diving to a depth of four meters. The collections were made in segments of the beaches of approximately 500 m in length. Four samplings were carried out in the rainy season, two

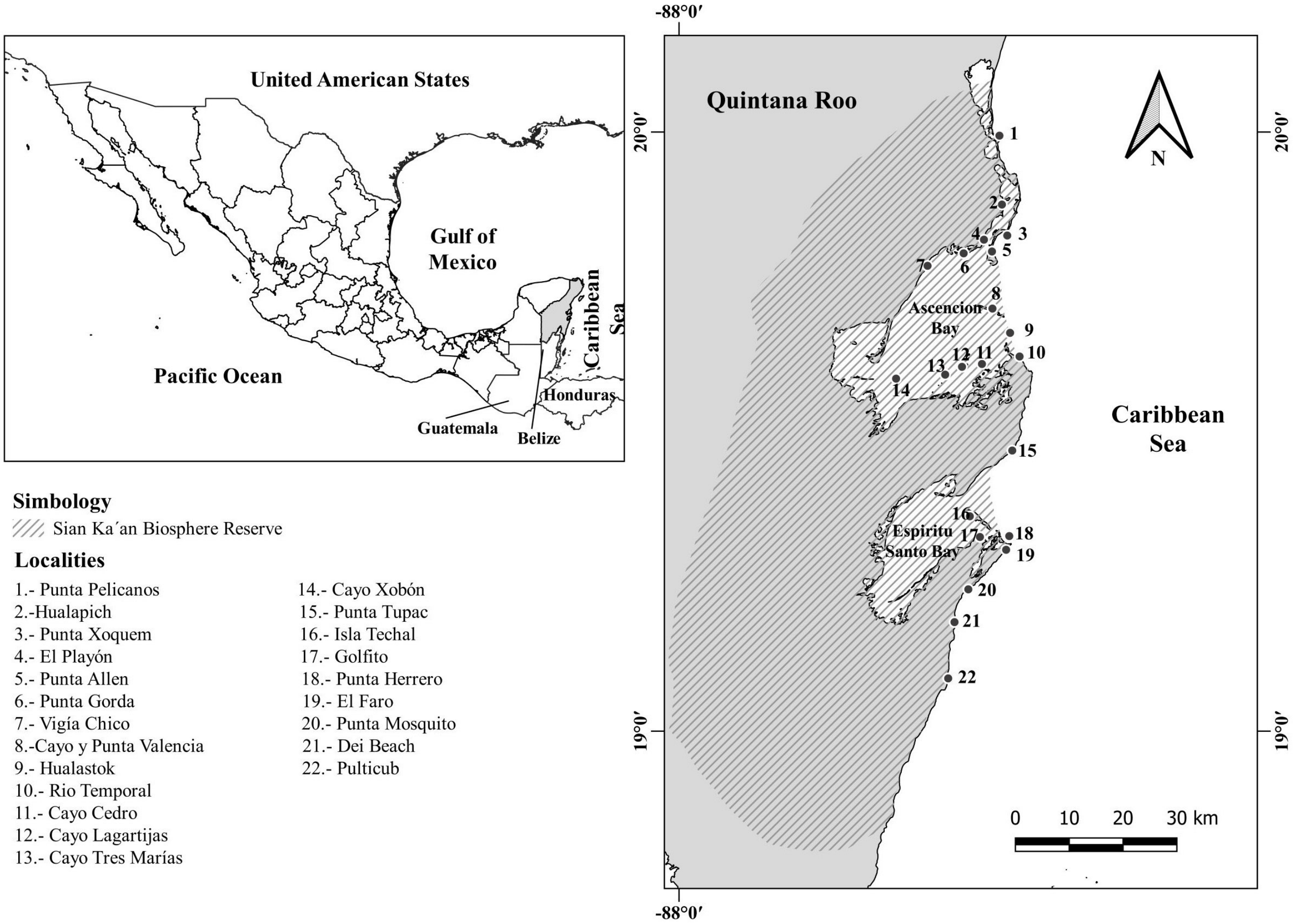

Figure 1. Study area.

in the winter rainy season (Northern) and four in the dry season, data on the GPS coordinates of the localities, substratum, wave exposure, marine or estuarine region, and maximum depth collection of the 22 sampling sites were recorded at Table 1. Specimens of nongeniculate coralline algae were borrowed from ENCB (Departamento de Botánica, Escuela Nacional de Ciencias Biológicas del Instituto Politécnico Nacional, CDMX, Mexico). Additional specimens of nongeniculate coralline algae were collected by reef-walking or snorkeling. Samples were preserved in 5% formalin/seawater for anatomical observations; duplicate samples of some specimens were preserved in silica gel for molecular analyses. Formalin preserved specimens were decalcified with 0.6M HNO_3 and dehydrated with ethyl alcohol at different concentrations: 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90% and absolute ethyl alcohol (Mateo-Cid et al. 2014). Small fragments were embedded in paraffin and sectioned 9–12 µm thick with a manual microtome, fixed on slides with Riuter's adhesive (Martoja & Martoja-Pierson 1970), and stained with aniline blue and hematoxilin eosine for anatomical observations and measurements. Procedures for morphological observations followed Kato et al. (2006); specimens for molecular analyses were deposited in NCU with duplicates in ENCB. Silica gel-dried samples for DNA

Table 1. Substrate characteristic, wave exposure, region, and maximum depth collection of the 22 sampling sites in the RBSK, Quintana Roo, Mexico. BA: Ascension, BE: Espiritu Santo bays.

No.	Samples sites	Latitude	Longuitude	Characteristics
1	Punta Pelicanos	19°59'38"	87°27'54"	Calcareous rocky with coral fragments and sandy areas with *Thalassia testudinum* meadows. BA outside. Euryhaline. Semi-protected. Subtidal, 0–1.5 m.
2	Hualapich	19°52'44"	87°27'40"	Calcareous rocky and rocks of different size. BA outside. Euryhaline. Exposed. Subtidal, 0–1 m.
3	Punta Xoquem	19°49'37"	87°27'08"	Rocky platform that extends from the intertidal zone to the subtidal zone where it is interspersed with sandy areas associated with *T. testudinum*. BA outside. Euryhaline. Exposed Intertidal-Subtidal 1.5 m.
4	El Playón	19°49'13"	87°29'28"	Sandy-muddy with shell fragments. Inside BA. Brackish. Protected. Subtidal 0-1 m.
5	Punta Allen	19°48'02"	87°28'39"	Sandy with *T. testudinum* meadows and wood dock. The shore is covered by *Rhizophora mangle*. Outside BA. Euryhaline. Protected. Subtidal 0–2 m.
6	Punta Gorda	19°47'51"	87°31'30"	Sandy with shell and coral fragments. The shore is covered by *R. mangle*. Inside BA. Brackish. Protected. Subtidal 0–1 m.
7	Vigía Chico	19°46'36"	87°35'07"	Muddy with *T. testudinum* patches and *R. mangle* in shore. Inside BA: Brackish. Protected. Subtidal 0–1 m.
8	Cayo Valencia	19°42'19"	87°28'37"	Sandy with *T. testudinum* meadows and *R. mangle*. Outside BA. Euryhaline. Semi-protected. Subtidal 0–1.5 m.
9	Hualastok	19°39'52"	87°26'51"	Sandy with *T. testudinum* meadows. Outside BA. Euryhaline. Semi-protected. Subtidal 0–3 m.
10	Rio Temporal	19°37'31"	87°25'54"	Sandy and calcareous rocky (0–2 m depth) and sandy with *T. testudinum* meadows (>2 m). Outside BA. Euryhaline. Semi-protected. Subtidal 0–4 m.
11	Cayo Cedro	19°36'46"	87°29'40"	Sandy with shell and coral fragments. *R. mangle* at shore. Inside BA. Brackish. Protected. Subtidal 0–1 m.
12	Cayo Lagartijas	19°36'29"	87°31'40"	
13	Cayo Tres Marías	19°35'42"	87°33'21"	
14	Cayo Xobón	19°35'17"	87°38'16"	
15	Punta Túpac	19°28'05"	87°26'38"	Rocky platform, rock of different size and sandy areas with *T. testudinum* meadows. *R. mangle* at shore. Outside BE. Euryhaline. Semi-protected. Subtidal 0–1.5 m
16	Isla Techal	19°21'31"	87°30'53"	Sandy-muddy with *T. testudinum* patches and *R. mangle*. Outside BE. Euryhaline. Protected. Subtidal 0–1.5 m.
17	Golfito	19°19'26"	87°29'52"	Muddy-sandy with shell fragments and *R. mangle* at shore. Inside BE. Brackish. Protected. Subtidal 0–1.5 m
18	Punta Herrero	19°19'32"	87°26'56"	Sandy-muddy with *T. testudinum* meadows. Outside BE. Euryhaline. Semi-protected-Subtidal 0–1.5 m.
19	El Faro	19°18'09"	87°27'14"	Rocky platform and sand areas with *T. testudinum* patches. Outside BE. Exposed. Euryhaline. Intertidal and Subtidal 0–4 m.
20	Punta Mosquitero	19°14'12"	87°31'02"	Sandy with *T. testudinum* patches and calcareous rocky of different sizes. Outside BE. Euryhaline. Semi-protected. Subtidal 0–1.5 m.
21	Playa Dei	19°10'54"	87°32'25"	Sandy with *T. testudinum* patches and calcareous rocky of different sizes. Outside BE. Euryhaline. Exposed. Subtidal 0–1.5 m.
22	Pulticub	19°05'17"	87°33'03"	Rocky platform with limestone and *T. testudinum* patches. Outside BE. Euryhaline. Exposed. Intertidal and Subtidal 0–1.5 m.

extraction were examined under high magnification with a dissecting microscope to check for red algal epiphytes. Clean fragments about 3 mm^3 total volume were placed in heavy paper packets and crushed and ground to a fine powder before being extracted following the protocol in Hughey et al. (2001) and the recommendations in Hughey & Gabrielson (2012). For DNA sequencing of collected specimens, markers chosen for PCR included the chloroplast-encoded genes *rbc*L, *psb*A as well as COI, and LSU (Richards et al. 2021). DNA was extracted from globally collected specimens at the University of North Carolina at Chapel Hill following the protocol established by Hughey et al. (2001) and modified by Gabrielson et al. (2011) for coralline algae. Amplification of *psb*A, *rbc*L, UPA, COI, and LSU followed the protocols and primers described in Richards et al. (2014, 2016). Voucher specimens are deposited in the herbarium of the Escuela Nacional de Ciencias Biológicas located in Mexico City, Mexico (ENCB), herbarium acronym follows Index Herbariorum (Thiers 2023). Also, information on species previously collected by other researchers was obtained of the herbarium ENCB; the determinations of some specimens were corrected and finally a bibliographic review of the studies carried out in the SKBR from 1989 to 2015, to obtain the records of Rhodophyta previously cited for the coast of the state and thereby compare it with the data obtained in the present study. To describe the geographical distribution of marine algae, Feldmann (1937) proposed the R/P index (number of Rhodophyta species divided by number of Phaeophyceae species), useful for knowing the geographical areas where algae are distributed and thus classifying the flora of a given region as a function of the latitudinal gradient. Thus, a value of the ratio $R/P > 4$ is found in tropical regions, while $R/P < 2$ corresponds to the phycoflora of temperate-cold regions. Cheney (1977) included the Chlorophyta (C) in an index like the one previously exposed $(R + C)/P$ and showed that values of the ratio $(R + C)/P \geq 6$ are obtained in tropical floras, while those from temperate-cold seas have indices <3, intermediate values suggest a mixed flora. The floristic list is accompanied by data on distribution, seasonality, environment, reproduction, habitat, observations, and herbarium number, new records for the RBSK and for Mexican Caribbean are indicated in Table 2. Species names are according to Wynne (2022) and Guiry & Guiry (2023).

Results

1. Floristics

During the study period (March 2009 to April 2015), 182 Rhodophyta taxa distributed in 4 classes, 15 Orders, 30 Families and 83 genera were determined (Table 2). The best represented Order was Ceramiales with 104 taxa (57.1%) followed by Corallinales with 29 (15.9%). The best represented families were Rhodomelaceae with 65 taxa (35.7%), followed by Ceramiaceae 13 (7.1%), Delesseriaceae with 12 (6.6%) and Spongitidaceae 10 (5.4%). Species of Bangiaceae, Liagoraceae, Galaxauraceae, Gelidiaceae, Cystocloniaceae, Peyssonneliaceae and Gracilariaceae represented by 1 or 5 species were also located (Table 2). The most representative genera in terms of the number of species were *Chondria* with 12, *Neogoniolithon* and *Laurencia* with 9 each, *Ceramium, Dasya* and *Polysiphonia* with 8 each. *Bangia, Asparagopsis, Lithothamnion, Melobesia, Wrightiella, Vertebrata, Gelidium* and *Gelidiella,* among others, are unispecific. The Rhodophyta determined in this work have been recorded in the tropical and temperate rocky areas of the world, including the coast of the Gulf of Mexico and the Mexican Caribbean (Wynne 2022, García-García et al. 2020). Considering previous studies of the studies of Acosta-Calderón et al. (2016) and Mateo-Cid et al. (2019) who listed the Chlorophyta and Phaeophyceae, respectively, from the RBSK, the Feldmann and Cheney indexes were calculated and compared with other localities and states of the Yucatan Peninsula (Table 3). Both the Feldmann and Cheney indices indicate that the RBSK phycoflora is of tropical affinity.

2. New records

The integration of the floristic list allowed us to recognize 25 new infrageneric records for the RBSK coastline, including *Harveylithon rupestre, Spongites fruticulosus, Acrochaetium barbadense, Dasya harveyi, Chondria pumila, Spermothamnion repens, Metapeyssonnelia milleporoides* and *M. tangerina*, representing new records for the Mexican Caribbean. Of the 168 previous infrageneric records, 116 taxa were found in this study and 51 were not found in the collected samples. Due to the above, the number of species recorded for the coast of the Sian Ka'an Biosphere Reserve increased to 233 infrageneric taxa of benthic marine and estuarine red algae, which represents an increase of 28% of the total Rhodophyta in the study area. Most of the new records for RBSK belong to genera of coralline algae and the Rhodomelaceae family such as *Chondria* and *Laurencia*.

3. Temporal variation

Figure 2 represents the number of taxa identified by climatic season, in general we can observe high richness in the three seasons, being in winter rains (northern) when the highest specific richness was located with 132, followed by rainy, 122 and finally dry with 107 taxa. Figure 3 shows the number of taxa per locality, it is observed that the locality corresponding to Punta Pelícanos presented the greatest richness (96 taxa), followed by Punta Xoquem (49) and Hualapich (45). The three localities have in common the fact of being found in a marine environment and be rocky beaches. The localities with the lowest specific richness are Golfito (11), Punta Allen and Golfito (10) and Punta Mosquitero (7), the first three are in an estuarine environment and only Punta Mosquitero is in a marine environment.

The number of taxa found in the different environments is represented in Figure 4, where it is observed that the highest species richness was found in the marine environment with 83 taxa, while in the estuarine environment 34 and 65 were found inhabiting in both marine and estuarine environments (Table 2).

4. Reproduction

The reproductive phase that was found most frequently in this study was the tetrasporic, which exceeded both the algae found with male or female gametic phase. These data allow us to consider that this generation has a longer survival with respect to the gametophytic generation, and other reproductive mechanisms such as vegetative propagation or apomeiosis. From the 182 taxa located in this study, 92.3% (168) were found in the fertile stage and only 7.6% (14) were found in the vegetative state, the sporophytic phase was found in 153 taxa, the gametophytic phase exclusively in 12 and finally 44 taxa

Table 2. Rhodophyta of the Sian Ka'an Biosphere Reserve, Quintana Roo (2009–2015). (The abbreviations are explained at the end of the table).

Division/species	**Localities**	**Seasonality**	**Environment**	**Reproduction**			**Habitat**	**Obs**	**ENCB Herbarium voucher number**
				Rains	**Winter rains (northern)**	**Dry**			
RHODOPHYTA									
Bangiophyceae **Bangiales** **Bangiaceae**									
1. *Bangia fuscopurpurea* (Dillwyn) Lyngbye	15	N	M		Ve		Epi/Sw		26451
Florideophyceae **Corallinales** **Corallinaceae**									
2. *Jania capillacea* Harvey	1, 2, 3, 6, 8, 10, 11, 13, 17, 19	Ll N S	M, E	Te	Te	Te	Epi/Sw Epi/Th R		20068 20296 20655 20656 21321 21322 21323 24986 26233 26234 26235 26408 26453 26465 26548 26579
3. *J. cubensis* Montagne ex Kützing	3, 5, 11	N S	M, E		Te	Te	Epi/Sw R		20069 26236 26452
4. *J. pedunculata* var. *adhaerens* (J.V. Lamouroux) A. S. Harvey, Woelkerling & Reviers	1, 11, 13	Ll N S	M, E	Te	Te	Te	Epi/Sw R		26237 26551 26552 26553
5. *J. rubens* (Linnaeus) J.V. Lamouroux	1, 12	Ll N	M, E	Te	Te		R		20133 21335
6. *Pneophyllum confervicola* (Kützing) Y.M. Chamberlain	3, 8, 14, 15, 19, 20, 22	Ll N S	M	Te Ci ♀♂	Te Ci ♂	Te Ci ♂	Epi/Th Epi/Sw		19638 20280 20171 23345 26549 26550 26575 26605
7. *P. fragile* Kützing	1, 3, 8	Ll N S	M	Te	Te Ci ♀♂	Te	Epi/Th Epi/Sw		20164 23348 26196 26576 26577 26578
Hydrolithaceae									
8. *Hydrolithon boergesenii* (Foslie) Foslie	1	Ll	M	Te			R Ez		17785
9. *H. farinosum* (J.V. Lamouroux) Penrose & Y.M. Chamberlain	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22	Ll N S	M, E	Te Ci ♂	Te Ci ♀♂	Te Ci ♀♂	Epi/Sw Epi/Th		19327 19638 19835 19839 19958 20280 20859 20866 20935 21544 23242 23369 23567 23616 23623 23641 24671 24954 26229 26422 26424 26425 26473 26474 26475 26476 26477 26478 26500 26525 26555 26556 26563 26574 26575 26581

Continue...

...Continuation

Division/species	Localities	Seasonality	Environment	Reproduction			Habitat	Obs	ENCB Herbarium voucher number
				Rains	Winter rains (northern)	Dry			
Lithophyllaceae									
10. *Amphiroa fragilissima* (Linnaeus) J.V. Lamouroux	1, 2, 7, 8, 11, 14, 19, 21, 22	Ll N S	M, E	Te	Ve	Ve	Epi/Sw R		17924 19344 19921 19922 20305 20793 20799 20815 26479 26480 26481 26482 26582
11. *A. rigida* J.V. Lamouroux	1, 2, 3, 5, 9, 15, 19, 20, 21, 22	Ll N S	M	Ci	Ve	Ve	R		18287 19258 19310 19311 19794 19918 19922 19928 19930 20060 20297 20653 20767 20772 20774 20801 20804 20805 26483 26484 26485
12. *A. tribulus* (J. Ellis & Solander) J.V. Lamouroux	1, 2, 3, 15, 19, 20, 21, 22	Ll N S	M	Ve	Ve	Ve	R Ez		19926 19932 20297 20638 20796 20797 22830 26486
13. *A. valonioides* Yendo	1	N	M		Te		Epi/Sw		20063
14. *A. vanbosseae* Me. Lemoine	1	S	M			Ve	R		19916 20058
15. *Lithophyllum corallinae* (P. Crouan & H. Crouan) Heydrich	15	N	M		Te		Ez		20145
16. *Titanoderma pustulatum* (J.V. Lamouroux) Nägeli	5, 9, 14, 15, 18, 20, 22	Ll N S	M, E	Te	Te	Te	Epi/Sw		19348 19638 23456 26452 26556 26584 26601
Porolithaceae									
17. *Harveylithon munitum* (Foslie & M. Howe) A. Rösler, Perfectti, V. Peña & J.C. Braga	1, 2	Ll N	M	Te	Te		R		20079 20080 20134 26188
18. *H. rupestre* (Foslie) A. Rösler, Perfectti, V. Peña & J.C. Braga	15	N	M		Te		Ez	**NRMC**	26228
19. *Porolithon antillarum* (Foslie & M. Howe) Foslie & M. Howe	1	N	M		Te		Ez	NRSK	26230
20. *P. onkodes* (Heydrich) Foslie	1	N	M		Te Ci ♀ ♂		Ez	NRSK	26189
Spongitidaceae									
21. *Neogoniolithon acropetum* (Foslie & M. Howe) W.H. Adey	1, 2, 3	Ll N S	M	Te	Te	Te	Ez R		19933 20131 20224 20263 20288 21442

Continue...

...Continuation

Division/species	Localities	Seasonality	Environment	Reproduction			Habitat	Obs	ENCB Herbarium voucher number
				Rains	**Winter rains (northern)**	**Dry**			
22. *N. fosliei* (Heydrich) Setchell & L.R. Mason	1	N	M		Te		Epi/Sw		20086
23. *N. mamillare* (Harvey) Setchell & L.R. Mason	1	Ll	M	Te			R		26190
24. *N. propinquum* (Foslie) Me. Lemoine	1, 2, 3, 22	Ll N S	M	Te Ci ♀	Te	Te	R		20081 20306 26191 26192
25. *N. rhizophorae* (Foslie & M. Howe) Setchell & L.R. Mason	1, 13	N	M, E		Te		Ez		26193 26232
26. *N. siankanense* L.E. Mateo-Cid, A.C. Mendoza-González & P.W. Gabrielson	1, 2	Ll S	M	Te		Te	R		20159 20225 20306
27. *N. solubile* (Foslie & M. Howe) Setchell & L.R. Mason	15, 22	N S	M		Te	Te	Ez		22395 26194
28. *N. spectabile* (Foslie) Setchell & L.R. Mason	1, 3, 7, 9, 10, 15, 22	Ll N S	M, E	Te	♂	Te	Ro		17920 19220 19750 19799 19914 20082 20132 20141 21447 22832
29. *N. strictum* (Foslie) Setchell & L.R. Mason	1,8, 10, 15, 19, 21, 22	Ll N S	M, E	Te	Ve	Te	Ro		19802 19803 19855 19915 19920, 19929 20142
30. *Spongites fruticulosus* Kützing	1	N	M		Te		Ez	**NRMC**	26195
Hapalidiales									
Hapalidiaceae									
31. *Lithothamnion sejunctum* Foslie	1	N	M		Te		Ez	NRSK	20073
32. *Melobesia membranacea* (Esper) J.V. Lamouroux	8, 15, 17	Ll S	M, E	Te		Te	Epi/Th		20090 20097 20171 21691
Acrochaetiales									
Acrochaetiaceae									
33. *Acrochaetium barbadense* (Vickers) Børgesen	1	S	M			Mn	Epi/Sw	**NRMC**	26281
Colaconematales									
Colaconemataceae									
34. *Colaconema daviesii* (Dillwyn) Stegenga	1	N	M		Mn		Epi/Sw		26280
35. *C. hypneae* (Børgesen) A.A. Santos & C.W.N. Moura	2	Ll	M	Mn			Epi/Sw		26366
Nemaliales									
Galaxauraceae									
36. *Galaxaura rugosa* (J. Ellis & Solander) J.V. Lamouroux	1, 2, 3, 18, 19, 22	Ll N S	M	♂	♂	Ci	R		19679 20300 20580 20639 20697 25036 26471 26472 26557 26558 26559

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...Continuation

Division/species	Localities	Seasonality	Environment	Reproduction			Habitat	Obs	ENCB Herbarium voucher number
				Rains	Winter rains (northern)	Dry			
Liagoraceae									
37. *Ganonema farinosum* (J.V. Lamouroux) K.-C. Fan & Y.-C. Wang	1, 3, 15, 22	Ll N S	M	Ci ♂♀	Ci ♂♀	♂♀	R		23220 24922 26281 26282 26500
38. *G. megagynum* (Børgesen) Huisman	1, 3, 22	Ll N S	M	Ci ♀	♂	Ci ♀	R		23309 23310 26283 26284 26285 26604
39. *Gloiocallis dendroidea* (P. Crouan & H. Crouan) Showe M. Lin, Huisman & D.L. Ballantine	1, 22	Ll N	M	♀	Ci ♀		R		23314 26286 26287
40. *Liagora ceranoides* J.V. Lamouroux	1,2, 3, 22	Ll N S	M	♂	♂	♂♀	R		23312 23313 26288 26289 26517
41. *Titanophycus validus* (Harvey) Huisman, G.W. Saunders & A.R. Sherwood	3, 22	S	M			Ci ♀	R	NRSK	20959 26292
42. *Trichogloeopsis pedicellata* (M. Howe) I.A. Abbott & Doty	4, 22	Ll N	M	Ci ♀	♂		R		26290 26291
Bonnemaisoniales									
Bonnemaisoniaceae									
43. *Asparagopsis taxiformis* (Delile) Trevisan	1, 11, 18, 19	N	M, E		Te		Epi/Sw		20114 22841 26266 26406
Ceramiales									
Callithamniaceae									
44. *Callithamnion corymbosum* (Smith) Lyngbye	8	Ll	E	Te Ci			Epi/Mg		26239
45. *Crouania attenuata* (C. Agardh) J. Agardh	1, 2, 3, 8	S	M, E			Te	Epi/Sw		20963 26384
46. *Crouanophycus latiaxis* (I.A. Abbott) A. Athanasiadis	3, 9, 10, 18	Ll N	M, E	Te	Te		Epi/Th Epi/Sw		20456 21002 21355 26507
47. *Spyridia aculeata* subsp. *complanata* (J. Agardh) Hommersand	1, 2	Ll S	M	Te		Te	R	NRSK	21082 26240
48. *S. filamentosa* (Wulfen) Harvey	6, 7, 8, 11	Ll N	E	Te ♂	Te Ci		Epi/Sw R		23274 23275 26241 26242 26243
49. *S. hypnoides* (Bory) Papenfuss	1, 2, 8	Ll N	M, E	Ve	Ve		Epi/Sw R		20932 21082 26244
Ceramiaceae									
50. *Centroceras gasparrinii* (Meneghini) Kützing	1, 2, 6, 8, 11, 14, 15	Ll N	M, E	Ci Te	Te		Epi/Mg Epi/Th Epi/Sw R	NRSK	26245 26246 26247 26393 26463 26509 26510
51. *C. hyalacanthum* Kützing	2	Ll	M	Te			Epi/Sw	NRSK	26400

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Division/species	**Localities**	**Seasonality**	**Environment**	**Reproduction**			**Habitat**	**Obs**	**ENCB Herbarium voucher number**
				Rains	**Winter rains (northern)**	**Dry**			
52. *C. micracanthum* Kützing	1, 8, 15, 19, 22	Ll N S	M	Te Ci	Te	Te	Epi/Sw R		19840 20113 22840 23277 23278 23279 26368 26510
53. *Ceramium brevizonatum* H.E. Petersen	12, 13	Ll S	E	Te		Te	Epi/Mg R		26248 26385
54. *C. brevizonatum* var. *caraibicum* H.E. Petersen & Børgesen	2, 6, 9, 11, 13, 15, 19	Ll N S	M, E	Te	Te Ci ♂	Te	Epi/Sw R		20695 26249 26430 26502 26510 26523 26562 26609
55. *C. cimbricum* f. *flaccidum* (H.E. Petersen) G. Furnari & Serio	8, 9, 18	Ll S	E	Te		Ve	Epi/Sw		20714 26502 QROO-12-89/03
56. *C. comptum* Børgesen	12	S	E			Te	Epi/Mg	NRSK	19783
57. *C. corniculatum* Montagne	2, 7, 8	Ll N S	M, E	♂ Ci	Te	Te	Epi/Th Epi/Mg R		20589 23276 26250
58. *C. cruciatum* Collins & Hervey	8, 15, 18	Ll N S	M	Te Ci	Te	Te	Epi/Sw Epi/Mg		19638 22845 26251
59. *C. luetzelburgii* O.C. Schmidt	10, 19, 22	Ll	M	Te			Epi/Sw		20706 26609 QROO-Rh/01
60. *C. nitens* (C. Agardh) J. Agardh	1, 2, 3, 6, 8, 9, 10, 22	Ll N S	M, E	Ve	Te	Ve	Epi/Th Epi/Sw R		26394 26396 26397 26467 26468 26497 26498 26499 26511 26512 26513
61. *Gayliella flaccida* (Harvey ex Kützing) T.O. Cho & L.J. McIvor	9, 15, 20	Ll N	M	Te		Te	Epi/Sw		19348 19638 23840
62. *G. transversalis* (Collins & Hervey) T.O. Cho & Fredericq	1, 3, 15, 22	Ll N	M	Te	Te		Epi/Mg Epi/Sw		19638 26386 26387 26471 26495
Delesseriaceae									
63. *Caloglossa leprieurii* (Montagne) G. Martens	6, 8, 16	Ll N S	E	Te	Te	Ve	Epi/Mg		24907 24908 26257
64. *Dasya baillouviana* (S.G. Gmelin) Montagne	2	Ll N	M	Te	Ve		R		23301
65. *D. caraibica* Børgesen	3	S	M			Ve	Epi/Mg R		26258
66. *D. collinsiana* M. Howe	3, 8	N S	M		Ve	Ve	Epi/Sw	NRSK	20926 26259
67. *D. corymbifera* J. Agardh	2	S	M			Te	Epi/Mg R		23300
68. *D. harveyi* Ashmead	1, 3	N	M		Te		R	**NRMC**	26260 26261
69. *D. ocellata* (Grateloup) Harvey	9	Ll	M	Te			Epi/Sw	NRSK	19348
70. *D. ramosissima* Harvey	1	Ll N	M	Te	Te		R Epi/Sw	NRSK	26262 26263 26264
71. *D. rigidula* (Kützing) Ardissone	7, 8	Ll N S	M, E	Te	Te	Te	Epi/Mg		20847 22446 23302 26265
72. *Heterosiphonia crispella* (C. Agardh) M.J. Wynne	1, 11, 18, 19	Ll N S	M, E	Te ♂	Ve	Ve	Epi/Sw		20396 23588 23627 26266
73. *Heterosiphonia crispella* var. *laxa* (Børgesen) M.J. Wynne	1, 2	Ll N	M	Te	Te		Epi/Sw		26515 26566

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Division/species	**Localities**	**Seasonality**	**Environment**	**Reproduction**			**Habitat**	**Obs**	**ENCB Herbarium voucher number**
				Rains	**Winter rains (northern)**	**Dry**			
74. *H. gibbesii* (Harvey) Falkenberg	1, 2, 3, 8, 9, 10, 18, 19	Ll N S	M, E	Te	Te	Te ♂	R		20984 23215 23297 23298 23299 24904 26267 26268 26269 26398 26399 26400
Rhodomelaceae									
75. *Acanthophora muscoides* (Linnaeus) Bory	1, 18	S	M			Ci	R		20934 23223 26401
76. *A. spicifera* (M. Vahl) Børgesen	1, 3, 8, 11, 15, 18	Ll N S	M, E	Te	Te	Te Ci	Epi/Mg R		19785 20588 20929 23221 23222 23318 24924 26437 26438 26439 26440
77. *Acanthosiphonia echinata* (Harvey) Savoie & G.W. Saunders	1	N	M		Te ♂Ci		R		25086
78. *Alsidium seaforthii* (Turner) J. Agardh	1	Ll	M	Ve			R		26518
79. *A. triquetrum* (S.G. Gmelin) Trevisan	1, 3	Ll N S	M	Te	Te	Ve	Epi/Mg R		23323 26375 26519
80. *Bostrychia binderi* Harvey	7	Ll	E	Te			Epi/Mg		26294
81. *B. montagnei* Harvey	5, 7, 8, 12	Ll N S	E	Te	Ve	Te Ci	Epi/Mg		20155 20958 23321 24925 26295
82. *B. moritziana* (Sonder ex Kützing) J. Agardh	5	N	E		Te		Epi/Mg		26296
83. *B. radicans* (Montagne) Montagne	11	N	E		Te		Epi/Mg		26297
84. *B. scorpioides* (Hudson) Montagne	4, 6, 7, 11	Ll N	E	Te	Ci		Epi/Mg		23322 26298 26441 26442 26520
85. *B. tenella (*J.V. Lamouroux) J. Agardh	1, 6, 7, 8, 11, 12, 19	Ll N S	M, E	Te	Te	Te Ci	Epi/Mg R		19907 24926 24927 24928 26443 26444 26445 26446
86. *Chondria atropurpurea* Harvey	7, 10	Ll S	E	Te		Te	Epi/Mg Epi/Sw Ez		23324 26560
87. *Ch. baileyana* (Montagne) Harvey	1, 8, 13, 18	Ll N S	M, E	Ci	Te	Te Ci ♂	Epi/Th R		19790 24929 26424 26564
88. *Ch. capillaris* (Hudson) M.J. Wynne	4, 9, 10	Ll N	E	Te	Ci		Epi/Mg Epi/Sw R		23225 26299 QROO-11-39/02
89. *Ch. cnicophylla* (Melvill) De Toni	2, 6, 17	Ll S	M, E	Te		Te	Epi/Mg R		20234 24930 26302 26523
90. *Ch. collinsiana* M. Howe	1, 6, 7, 9, 10, 12, 19	Ll N S	M, E	Te ♂ Ci	Te	Te Ci	Epi/Mg Epi/Th R		19834 19921 21042 23325 23326 26300 26301 26521

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Division/species	**Localities**	**Seasonality**	**Environment**	**Reproduction**			**Habitat**	**Obs**	**ENCB Herbarium voucher number**
				Rains	**Winter rains (northern)**	**Dry**			
91. *Ch. dasyphylla* (Woodward) C. Agardh	4, 6, 7, 11, 12, 13, 18, 19	Ll N S	M, E	Te	Te	Te	Epi/Mg Epi/Sw R		20116 22846 23226 23328 24932 26304 26305 26306 26587
92. *Ch. floridana* (Collins) M. Howe	19	Ll	M	Te			R		24931
93. *Ch. leptacremon* (Melvill ex G. Murray) De Toni	10, 19	Ll	M, E	Te			R	NRSK	24933 24934 26307
94. *Ch. littoralis* Harvey	1, 3, 7, 9	N S	M, E		Te	Te	R		20154 20931 23227 23329 23330 26308 26309
95. *Ch. polyrhiza* Collins & Hervey	8, 10, 19	Ll S	E	Te		Te	Epi/Th		21607 RhC-12/01, 02
96. *Ch. pumila* Vickers	5	N	E		Te		Epi/Sw	**NRMC**	26310
97. *Ch. pygmaea* Garbary & Vandermeulen	3	N	M		Te		Epi/Th		26522
98. *Chondrophycus anabeliae* Senties, M.T. Fujii, Cassano & Dreckmann	1	N	M		♂		R	NRSK	26311
99. *Digenea mexicana* G.H. Boo & D. Robledo	1, 2, 3, 4, 5, 6, 7, 10, 11, 13, 14, 15, 17, 22	Ll N S	M, E	Te	Te	Te Ci	Epi/Mg R		17732 20314 22462 23331 23332 24935 26447 26448 26449 26450 26451 26452 26488 26523 26524 26525 26526 26565 26566
100. *Dipterosiphonia dendritica* (C. Agardh) F. Schmitz	1	N	M		Te		Epi/Sw		26527
101. *D. rigens* (C. Agardh) Falkenberg	18, 19	Ll	M	Te Ci ♀			Epi/Sw	NRSK	26312 26528
102. *Herposiphonia bipinnata* M. Howe	6, 10, 11, 12, 13, 18	Ll N S	M, E	Te	Ve	Te Ci ♂	Epi/Th Epi/Sw		19702 20027 21536 26313 26314 26425 26529
103. *H. pecten-veneris* (Harvey) Falkenberg	6, 10, 13	Ll N S	E	Te	Ve	Te	Epi/Mg Epi/Th Epi/Sw R		26315 26316 26317 26530
104. *H. secunda* (C. Agardh) Ambronn	1, 9, 19, 21	Ll N S	M	Te	Te	Te	Epi/Sw		20907 23518 26318 26319 26418 26606
105. *H. tenella* (C. Agardh) Ambronn	1, 7, 8, 10, 11, 15, 18, 19, 22	Ll N S	M, E	Te Ci	Te	Ci	Epi/Sw Pe		19702 19844 20114 20373 20417 20706 20819 20997 20112 24749
106. *Heterodasya mucronata* (Harvey) M.J. Wynne	1	N	M		Te		R		26320

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...Continuation

Division/species	**Localities**	**Seasonality**	**Environment**	**Reproduction**			**Habitat**	**Obs**	**ENCB Herbarium voucher number**
				Rains	**Winter rains (northern)**	**Dry**			
107. *Laurencia caduciramulosa* Masuda & S. Kawaguchi	3	N	M		Te		Ez	NRSK	26321
108. *L. caraibica* P.C. Silva	1	Ll N	M	Te	Te		R		26322 26323
109. *L. dendroidea* J. Agardh	7, 10, 19	Ll N S	M, E	Te	Ve	Te	Epi/Sw R		22463 26324 26325
110. *L. filiformis* (C. Agardh) Montagne	3, 6, 7, 9, 10, 11	Ll N S	M, E	Te	Te	Te	Epi/Sw R		19782 20314 23378 23379 23380 26326 26588
111. *L. intricata* J.V. Lamouroux	1, 2, 3, 4, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 19	Ll N S	M, E	Te	Te	Te	Epi/Th Epi/Mg Epi/Sw		20117 20118 20966 23231 23232 23384 24936 23388 23390 26453 26454 26455 26456 26457 26458 26459 26460 26461 26462 26489 26531 26561 26567
112. *L. laurahuertana* Mateo-Cid, Mendoza-González & Senties	3	N	M		Te		Epi/Th		26327
113. *L. microcladia* Kützing	1, 7, 8, 18, 19, 21, 22	Ll N S	M, E	Te Ci	Te	Te	Epi/Sw Epi/Th R		20443 23391 24937 26328 26407 26532 26533 26589
114. *L. obtusa* (Hudson) J.V. Lamouroux	1, 2, 3, 7, 8, 17, 18, 19, 21, 22	Ll N S	M, E	Te Ci	Te	Te	R		20313 20963 20964 23233 23392 23393 24938 26402 26403 26404 26405 26406 26534 26535 26568 26569 26590 26591
115. *L. venusta* Yamada	1, 10, 16, 17, 18	Ll S	M, E	Te		Te	Epi/Sw R		23234 26536 26570
116. *Laurenciella marilzae* (Gil-Rodríguez, Sentíes, Díaz-Larrea, Cassano & M.T. Fujii) Gil-Rodríguez, Sentíes, Díaz-Larrea, Cassano & M.T. Fujii	1, 12	Ll N	M, E	Te	Te		R	NRSK	23377 26333
117. *Lophocladia trichoclados* (C. Agardh) F. Schmitz	1, 2, 3, 22	Ll N S	M	Te	Te	Te	Epi/Sw R		23400 26329 26330 26331 26332 26537 26541
118. *Lophosiphonia cristata* Falkenberg	3	S	M			Te	Epi/Sw		26334

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Division/species	**Localities**	**Seasonality**	**Environment**	**Reproduction**			**Habitat**	**Obs**	**ENCB Herbarium voucher number**
				Rains	**Winter rains (northern)**	**Dry**			
119. *L. obscura* (C. Agardh) Falkenberg	1	Ll N	M	Te	Ve		Epi/Sw		25085 26335
120. *Melanothamnus ferulaceus* (Suhr ex J. Agardh) Díaz-Tapia & Maggs	1, 3, 6, 9, 19	Ll N S	M, E	Te Ci	Te	Te Ci	Epi/Sw R		20709 20961 23398 24939 26336 26337 26338 26491
121. *M. sphaerocarpus* (Børgesen) Díaz-Tapia & Maggs	1, 2, 7, 12, 15, 16	Ll N S	M, E	Te Ci	Te Ci	Te	Epi/Th Epi/Mg Epi/Sw R		20762 24940 24941 24942 26339 26340 26341
122. *Meridiocolax polysiphoniae* (E.C. Oliveira & Ugadim) J. Morrill	7, 19	Ll	M, E	Te Ci ♂			Par		QR12A/01 QR08B/02.
123. *Murrayella periclados* (C. Agardh) F. Schmitz	8, 11, 13, 14	Ll N S	E	Te	Te	Te	Epi/Mg R		23399 24943 26408 26409 26410 26538
124. *Palisada corallopsis* (Montagne) Sentíes, Fujii & Díaz-Larrea	4, 5, 11, 14, 19	Ll N	M, E	Te	Te		Epi/Mg R		24944 26342 26343 26411 26412
125. *P. flagellifera* (J. Agardh) K.W. Nam	11	S	E			Te	Ez		26344
126. *P. perforata* (Bory) K.W. Nam	1, 2, 3, 6, 7, 8, 9, 15, 18, 19, 22	Ll N S	M, E	Te	Te ♂	Te	Epi/Mg R		20156 20935 21079 24945 24969 26413 26414 26415 26416 26417 26418 26463 26464 26492 26539 26540 26541 26571
127. *Polysiphonia atlantica* Kapraun & J.N. Norris	1, 7	Ll N	M, E	Te	Te		Epi/Mg		19594 23396
128. *P. binneyi* Harvey	1, 7, 13, 18	Ll N S	M, E	Te ♂ Ci	Te	Ci	Epi/Mg R		23230 23397 26345 26542
129. *P. exilis* Harvey	1, 2, 18, 19, 22	Ll N	M	Te Ci	Ci ♂		Epi/Sw R		26346 26347 26348 26349 26543
130. *P. havanensis* Montagne	2, 4, 7, 18	Ll N S	M, E	Te Ci	Te	Te	Epi/Sw		20737 22461 26350 26351
131. *P. scopolorum* Harvey	6	N	E		Ci		Epi/Mg		26352
132. *P. sertularioides* (Grateloup) J. Agardh	6, 7, 13, 22	N S	E		Te	Te	Epi/Mg Epi/Sw		26316 26353 26562 26500
133. *P. subtilissima* Montagne	4, 7, 9, 13, 14	N S	M, E		Te	Te	Epi/Mg Epi/Sw		23263 26356 26357 26358 26526 26544
134. *P. villum* J. Agardh	3, 13	N	E		Te		Epi/Sw		26359 QROO-11-189/07
135. *Vertebrata foetidissima* (Cocks ex Bornet) Díaz-Tapia & Maggs	1, 15, 19	Ll	M	Te Ci			R		21465 24947 25087

Continue...

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Division/species	Localities	Seasonality	Environment	Reproduction			Habitat	Obs	ENCB Herbarium voucher number
				Rains	Winter rains (northern)	Dry			
136. *Wilsonosiphonia howei* (Hollenberg) D. Bustamante, Won & T.O. Cho	1, 2, 3, 10, 11, 13, 14, 15, 19	Ll N S	M, E	Te Ci	♂ Te	Te	Epi/Mg Epi/ Sw Ez R		19844 20314 21078 26360 26361 26363 26364 26365 26366 26367 26368 26540
137. *Wrightiella tumanowiczii* (Gatty ex Harvey) F. Schmitz	1	S	M			Ve	R		26369
138. *Yuzurua poiteaui* (J.V. Lamouroux) Martin-Lescanne	1, 4, 6, 7, 9, 10, 11, 12, 13, 14, 15, 16	Ll N S	M, E	Te ♂	Te	Te	Epi/Mg Epi/ Sw R		20587 20936 23748 26362 26370 26419 26420 26421 26422 26465 26466 26493 26494 26545 26572
139. *Y. poiteaui* var. *gemmifera* (Harvey) M.J. Wynne	1, 3, 6, 10, 11, 12, 14, 17, 22	Ll N S	M, E	Te	Te ♂	Te	Epi/Mg Ez R		21535 26371 26372 26373 26374 26423 26495 26496 26573 26574
Wrangeliaceae 140. *Anotrichium tenue* (C. Agardh) Nägeli	1, 3, 4, 7, 8, 11, 12, 13, 14, 21	Ll N S	M, E	Te	Te	Te	Epi/Mg Epi/Th Epi/ Sw R		20561 20832 20997 23332 23660 26376 26377 26378 26379 26380 26546 26563
141. *Griffithsia globulifera* Harvey ex Kützing	18, 19	Ll N	M	Te	Te		Epi/Sw		20114 22841
142. *G. heteromorpha* Kützing	8, 19	Ll	M, E	Te			Epi/Sw		26606 QROO-10-Rh/C
143. *Ptilothamnion speluncarum* (Collins & Hervey) D.L. Ballantine & M.J. Wynne	8	S	E			Te	Epi/Sw		21031
144. *Spermothamnion investiens* (P. Crouan & H. Crouan) Vickers	11	N	E		Te		Epi/Sw		26381
145. *S. repens* (Dillwyn) Magnus	8	S	E			Te	Epi/Mg	**NRMC**	24968
146. *Spongoclonium caribaeum* (Børgesen) M.J. Wynne	1	N	M		Te		Epi/Sw		19834
147. *Wrangelia bicuspidata* Børgesen	1, 3	N S	M		Te	Te	Epi/Sw R		19844 26382
148. *W. penicillata* (C. Agardh) C. Agardh	2, 3	Ll N S	M	Te	Ci	Te	Epi/Sw R		26383 26547 26548
Gelidiales **Gelidiaceae** 149. *Gelidium pusillum* (Stackhouse) Le Jolis	17	S	E			Te	Ez		23306

Continue...

...Continuation

Division/species	**Localities**	**Seasonality**	**Environment**	**Reproduction**			**Habitat**	**Obs**	**ENCB Herbarium voucher number**
				Rains	**Winter rains (northern)**	**Dry**			
Gelidiellaceae									20120 20960
150. *Gelidiella acerosa* (Forsskål) Feldmann & Hamel	1, 2, 3, 15, 19, 22	Ll N S	M	Te	Te	Ve	R		20962 23307 24919 26278 26433 26434 26435 26436 26516
Pterocladiaceae									RhP-10/B1
151. *Pterocladiella sanctarum* (Feldmann & Hamel) Santelices	6	S	E			Te	Epi/Mg		
Gigartinales									
Cystocloniaceae									
152. *Hypnea cervicornis* J. Agardh	11, 15	Ll N	M, E	Te	Te		Epi/Mg Epi/Sw		26254 26503
153. *H. musciformis* (Wulfen) J.V. Lamouroux	2, 8, 11,18	Ll N S	M, E	Te Ci	Te	Te	Epi/Mg Epi/Sw R		20591 23267 23739 26432 26501
154. *H. spinella* (C. Agardh) Kützing	1, 2, 9, 13, 15, 18, 19	Ll N S	M, E	Te	Te	Te	Epi/Mg Epi/Sw R		20352 20457 20464 26255 26431 26502 26586
155. *H. valentiae* (Turner) Montagne	9, 22	Ll S	M	Ve		Te	Epi/Mg Epi/Th Epi/Sw		26256
156. *Hypneocolax stellaris* Børgesen	10	Ll	E	♂			Par		Rh-Par-13
Caulacanthaceae									22436 22439
157. *Catenella caespitosa* (Withering) L.M. Irvine	7, 10	Ll S	E	Te		Te	Epi/Mg		
158. *C. impudica* (Montagne) J. Agardh	4, 6, 7, 8, 9, 10, 11, 12, 14	Ll N S	E	Te	Te Ci	Te	Epi/Mg	NRSK	19780 22437 22438 23295 23296 24891 26426 26388 26426 26427 26428 26429 26505 26506
Rhizophyllidaceae									
159. *Ochtodes maguachaveziae* Mendoza-González, Mateo-Cid & Sentíes	1	S	M			Te Ci ♀ ♂	R		20661
160. *O. secundiramea* (Montagne) M. Howe	22	S	M			Te	R		20667
Gracilariales									
Gracilariaceae									
161. *Gracilaria blodgettii* Harvey	8	N	E		Te		R		26273
162. *G. cervicornis* (Turner) J. Agardh	1, 2	Ll S	M	Te	Ci		R		26274 26275 26276
163. *G. crassissima* (P. Crouan & H. Crouan) P. Crouan & H. Crouan	1, 22	Ll N	M	Te	Te		R		23308 26270 26271
164. *G. cylindrica* Børgesen	8	N	E		Ve		Ez		26277

Continue...

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Division/species	**Localities**	**Seasonality**	**Environment**	**Reproduction**			**Habitat**	**Obs**	**ENCB Herbarium voucher number**
				Rains	**Winter rains (northern)**	**Dry**			
165. *G. damicornis* J. Agardh	2	Ll S	M	Te		Ve	R		21083 24920
166. *G. tikvahiae* McLachlan	10	Ll	E	Te			R		19953
Peyssonneliales									
Peyssonneliaceae									
167. *Agissea simulans* (Weber Bosse) Pestana, Lyra, Cassano & J.M.C. Nunes	1, 2, 8, 19	Ll N S	M, E	Te Ci	Te	Ve	Epi/Sw Ez		20186 20471 26593 26594 26595
168. *Metapeyssonnelia milleporoides* D.L. Ballantine & H. Ruiz	1	N	M		Te		Ez	**NRMC**	26238 26598
169. *M. tangerina* D.L. Ballantine, C. Lozada-Troche & H. Ruiz	1, 22	N	M		Te		R Ez	**NRMC**	21316 26197
170. *Peyssonnelia armorica* (P. Crouan & H. Crouan) Weber Bosse	3, 8	N S	M, E		Te	Te	Epi/Sw Ez		20180 26487 26596
Rhodymeniales									
Champiaceae									
171. *Champia parvula* (C. Agardh) Harvey	1, 3, 8	Ll N S	M, E	Ci Te	Te	Po♀	Epi/Th Epi/Mg Epi/Sw		19840 20965 20997 24895 26389 26390 26514
172. *Champia parvula* var. *prostrata* L.G. Williams	7, 8, 12	Ll N	E	Te	Te		Epi/Th		24896 26252
173. *C. salicornioides* Harvey	3	N	M		Te		Epi/Th		26253
174. *Coelothrix irregularis* (Harvey) Børgesen	1, 6, 14, 19, 22	Ll N	M, E	Ve	Te		Epi/Mg R		20119 23266 24897 26391 26392
Halymeniaceae									
175. *Cryptonemia crenulata* (J. Agardh) J. Agardh	1, 2	Ll N	M	Te	Te		Ez		26279 26280
176. *Phyllymenia gibbesii* (Harvey) Showe M. Lin, Rodríguez-Prieto, De Clerck & Guiry	5	S	E			Te	Pe		20226
Lomentariaceae									
177. *Ceratodictyon intricatum* (C. Agardh) R.E. Norris	1	S	M			Ve	R		26293
Compsopogonophyceae									
Erythropeltales									
Erythrotrichiaceae									
178. *Erythrocladia irregularis* Rosenvinge	1, 3, 9, 16, 18, 21	Ll N S	M	Ve	Ve	Ve	Epi/Sw		20763 24954 26267 26322 26347 26402 26487 26532
179. *Erythrotrichia carnea* (Dillwyn) J. Agardh	1, 2, 3, 4, 7, 8, 9, 13, 15, 16, 17, 18, 20, 22	Ll N S	M, E	Ve	Ve	Ve	Epi/Sw		20732 20737 20866 20887 23302 24954 26267 26306 26317 26318 26347 26366 26385 26483 26500 26546 26541 26561 26605 26608

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Division/species	Localities	Seasonality	Environment	Reproduction			Habitat	Obs	ENCB Herbarium voucher number
				Rains	Winter rains (northern)	Dry			
180. *Sahlingia subintegra* (Rosenvinge) Kornmann	2, 11, 13, 14, 17, 18	Ll N S	M, E	Ve	Ve	Ve	Epi/Sw		24954 26237 26385 26528 26532 26565 2661017,
Stylonematophyceae									24954 26242
Stylonematales									26292 26338
Stylonemataceae									26377 26562
181. *Chroodactylon ornatum* (C. Agardh) Basson	6, 11, 13, 16, 22	N S	M, E		Ve	Ve	Epi/Sw		
182. *Stylonema alsidii* (Zanardini) K.M. Drew	1, 2, 6, 8, 11, 14, 16 18, 22	Ll N S	M, E	Ve	Ve	Ve	Epi/Sw		19958 20737 20864 20933 20936 26240 26302 26312 26377 26523 26527 26528 26568

SIMBOLS: Localities: 1. Punta Pelícanos, 2. Hualapich, 3. Punta Xoquem; 4. El Playón, 5. Punta Allen, 6. Punta Gorda, 7. Vigía Chico, 8. Cayo y Punta Valencia, 9. Hualastok, 10. Río Temporal, 11. Cayo Cedro, 12. Cayo Lagartijas, 13. Cayo Tres Marías, 14. Cayo Xobón, 15. Punta Tupac, 16. Isla Techal, 17. Golfito, 18. Punta Herrero, 19. El Faro, 20. Punta Mosquitero, 21. Playa Dei, 22. Pulticub. Seasonality: Ll = rains (September, 2009, June 2010, August and September 2012), N = Winter rains (northern) (January 2011, December 2011); S = Dry (March, 2009, April, 2010, 2012, 2015). Environment: M = marine, E = estuarine. Reproduction: Ve = vegetative, Mn = Monosporangio, Po = Poliesporangia, Te = Tetrasporangia, Ci = Carpoporophyte, ♀ = Carpogonia, ♂ = spermatie. Habitat: Epi/Sw = epiphyte on other macroalgae, Epi/Th = epiphyte on *Thalassia testudinum*, Epi/Mg = epiphyte on mangrove roots, Ez = Epizoic, Ro = Rodolithes, R = Rocky, Par = Parasite. Obs (Observations): NRSK = New record of RBSK, NRMC = New record of Mexican Caribbean.

Table 3. Species not located in the study period (Reported by Valadez-Cruz et al., 2014, García-García et al. 2020).

Species	Observations
Florideophyceae	
Corallinales	
Corallinaceae	
1. *Jania pumila* J.V. Lamouroux	RD
2. *Jania subulata* (Ellis & Solander) Sonder	
3. *Jania tenella* (Kützing) Grunow	RD
Mesophyllumaceae	
4. *Mesophyllum incertum* (Foslie) Me.Lemoine	
Spongitidaceae	
5. *Neogoniolithon trichotomum* (Heydrich) Setchell & L.R. Mason	RD
Orden Nemaliales	
Galaxauraceae	
6. *Tricleocarpa fragilis* (L.) Huisman & Townsend	
Ceramiales	
Callithamniaceae	
7. *Aglaothamnion cordatum* (Børgesen) Feldmann-Mazoyer	
8. *Aglaothamnion halliae* (Collins) Aponte, D.L. Ballantine & J.N. Norris	
9. *Crouania pleonospora* W.R. Taylor	
Ceramiaceae	
10. *Centroceras clavulatum* (C. Agardh) Montagne	RD
11. *Ceramium cimbricum* H.E. Petersen	
12. *Ceramium cimbricum* f.*flaccidum* (H.E. Petersen) G. Furnari & Serio	
13. *Ceramium subtile* J. Agardh	
14. *Ceramium virgatum* Roth	
Delesseriaceae	
15. *Dasya mollis* Harvey	
16. *Martensia fragilis* Harvey	
Rhodomelaceae	
17. *Amansia multifida* J.V. Lamouroux	
18. *Carradoriella denudate* (Dillwyn) Savoie & G.W. Saunders	
19. *Chondria curvilineata* Collins & Hervey	
20. *Chondria platyramea* Joly & Ugadim	
21. *Digenea simplex* (Wulfen) C. Agardh	RD
22. *Laurencia minuta* Vandermeulen, Garbary & Guiry	
23. *Melanothamnus harveyi* (Bailey) Díaz-Tapia & Maggs	
24. *Melanothamnus hawaiiensis* (Hollenberg) Díaz-Tapia & Maggs	RD
25. *Melanothamnus pseudovillum* (Hollenberg) Díaz-Tapia & Maggs	
26. *Melanothamnus tongatensis* (Harvey ex Kützing) Díaz-Tapia & Maggs	RD
27. *Polysiphonia breviarticulata* (C. Agardh) Zanardini	
28. *Polysiphonia opaca* (C. Agardh) Moris & De Notaris	
29. *Wrightiella blodgettii* (Harvey) F. Schmitz	
Wrangeliaceae	
30. *Grallatoria reptans* M. Howe	

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31. *Griffithsia heteromorpha* Kützing
32. *G. radicans* Kützing
33. *Haloplegma duperreyi* Montagne
34. *Spermathamnion gymnocarpum* M. Howe
35. *Tiffaniella gorgonea* (Montagne) Doty & Meñez
36. *Wrangelia argus* (Montagne) Montagne

Gigartinales
Gigartinaceae
37. *Chondracanthus acicularis* (Roth) Fredericq
38. *C. teedei* (Mertens ex Roth) Kützing

Kallymeniaceae
39. *Kallymenia limminghei* Montagne

Solieriaceae
40. *Eucheumatopsis isiformis* (C. Agardh) Núñez-Resendiz, Dreckmann & Sentíes
41. *Wurdemannia miniata* (Sprengel) Feldmann & Hamel

Gracilariales
Gracilariaceae
42. *Gracilaria armata* (C. Agardh) Greville
43. *Gracilaria cornea* J. Agardh
44. *Gracilaria debilis* (Forsskål) Børgesen

Peyssoneliales
Peyssonneliaceae
45. *Peyssonnelia conchicola* Piccone & Grunow

Halymeniales
Halymeniaceae
46. *Corynomorpha clavata* (Harvey) J. Agardh
47. *Halymenia duchassaingii* (J. Agardh) Kylin

Nemastomatales
Schizymeniaceae
48. *Platoma cyclocolpum* (Montagne) F. Schmitz

Rhodymeniales
Champiaceae
49. *Gastroclonium parvum* (Hollenberg) C.F. Chang & B.M. Xia

Rhodymeniaceae
50. *Botryocladia pyriformis* (Børgesen) Kylin
51. *Chrysymenia planifrons* (Melvill) J. Agardh

RD = Uncertain record.

and they were found both in the sporophytic phase (sporophyte and carposporophyte) and in the gametophytic phase (Table 2).

5. *Epiphytism*

Altogether 119 epiphytic taxa were identified (Table 2), by host we have that, from them, 54 grew exclusively on other Rhodophyta, 29 lived on the roots or bark of mangrove (*Rhizophora mangle* Linnaeus), 8 in *Thalassia testudinum* Banks ex König, 12 both in mangrove as in other Rhodophyta, 7 in other Rhodophyta and *Thalassia,* only 3 were inhabitants of both *T. testudinum* and mangrove roots and finally 6 taxa were located in all hosts (Figure 5). The highest number of epiphytes was obtained in the dry season with 92, observing the highest number of species of the families Rhodomelaceae, Wrangeliaceae and Ceramiaceae.

Discussion

1. *Floristics*

The total number of taxa found in this study is greater than that recorded on the coast of the island of Cozumel Mateo-Cid & Mendoza-González (1991) cited 168 Rhodophyta taxa; Mateo-Cid & Mendoza-González (1992) recorded 122 red algae off the coast of Isla Mujeres; Dreckmann et al. (1996) recorded 109 Rhodophyta in Puerto Morelos. On the other hand, Cetz-Navarro et al. (2008) listed 53 Rhodophyta taxa for Quintana Roo in works after the catalog by Ortega et al. (2001). In the case of Valadez-Cruz et al. (2014) these authors documented 172 Rhodophyta taxa for the Sian Ka'an Biosphere Reserve, which shows that the RBSK has a great specific richness of red algae from the Quintana Roo coast, with numerous taxa characteristic of the region. In addition, the results obtained suggest that the RBSK is an area with high floristic diversity, if one considers that 50.4% of the Rhodophyta known for the coast of Quintana Roo can be found on its coastline, which is 451 species and 13 infraspecific categories of red algae (García-García et al. 2020).

The best represented family in our study was Rhodomelaceae with 65 taxa, a figure greater than that found by Mateo-Cid & Mendoza-González (1991) where the authors recorded 38 Rhodomelaceae taxa for Cozumel Island, Dreckmann et al. (1996) cite 34 for Puerto Morelos and Senties & Dreckmann (2014) recorded 26 species of the Rhodomelaceae family for the coast of Campeche. On the other hand, Senties & Dreckmann (1990) indicate that the Rhodomelaceae family (order Ceramiales) is the most numerous not only within the Order, but also within the Rhodophyta division. The species of this order have a greater affinity for tropical, subtropical, and temperate zones, occupying mostly rocky substrates and some epiphytes in intertidal and subtidal environments, characteristics that our study locations present. The specific richness and the presence of the species of the order Ceramiales in all the localities of the RBSK can be explained in several ways; one of them is that red algal order Ceramiales contains the 37.6% of all floridean red algal species (Guiry & Guiry 2023). It is a highly diverse group in terms of number of species, with over 330 genera and over 2690 species. The order is represented in all marine and brackish habitats worldwide and is comprised of five families: Callithamniaceae, Ceramiaceae, Delesseriaceae, Rhodomelaceae and Wrangeliaceae (Guiry & Guiry 2023). In addition to their high diversity, the Ceramiales have a great adaptability to develop in different environments. For example, the Rhodomelaceae species occupy various marine habitats: they can grow as free-living plants on stones, rocks, shells, and different artificial substrata, or colonize other algae either as obligate epiphytes or as parasites. Also, there are cosmopolitan species growing within a broad range of temperature (0–28 °C), salinity (6.0–32.5‰), and vertical distribution. In different locations it may occur in the low-intertidal zone, in rock pools, in shallow or deep (15–17 m) subtidal water along open, wave-exposed coasts and in sheltered habitats (Tarakhovskaya et al. 2022). On the other hand, many studies show that the species of the order Ceramiales are successful, due to their asexual reproduction and the vegetative multiplication mechanisms as fragmentation, multicellular propagules, and monopodial stoloniferous growth (Kilar & McLachlan 1986, Kapraun 1977, Haroun & Gil-Rodriguez 1995, Husa & Sjøtun 2006, Cecere et al. 2007).

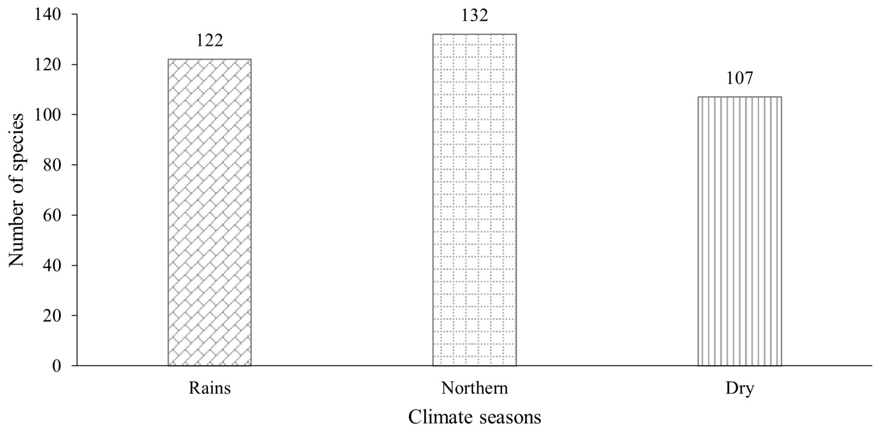

Figure 2. Number of taxa by climatic season.

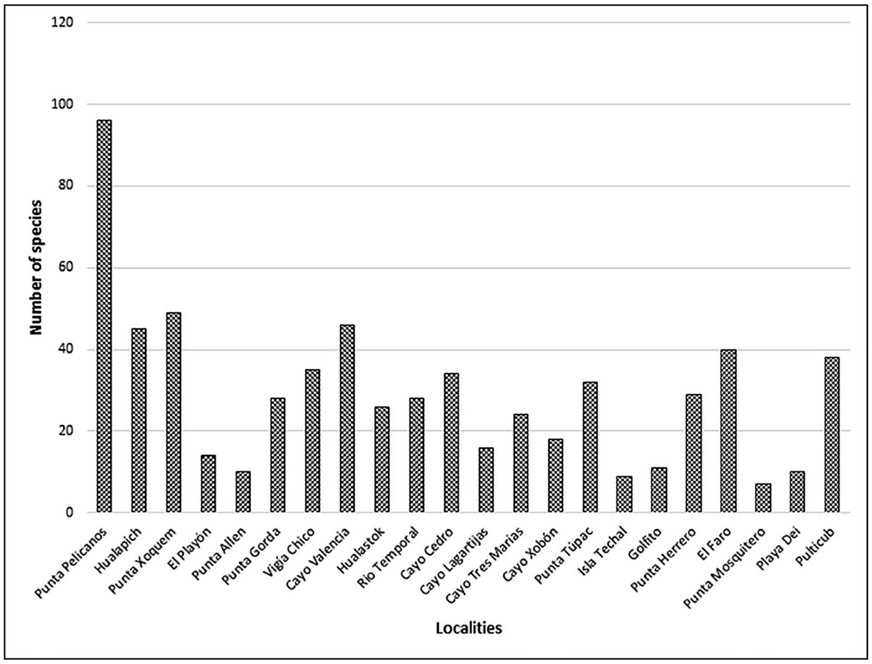

Figure 3. Number of taxa per locality.

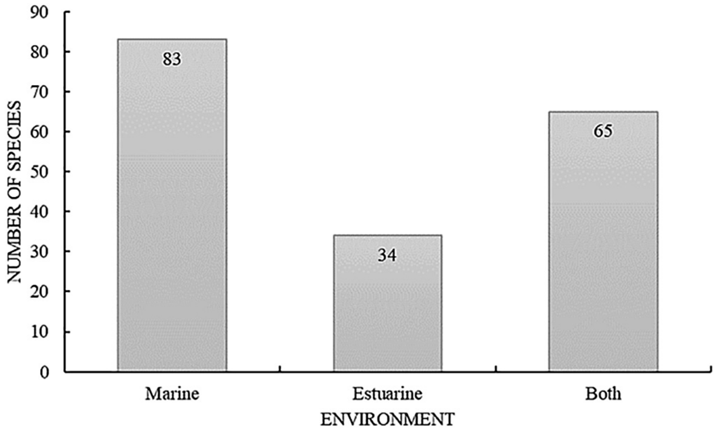

Figure 4. Number of taxa by environment.

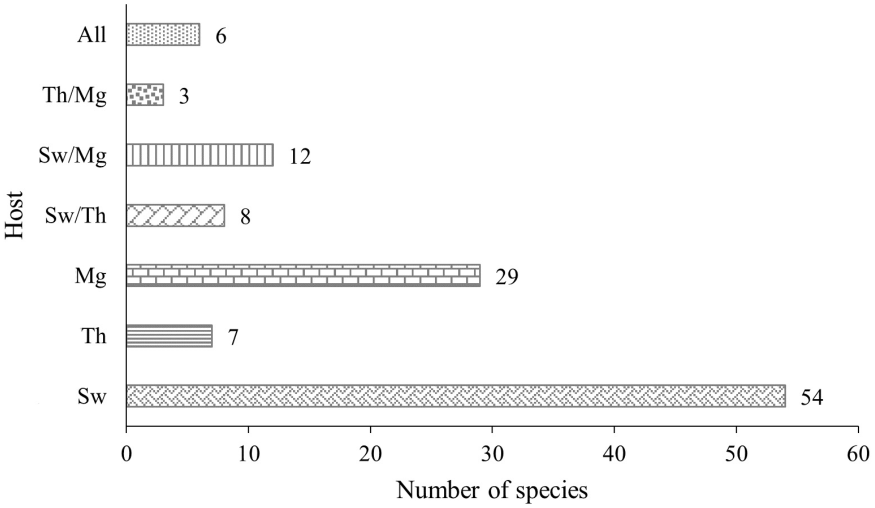

Figure 5. Number of epiphytes by host (abbreviations = Mg = *Rhizophora mangle*, Th = *Thalassia testudinum*, Sw = Other macroalgae).

Table 4. Feldmann and Cheney indices for some marine environments of the coast of the Gulf of Mexico and the Mexican Caribbean.

Locality/state	Feldmann index (R/P)	Cheney index (R + C)/P
Mujeres island, Quintana Roo	4.50	7.15
Cozumel island, Quintana Roo	4.40	7.04
Puerto Morelos, Quintana Roo	3.40	5.60
Yucatán coast	6.00	9.00
Campeche coast	5.37	9.30
Sian Ka'an Biosphere Reserve (This study)	**4.68**	**7.26**

Of the 182 taxa determined in this study for the RBSK coastline, 25 represent new records for the study area (NRSK) and of these, 8 are new records for the Mexican Caribbean (Table 2); on the other hand, 51 previously recorded species were not located (Table 3), perhaps due to changes in the environments where these algae inhabit, where there is currently a greater human influence that has modified the architecture of the landscape, as well as natural events such as hurricanes and Tropical storms. Entirety, previous records, and those obtained in this study constitute a total of 233 registered species for the RBSK, however, it is important to highlight that the Espiritu Santo Bay has not been sufficiently studied, so to know the phycofloristic composition throughout the reserve, more studies are required in this bay.

There are also doubtful records of some species, to name a few, Won et al. (2009) in their work on the morphological and molecular characterization of the genus *Centroceras*, found that samples identified under the concept of "*Centroceras clavulatum*" represented 9 morphological groups that corresponded to different clades in their phylogenetic analysis and determined that the distribution of *C. clavulatum* is restricted to northern Chile, Peru, southern California, southern Australia and New Zealand, which makes its presence in the Mexican Caribbean region unlikely. Díaz-Tapia et al. (2017) sought to clarify the relationships in the *Neosiphonia/Polysiphonia* complex using a combination of molecular and morphological analyses, based on their results they transferred 46 species of *Neosiphonia* to *Melanothamnus*, including *Melanothamnus hawaiiensis* (type locality: Waikiki, Oahu, Hawaiian Islands) also indicating, the distribution of the genus *Melanothamnus* is predominantly in the Indo-Pacific, so it is necessary to reevaluate the species of the genus *Melanothamnus* that have been cited in the Mexican Caribbean.

Particularly for the genus *Jania*, it is widely known about its complicated scenario to establish limits between species due to the substantial morphological variation that it exhibits, consequently, the correct application of names for many species of *Jania* is surrounded by uncertainty and, therefore, lacks knowledge of a stable nomenclatural foundation, and descriptions are often brief and inadequate as well (Harvey et al. 2020). Harvey et al. (2020) in a study of the genus *Jania* in Australia evaluated 79 diagnostic characters to delimit the species of this genus, finding that many of these characters' overlap each other or are inadequately explained, some characters or character states were not found in species from south-eastern Australia or its nomenclatural types and therefore could not be assessed. Others were present in all specimens and thus were of no value in delineating species found in south-eastern Australia and which records of some species from south-eastern Australia involve misidentified specimens. In their study, Harvey et al. (2020) transferred *J. adhaerens* as a synonym of *Jania pedunculata* var. *adhaerens*, indicating that, in the published literature, the concept of the morphoanatomy of *J. adhaerens* varies considerably from publication to publication. In addition, there is no consensus in the literature regarding what defines *J. adhaerens* as a species from a morphoanatomical point of view, so it is necessary to review the type of material and molecular sequence data may also be useful. Finally, the authors excluded *J. rubens* from south-eastern Australia because the records are based on misidentifications. The type locality of *J. rubens* is 'Insulae Stoechades' [Îles d' Hyères, Francia, Mediterráneo], in the prologue Linnaeus (1758, p. 806) indicated 'Habitat en Oceano Europæo' and it is not known whether this includes the Mediterranean (Guiry & Guiry 2023). Regarding *J. tenella*, the type locality is the Gulf of Naples (Italy), and the distribution of this species is mainly in the Pacific islands, Japan, and

Taiwan (Guiry & Guiry 2023). It is evident that the *Jania* species cited in the Mexican Caribbean require morphological and molecular studies to find the true taxonomic and phylogenetic affinities of these species, as well as to delimit their distribution in the study area.

The use of morphoanatomical characters in the determination of non-geniculate coralline algae collected in the RBSK has been problematic; this fact is consistent with what was reported by Kato et al. (2013), Mateo-Cid et al. (2014) and Richards et al. (2021), due to the above and based on sequencing only 20 specimens from the rather narrow study area, we have recovered 9 species of *Neogoniolithon*, and 2 *Harveylithon* and *Porolithon* each, in the case of *Spongites* and *Lithothamnion* specimens lack many morphoanatomical characters needed to adequately describe them, particularly those characters associated with reproduction. We have not sequenced any specimens that morphoanatomical we call *S. fruticulosus* and *L. sejunctum*. We recognize that acceptance of each of these names for our local species will depend upon sequencing some specimens.

2. *Biogeography*

The results of the present study were examined with the Feldmann and Cheney indices and were contrasted with what was found by Mateo-Cid & Mendoza-González (2007) for Isla Cozumel; Mendoza-González et al. (2007) from Isla Mujeres, Dreckmann et al. (1996) for Puerto Morelos and Huerta-Múzquiz et al. (1987), Ortegón-Aznar et al. (2001, 2009) and Sánchez-Molina et al. (2007) for the Yucatan coast. Table 4 shows the data obtained from the Feldmann and Cheney indices calculated in the four regions mentioned; the phycoflora of the study area is similar to that obtained for the Isla Cozumel and Isla Mujeres, completely Caribbean localities. The indices used allow us to establish that the marine and estuarine algae of the Sian Ka'an Biosphere Reserve have a predominant tropical distribution and that, accordingly, the presence of *Jania cubensis, Amphiroa fragilissima, A. tribulus*, *Neogoniolithon spectabile*, *Titanophycus validus, Ceramium nitens, Dasya caraibica, Bostrychia binderi, Chondria littoralis, Wrangelia penicillata, Gracilaria blodgettii* and *G. crassissima*, were recorded among others.

3. *Temporal variation*

In the present work, the highest species richness was found in the northern (winter rains), followed by summer rains, and the lowest species richness was found in the dry season. This can be justified with what is reported by Pech-Poll et al. (2010) who relate the physicochemical parameters with the abundance and diversity of species, in addition to the amount of nutrients available in the habitat, in the case of the summer or winter rainy season, the supply of nutrients is greater due to runoff along the coast, this would also justify the fact that a high species richness is present in the northern rainy climatic season, not varying in great number with the rainy season. On the other hand, the dry climatic season provides a more adverse habitat due to the low rainfall that exists in the season, as well as the high temperature that occurs, since it can reach more than 30 °C, which increases the evaporation of seawater and therefore salinity. Mateo-Cid & Mendoza-González (1991) mention that seasonality in the Mexican Caribbean is related to large temperature fluctuations throughout the year.

The changes in each community at each time of the year are largely regulated by the biological rhythms of the organisms that constitute it, which in turn are related to environmental fluctuations (Núñez-López 1996), which modify the physicochemical characteristics of seawater associated with the seasonality of the environment. The spatial and temporal variability is affected by factors such as the complexity of the substrate, as well as temperature and salinity, since at high atmospheric temperature water evaporation is greater, generating hot water and higher salinity, on the contrary, when there is a high rate of rainfall, a considerable discharge of fresh water is caused along the coast (Pech-Poll et al. 2010).

In this context, Punta Pelicanos, Hualapich, Punta Xoquem and Pulticub provide adequate conditions for the high specific richness of red algae that are present, this is because in the intertidal zone there are platforms and rocky plains with gentle waves, in addition these beaches are in a conserved region for being within the reserve. In the same way, the localities where there was a low specific richness correspond to Cayo Lagartijas, Cayo Xobón, Punta Allen, Isla Techal and Golfito, localities that are located within the bays, purely estuarine areas, in which there are no adequate conditions for the establishment and development of the Rhodophyta, especially the type of substrate that is mostly sandy and the presence of seagrass beds and mangroves. It is important to highlight that a high percentage of the Rhodophyta species of the Mexican Caribbean have been collected in rocky substrate, Santelices (1977), Mateo-Cid & Mendoza-González (1991), Mendoza-González & Mateo-Cid (1992) and Ortega et al. (2001) indicate that this substrate exposed to waves is the place where a great diversity of marine algae is located.

4. *Reproduction*

The reproductive stage best represented in this study was the sporic stage, which coincides with the results obtained by Mateo-Cid & Mendoza-González (1991), Mendoza-González & Mateo-Cid (1992), Mateo-Cid et al. (2013), and Lucio & Nunes (2002), the latter authors mention that the dominance of a reproductive phase may be influenced by temporary changes in local environmental factors. On the other hand, Ardito & Gómez (2005) consider that the sporophytic generation has a longer survival than the gametophytic generation, in addition to other reproductive mechanisms such as vegetative propagation or apomeiosis.

The sexual stages were poorly represented in this study, according to Santelices (1977) asexual reproduction has the advantage of requiring less energy expenditure for the formation of spores and their rapid dissemination, compared to the formation of sperm and carpogonium that give rise to the carposporophytic phase, which are only present when environmental conditions become adverse.

5. *Epiphytism*

The highest number of epiphytes was obtained in the dry season with 92, observing the highest number of species from the Rhodomelaceae, Wrangeliaceae and Ceramiaceae families with 11 each, most of these species are filamentous, small, and annual. Most of the epiphytes were found growing frequently on other larger Rhodophyta such as *Gracilaria*, *Laurencia*, *Palisada*, *Acanthophora*, *Alsidium*, and *Digenea*. It has been suggested that host longevity must be long enough to allow these organisms to complete their life cycle and that this could be a reason for the absence of epiphytes in algae with short and ephemeral lifecycles (Santelices 1977). Regarding the rainy season, 87 species were identified, a number very close to that found in the dry season. In this season it was observed that fleshy corticated macroalgae grew both on rocky substrates and epiphytes of other macroalgae, which can be attributed to the fact that the populations of both epilithic and epiphytic benthic marine algae are growing. On the other hand, it is necessary to consider that in the RBSK there are seagrass meadows and mangroves, both populations of vascular plants offer an adequate substrate for the fixation and growth of epiphytic algae (Nava-Olvera et al. 2017, Peña-Salamanca 2017).

Seagrass meadows *Thalassia testudinum* represent a coastal ecosystem of great value in the RBSK, mainly due to the ecosystem services they offer, the vertical and horizontal structure of the seagrass plants favours the appearance of many microhabitats, transforming the leaves into an ideal substrate for the development of many epiphytic organisms (Díaz-Merlano et al. 2003, Nava-Olvera et al. 2017). Nava-Olvera et al. (2017) in their study of epiphytic algae in Veracruz and Quintana Roo, determined 46 epiphytic algae taxa on *T. testudinum* in Santa Rosa, Quintana Roo, 38 of them correspond to Rhodophyta, which highlights its high contribution quantitatively compared to other groups of algae. This dominance is consistent with previous records in other regions, where red algae have been documented to dominate in species composition and biomass (Mendoza-González & Mateo-Cid 1992, Quan-Young et al. 2006). Records of Rhodophyta in studies of epiphytic floras, both in marine angiosperms (Ibarra-Obando & Aguilar-Rosas 1985, Barrios & Díaz 2005), and in macroalgae (Montañés et al. 2003, Quan-Young et al. 2006, Ortuño-Aguirre & Riosmena-Rodríguez 2007), point out that red algae are the group with the greatest specific richness within epiphytism, since they present life forms and reproductive strategies that allow them to remain longer in the phorophyte (Albis-Salas 2010). Regarding mangroves, the roots and remains of these trees constitute a firm and safe substrate for the organisms that inhabit them; regarding epibiont algae and invertebrate communities, the roots provide a large moist surface available for colonization. It has been proven that the tolerance of mangrove algae to variations in salinity and periods of desiccation is due to their ability to synthesize, accumulate and regulate organic compounds that protect them from unfavourable factors for them (Ríos et al. 2019).

In our study, a total of 29 exclusive epiphytic species were located in mangrove roots and bark, mainly from the genus *Bostrychia* with 6 species, *Caloglossa* and *Murrayella* with one species each and *Catenella* 2. These results agree with what was recorded by other authors such as Peña-Salamanca (2017) and Ríos et al. (2019) who mention that the association of the Bostrychietum complex is well known, which is a group of algae associated with mangrove roots in tropical and subtropical areas, composed mainly of the genera *Bostrychia, Caloglossa, Catenella,* and *Murrayella*, as well as other genera. Epiphytes that were also found in the mangrove roots were *Polysiphonia* and *Dasya* with 5 taxa each and *Chondria* with 3, most of the species that make up the Bostrychietum algal complex such as the genera *Polysiphonia, Dasya* and *Chondria* they belong to the order Ceramiales which has the highest specific richness within Rhodophyta and its species have a wide worldwide distribution (Guiry & Guiry 2023).

Conclusion

The analysis and integration of previous studies of Rhodophyta in the study area and the results obtained confirm the importance of carrying out phycofloristic inventories in little-worked coastal regions of the RBSK, which will result in a better understanding of the diversity of this important cluster. These results are the basis for future ecological, sustainable management and conservation studies, so it is recommended to continue with the sampling in the localities visited to observe the spatial and temporal changes of the flora that allow identifying possible alterations in the environmental conditions of the area of the RBSK.

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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

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Article

Dung beetles in South American pasturelands

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Abstract: Pasturelands are characterized as grasslands utilized for cattle raising and consist of natural or exotic vegetation, predominantly grasses. In the context of sustainable production, the biodiversity of insects within grazing environments holds significant value. Dung beetles play a crucial role in sustaining pasturelands as the burial of feces by these beetles fosters ecological services indispensable for maintaining a robust and healthy environment. Given that different dung beetle species contribute to distinct environmental benefits, a comprehensive understanding of the species present in pasturelands, their origins, and the ecological services they provide is imperative. This study endeavors to compile comprehensive information on dung beetle species native to South America, emphasizing taxonomic precision and a confirmed affinity for cattle dung. Our findings are derived from a synthesis of literature and observational data, incorporating location information obtained from taxonomic revisions and specimen labels of specimens housed at CEMT. In South America, a total of 57 dung beetle species are documented that inhabit grazing areas and actively feed on cattle manure. These areas span diverse biomes encompassing native and/or introduced grasslands, which may include deforested sections within forest biomes such as Chaco, Pantanal, Cerrado, Caatinga, Pampa, Atlantic Forest, Amazon Forest, Paramo, Puna, Llanos, and Patagonia. The preponderance of species identified fall within the paracoprid category, recognized as particularly vital for the sustainability of pasturelands. Despite their acknowledged importance, a noticeable knowledge gap impedes the effective conservation of these species. This gap is a focal point of discussion in this study, addressing the challenges and opportunities for enhancing conservation efforts. The species documented in this research exhibit notable economic and environmental relevance in the context of sustainable livestock production, emphasizing the urgency and significance of initiatives that prioritize their conservation.

Keywords*: Scarabaeinae; livestock; grasslands; conservation.*

Besouros rola-bostas em pastagens sul-americanas

Resumo: Pastagens são áreas formadas por vegetação nativa ou exótica, principalmente gramíneas, e são utilizadas na pecuária. A diversidade de insetos em áreas de pastagens é muito valiosa, especialmente quando consideramos os métodos de produção sustentável. Besouros rola-bostas são importantes para a sustentabilidade em pastagens porque o enterrio de esterco promove benefícios essenciais para a manutenção do ambiente pastoril. Espécies diferentes exercem diferentes serviços ecossistêmicos, logo é necessário saber quais espécies estão presentes em áreas de pastoreio para saber quais são os benefícios que elas podem proporcionar. Aqui reunimos todas as informações disponíveis para as espécies taxonomicamente bem definidas de rola-bostas nativos da América do Sul e que são conhecidas por utilizar fezes bovinas como recurso para alimentação e nidificação. Usamos dados encontrados na literatura, em observações de campo e em etiquetas de espécimes depositados na CEMT. São registradas 57 espécies de rola-bostas nativos da América do Sul que se alimentam e nidificam em fezes bovinas, e estas estão distribuídas nos seguintes biomas: Chaco, Pantanal, Cerrado, Caatinga, Pampa, áreas abertas da Mata Atlântica e da Floresta Amazônia, Paramo, Puna, Llanos e Patagônia. A maioria das espécies são de paracoprídeos e estes são considerados os mais importantes para as áreas de pastagem. No entanto, existe uma grande lacuna de conhecimento em história natural, o que dificulta a efetividade da conservação dessas espécies. Todas as espécies listadas neste trabalho têm potencial relevância econômica e ambiental na pecuária sustentável e, portanto, o estudo e conservação delas devem ser priorizadas.

Palavras-chave*: Scarabaeinae; pecuária; áreas abertas; conservação.*

Introduction

Pasturelands characterized by grasses and used for cattle raising are a significant component of South American landscapes. These grasslands exhibit diverse ecological characteristics, ranging from tropical to temperate climates. While tropical grasslands dominate regions such as the Cerrado, Chaco, Pantanal, Llanos, and Caatinga, temperate or temperate-like grasslands are prevalent in the Pampas, Patagonia, Paramo, and Puna (the latter two being high altitude grasslands) (Dixon et al. 2014). The term "derived savannas" refer to areas that were once forests but were deforested for crop cultivation or livestock management. Despite this transformation, natural grasslands remain highly attractive to farmers due to their flat terrain and cost-effective deforestation methods. However, the widespread conversion of natural grasslands into croplands or extensive planted pastures raise significant conservation concerns (Overbeck et al. 2015, Oliveira et al. 2017).

Insect biodiversity in grazing environments is highly valuable, especially when sustainable production is considered crucial. Bioindicators, which include several animal groups (such as dung beetles, birds, mammals, and butterflies) play a vital role in evaluating environmental quality. Our focus here is on dung beetles (Coleoptera, Scarabaeinae), known for their sensitivity to grazing intensity, land conversion, and abandonment (Tonelli et al. 2019). Dung beetles offer economically efficient means of assessing pasturelands, whether they are natural or disturbed habitats, thanks to cost-effective standardized protocols for evaluating dung beetle richness, abundance, and community structure (Halffter & Favila 1993, Gardner et al. 2008, Tonelli et al. 2019).

Dung beetles play a pivotal role in ensuring sustainability within pasturelands through the burial of feces, thereby fostering bioturbation. This process enhances aeration, humidity, and the redistribution of organic matter and microorganisms across varying depths, consequently increasing the nutritional value of grasses (Bornemissza & Williams 1970, Bang et al. 2005, Farias & Hernández 2017, Barragán et al. 2022). Furthermore, dung beetles contribute significantly to parasitic control, targeting flies and nematodes (Bornemissza 1960, 1970, Nichols et al. 2008, Sands & Wall 2016). Noteworthy environmental benefits include a reduction in greenhouse gas emissions with a decrease of 7% in dung pads and 12% in pasture ecosystems (Slade et al. 2016). This is predominantly due to mitigating methane (CH_4) emissions, a gas that typically forms under anaerobic conditions, since dung beetle activities facilitate oxygenation within pads, therefore diminishing methanogenesis (Slade et al. 2016).

The functional classification of dung beetles into three types reflects their distinct approaches to managing and storing food and nest resources: telecoprids (rollers), paracoprids (tunnellers), and endocoprids (dwellers) (Halffter & Matthews 1966) (Figure 1). There is a fourth guild called "kleptocoprids" (Halffter & Matthews 1966), but precise information is lacking on how deep or how far they nest, or even if it is within their host nest, thus we use this class apart from the three main functional types. Although these functional types are common in grasslands, they exhibit disparities in terms of soil preferences and when they are active (Halffter & Edmonds 1982). According to Farias & Hernández (2017), paracoprids exhibit a positive association with soil organic matter components and quantity, while telecoprids typically favor specific soil textures, particularly sandy soil. Endocoprids, on the other hand, exhibit no particular preference for soil components, nesting either within the dung pad or at the interface between soil and dung. Notably, they tend to be active during drier periods of the day, strategically avoiding competition with tunnellers and rollers, which thrive in more humid conditions (Halffter & Edmonds 1982).

Diverse body sizes and distinct food preferences among dung beetle species yield varied environmental benefits. Hence high species diversity within pastures correlates with many advantages. These benefits encompass diverse levels of bioturbation, characterized by shallow, medium, or deep burrows, nests, and galleries containing one, two, or multiple chambers. Furthermore, disparate rates of feces disaggregation and the integration of organic matter into the soil occur across various horizontal levels (Flechtmann et al. 1995a, Bornemissza 1960, Halffter & Edmonds 1982).

In the Brazilian context, 76 dung beetle species are documented in grazing areas (Tissiani et al. 2017). However, a reassessment of this list is imperative due to discrepancies observed in feeding habits or habitat preferences of some reported species, particularly in open conditions. Additionally, several taxonomic revisions have been published since the publication of this list. Although recent efforts have comprehensively reviewed published information on the ecological functions of dung beetles in South American pasturelands (Arellano et al. 2023), the need for a comprehensive taxonomic list remains. This study aims to compile a taxonomically well-defined list of dung beetle species native to South America, focusing on those known to feed on cattle dung. Such endeavor not only contributes to a clearer understanding of biodiversity but also highlights the potential economic and environmental relevance of these species within pastureland ecosystems (Losey & Vaughan 2006, Beynon et al. 2015).

Material and Methods

We compiled a list of dung beetle species exhibiting coprophagous behavior, specifically those associated with cattle dung in pastures. This compilation is grounded in bibliographic sources and observational data. Our methodology involved an exhaustive bibliographic search focused on dung beetle species within South American pasturelands. To accomplish this, we employed a systematic review across two prominent academic databases: Web of Science for comprehensive bibliographic coverage and SciELO for papers presented in Portuguese and Spanish. The search query was: "(dung beetle* OR Scarabaeinae*) and (pastures* OR grasslands*) and (cattle dung) and (South America* OR Argentina* OR Brazil* OR Bolivia* OR Chile* OR Colombia* OR Ecuador* OR French Guiana* OR Guyana* OR Paraguay* OR Uruguay* OR Peru* OR Venezuela*)". All articles meeting the predetermined criteria and published until 2022 were included, with books and technical reports also considered, even if not explicitly listed in the systematic search. Our focus was on papers presenting lists of dung beetle species collected from native or exotic pasturelands within the South American territory.

To address historical nomenclature challenges, wherein certain Geotrupidae and Aphodiinae (Scarabaeidae) species have been designated as "dung beetles," we made a deliberate choice to exclusively concentrate on Scarabaeinae (Coleoptera: Scarabaeidae) species in this study. Geotrupidae species associated with feces are confined to Southern Argentina and Chile (Lobo & González-Chang 2022), and

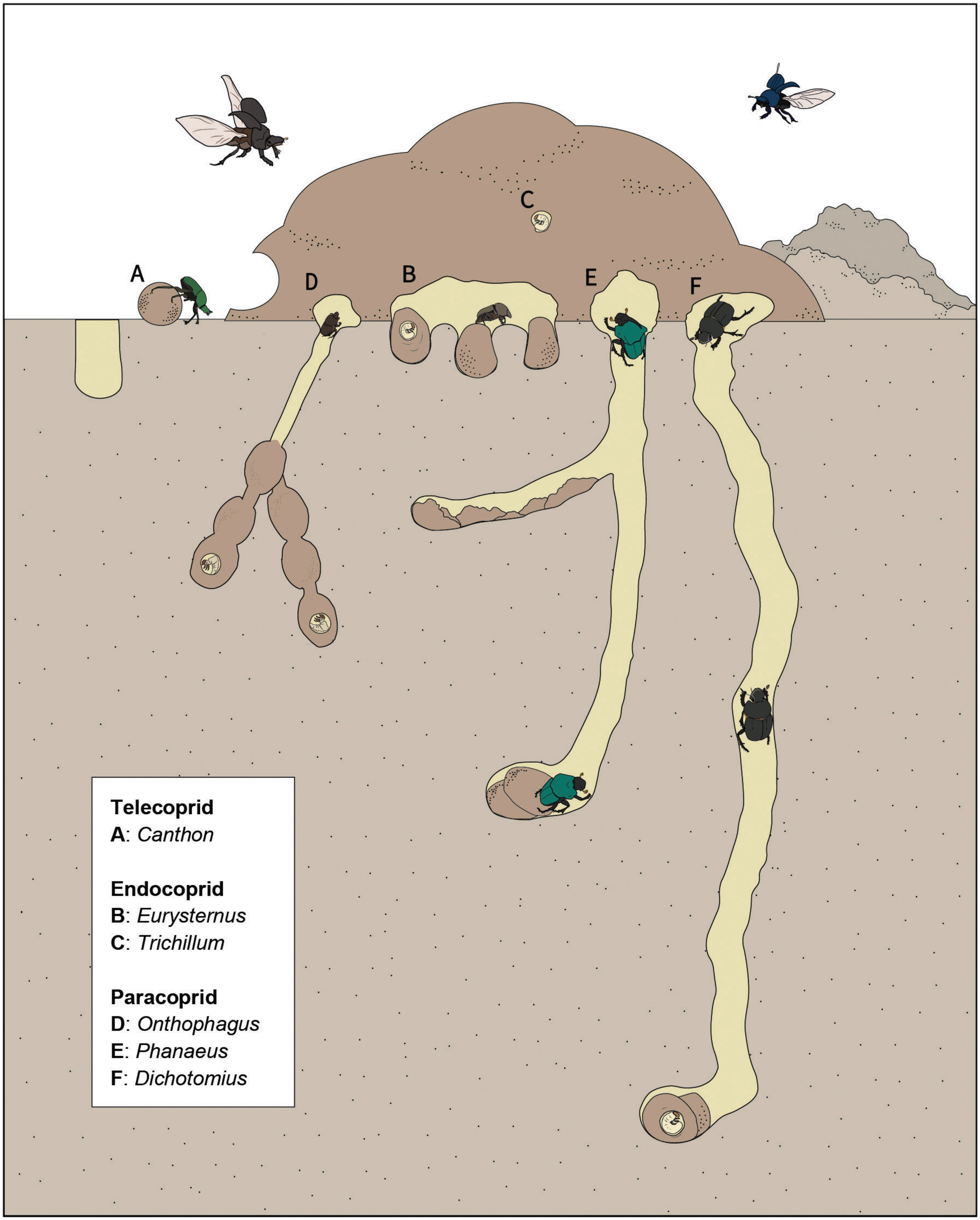

Figure 1. Functional groups of dung beetles based on nesting behavior. Illustration: Bruna Bordin.

Aphodiinae are small dwellers, whose present identification challenges in tropical regions of the continent. Additionally, our focus was refined to exclude Scarabaeinae species that, while inhabiting pasturelands, do not commonly engage in coprophagous behavior on cattle dung.

To compile our list, we relied on reported localities derived from taxonomic revisions and specimen labels housed at Coleção Entomológica de Mato Grosso Eurides Furtado (CEMT). This effort yielded 9,558 geographical records, including 5,935 from CEMT, 2,603 from bibliographic sources, and 1,020 yet unpublished records from ongoing taxonomic revisions provided by respective authors (Supplementary Material).

Geospatial maps were generated using a suite of R packages, including "ggsn," "RColorBrewer," "raster," "rgdal," "sf," "tidyverse," "wesanderson," "ggspatial," "viridis," and "scales" (R Core Team 2022). We chose not to include a map (or layer) of South American pasturelands because the available data is outdated, however, this product is being actively developed as part of the Global Pasture Watch initiative. The initial maps expected in the second quarter of 2024 [https://www.landcarbonlab.org/news-updates/tag/global+pasture+watch]. High-quality photographic documentation was facilitated using a Leica model m205C (7.8 × –160.0 ×) stereo microscope equipped with an MC190 HD image capture system.

Results

During our comprehensive search, we identified 43 articles containing reports on dung beetle species collected on cattle dung in South American pasturelands. It is pertinent to note that dung beetle species observed in cattle dung in forests or within forested areas were excluded from our consideration. The resultant list comprises 57 species documented in South American pasturelands actively feeding on cattle dung (Table 1). Notably, in Brazil, where the largest pasturelands in the Neotropical region are found, a total of 48 dung beetle species engaging in the consumption of cattle manure have been recorded in grazing areas. These occurrences span various biomes with native and/or introduced grasses, including Chaco, Cerrado, Caatinga, Pampa, Atlantic Forest, and Amazon Forest, as detailed in Table 1 and Figures 2–11. Furthermore, our findings extend beyond Brazil, encompassing nine species in other South American countries that exhibit coprophagous behavior on cattle dung. These countries host unique biomes not found within Brazil. Specifically, these biomes include Paramo (Colombia and Peru), Puna (Peru to Argentina), Llanos (Venezuela and Colombia), and Patagonia (Chile and Argentina) (Figures 2–11). This comprehensive listing provides a nuanced understanding of the distribution and feeding habits of dung beetle species across diverse South American ecosystems.

Discussion

In the context of climate variables, distribution of dung beetles is predominantly shaped by temperature and precipitation dynamics (Halffter & Edmonds 1982). Nevertheless, at finer spatial scales, factors such as landscape configuration, soil composition, vegetation structure, and habitat heterogeneity emerge as primary influencers on dung beetle communities (Sowig 1995, Almeida & Louzada 2009, Louzada et al. 2010, Silva et al. 2010, Almeida et al. 2011). Species inhabiting cattle pastures are generally exposed to higher temperatures, lower humidity, and higher soil compaction compared to those in forests (Soto et al. 2019). Species adapted to natural grasslands may be more resilient to these variables, and, indeed, we find that the most common dung beetle species in pastures are native to the Cerrado, Caatinga, or other natural South American grasslands (Almeida & Louzada 2009, Louzada & Carvalho e Silva 2009, Louzada et al. 2010, Silva et al. 2014).

Southwestern Amazonian pasturelands were colonized by dung beetle species from the Cerrado and other adjacent dryer habitats; these habitats typically serve as the primary source of native species for introduced grasslands (Silva et al. 2014). Northern Amazon pasturelands exhibit a dung beetle fauna similar to that found in intra-Amazonian savannas and Llanos (Matavelli & Louzada 2008). However, as certain species are found in Cerrado areas south of the Amazon, we hypothesize that these populations may have dispersed along with large groups of cattle transported during the northern expansion of grasslands (and consequently, of cattle) from the Cerrado areas.

A comparable pattern is observed in pastures located in Atlantic Forest areas, where dung beetle fauna is allochthonous (see Louzada & Carvalho e Silva 2009). Based on our understanding, it is expected that species adapted to forests would not endure in dry environments, and this indeed occurs in pasturelands established in areas where there was once a closed canopy. In Northeastern Brazil, the species found in pastures also inhabit Cerrado and/or Caatinga areas. However, for the Central and Southern regions of Brazil, the dung beetle fauna found in pasturelands is similar to that in Cerrado and/or Pampa regions.

The species composition between pasturelands and forests differs, and presence of surrounding forests does not increase dung beetle richness in pastures (Silva et al. 2014). Feeding guilds of dung beetles in forests consist of 40% specialists and 60% generalists, while in pastures, 75% of dung beetle species are specialists (coprophagous), and 25% are generalists (Silva et al. 2014). It has been suggested that the development and dominance of coprophagous behavior began in savannas, potentially influenced by herds of large herbivorous mammals (Halffter & Matthews 1966). An intriguing fact is that the greatest diversity of coprophagous dung beetles in Africa is found in savannas, while in South America, where megafauna became extinct during the Pleistocene, dung beetles in savannas also exhibit frugivorous and necrophagous behaviors (Halffter & Matthews 1966).

In the context of large dung pats and their remarkable diversity, it is frequently observed that species colonizing a pat exhibit varying sizes, even when the allocation strategy is alike. This diversity in size may account for the coexistence of numerous species (and specimens) within a dung pat (Hanski & Cambefort 1991). The abundance of specimens in a dung pat can each over 1500 individuals, encompassing all three functional types with a predominant representation by small endocoprids (Flechtmann et al. 1995b). This is reasonable given that paracoprids and telecoprids tend to swiftly disappear after extracting a portion from the source.

Dung removal is directly correlated with the body size of dung beetles, with the largest species excavating the deepest galleries (Gregory et al. 2015). The most extensive tunnel documented, created by the native North American dung beetle *Dichotomius carolinus* (Linnaeus, 1767), measured 162 cm in length and 55 cm in depth (Lindquist 1933). While substantial research on dung beetle's nesting behavior was compiled by Halffter and Edmonds (1982) there remains much to uncover. Although different specimens of the same species share

Table 1. List of dung beetle species registered in South American pasturelands.

Species	Author	Region	Functional Type	Size (mm)	Burial depth (cm)	Reference
Agamopus unguicularis	(Harold, 1883)	Cerrado	Kleptocoprid	4.5	–	Harold (1883); Vaz-de-Mello (2007); Costa-Silva et al. (2022); CEMT.
Agamopus viridis	Boucomont, 1928	Cerrado	Kleptocoprid	4.5	–	Boucomont (1928); Vaz-de-Mello (2007); Costa-Silva et al. (2022); CEMT.
Ateuchus striatulus	(Preudhomme de Borre, 1886)	Cerrado	Paracoprid	5	unknown	Cupello (2023) personal communication – to be published); CEMT.
Ateuchus vividus	Germar, 1823	Cerrado	Paracoprid	5	unknown	Cupello (2023) (personal communication – to be published); CEMT.
Canthon septemmaculatus histrio	(Lepeletier de Saint-Fargeau & Audinet-Serville, 1828)	Cerrado, Caatinga, Chaco, Pantanal, Amazon	Telecoprid	6–11	shallow*	Halffter & Edmonds (1982); Nunes (2015)[1]; Correa & da-Silva (2022); Correa et al. (2022); CEMT.
Canthon ornatus bipunctatus	(Burmeister, 1873)	Chaco, Pantanal	Telecoprid	6–9	shallow*	Burmeister (1873); Halffter & Edmonds (1982); CEMT.
Canthon ornatus ornatus	Redtenbacher, 1868	Cerrado	Telecoprid	6–8	shallow*	Balthasar (1939); Halffter & Edmonds (1982); Tissiani et al. (2015); CEMT.
Canthon ornatus thoracicus	Harold, 1868a	Pampa	Telecoprid	7–9	shallow*	Halffter & Edmonds (1982); CEMT
Canthon rutilans cyanescens	Schmidt, 1922	Pampa, Atlantic Forest	Telecoprid	10	shallow*	Harold (1868); Halffter & Edmonds (1982); Medina Hernández et al. (2020); Hensen et al. (2021)[2]; CEMT.
Canthon rutilans rutilans	Castelnau, 1840	Pampa	Telecoprid	9–11.5	shallow*	Castelnau (1840); Halffter & Edmonds (1982); Hensen et al. (2021)[2]; CEMT.
Canthon septemmaculatus linearis	Schmidt, 1920	Llanos, Amazon	Telecoprid	8–11	shallow*	Halffter & Edmonds (1982); Nunes (2015); CEMT.
Diabroctis mimas	(Linnaeus, 1758)	South America	Paracoprid	20–32	unknown	Valois et al. (2018); CEMT.
Dichotomius bos	(Blanchard, 1845)	Cerrado, Atlantic Forest, Chaco, Pantanal	Paracoprid	25–28	>100**	Luederwaldt (1929); Lindquist (1933); Correa & da-Silva (2022); Correa et al. (2022); CEMT.
Dichotomius cotopaxi	(Guérin-Méneville, 1855)	Paramo	Paracoprid	16–24	unknown[1]	Luederwaldt (1929); CEMT.
Dichotomius crinicollis	(Germar, 1823)	Cerrado	Paracoprid	20–28	unknown[1]	Luederwaldt (1929); CEMT.
Dichotomius cuprinus	(Felsche, 1901)	Cerrado	Paracoprid	15–20	unknown[1]	Luederwaldt (1929); Cassenote et al. (2023) (personal communication – to be published); CEMT.
Dichotomius fimbriatus	(Harold, 1869)	Atlantic Forest	Paracoprid	16–23	unknown[1]	CEMT

Continue...

Continuation

Species	**Author**	**Region**	**Functional Type**	**Size (mm)**	**Burial depth (cm)**	**Reference**
Dichotomius geminatus	(Arrow, 1913)	Northern Atlantic Forest, Caatinga	Paracoprid	12.5–13.5	unknown[!]	Luederwaldt (1929); CEMT.
Dichotomius glaucus	(Harold, 1869)	Cerrado	Paracoprid	17–19	unknown[!]	Luederwaldt (1929); Cassenote et al. (2023) (personal communication – to be published); CEMT.
Dichotomius longiceps	(Taschenberg, 1870)	Amazon, Cerrado	Paracoprid	27–33	>100**	Luederwaldt (1929); Lindquist (1933); CEMT.
Dichotomius lycas	(Felsche, 1901)	Amazon, Cerrado	Paracoprid	15–20	unknown[!]	Felsche (1901); Cassenote et al. (2023) (personal communication – to be published); CEMT.
Dichotomius monstrosus	(Harold, 1875)	Paramo	Paracoprid	27–33	>100**	Luederwaldt (1929); Lindquist (1933); CEMT.
Dichotomius nisus	(Olivier, 1789)	South America	Paracoprid	16–25	unknown[!]	Luederwaldt (1929); CEMT.
Dichotomius opacipennis	(Luederwaldt, 1931)	Chaco, Pantanal	Paracoprid	12–14	unknown[!]	Luederwaldt (1931); Tissiani et al. (2015); Correa & da-Silva (2022); Correa et al. (2022); CEMT.
Dichotomius opacus	(Blanchard, 1845)	Chaco, Pantanal, Cerrado, Atlantic Forest	Paracoprid	14–17	unknown[!]	Cassenote et al. (2023) (personal communication – to be published); CEMT.
Dichotomius rugatus	(Luederwaldt, 1935)	Paramo	Paracoprid	23–27	>100**	Luederwaldt (1935); Lindquist (1933); CEMT.
Dichotomius semiaeneus	(Germar, 1823)	Cerrado	Paracoprid	11–15	90**	Luederwaldt (1929); CEMT.
Dichotomius semisquamosus	(Curtis, 1844)	Atlantic Forest, East Amazon, Caatinga	Paracoprid	20–25	unknown[!]	CEMT
Digitonthophagus gazella	(Fabricius, 1787)	South America	Paracoprid	7–13	20–25	Génier & Moretto (2017); CEMT; DBI (2023).
Eurysternus caribaeus	(Herbst in Jablonsky & Herbst, 1789)	South America	Endocoprid	10.5–20	–	Génier (2009); CEMT.
Eurysternus deplanatus	Germar, 1823	Atlantic Forest	Endocoprid	8–11	–	Génier (2009); CEMT.
Eurysternus jessopi	Martínez, 1988	Cerrado, Atlantic Forest, Amazon	Endocoprid	9–13	–	Génier (2009); CEMT.
Eurysternus nigrovirens	Génier, 2009	Cerrado, Caatinga, Atlantic Forest	Endocoprid	5–7.5	–	Génier (2009); CEMT.
Eurysternus parallelus	Castelnau, 1840	Atlantic Forest	Endocoprid	9.5–14	–	Génier (2009); CEMT.

Continue...

Continuation

Species	Author	Region	Functional Type	Size (mm)	Burial depth (cm)	Reference
Genieridium bidens	(Balthasar, 1938)	Cerrado	Endocoprid	3.8–5.3	–	Vaz-de-Mello (2008); CEMT.
Gromphas lacordairii	(Oken, 1834)	Pampa, Chaco, Pantanal	Paracoprid	9.3–17.4	unknown	Cupello & Vaz-de-Mello (2013); Cupello (2024); CEMT
Homocopris achamas	(Harold, 1867)	Paramo	Paracoprid	20–31	unknown	CEMT
Ontherus appendiculatus	(Mannerheim, 1829)	South America	Paracoprid	7–13	>10***	Génier (1996); CEMT.
Ontherus dentatus	Luederwaldt, 1930	Cerrado, Chaco, Pantanal	Paracoprid	8–9	10***	Génier (1996); CEMT.
Ontherus sulcator	(Fabricius, 1775)	Pampa, Chaco, Pantanal	Paracoprid	9–18	>10***	Génier (1996); Gregory et al. (2015); Tissiani et al. (2015); CEMT.
Onthophagus bidentatus	Drapiez, 1819	Llanos, Amazon	Paracoprid	4–7	10–20**	Zunino & Halffter (1997); CEMT; DBI (2023).
Onthophagus buculus	Mannerheim, 1829	Cerrado, Chaco, Pantanal, Pampa	Paracoprid	4–12	10–30**	Rossini et al. (2018); CEMT; DBI (2023).
Onthophagus hircus	Billberg, 1815	Cerrado, Chaco, Pantanal, Pampa	Paracoprid	4–12	10–30**	Rossini et al. (2018); CEMT; DBI (2023).
Onthophagus ptox	Erichson, 1847	South America	Paracoprid	4–7	10–20**	Zunino & Halffter (1997); CEMT; DBI (2023).
Onthophagus ranunculus	Arrow, 1913	Caatinga, Atlantic Forest, Cerrado	Paracoprid	4–6	10–15**	CEMT
Oruscatus davus	(Erichson, 1847)	Puna	Paracoprid	12–19	unknown	CEMT
Oruscatus opalescens	Bates, 1870	Paramo	Paracoprid	18–29	unknown	Chamorro et al. (2014); CEMT
Oxysternon palemo	Castelnau, 1840	Cerrado, Chaco, Pantanal	Paracoprid	12–18	15–25**	Halffter & Matthews (1966); Edmonds & Zídek (2004); CEMT.
Phanaeus kirbyi	Vigors, 1825	Cerrado, Chaco, Pantanal	Paracoprid	13–20	15–35**	Edmonds (1994); CEMT.
Phanaeus palaeno	Blanchard, 1845	Cerrado, Chaco, Pantanal	Paracoprid	16	15–30**	Blanchard (1845); Edmonds (1994); Price & May (2009); Correa & da-Silva (2022); Correa et al. (2022); CEMT.
Sulcophanaeus menelas	(Castelnau, 1840)	Cerrado, Pantanal, Pampa	Paracoprid	11–20	25–30**	Edmonds (2000); Matthews (1966); CEMT.
Tetraechma liturata	(Germar, 1813)	South America	Telecoprid	5–6.5	shallow*	Balthasar (1939); Nunes & Vaz-de-Mello 2022; CEMT.
Trichillum adjunctum	Martínez, 1969	Cerrado	Endocoprid	4–5	–	Vaz-de-Mello (2008); CEMT.

Continue...

Continuation

Species	Author	Region	Functional Type	Size (mm)	Burial depth (cm)	Reference
Trichillum externepunctatum	Preudhomme de Borre, 1880	Cerrado, Atlantic Forest, Chaco, Pantanal	Endocoprid	3–3.5	–	Vaz-de-Mello (2008); Tissiani et al. (2015); Correa & da-Silva (2022); Correa et al. (2022); CEMT.
Uroxys coarctatus	Harold, 1867	Paramo	Paracoprid	7–12	unknown	CEMT
Uroxys latesulcatus	Bates, 1892	Paramo	Paracoprid	10–15	unknown	CEMT
Uroxys rugatus	Boucomont, 1928	Paramo	Paracoprid	7–11	unknown	CEMT

*Halffter & Edmonds (1982) defined patterns of nests and, however with no measure, Deltochilini species were classified as telecoprids with shallow or superficial nests, i.e. close to soil surface.

**Estimated based on close species (same genus) with same or approximate size.

***Based on mean values published by Gregory et al. (2015).

[1] *Dichotomius* species with potential to burrow deep galleries with no close species (in size or same subgenus) to estimate depth.

[1] Nunes (2015) cite that *Canthon* histrio does not occur in the Amazon Region, but it does, as we observed in recent specimens deposited at CEMT.

[2] Hensen et al. (2021) cite that the geographical distribution of *Canthon rutilans rutilans* and *Canthon rutilans cyanescens* include French Guiana, but that is probably a citation mistake, as these species do not occur in Amazon Region.

Observation: South America is here considered three or more biomes located East of Andes. Exception: *Eurysternus caribaeus* occurs in both East and West of Andes. Pampa here comprehend Patagonia species.

nesting patterns, their nests can still vary in depth and length (Lindquist 1933). We utilized published data on known species to estimate the potential depth that closely related species might achieve (Table 1). However, we strongly advocate for future research to undertake these measurements on a species-specific basis.

A comparison between the native *Dichotomius bos* (Blanchard 1845) and the introduced species *Digitonthophagus gazella* (Fabricius 1787) highlights that *D. bos* is more effective than *D. gazella* in terms of dung removal and nutrient intake from the soil (Galbiati et al. 1995). While *D. bos* is indeed larger than *D. gazella*, the more crucial factor is that *D. bos* is native to South America. Given its larger size and superior efficiency compared to *D. gazella*, *D. bos* emerges as a preferable choice for dung beetle conservation in pasturelands. While a high number of native species, along with their abundance, might have a negative impact on the presence and invasion of *D. gazella* (Matavelli & Louzada 2008), as observed in intra-Amazonian savannas, the same effect was not observed in the Cerrado region (Mesquita-Filho et al. 2018), probably due to high specialization of *D. gazella* in broader savanna-like habitats (Matavelli & Louzada 2008).

Even without considering Aphodiinae species in this study, it is essential to emphasize their significance in pasturelands. Although not typically recognized as paracoprids, some Aphodiinae larvae create small cavities in the ground for pupation, a behavior similar to paracoprids (Yamada et al. 2007, Tonelli 2022). Even species exclusively identified as endocoprids play a crucial role in pastures disintegrating dung pats from the inside out (Flechtmann et al. 1995a). The knowledge of Aphodiinae in Brazil and most other South American countries is limited, and we emphasize the urgent need for studies on this group.

This work gathers all available information on dung beetle species that feed on cattle dung and inhabit pasturelands in South America, including estimates of burrow capacities and distribution maps. However, it is important to regard this review as a new starting point for dung beetle conservation and its applicability to sustainable livestock production, complementing the works of Martínez & Lumaret (2022) and the ecological functions review by Arellano and colleagues (Arellano et al. 2023). The current scenario is concerning, given the vulnerability of dung beetles to parasiticides (Correa et al. 2021), competition with *D. gazella*, and anticipated climate change impacts (Noriega et al. 2020, Maldaner et al. 2021). To preserve the ecological functions provided by dung beetles in pasturelands, sustainable practices must become a priority in livestock production, drawing inspiration from successful examples in Mexico and South America (Halffter et al. 2018).

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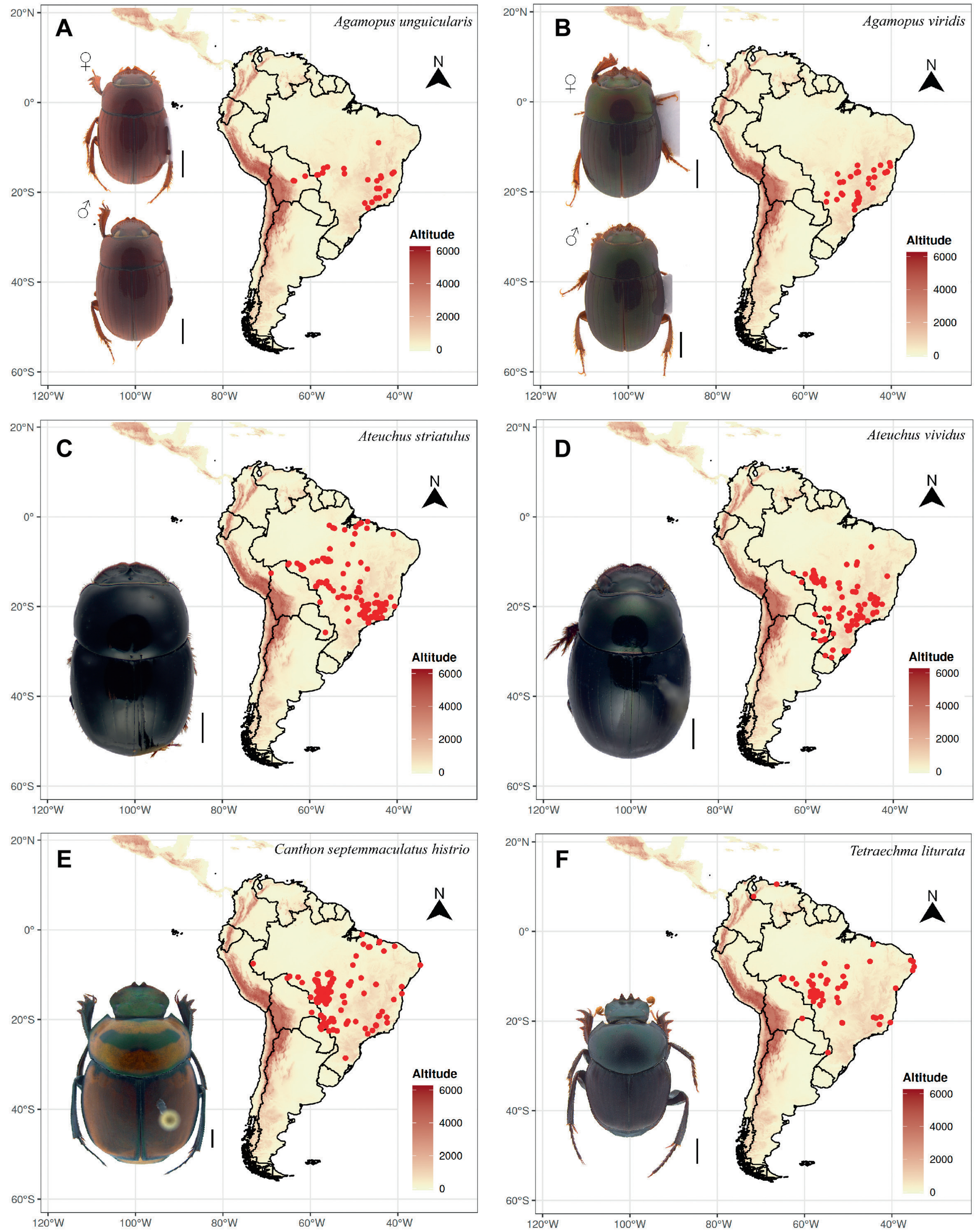

Figure 2. Geographical distribution and dorsal view of specimens for each species. (A) *Agamopus unguicularis*. (B) *Agamopus viridis*. (C) *Ateuchus striatulus* and (D) *Ateuchus vividus* (Photos: Mario Cupello). (E) *Canthon septemmaculatus histrio*. (F) *Tetraechma liturata*. Scale: 1 mm.

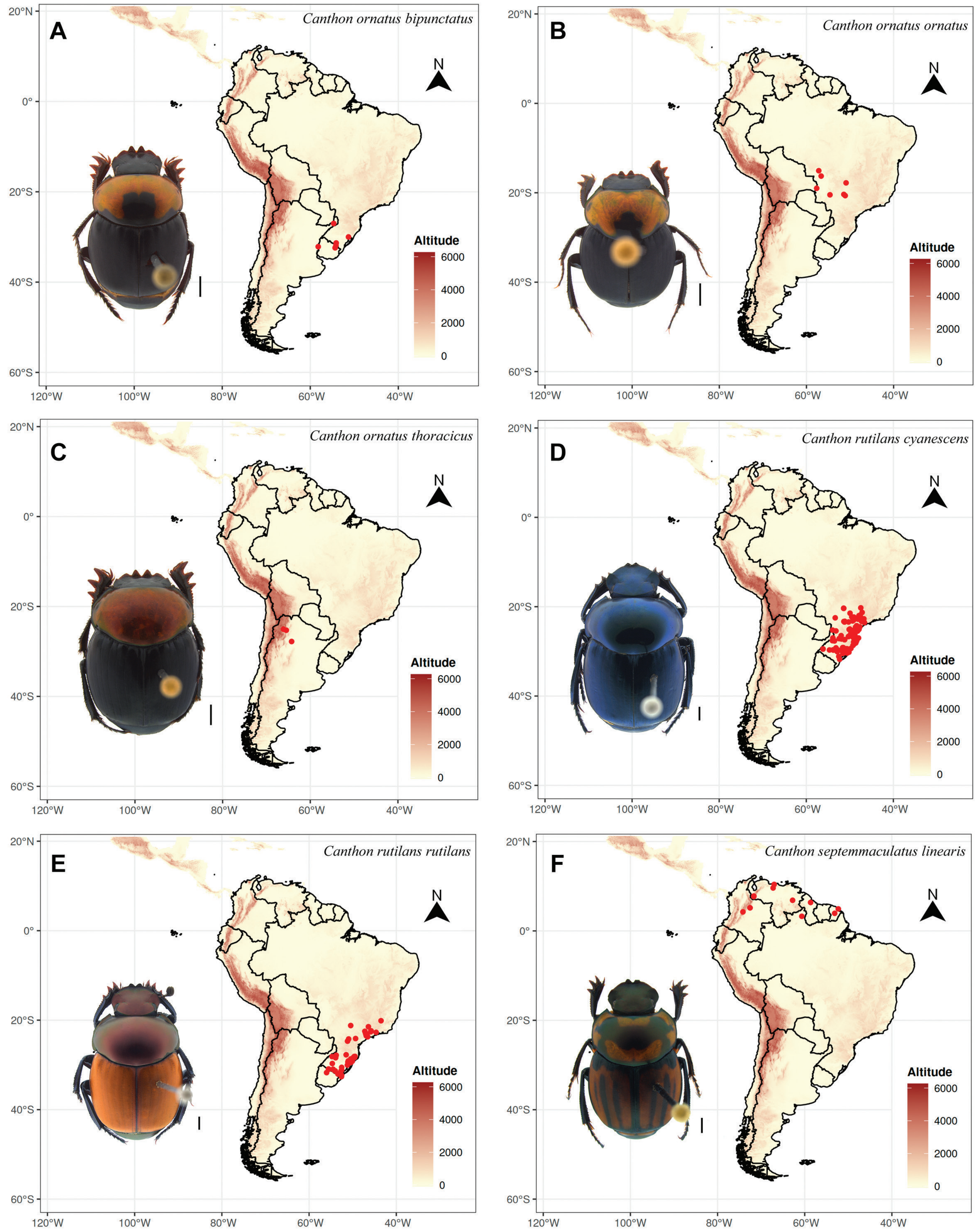

Figure 3. Geographical distribution and dorsal view of specimens for each species. (A) *Canthon ornatus bipunctatus*. (B) *Canthon ornatus ornatus*. (C) *Canthon ornatus thoracicus*. (D) *Canthon rutilans cyanescens*. (E) *Canthon rutilans rutilans*. (F) *Canthon septemmaculatus linearis*. Scale: 1 mm.

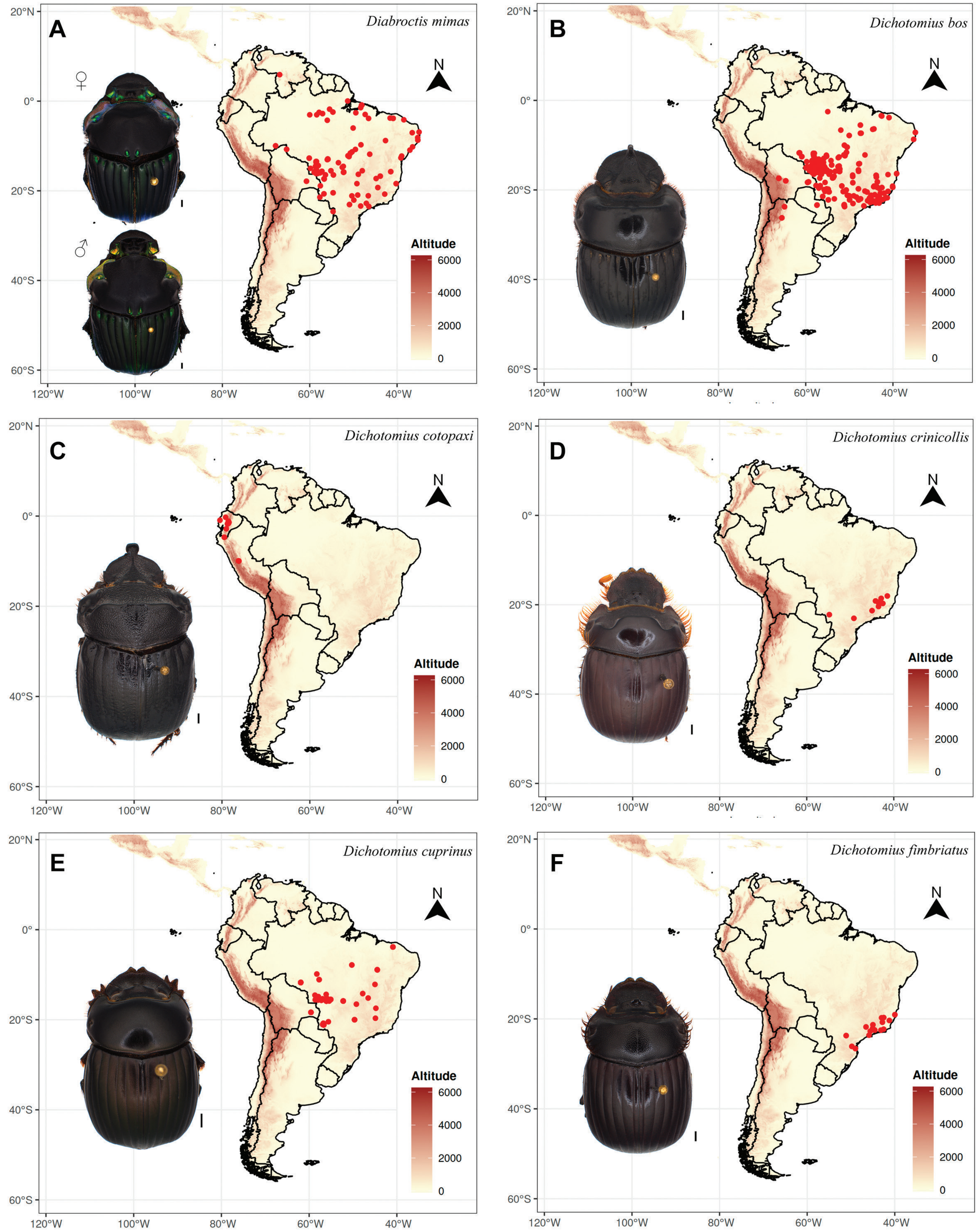

Figure 4. Geographical distribution and dorsal view of specimens for each species. (A) *Diabroctis mimas*. (B) *Dichotomius bos*. (C) *Dichotomius cotopaxi*. (D) *Dichotomius crinicollis*. (E) *Dichotomius cuprinus*. (F) *Dichotomius fimbriatus*. Scale: 1 mm.

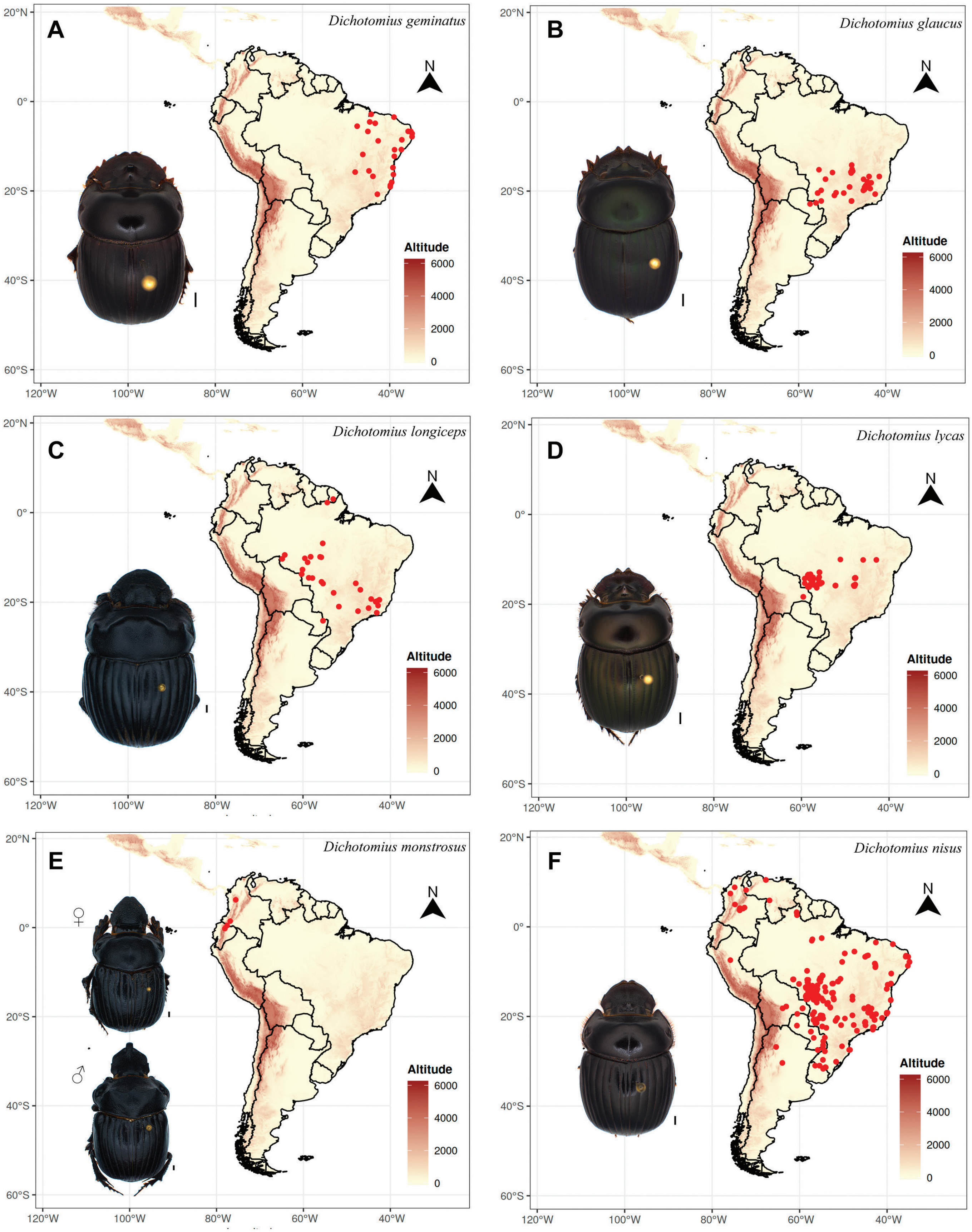

Figure 5. Geographical distribution and dorsal view of specimens for each species. (A) *Dichotomius geminatus*. (B) *Dichotomius glaucus*. (C) *Dichotomius longiceps*. (D) *Dichotomius lycas*. (E) *Dichotomius monstrosus*. (F) *Dichotomius nisus*. Scale: 1 mm.

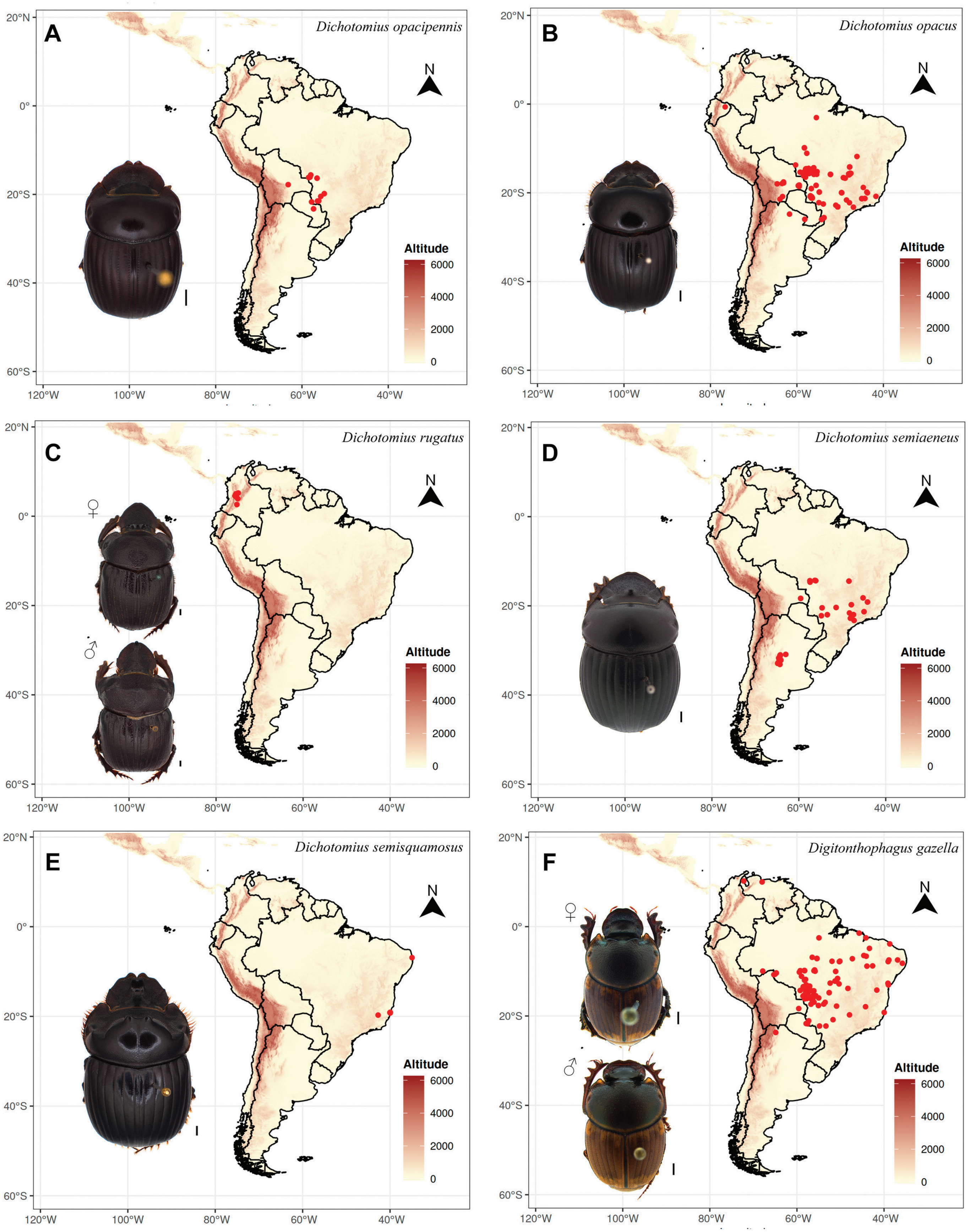

Figure 6. Geographical distribution and dorsal view of specimens for each species. (A) *Dichotomius opacipennis*. (B) *Dichotomius opacus*. (C) *Dichotomius rugatus*. (D) *Dichotomius semiaeneus*. (E) *Dichotomius semisquamosus*. (F) *Digitonthophagus gazella*. Scale: 1 mm.

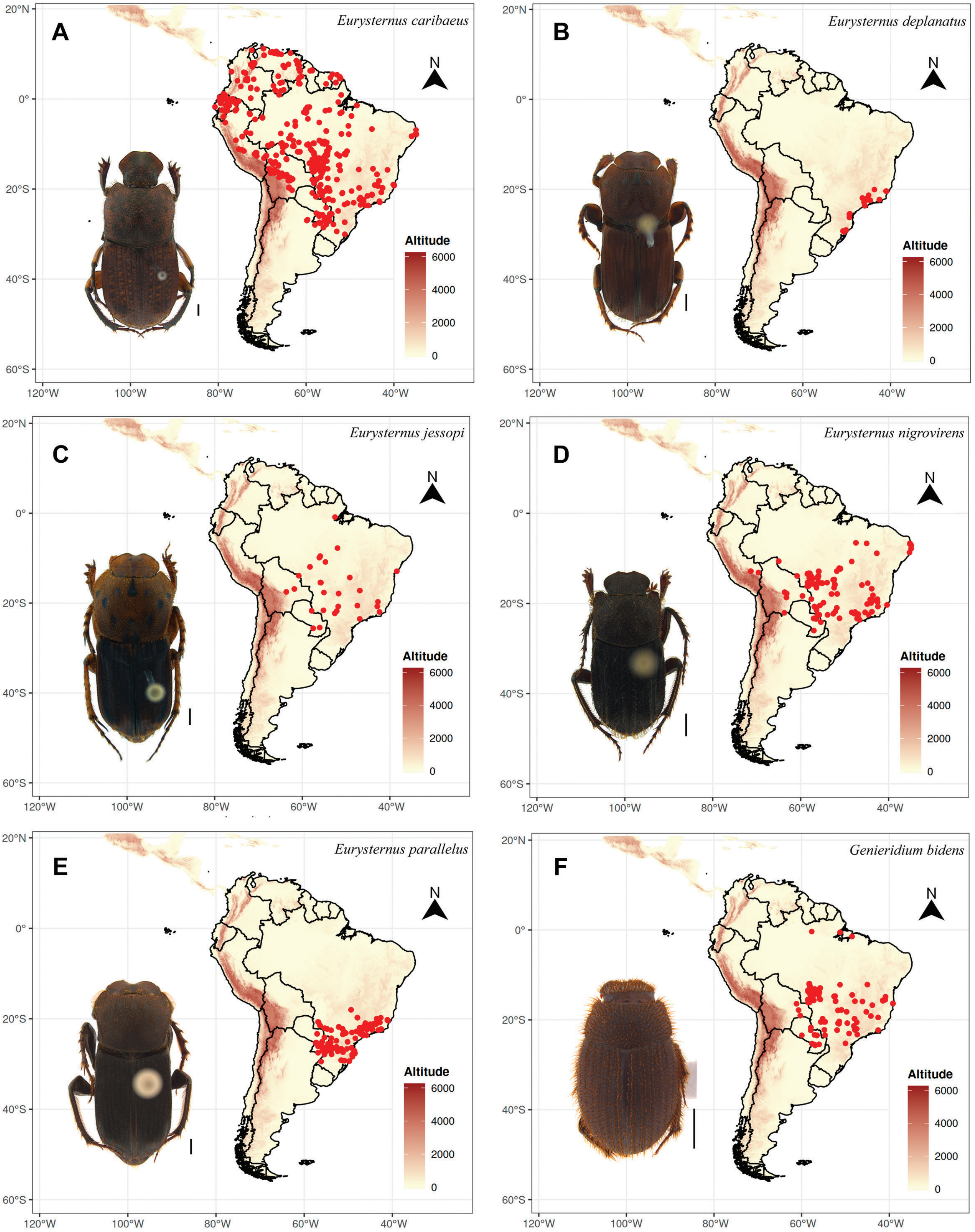

Figure 7. Geographical distribution and dorsal view of specimens for each species. (A) *Eurysternus caribaeus*. (B) *Eurysternus deplanatus*. (C) *Eurysternus jessopi*. (D) *Eurysternus nigrovirens*. (E) *Eurysternus parallelus*. (F) *Genieridium bidens* (Photo: Edrielly Carvalho). Scale: 1 mm.

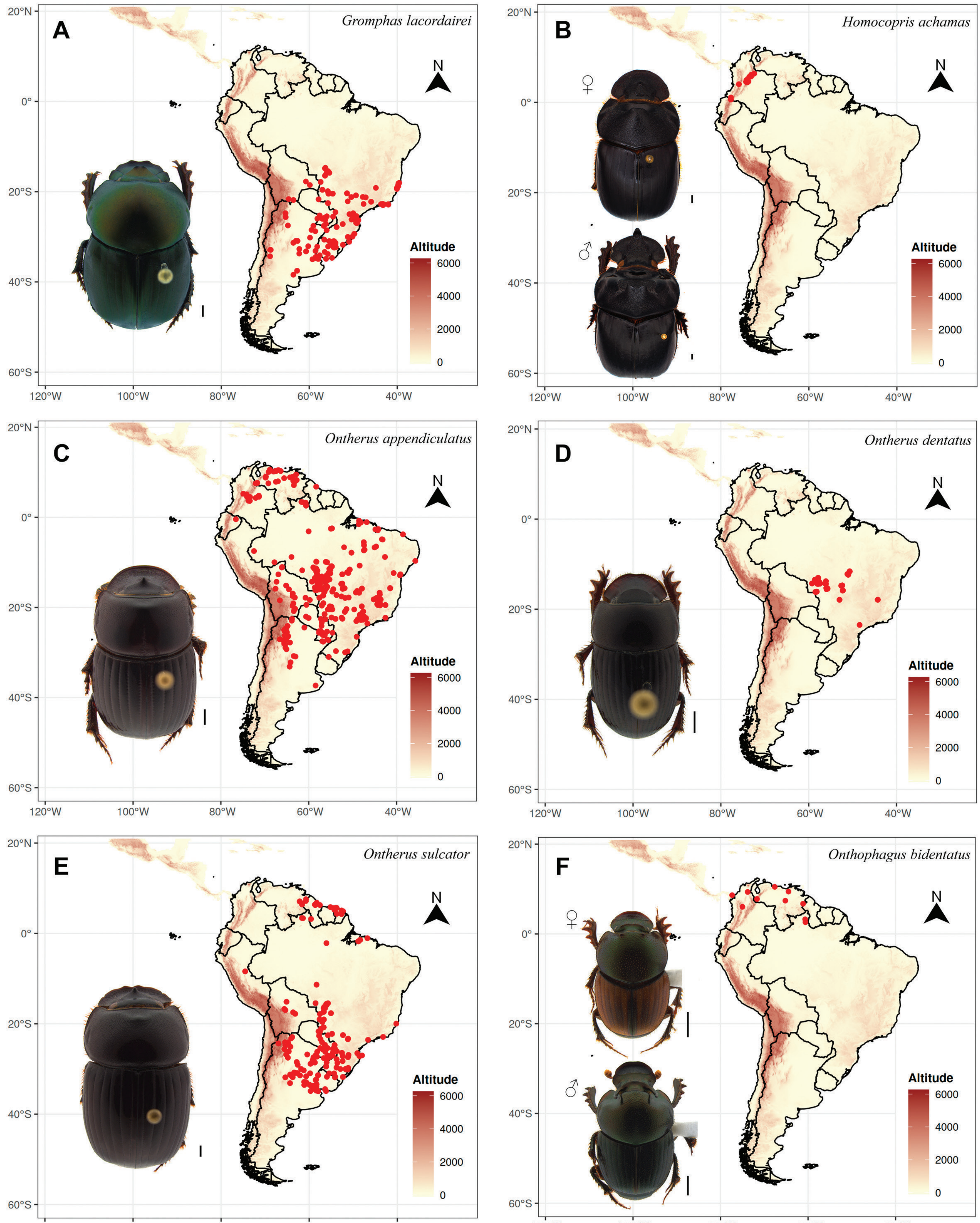

Figure 8. Geographical distribution and dorsal view of specimens for each species. (A) *Gromphas lacordairei*. (B) *Homocopris achamas*. (C) *Ontherus appendiculatus*. (D) *Ontherus dentatus*. (E) *Ontherus sulcator*. (F) *Onthophagus bidentatus*. Scale: 1 mm.

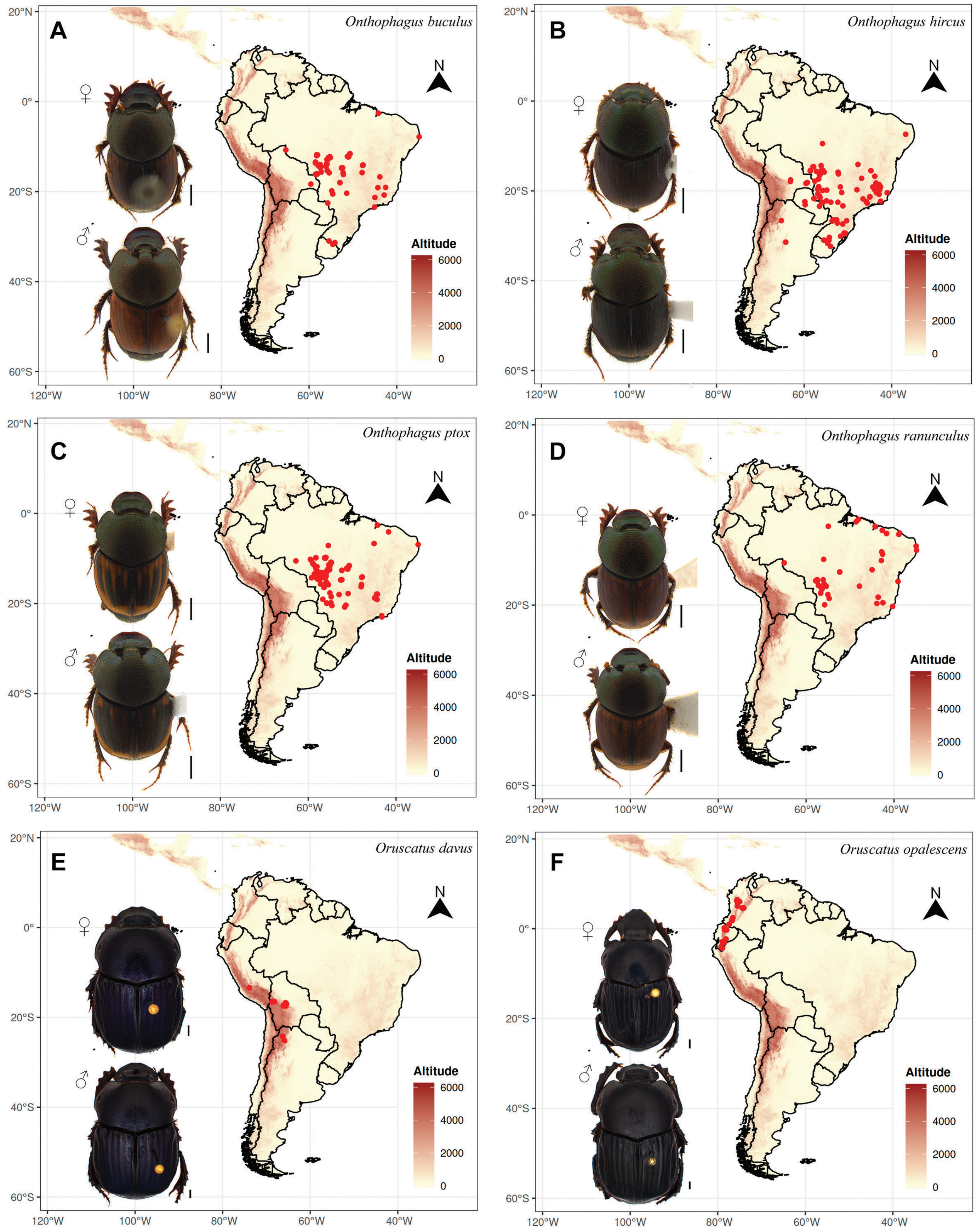

Figure 9. Geographical distribution and dorsal view of specimens for each species. (A) *Onthophagus buculus*. (B) *Onthophagus hircus*. (C) *Onthophagus ptox*. (D) *Onthophagus ranunculus*. (E) *Oruscatus davus*. (F) *Oruscatus opalescens*. Scale: 1 mm.

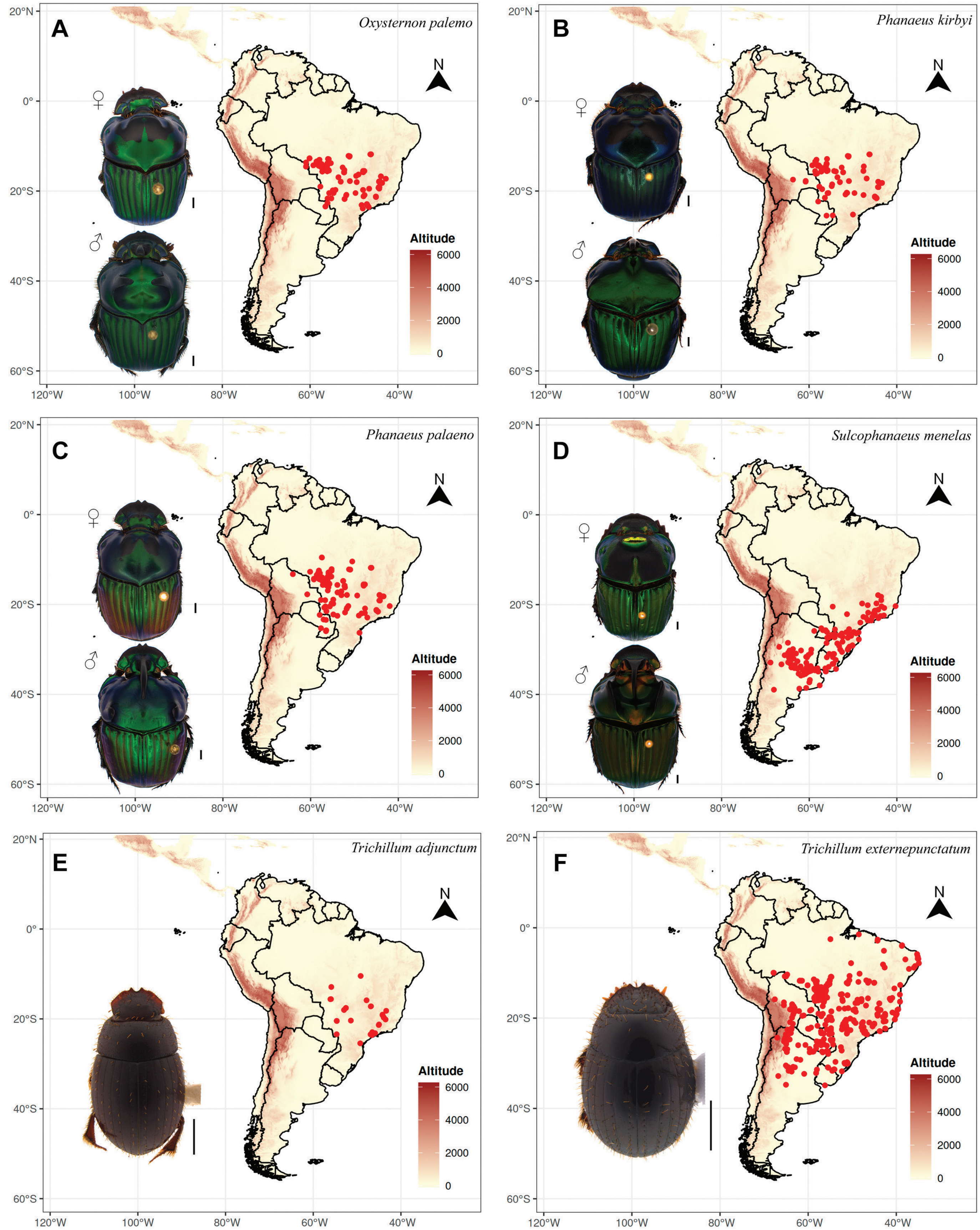

Figure 10. Geographical distribution and dorsal view of specimens for each species. (A) *Oxysternon palemo*. (B) *Phanaeus kirbyi*. (C) *Phanaeus palaeno*. (D) *Sulcophanaeus menelas*. (E) *Trichillum adjunctum*. (F) *Trichillum externepunctatum*. Scale: 1 mm.

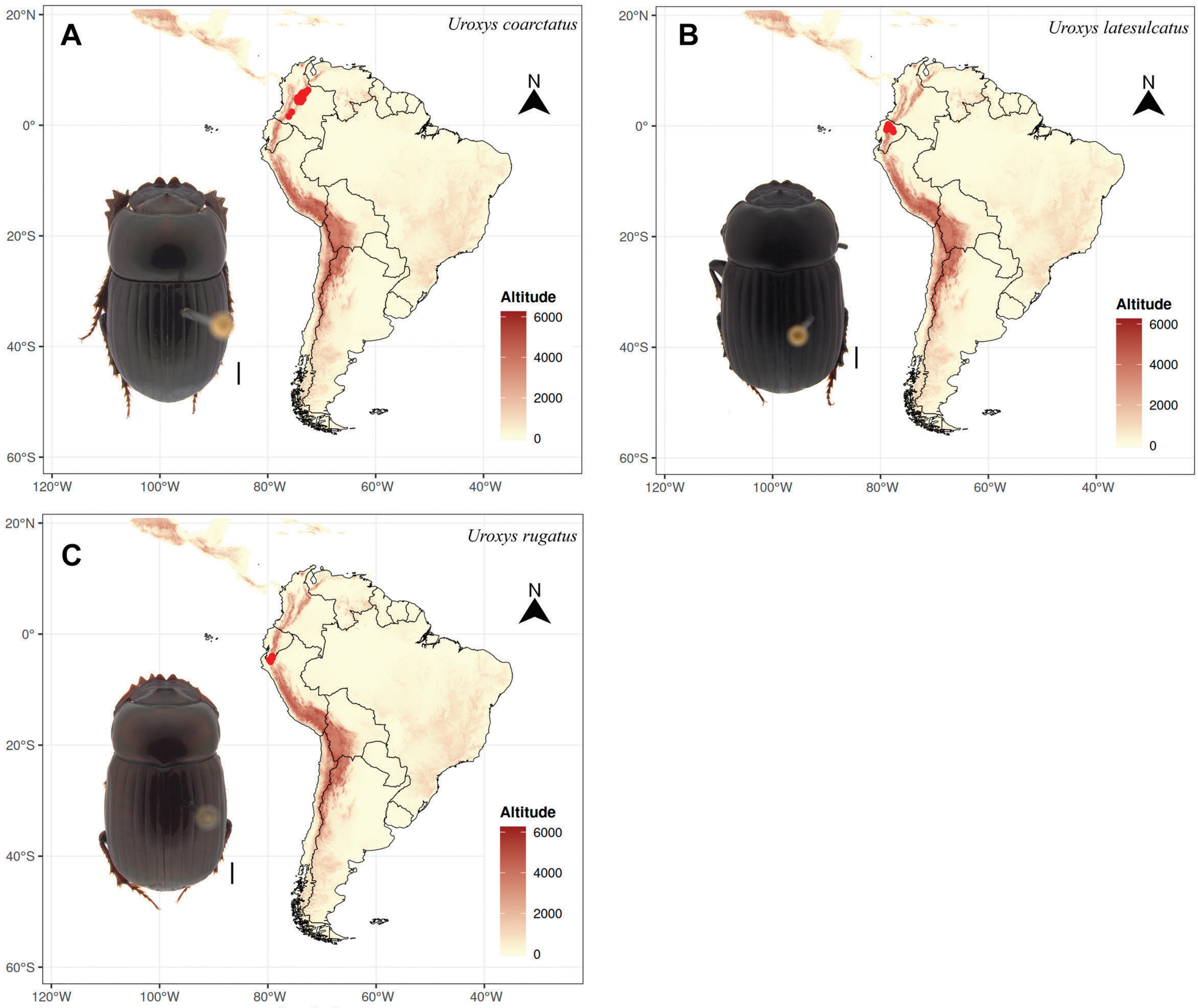

Figure 11. Geographical distribution and dorsal view of specimens for each species. (A) *Uroxys coarctatus*. (B) *Uroxys latesulcatus*. (C) *Uroxys rugatus*. Scale: 1 mm.

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Fernando Z. Vaz-de-Mello: Conceptualization, Resources, Methodology, Writing – review & editing.

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 an Institutional Committee.

Data Availability

The datasets generated during and/or analyzed during the current study are available at: https://doi.org/10.48331/scielodata.82AEC8

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Article

Amphibians and reptiles of the Refúgio Biológico Bela Vista – Itaipu Dam, state of Paraná, southern Brazil

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Abstract: Information regarding species occurrence is fundamental to understanding biodiversity distribution. However, the biodiversity from the west of the state of Paraná has been historically less studied, especially amphibians and reptiles. For this reason, we present the first reptile list of species from the west of the state of Paraná and extend the current list of anurans for the municipality of Foz do Iguaçu. The species list was based on a systematic field study conducted at Refúgio Biológico Bela Vista (RBV) a conservation area within the Hydroelectric Power Itaipu Binacional. We integrated the species list with previous species observations available in the literature for the same place where our sampling was conducted. A total of 41 species of amphibians and reptiles are presented. All amphibians species found were recorded in the field; however, from the 22 species of reptiles recorded, three were historical records obtained before this study. Species were all classified as Least Concern and/or had stable populational status according to the IUCN. Sampling sufficiency was achieved for anurans but not for reptiles, probably due to low abundance of several snake species. The most abundant species of anuran was *Dendropsophus nanus*, from the Hylidae family, whereas *Leptodactylus plaumanni* and *Scinax squalirostris* were represented by only one individual each. The lizard *Salvator merianae* was the most abundant reptile, and seven species were represented by only one individual each. The most successful sampling method for adult anurans was active search in water bodies whereas most of reptile species were observed by accidental encounters and not through a systematic sampling method. We found that herpetofauna composition from RBV was similar to other communities from Paraná state that also occur within the Semideciduous Seasonal Forest. Finally, as additional information to the species list, we offer species identification keys and discuss the importance of Refúgio Biológico Bela Vista to harbor the anuran and reptile diversity of the region.

Keywords: *Atlantic Forest; Herpetofauna; Identification keys; Semideciduous forest; Species inventory.*

Anfíbios e répteis do Refúgio Biológico Bela Vista – hidrelétrica Itaipu, estado do Paraná, sul do Brasil

Resumo: Informações sobre a ocorrência de espécies são fundamentais para a compreensão da distribuição da biodiversidade. Porém, a biodiversidade do oeste do Estado do Paraná tem sido historicamente menos estudada, especialmente a de anfíbios e répteis. Por esse motivo, apresentamos a primeira lista de espécies de répteis do oeste do Estado do Paraná e ampliamos a lista atual de anuros para o município de Foz do Iguaçu. A lista de espécies foi baseada em um estudo sistemático de campo realizado em uma área de conservação dentro da Usina Hidrelétrica Itaipu Binacional. Integramos a lista de espécies com observações de espécies anteriores disponíveis na literatura para o mesmo local onde nossa amostragem foi realizada. Um total de 41 espécies são apresentadas. Todas as espécies de anuros encontradas foram registradas em campo; entretanto, das 22 espécies de répteis registradas, três foram registros obtidos antes deste estudo. Todas as espécies foram classificadas como "Pouco Preocupante" e/ou tinham status de "População Estável" de acordo com a IUCN. A suficiência amostral foi alcançada para anuros, mas não para répteis, provavelmente devido à baixa abundância de diversas espécies de serpentes. A espécie de anuro mais abundante foi *Dendropsophus nanus*, da família Hylidae, enquanto *Leptodactylus plaumanni* e *Scinax squalirostris* foram representados por apenas um indivíduo cada. O lagarto *Salvator merianae* foi o réptil mais abundante, e sete espécies foram representadas por um indivíduo cada. O método de amostragem mais bem sucedido para anuros adultos foi a busca ativa em corpos d'água, enquanto a maioria das espécies de répteis foi observada por encontros acidentais e não através de um método de amostragem sistematizado. Descobrimos que a composição da herpetofauna do Refúgio Biológico Bela Vista foi semelhante à de outras comunidades do estado do Paraná que também ocorrem dentro da Floresta Estacional Semidecidual. Por fim, como informações adicionais à lista de espécies, oferecemos chaves de identificação das espécies e discutimos sobre a importância da área de Itaipu para abrigar a diversidade de anuros e répteis da região.

Palavras-chave: *Mata Atlântica; Herpetofauna; Chave de identificação; Floresta semidecidual; Inventário de espécies.*

Introduction

The urgency of inventorying and monitoring biodiversity is paramount in light of the ongoing biodiversity crisis we are currently experiencing. The conduct of species inventories represents the most elementary information requisite for comprehending biodiversity distribution (Silveira et al. 2010). Herpetofauna occurrence data contribute to our knowledge of species' geographical distribution and are helpful in delineating effective management plans in threatened areas (Oliveira et al. 2016, Trindade-Filho et al. 2012). One of these areas is the Atlantic Forest, a biodiversity hotspot (Myers et al. 2000), which houses over 50% of all amphibians from Brazil, with prominent endemism (Rossa-Feres et al. 2017, Rojas-Padilla et al. 2020) and ca. 33% of all reptile species (Silva 2017). This higher biodiversity, however, may be linked to well-preserved areas, mainly in mountain areas in the Atlantic Forest (Silva et al. 2012; Rossa-Feres et al. 2017). In contrast, in human-modified or anthropized Atlantic Forest landscapes, species richness should be lower mainly due to habitat loss and degradation (Rodrigues 2005, Fiorillo et al. 2018). Novel studies on herpetofauna communities in modified tropical landscapes are necessary to elucidate species' sensitivity to disturbed environments (Ganci et al. 2022). Since community response to environmental modification might have regional-dependent characteristics (Pelinson et al. 2022), these studies can provide data that increase conservation planning and action on a regional and local scale (Palmeirim et al. 2017, Figueiredo et al. 2019).

Despite their enormous original extension, the Atlantic Forest is currently the most deforested Brazilian tropical forest (SOS Mata Atlântica 2018). It is estimated that only ca. 8 to 12% of its original area endured the deforestation that has taken place since the colonization (Myers et al. 2000, Ribeiro et al. 2009, Silva et al. 2017). In the state of Paraná, the original area of the Atlantic Forest from the Third Plateau of Paraná - the lower plateau in the western side - comprised ca. 45% of the state's vegetational formation (SOS Mata Atlântica 2018). The forest of this region is classified as Semideciduous Seasonal Forest (SSF), characterized by vegetation with deciduous leaves that during winter can lose up to 50% of the canopy cover (Veloso et al. 1991, Giraudo et al. 2003). The SSF is a critically threatened vegetational formation in the state of Paraná - because of its countryside position, this formation suffered the advance of cattle ranching and monoculture - remaining only ca. 0.1% of its original distribution (Medri et al. 2002). Hence, remnants of the SSF are mainly distributed in sparse fragments along the west side in the state of Paraná (Ribeiro et al. 2009), with the majority of these fragments lacking inventories of amphibians and reptiles.

One of the largest forest fragments in the western region of the state of Paraná is the Refúgio Biológico Bela Vista (RBV). The Itaipu Binacional Hydroelectric Power Plant (a binational entity of Brazil and Paraguay) established several extensive conservation areas as a compensatory program during hydroelectric dam construction (Ziober et al. 2014), with a substantial portion of this area referred to as the Refúgio Biológico Bela Vista. These areas were created primarily to shelter and protect regional biodiversity from the flooding derived from the dam construction, but it also have the potential for conservation over a longer period. These conservation areas are located marginally in the Paraná River, which was originally surrounded by riparian SSF forest. The Refúgio Biológico Bela Vista (RBV) is the largest Itaipu conservation area on the Brazilian side, classified as an Advanced Station in the Atlantic Forest Biosphere Reserve by UNESCO. Although the history of the area's establishment is well-documented, there is a lack of herpetofauna inventories in the region. There are no historical records of amphibians for the area, however, data on reptile species richness are available, which were collected during the creation of the Itaipu Dam (Ziober & Zanirato 2014), but the species composition is unavailable. Due to a long history of different types of land use in the region, the RBV is characterized by a miscellaneous of land uses, however, including reforestation areas and secondary forests in advanced successional stages that have not been interfered for over 30 years. Notwithstanding, the herpetofauna community of RBV could reflect recolonization events from surrounding communities since the Itaipu reservoir construction.

The forest remnants preserved by Itaipu Dam are interesting for studying long-term biological community response to landscape modification and, at the same time, provide essential information on species geographical distribution for understudied areas where no survey has been placed. A large gap in knowledge on herpetofauna communities remains for Western Paraná, where inventories are scarce. Only punctual records of reptile species have been observed for the region (e.g., Moura-Leite et al. 1996), and one study focused on amphibian community (Leivas et al. 2018). Due to the intensive degradation of the entire extension of SSF, inventories are important to understand how biodiversity currently occupies this threatened vegetational formation. Furthermore, comparing the composition of communities along different SSF localities can also provide insights into the regions that are somehow harboring similar species and, therefore, indistinguishable from each other; and consequently, which regions are unique in its composition.

Here, we provide a species inventory of amphibians and reptiles in a conservation area of the Semideciduous Seasonal Forest on the most Western side of the state of Paraná. More specifically, our study had the following aims: (i) we presented the comprehensive inventory of amphibians and reptile for this region, which is the first reptile species list in the region; (ii) we evaluated the effectiveness and synergistic potential of a range of methodologies used in the collection of amphibian and reptile data; (iii) we carried out a comparative analysis of the compositions of amphibian and reptile communities in contrast to other herpetofauna communities in the Semideciduous Seasonal Forest, shedding light on their distinctions and similarities; and (iv) we produced taxonomic identification keys, specifically designed to expedite the identification of amphibian species, encompassing both adults and tadpoles, as well as reptilian fauna. We expect that the species composition among communities will be related to geographic distance. The similarity of species composition between communities tends to decrease with increased distance, this pattern is observed across various taxa (Astorga et al. 2012), including amphibians (Garey & Silva 2010). This is attributed to limitations in dispersion and the spatial structuring of environmental characteristics (Astorga et al. 2012). Even though some differences might appear due to the land-use history of the locals. We discuss some remarkable records and the importance of this area for herpetofauna conservation.

Materials and Methods

1. *Study area*

This study was conducted in the conservation area Refúgio Biológico Bela Vista (RBV) maintained and managed by Itaipu Binacional, situated in Foz do Iguaçu municipality, state of Paraná, Brazil (25°44′90″S, 54°55′42″W) (Figure 1). Foz do Iguaçu is located in the south of Brazil, in the western portion of Paraná state, neighboring territories with Paraguay and Argentina. The local climate is temperate and humid with hot summer, Cfa, following Köppen's classification (Alvares et al. 2013). The region has one of the biggest annual thermal amplitudes in the state of Paraná, an approximate value of 11 °C of the average difference between the winter (June to August) and summer (December to March). Summers usually average around 33 °C, eventually surpassing the 40°C. Conversely, winter can present temperatures below zero during the passage of cold fronts with polar air masses. Rainfalls are usually evenly distributed throughout the year, with a slight decrease during winter, with annual precipitation totaling around 1800mm (Delgado et al. 2016). The area belongs to the morphostructural subunit of the Foz do Iguaçu plateau, characterized by flat and gently undulating top relief not exceeding 540 m in elevation (Santos et al. 2006).

The RBV represents 1.920 ha from 41.039 ha of the Itaipu area and has an altitudinal variation from ca. 100 to ca. 250 m. a.s.l. RBV was characterized by a heterogeneous landscape with different formations that endured three asynchronous types of land use transformation (secondary forest, reforestation, and anthropized). Before the hydroelectric construction, the area was partly covered by SSF vegetation (Roderjan et al. 2002) that experienced selective cutting and partly by grazing pasture. After the construction of the reservoir, the remnants of pasture fields were initiated in reforestation activities approximately 40 years ago. Excluding forested landscapes, other areas were profoundly anthropized, corresponding to the locations where Itaipu constructions were present. It can be found in these areas open fields, buildings, roads, and a fish pass system liking the Paraná River to Itaipu Reservoir that allowed migratory fishes to find suitable spawning in tributaries of Itaipu Reservoir and the floodplain located upstream (See Makrakis et al. 2007 for more details), called Canal da Piracema. The RBV is not a conservation unit under any government office (federal, state, or municipal) or a private reserve; hence it is administrated only by Itaipu Binational.

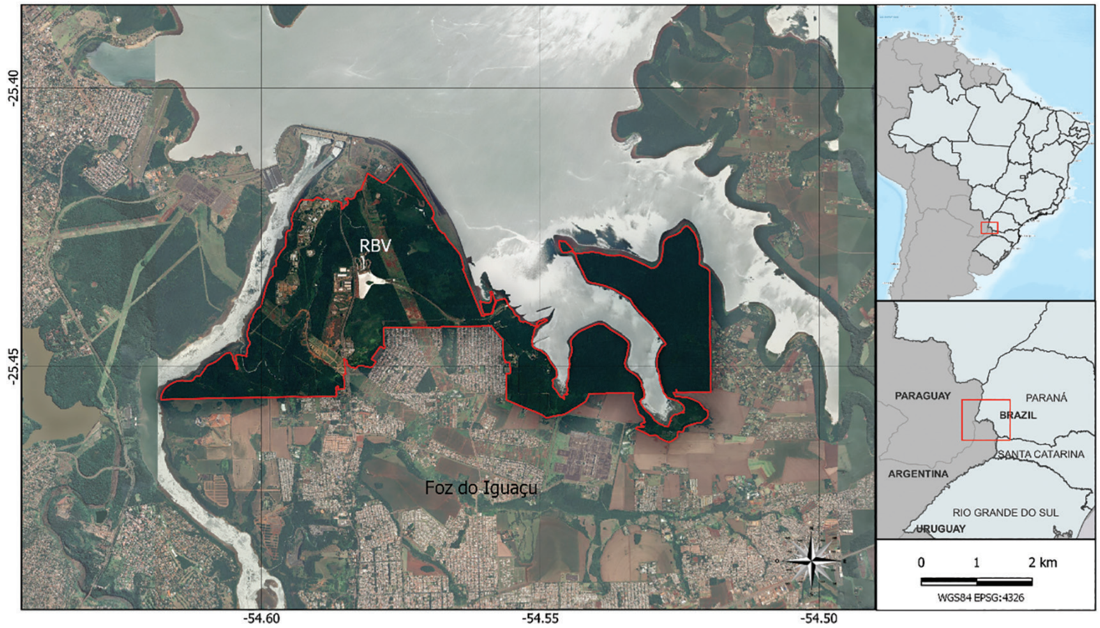

Figure 1. Geographical location of the study area: Refúgio Biológico Bela Vista (RBV), Foz do Iguaçu municipality, state of Paraná, Southern Brazil.

2. *Data collection*

We sampled amphibians and reptiles from January 2021 to July 2022. Sampling events were carried out bimonthly, with 15 days of field activities and a 45-day interval between sampling events, totaling 120 days of fieldwork. Over these 15 days, we sampled adult anurans, anuran larvae (tadpoles), and reptiles from terrestrial and aquatic environments. Additionally, to incorporate our database and embrace a better temporal perspective of the species that could be found in the RBV, we provide information on the species recorded previously to this study (historical records), even though they were not included in the rarefaction or cluster analyses.

Sampling amphibians and reptiles in terrestrial environments was performed by visual encountering through time-constrained searches in transects (Mackey et al. 2010), pitfall traps with drift fences (Greenberg et al. 1994, Cechin & Martins 2000), and accidental encounters (Martins & Oliveira 1998). Our sampling design for time-constrained searches in transects consisted of 18 transects of 100 m with a sampling effort of one hour in each transect. Each transect was searched two times, once in the first week at daylight and night during the second week, totaling 288 hours. We used 24 pitfall traps; each was a straight line of drift fence made of a black canvas of 70 cm height and 100-m long, and with five plastic buckets of 60 L, equally spaced by 20-m. We perforated the bottom of the buckets and added a small piece of polystyrene to prevent animal death by drowning in the case of rain. During the first week of each expedition, all 24 pitfall traps were checked daily for herpetofauna specimens, totaling 960 hours. Finally, accidental encounters included all specimens visualized by the researchers and civilians at any location and day, as long as it was within the Itaipu border and occurred within the study period (2021 to 2022). Only individuals found through accidental encounters identified by the researchers of this study were part of our database.

In aquatic habitats, we registered adult anurans through surveying at breeding sites (Scott et al. 1994), herein named as time-constrained searches (*sensu* Corn & Bury 1990) in water bodies, and tadpoles by a quantitative sampling of tadpoles (Scott et al. 1994). Reptiles were sampled using double-ended funnel traps (Greenberg 1994). In time-constrained searches in water bodies, we sampled adult anurans and tadpoles at 16 water bodies: one temporary lotic, two perennials lotic, six temporary lentic, and seven perennial lentic water bodies. Time-constrained searches in water bodies sampling occurred at night, with a sampling effort of one hour in each water body, totaling 128 hours. During the campaigns, the sampling order of the environments was randomized to minimize the effects of variation in species activity throughout the night. Tadpole sampling occurred during the daylight by sweeping dipnets in the same water bodies where adults were sampled. Dipnets consisted of a round 30-cm diameter frame supporting a 3 mm nylon mesh with a 1.5-m handle. Each water body was sampled for tadpoles for one hour in each campaign, totaling 128 hours of sampling effort. All species seen or heard were recorded for further identification. Four funnel traps were placed in water bodies and with the longitudinal half portion immersed in the water. Funnel traps were left in water bodies for five days consecutively during each campaign, totaling 3840 hours. Funnel traps consisted of a 100 cm long cylinder of nylon line net with two funnels - oriented to the inside - on both extremities (double-ended trap) made of aluminum hoops; the large hoop of the funnel had 45 cm of diameter, and the smaller hoop 20 cm of diameter. Chicken giblets and cow's kidneys were used as baits inside a 15 cm plastic pipe to attract freshwater turtles and alligators.

We obtained the abundance data for each species by summing the total number of individuals observed during a single sampling campaign when the species exhibited the highest abundance considering all sampling methods together. We provided the conservation status for each species of amphibians and reptiles at international, federal, and state levels. Status was attributed based on the IUCN Red List (2022) for the international level classification, the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio 2018a, b) for federal and the Livro Vermelho de Fauna Ameaçada no Estado do Paraná (Mikich & Bérnils 2004) for the state level classification.

We collected some voucher specimens following ethical and legal guidelines according to Brazilian laws (collection license ICMBio/SISBIO 73800 and 73839). The identity of the species was validated by specialists in the taxonomy of tadpoles (PhD. Denise de C. Rossa Feres) and adults of anurans (PhD. Célio F. B. Haddad) and reptiles (PhD. Júlio C. Moura Leite). Voucher specimens were posteriorly deposited in the herpetological collection of Universidade Federal da Integração Latino-Americana (UNILA), Foz do Iguaçu municipality, state of Paraná, Brazil. See the Supplementary Material to access the specimens collected and included in the Bertha Lutz Herpetological Collection.

3. *Data analyses*

Sample success was described as the proportion of the richness sampled by each sampling method in relation to the total richness, separated between anurans (adults and tadpoles) and reptiles. Sampling sufficiency was evaluated through individual-based rarefaction curves and extrapolation (Gotelli & Colwell 2001). We generated 1000 rarefaction curves based on individual randomization using interpolation and extrapolation methods from the *iNEXT* package (Hsieh et al. 2016). We created a rarefaction curve for total of reptiles and the total of amphibians separately because of contrasting observed abundances. We implemented the Hill series with the q exponent of 0, which is a measure of observed richness, without considering abundance (Chao et al. 2014).

In addition, we compared the RBV herpetofauna community with other inventories from the Semideciduous Seasonal Forests formation of the Atlantic Forest. For this analysis, only species identified up to the species level were considered. Therefore, species with uncertain taxonomy (e.g., 'sp.', 'gr.', 'aff.', and 'cf.') were not included. The assemblages included in the cluster were: Bertoluci et al. (2009), Cacciali et al. (2015), Garey & Silva (2010), Leivas et al. (2018), López & Garey (2021), López & Prado (2012), Mesquita et al. (2018), Moura et al. (2012), Neves et al. (2017), Protázio et al. (2021), Rampim et al. (2018), Shibatta et al. (2009), Souza Filho & Oliveira (2015), Souza-Costa et al. (2020), Souza et al. (2012), Uetanabaro et al. (2007), Zina et al. (2007). Due to methodological differences among studies, we only considered data on the presence and absence of species in each inventory. We constructed two dendrograms, one for squamates and one for amphibians, based on a Jaccard similarity index (*vegan* package; Oksanen et al. 2022). Reptile clustering accounted only for squamates because of the difficulty of finding more studies that included all types of reptiles in SSF assemblages. Therefore, we did not construct a cluster for all reptiles so as not to inflate assemblages' differences. We chose the best clustering method that had the higher cophenetic correlation score; the competitive methods tested were: Single Linkage, Complete Linkage, Unweighted Pair-Group Method using Arithmetic average (UPGMA), Weighted Pair-Group Method using Arithmetic average (WPGMA), Unweighted pair-group method using centroids (UPGMC), Weighted pair-group method using centroids (WPGMC) and Ward's Minimum Variance Clustering. Dendrograms were constructed using UPGMA for both anurans and reptiles. All statistical analyses were conducted in R environment (R Core Team 2022).

The identification key was elaborated to separate anurans, tadpoles, and reptiles at species terminal level. We used external morphology characters that can be easily observed from naked eye or using a stereomicroscopes. The identification key of adult anuran was elaborated based only on the specimens collected at Refúgio Biológico Bela Vista. As we were unable to record tadpoles of all species in RBV, we utilized specimens already included in the collection and relied on external morphological characteristics available in the articles (De Sá et al. 1997, Rossa-Feres & Nomura 2006). For reptiles, some species characters were described based on general morphology of individuals of the species because we did not have testimony specimens, i.e., *Caiman latirostris, Phrynops geoffranus, Chelonoidis carbonarius*, *Eunectes noteaus, Erythrolamprus aesculapii, Oxyrhopus guibei* and *Xenodon merremi.*

Results

We recorded 38 species of amphibians and reptiles from the Anura, Squamata, Crocodylia, and Testudines orders. A representative fraction of the species collected is shown in Figures 2 and 3. Adding the historical records with the species sampled during this study, the RBV presented 41 species of anurans and reptiles. Based solely on species recorded from our field data, we found 19 species of anurans from five families (Table 1, Figure 4), at least one adult of the same species was collected for each tadpole species sampled.

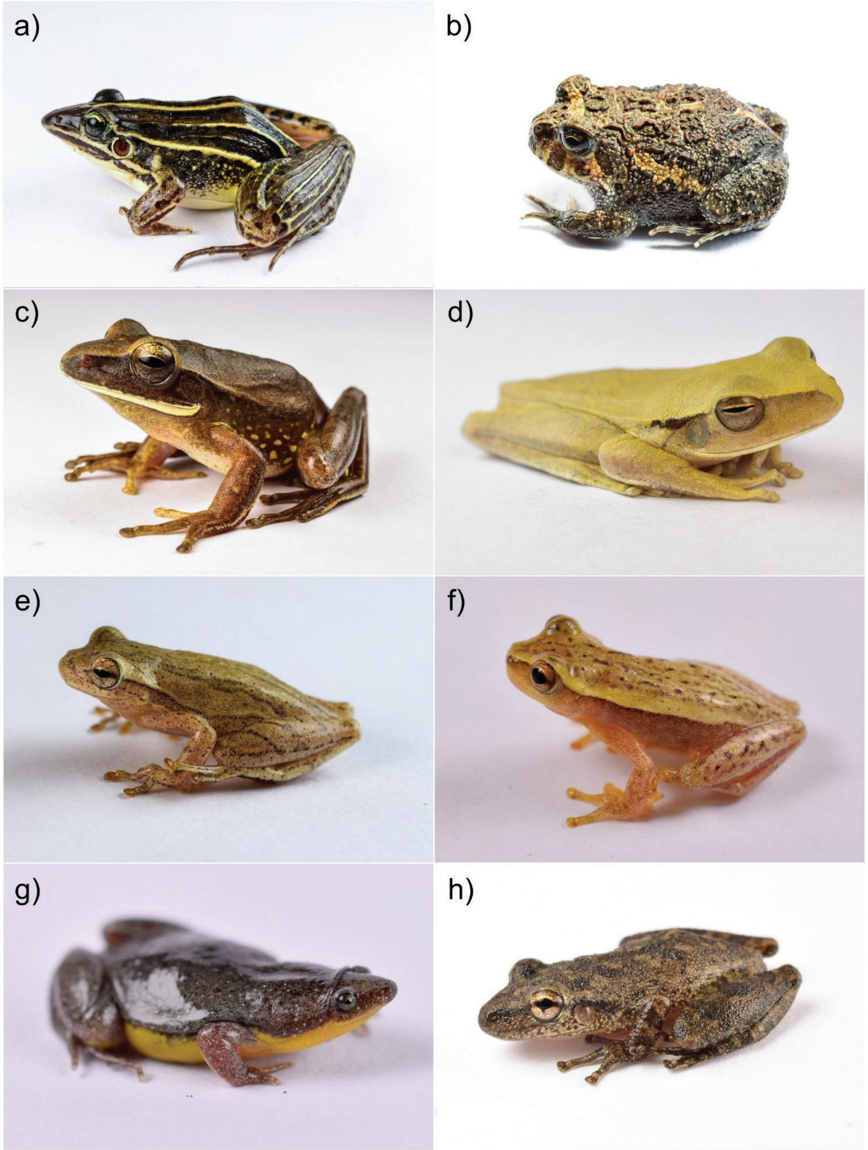

Figure 2. Some anuran species recorded in the Refúgio Biológico Bela Vista (RBV) at Foz do Iguaçu, state of Paraná. (a) *Leptodactylus plaummani*; (b) *Odontophrynus reigi*; (c) *Boana albopunctata*; (d) *Boana raniceps*; (e) *Dendropsophus nanus*; (f) *Dendropsophus minutus*; (g) *Elachistocleis bicolor*; (h) *Scinax berthae* (Photos by GSVF and TAK).

Figure 3. Some reptile species recorded in the Refúgio Biológico Bela Vista (RBV) at Foz do Iguaçu, state of Paraná. (a) *Bothrops jararaca*; (b) *Bothrops moojeni*; (c) *Erythrolamprus macrossomus*; (d) *Micrurus corallinus*; (e) *Dipsas mikanii*; (f) *Liotyphlops beui*; (g) *Amphisbaenia mertensi*; (h) *Tropidurus catalanensis* (Photos by GSVF and TAK).

For reptiles, we recorded 19 species, one of which is a species of alligator from the Alligatoridae family, two are tortoises from Testudinidae, eleven snake species from four families, and five lizard species from five families at Refúgio Biológico Bela Vista (RBV), Foz do Iguaçu, state of Paraná, southern Brazil. Based on adult anuran individuals, the most abundant species was *Dendropsophus nanus* representing ca. 38% of the total anurans, and the least abundant was both *Leptodactylus plaumanni* and *Scinax squalirostris*, representing less than 1% of the anurans total (one individual of each species). For the reptiles, *Salvator merianae* ca. 20% of the total reptiles. *Caiman latirostris*, the second highest abundant reptile, representing ca. 17%, and *Bothrops moojeni*, counted ca. 15% of the total. Several species were equally rare and were represented by only one individual. These species were *Bothrops jararaca, Bothrops moojeni, Bothrops jararacussu, Philodryas olfersii, Micrurus corallinus,* and *Chelonoidis carbonarius*, each representing less than 1% of the total of reptiles.

Approximately 74% of the amphibian species recorded in RBV exhibit stable populations, while 16% have unknown population trends, and 10% of species remain unassessed (Table 1). As for reptiles, 50% of species display stable populations, 32% have unknown status, and 18% have not been evaluated by the IUCN (Table 1). Species recorded at RBV were not classified as threatened in any of the endangered list of species: state (Paraná red list), national (ICMBio), or international (IUCN Red List). Notwithstanding, the Cope's toad *Rhinella diptycha* is assessed as Data Deficient, and consequently, its populational trend is Unknown due to its taxonomic status, the extent of occurrence, and ecological requirements (IUCN Red List). This species is common in the region where the study was conducted, possibly with stable and high populational density. Still, some species have been recently elevated to the taxonomic category of species, and no information is available on the IUCN Red List (Table 1).

Table 1. List of herpetofauna species recorded in the Refúgio Biológico Bela Vista (RBV), municipality of Foz do Iguaçu, state of Paraná, southern Brazil. Maximum abundance per species (N), sampling method (Method), and habitat type (Habitat). TCW – time-constrained search in water bodies, TCT – time constrained in transects, PT – pitfall traps with drift fences, AE – accidental encounter. SF – secondary forest, RE – restoration forest, DI – disturbed areas. Population status according to the IUCN (2022): Stb – stable, Unk – Unknown, Dec – Decreasing, Inc – Increasing.

TAXA	N	Method	Habitat	IUCN
AMPHIBIA				
ANURA				
Bufonidae				
Rhinella diptycha (Cope, 1862)	37	TCW, TCT, PT, AE	SF, RE, DI	Unk
Hylidae				
Boana albopunctata (Spix, 1824)	53	TCW, TCT	SF, RE, DI	Stb
Boana raniceps (Cope, 1862)	55	TCW, TCT	SF, RE, DI	Stb
Dendropsophus minutus (Peters, 1872)	333	TCW, TCT	SF, RE, DI	Stb
Dendropsophus nanus (Boulenger, 1889)	745	TCW, TCT	SF, RE, DI	Stb
Scinax berthae (Barrio, 1962)	2	TCW	SF	Stb
Scinax fuscovarius (Lutz, 1925)	31	TCW, TCT, PT, AE	SF, RE, DI	Stb
Scinax granulatus (Peters, 1871)	12	TCW, TCT	SF, RE, DI	Stb
Scinax squalirostris (Lutz, 1925)	1	TCW	RE	Stb
Trachycephalus typhonius (Linnaeus, 1758)	15	TCW, TCT	SF, RE, DI	Stb
Microhylidae				
Elachistocleis bicolor (Guérin-Méneville, 1838)	62	TCW, TCT, PT	SF, RE, DI	Stb
Leptodactylidae				
Leptodactylus elenae Heyer, 1978	70	TCW, TCT, PT	SF, RE, DI	Unk
Leptodactylus fuscus (Schneider, 1799)	86	TCW, TCT	SF, RE, DI	Stb
Leptodactylus plaumanni Ahl, 1936	1	TCW	DI	Stb
Leptodactylus luctator (Steffen, 1815)	58	TCW, TCT, PT	SF, RE, DI	NA
Leptodactylus podicipinus (Cope, 1862)	284	TCW, TCT, PT	SF, RE, DI	Stb
Physalaemus cuvieri Fitzinger, 1826	99	TCW, TCT, PT, AE	SF, RE, DI	Stb
Odontophrynidae				
Odontophrynus reigi Rosset, Fadel, Guimarães, Carvalho, Ceron, Pedrozo, Serejo, Souza, Baldo, and Mângia, 2021	4	TCW, TCT	DI	NA
Proceratophyrs avelinoi Mercadal de Barrio and Barrio, 1993	7	TCW, PT	SF, RE	Unk
REPTILIA				
CROCODYLIA				
Alligatoridae				
Caiman latirostris (Daudin, 1801)	16	TCT	SF, RE, DI	Stb
TESTUDINES				
Chelonoidis carbonarius (Spix, 1824)	1	-	-	NA
Phrynops geoffroanus (Schweigger, 1812)	1	-	-	NA
SQUAMATA				
Amphisbaenidae				
Amphisbaenia mertensi Strauch, 1881	3	TCT, PT	SF, RE, DI	Unk
Hemidactylidae				
Hemidactylus mabouia (Moreau de Jonnès, 1818)	5	AE	DI	Stb
Tropiduridae				
Tropidurus catalanensis Gudynas & Skuk, 1983	11	AE	DI	Unk
Teiidae				
Salvator merianae (Duméril & Bibron, 1839)	19	PT, AE	SF, RE, DI	Stb

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TAXA	N	Method	Habitat	IUCN
Scincidae				
Notomabuya frenata (Cope, 1862)	3	PT	SF	Stb
Anomalepididae				
Liotyphlops ternetzii (Amaral, 1924)	4	TCT, PT	SF, DI	Unk
Boidae				
Eunectes notaeus Cope, 1862 ^{P}	-	-	-	Stb
Colubridae				
Dipsas mikanii Schlegel, 1837	4	TCT, PT, AE	RE, DI	Stb
Erythrolamprus macrosomus (Amaral, 1936)	4	PT, AE	SF, RE, DI	NA
Erythrolamprus aesculapii (Linnaeus, 1758) ^{P}	-	-	-	Stb
Leptophis marginatus (Cope, 1862)	2	AE	DI	NA
Philodryas olfersii (Lichtenstein, 1823)	1	AE	DI	Stb
Dryophylax hypoconia (Cope, 1860)	2	TCT	SF, DI	Stb
Xenodon merremi (Wagler, 1824) ^{P}	-	-	-	Stb
Oxyrhopus guibei Hoge & Romano, 1977	1	AE	SF	Stb
Elapidae				
Micrurus corallinus (Merrem, 1820)	1	AE	RE	Unk
Viperidae				
Bothrops jararaca (Wied-Neuwied, 1824)	1	AE	SF	Unk
Bothrops jararacussu Lacerda, 1884	1	TCT	RE	Unk
Bothrops moojeni Hoge, 1966	14	TCT, PT, AE	SF, RE, DI	Unk
Total = 41	2049			

P (previous observations) – Historical records: species that were previously recorded at the Refúgio Biológico Bela Vista, which were not found in the present study.

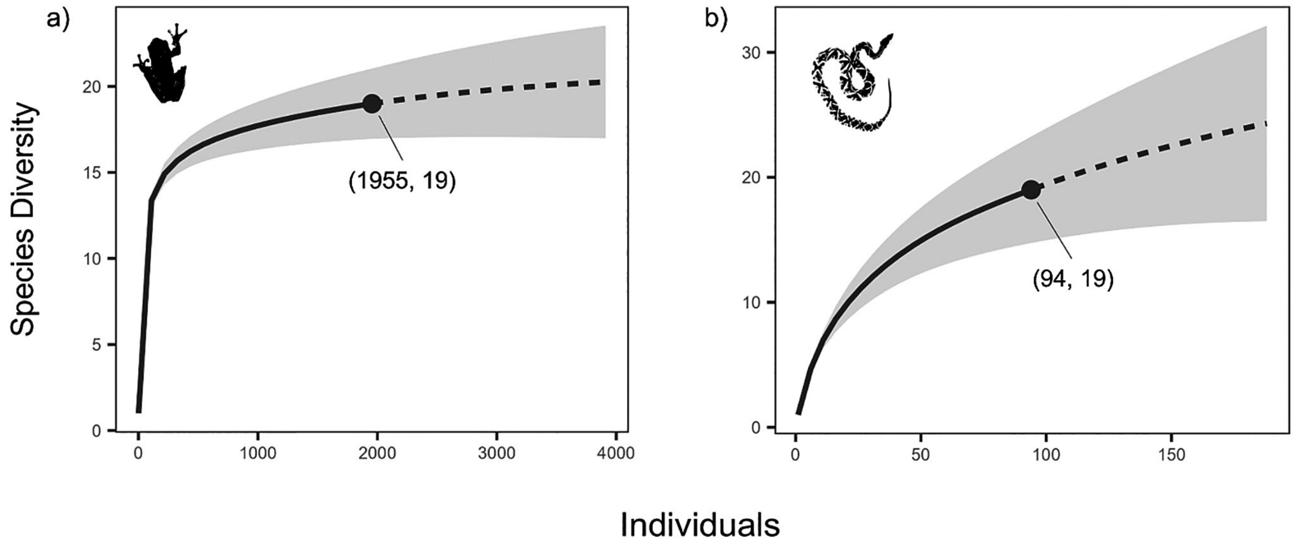

Figure 4. Anuran (adults and tadpoles) and reptile individual-based rarefaction curves and species richness estimation. Solid lines are interpolated diversity, and the dot, in the end, represents the observed abundance; the dashed line is the extrapolated diversity with the end at the observed abundance of anurans. The curve is based on species diversity rarefaction according to Hill number of q = 0, equivalent to species richness.

The reptile rarefaction curve of richness indicated that more species might be found in the sampled area (Figure 4b). Estimation on asymptote suggested a potential an additional five species of reptiles after hypothetically sampling more than 188 individuals (ca. 24 species ± 17.00 – 32 95% CI). By comparison, the anuran's curve is much closer to the asymptote (Figure 4a). Estimation on asymptote for anuran suggested the addition of two species if the double of individuals is recorded (ca. 20 species ± 17.00 – 23 95% CI).

Table 2. Sampling success obtained by each method. Number of species sampled by method (Observed), accompanied by the relative percentage of the total richness of anurans and reptiles separately. Methods implemented are pitfall traps with drift fence (Pitfall trap), time-constrained searches in transects (TCSt), time-constrained search in water bodies for adult anuran (TCSw), time-constrained search in water bodies for tadpole (tadpoles), double ended funnel trap (FT) and accidental encounter (AE).

Sampling method	Observed	% of total richness
Anurans		
Pitfall trap	8.00	8%
TCSt	15.00	78%
TCSw	19.00	100%
Tadpoles	13.00	68%
AE	2.00	10%
Reptiles		
Pitfall trap	7.00	36%
TCSt	7.00	36%
AE	13.00	68%
FT	1.00	0.5%

Sample efficiency was different among groups accordingly to the sampling method used (Table 2). Considering species incidence, active search on water bodies was the most effective method, registering all 19 anuran species, whereas the least effective was accidental encounters, registering only two species. In contrast, 13 reptile species were recorded by the accidental encounter, and both active searches in transects and pitfall traps registered seven species each. The funnel-trap was the most time consuming method – more than three thousand hours of effort – and sampled only one individual of *Caiman latirostris*. Several species were recorded only by one method for both anurans and reptiles (See Table 1).

The cluster analysis revealed that the assemblage of anurans at RBV is closer to Parque Nacional do Iguaçu (a western Paraná) and Misiones in Argentina, positioning Londrina municipality as a sister group of the western Paraná and Misiones group (Figure 5a). For reptiles, the assemblage that grouped with RBV was also Londrina municipality, but in this case, both assemblages formed a closed group; in other words, RBV had its composition more similar to Londrina than with any other assemblage studied (Figure 5b). In general, the most dissimilar assemblages for both anurans and reptiles were those from northeast Brazil, i.e., Pernambuco and Bahia states (Figure 5b). However, the most different reptile assemblage included was from Araçatuba municipality.

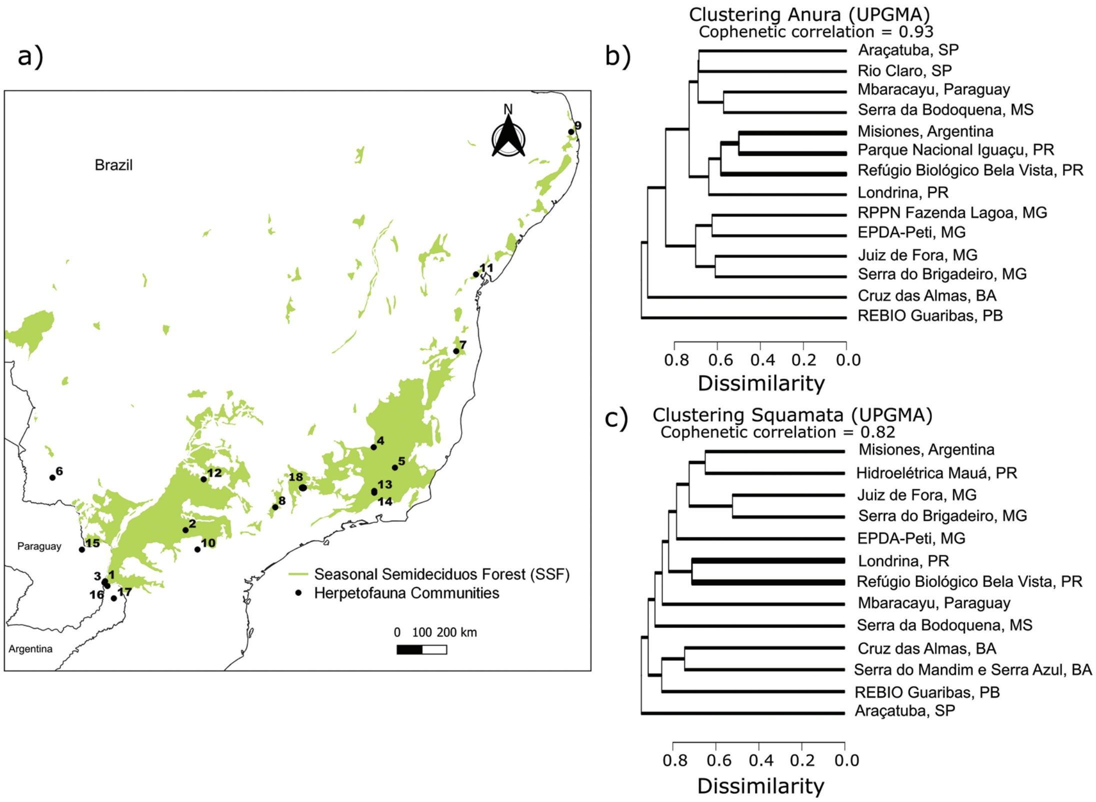

Figure 5. Dendrograms of cluster analyses using Jaccard Indices and map distribution of herpetofauna communities. a) map of the herpetofauna communities (black points) used to create the clustering b) dendrogram of the anuran and; c) reptile species composition from 17 localities in the Semideciduous Seasonal Forest in the Atlantic Forest. Numbers represent herpetofauna from 1 – Refúgio Biológico Bela Vista (RBV); 2 – Londrina, PR; 3 – Parque Nacional do Iguaçu (PNI), PR (anurans); 4 – EPDA, Peti, MG; 5 – Serra do Brigadeiro, MG; 6 – Serra da Bodoquena, MS; 7 – Serra do Mandim e Serra Azul, BA (reptiles); 8 – Rio Claro, SP (anurans); 9 – REBIO Guaribas, 10 – Hidrelétrica de Mauá, PR; 11 – Cruz das Almas, BA; 12 – Araçatuba, SP; 13 – Juiz de Fora, MG (reptiles); 14 – Juiz de Fora, MG (anurans); 15 – Mbaracayú, Paraguay; 16 – Misiones, Argentina (anurans), 17 – Misiones, Argentina (reptiles), 18 – RPPN Fazenda Lagoa, Monte Belo, MG (anurans). Green area represents the Semideciduous Seasonal Forest within Brazil border according to Brazil National Agency of Water (Agência Nacional de Águas – ANA).

Discussion

We registered 19 species of anurans and 19 reptiles in a mosaic of land cover within Itaipu in western Paraná state. At least to our knowledge, this is the first study to list the species of reptiles from a locality in the west of Paraná state. Even though records of the snake species *Eunectes notaeus* from the Boidae family, and *Xenodon merremi* and *Erythrolamprus aesculapii* from the Dipsadidae family have been found in the literature in the same area studied here (Morato 1996, Moutra-Leite et al. 1996). The presence of *Phrynops geoffroanus* in the surroundings of RBV has also been recorded by workers of RBV, who took photographs that enabled us to confirm the species identification. Also, we registered two new occurrences of anuran species for the region that have not been included in previous lists of species for the west of Paraná (i.e., Leivas et al. 2018): *Leptodactylus plaumanni* and *Odontophrynus reigi.* Therefore, the species richness of anurans recorded at RBV in the present study represents ca. 13% of the species occurrence for the state of Paraná (137 total; Santos-Pereira et al. 2018) and ca. 44% of the species occurrence for the west of Paraná (36 total; Leivas et al. 2018). The reptiles represent 10% of the state (156 total; Costa et al. 2022).

The rarefaction curve of anuran richness is very close to the asymptote, indicating that we were able to sample the community sufficiently; that is, our composition and richness data are representative of the species pool. On the other hand, the reptile rarefaction curve showed that six more species are pruned to be collected if more sampling effort is made. However, due to the wide range of microhabitats used by reptiles, including high heights in the vegetation, cryptic habitats, and seasonal abundance peaks that are not necessarily yearly, possibly only long-duration studies would approximate the real reptile richness (Henderson et al. 2016, Michael et al. 2018).

Sampling method showed different sampling success as demonstrated in previous studies (Hutchens & DePerno 2009). Sampling efficiency was different for anurans and reptiles. For capturing anurans, active search in water bodies was the most efficient method whereas accidental encounter was the least effective. On the other hand, reptiles were mostly sampled through accidental encounters and funnel trap only recorded one individual of a juvenile *Caiman latirostris*. Even though the funnel trap was the most time-consuming method, there were only four funnel traps distributed, which could be one explanation for its low success in capturing aquatic reptiles, particularly alligators. Capturing success is expected to vary due to its bias toward specific functional groups. For example, pitfall traps are pruned to sample terrestrial and fossorial reptiles and anurans (e.g., Ribeiro-Júnior et al. 2008, Ali et al. 2018). Considering that most anurans lives associated with water bodies for reproduction, it is expected less anuran species captured by pitfall traps rather than by active searching in water bodies. Some reptiles, like snakes, are secretive animals, therefore, it is common that individuals are found occasionally when moving around the area more than by in pitfall traps or active search, particularly in forested environments where several species use arboreal substrate (Bernarde 2012).

As expected, the anuran species composition from RBV is mostly similar to Parque Nacional do Iguaçu anuran assemblage, likely due to its geographic proximity (ca. 20 km). Hence, the assemblage from The Parque Nacional do Iguaçu and its surroundings have been registered with 36 species of anuran (Leivas et al. 2018), 17 more than we found at RBV. Both assemblages share 16 species, meaning that species from RBV are not necessarily a portion of Parque Nacional do Iguaçu. However, it also includes three species that were not in Leivas et al. (2018), such as *Odontophrynus reigi, Leptodactylus elenae,* and *Leptodactylus plaumanni.* Leivas et al. (2018) indicated the occurrence of *Trachcephalus dibernadoi* in Parque Nacional do Iguaçu; however, upon consulting the mentioned specimen, we have determined that it is an individual of *T. typhonius*. In another survey conducted at Parque Nacional do Iguaçu, *O. reigi*, and *L. plaumanni* were also not registered (Nazaretti 2016). For anurans, the most dissimilar assemblages included in the cluster analysis were those from northeast Brazil. However, the separation of the northeast group from the southern assemblages could be explained by the biogeographic barrier imposed by the Rio Doce river present in the states of Espírito Santo and Minas Gerais. A study that compiled data on anurans from the entire extension of the Atlantic Forest has demonstrated that Rio Doce is a geographical feature that can explain part of the composition of amphibian species and traits along the Atlantic Forest (Lourenço-de-Moraes et al. 2019). Hence, despite the similar vegetational formation, Semideciduous Seasonal Forest assemblages are expected to differ positively with increasing geographic distance, as it harbors differences in spatially structured environmental variables (Chen et al. 2011).

For reptiles, the positioning of Araçatuba reptile assemblage as an outgroup was unexpected. Araçatuba municipality is located in São Paulo state and is geographically closer to RBV (ca. 630 km) than the assemblages from the state of Minas Gerais, e.g., Juiz de Fora (ca. 1,215 km), and Serra do Brigadeiro (ca. 1,345 km). The dissimilarity between Araçatuba with the other southern assemblages might be because the reptiles and amphibians of Araçatuba were sampled from urbanized and rural environments. Assemblages sampled from modified environments, like grazing pastures, are pruned to present a composition different from the expected from natural areas (Ernst & Rodel 2005). Especially for modified Semideciduous Seasonal Forests, the process of savannization and physiognomic changes could have induced compositional shifts that tend to be more similar to the Cerrado biome (Sales et al. 2020). On the other hand, the greatest similarity in composition was observed between RBV and Londrina. This result was already expected due to the geographic proximity. Londrina is the only assemblage in the analysis that belongs to Paraná state and is relatively close to RBV (ca. 500 km). Besides geographical proximity, both assemblages were sampled from forest and modified environments, which could also contribute to compositional similarity (Silva et al. 2011, Figueiredo et al. 2019). Even though the closer assemblage from RBV included in the cluster is Misiones, this assemblage is positioned distant from RBV. One explanation could be the extremely large area of Misiones province where the assemblage was sampled (over 29,000 km^2). Hence, species composition from the south edge of the province could be more similar to a Pampa phytophysiognomy (Arana, 2017) and then generate an assemblage composition different from the north edge, which is the region closer to RBV.

The only evidence of reptile richness from the past in the extreme western region of Paraná registered 17 species. This number refers to reptiles rescued during the construction of the Itaipu Dam (Ziober & Zanirato 2014). Based on this information, our study reveals that no substantial richness loss has happened in the region compared to past decades. Although, no conclusions can be made regarding composition turnover that could have occurred since the construction of Itaipu and the RBV because any species list has been previously published. Information of previous species recorded at Itaipu was also sampled years after its construction and accounts for only three snake species (Morato 1996, Moutra-Leite et al. 1996). Surveys in other localities in western Paraná could increase the chance of adding new occurrences of species to the list. For example, inventories at the Parque Nacional do Iguaçu would probably register new species occurrences due to their large area and more preserved environment (Leivas et al. 2018).

The prevalence of species classified as "Least Concern" and populational trend as "Stable" are related to the predominance of common and relatively abundant species. Anuran species, like *D. nanus, D. minutus,* and *L. podicipinus,* and reptile species, like the snakes from the *Bothrops* genus and the lizard *S. merianae* are widely distributed and are frequently associated with disturbed environments and urbanization (Oda et al. 2017, Lima et al. 2009). Anurans assemblages found in modified habitats are usually composed of species that present traits that allow survival in anthropic environments, attributes that differ from intact forests associated with particular environmental variables, like less water availability and microhabitat availability (Riemann et al. 2017). Therefore, even though RBV has a great area of preserved SSF, its anuran composition could reflect its land cover composed of forested areas proximal to urbanized areas.

Due to the absence of previous compositional information on reptile species from western Paraná, we cannot conclude whether the RBV assemblage is similar to previous assemblages that naturally occurred in the region or has experienced species turnover through time. Also, when comparing reptile assemblages from SSF, one should consider the longitudinal and latitudinal gradients. Climatic, pluviometry, and seasonality vary among longitudes and latitudes within SSF (Oliveira-Filho et al. 2000), and it could interfere with the historical processes conducting herpetofauna composition structure. Thus, more studies on the western limits of SSF formation are necessary to fill the gaps where no surveys have been done. For example, an information gap exists regarding the herpetofauna from the south of Mato Grosso do Sul state and the northwest, western, and central areas of Paraná state. These localities are close to Foz do Iguaçu and are linked by the presence of the Paraná and Iguaçu rivers which probably contributed to the region's biogeography. Furthermore, the largest fragment of SSF in Brazil is the Parque Nacional do Iguaçu, which has never been systematically inventoried for reptiles.

In conclusion, our study registered two new occurrences of anuran species of anurans for the western Paraná found in an area of conservation and restoration. Moreover, we show that even though species found in RBV are not a conservation priority, the RBV can function as an important refugee to anuran and reptile biodiversity, housing more than 13% of amphibians and 10% of reptiles from the state of Paraná. The RBV could, eventually, harbor anuran species of conservation priority present at Parque Nacional do Iguaçu, e.g., *Crossodactylus schmidti, Proceratophrys bigibbosa, Vitreorana uranoscopa* and *Limnomedusa macroglossa (*Leivas et al. 2018, IUCN 2022*)*. The possible exchange of species between Parque Nacional do Iguaçuand the RBV must be explored in future studies. Thus, investigations aiming to understand how biological corridors influence the community structure between these areas are crucial for regional conservation actions. Currently, two extended and preserved fragments of vegetation could function as a bridge: the riparian forest of the Paraná River and the "Ecological Corridor of Santa Maria", a band of remnant forest that passes through rural properties. In addition, due to the history of land use in the state of Parana countryside, more surveys on current herpetofauna could clarify how diversity is distributed and how community structure and dynamics relate to a modified environment by anthropogenic actions.

Identification keys – Adult Anurans (see Figure 6)

Identification key to Family or Species

1. Paratoid glands present...... **BUFONIDAE *Rhinella diptycha***
   Paratoid glands absent... 2
2. Robust body shape; rough skin all over the body .... **ODONTOPHRYNIDAE**
   Elongated body shape; smooth or lumpy skin 3
3. Oval body shape in dorsal view; reduced head and forelimbs .... **MICROHYLIDAE *Elachistocleis bicolor***
   Body of another shape 4
4. Fingertip dilated forming an adhesive disc ...... **HYLIDAE**
   Fingertip not dilated .... **LEPTODACTYLIDAE**

Identification key to Species

ODONTOPHRYNIDAE

1. Skin bulges at edge of eyelid present; white stripe in the middle dorsal region absent .... ***Proceratophrys avelinoi***
   Skin bulges at the edge of the eyelid absent; white stripe in the middle dorsal region present ....***Odontophrynus reigi***

LEPTODACTYLIDAE

1. Snout–vent length (SVL) from 15 to 35 mm; dark dots on the gular region extending below the pectoral region present ....*(Physalaemus)* ***Physalaemus cuvieri***
   Greater than 35 mm of SVL; dark spots on the gular region absent or if present limited to above the pectoral region ....(*Leptodactylus*) 2
2. Presence of a white stripe in the middle dorsal region, extending from the pelvic girdle to the middle of the head and medial location of the nostril between the eye and snout .... ***Leptodactylus plaumanni***
   Absent of a white stripe in the middle dorsal region of the dorsum, but if present, the nostril is positioned closer to the snout than the eyes 3
3. Pair of dorsolateral white stripes on each side of the body starting at the pelvic girdle present 4
   Pair of dorsolateral white stripes on each side of body starting at pelvic girdle absent 5

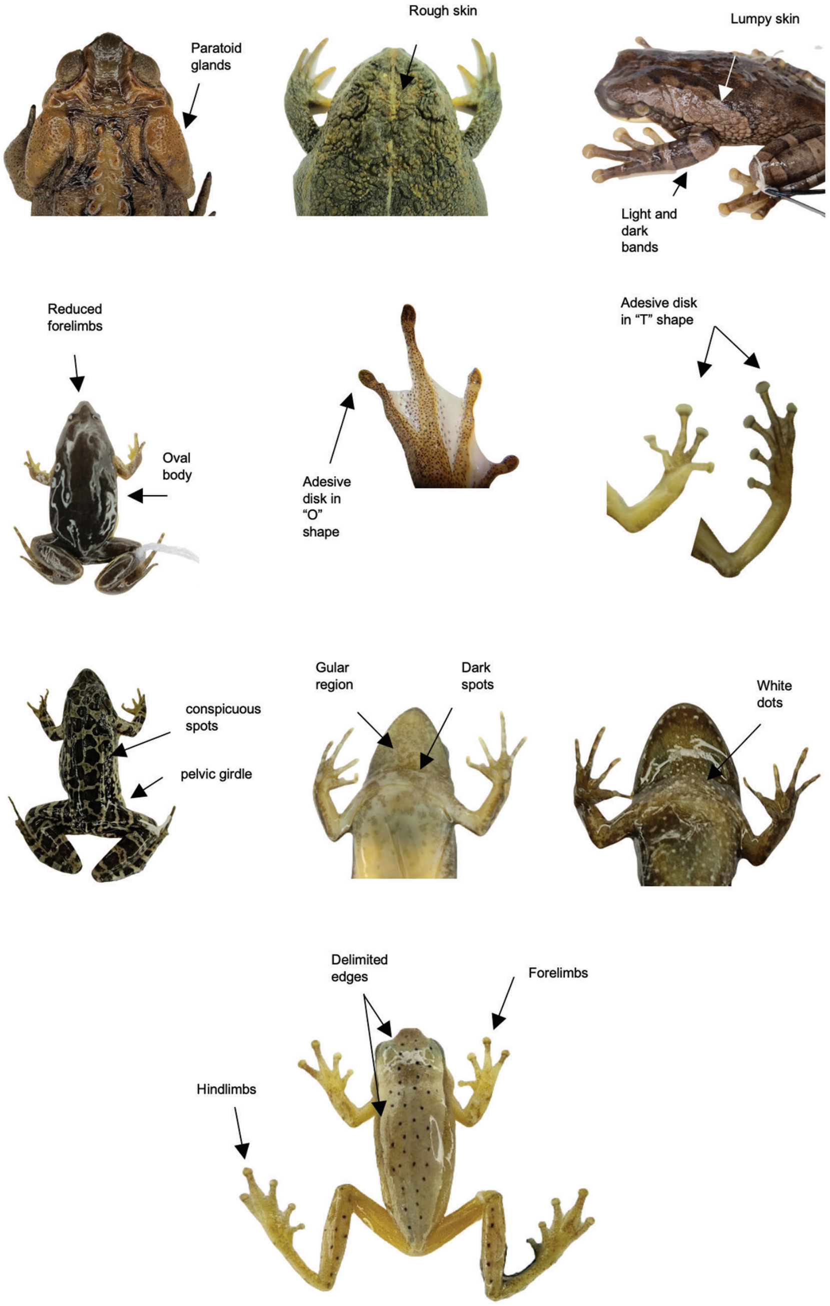

Figure 6. Morphological structures of adult anurans used in the identification key.

4. Dark and conspicuous blotches on the dorsum .... ***Leptodactylus fuscus***
   Gray dorsum or with light spots; a black stripe on the side of the head, crossing the eyes and the tympanum over a white stripe above the lips .... ***Leptodactylus elenae***
5. White dots scattered along all the ventral region present ....***Leptodactylus podicipinus***
   White dots in the ventral region absent; trapezium-shaped interocular spot .... ***Leptodactylus luctator***

HYLIDAE

1. Lumpy skin on the dorsolateral and ventral region; light and dark bands around fore and hind limbs .... *(Trachycephalus)* ***Trachycephalus typhonius***
   Smooth skin on the dorsolateral and ventral region 2
2. Adhesive disks of the digits and toes in a "T" shape (except for *Scinax squalirostris*) *Scinax* 3
   Adhesive disks digits and toes in an "O" shape 5
3. SVL less than 28 mm; pair of white stripes absent; uniformly brown dorsal region ....***Scinax berthae***
   SVL greater than 28 mm 4

4. SVL greater than 40 mm; adhesive disk of the longest digit of the forelimb smaller than the diameter of the tympanum (proportion of 3/4 of the ratio) ....***Scinax fuscovarius***
SVL less than 37 mm; adhesive disc of the longest digit of the forelimb smaller than the diameter of the eardrum (4/5 ratio of the ratio) ....***Scinax granulatus***
5. Pair of longitudinally oriented white stripes on the dorsolateral region present; elongated snout ... .***Scinax squalirostris***
Pair of longitudinally oriented white stripes on dorsolateral region absent 6
6. SVL greater than 40 mm ....*Boana* 7
SVL less than 40 mm ....*Dendropsophus* 8
7. Sparse white dots on the back of the thigh ....***Boana albopunctata***
Dark stripes on the ventral thigh .... ***Boana raniceps***
8. Irregular dark-colored spots on the back of the body or homogeneous color .... ***Dendropsophus minutus***
Dorsum light-colored with delimited edges ....***Dendropsophus nanus***

Identification key – Tadpoles (see Figure 7)

Identification key to Species

1. Oral disc with labial flap; nostrils absent ....***Elachistocleis bicolor***
Oral disc without labial flap and nostrils present 2
2. Oral disc with keratinized structures and papillae 3
Modified oral disc in protractile tube ....***Dendropsophus nanus***
3. Marginal papillae row with gap on the anterior and posterior lips 4
Marginal papillae row with gap only on the anterior lip......5
4. Body black; inclined snout (side view) .....***Rhinella diptycha***
Body brown; round snout (side view) ... ***Physalaemus cuvieri***
5. One or no row of anterior labial teeth; body triangular (lateral view) .... ***Dendropsophus minutus***
Two or more rows of anterior labial teeth 6
6. Four or more rows of anterior labial teeth .... ***Trachycephalus typhonius***
Three or two rows of anterior labial teeth 7
7. Oral disc not emarginated 8
Oral disc emarginated 10
8. Lower jaw W-shaped ....***Scinax berthae***
Lower jaw in another shape 9
9. Lower jaw U-shaped ....***Leptodactylus plaumanni***
Lower jaw V-shaped .... ***Leptodactylus fuscus***
10. Oral disc laterally emarginated 11
Oral disc not laterally emarginated 13
11. Oral disc prominently emarginated.................................... .... ***Proceratophrys avelinoi***
Oral disc with regularly emarginated.............................12
12. Tadpoles with a total length greater than 45 mm; oral disc uniformly pigmented around the jaws (brown) ....***Odontophrynus reigi***
Tadpoles with total length below 35 mm; oral disc not uniformly pigmented around the jaws .... ***Leptodactylus elenae***
13. Posterior labial teeth without gap 14
Posterior labial teeth with gap (any row) 15

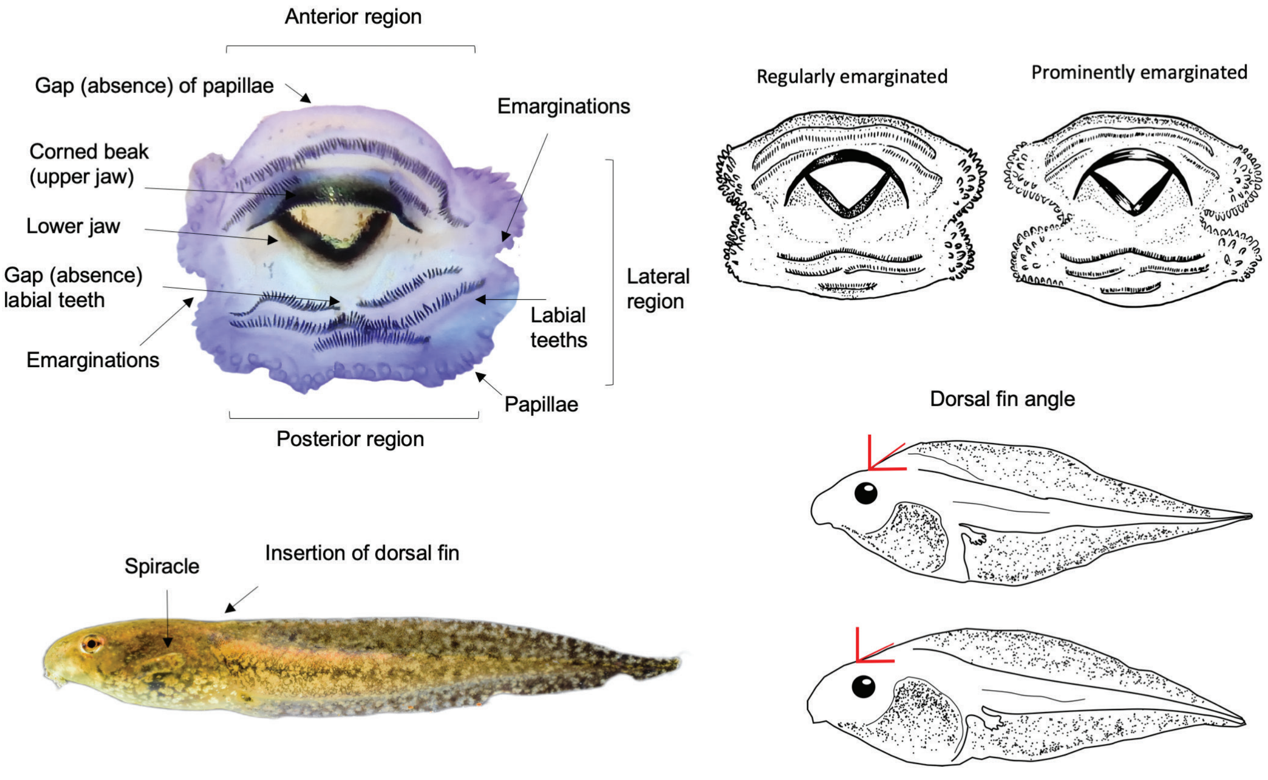

Figure 7. Morphological structures of tadpoles used in the identification key.

14. Second anterior (A2) labial tooth row with gap .... ***Leptodactylus podicipinus***
    Second anterior (A2) labial tooth row without gap .... ***Leptodactylus luctator***
15. Spiracle inner wall not fused with the body; globular body (lateral view) 16
    Spiracle inner wall fused with the body; triangular body (lateral view) 17
16. Body and tail yellowish; dorsal fin with pronounced tapering with triangular margin .... ***Boana raniceps***
    Dorsal region of body lighter than the dorsolateral region; dorsal fins with gradual tapering, with convex margin .... ***Boana albopunctata***
17. Body elongated-oval (dorsal view); base of tail muscle higher than the body .... ***Scinax squalirostris***
    Body depressed (dorsal view) 18
18. The angle between where dorsal fin originates and the body surface close to 45 degrees; mostly silver cover over the intestine (ventral region of the body); ventral fin margin extends beyond the body .... ***Scinax fuscovarius***
    The angle between where dorsal fin originates and the body surface less than 45 degrees; mostly brownish cover over intestine (ventral region of the body); ventral fin margin does not extend beyond the body ...... ***Scinax granulatus***

Identification keys – Reptiles

Identification Key to Family or Species

1. Body protected by carapace and plastron 2
   Body without carapace and plastron 3
2. 11 to 12 shields in the plastron ....**TESTUDINIDAE *Chelonoidis carbonarius***
   13 shields in the plastron .... **CHELIDAE *Phrynops geoffranus***
3. Body with front and hind limbs 4
   Body elongated without limbs 5
4. A double vertical row of caudal crests starting at the dorsal region of the tail base .... **ALLIGATORIDAE *Caiman latirostris***
   Absence of vertical crests on the dorsal region of the tail 11
5. Vestigial eyes, covered by scales 6
   Developed eyes, without coverage scales 7
6. Pre-cloacal pores present ....**AMPHISBAENIDAE *Amphisbaena mertensii***
   Pre-cloacal pores absent 7
7. Undifferentiated dorsal and ventral scales ....**ANOMALEPIDIDAE *Liotyphlops ternetzii***
   Differentiated dorsal and ventral scales 8
8. Ventral scales differentiated from the dorsal scales and covering the entire ventral 9
   Ventral scales differentiated from the dorsal scales but narrower, without occupying the entire ventral region .... **BOIDAE *Eunectes notaeus***
9. Solenoglyphous fang .... **VIPERIDAE**
   Other type of dentition 10
10. Proteroglyphous fang .... **ELAPIDAE *Micrurus corallinus***
    Opisthoglyphous fang or aglyphous dentition .... **COLUBRIDAE**
11. A pair of internasals scales in contact with each other 12
    Three or more scales in the nasal region 13
12. Pores on the ventral region and on the inner surface of the thighs present .... **TEIIDAE *Salvator merianae***
    Pores on the ventral region and on the inner surface of the absent .... **SCINCIDAE *Notomabuya frenata***
13. A large intraparietal scale, much larger than all other surrounding scales ....**TROPIDURIDAE *Tropidurus catalanensis***
    Head scales numerous and of uniform size, without great differentiation .... **GECKONIDAE *Hemidactylus mabouia***

Identification Key to Species

VIPERIDAE

1. Area between dorsal dark triangular spots 1.5 to 2 times larger than the spots 2
   Area between dorsal dark triangular spots approximately the same size as the spots; white marks around sharp spots; lateral band on head broad and dark .... ***Bothrops jararacussu***
2. Well-demarcated dorsal dark triangular spots; spaces between spots without darker circular marks .... ***Bothrops jararaca***
   Blurred dorsal dark triangular spots, light brown post-orbital band, spaces between spots with several dark circular marks .... ***Bothrops moojeni***

COLUBRIDAE

1. Banded/coralline coloration pattern (red, black and white) 2
   Other coloring pattern 3
2. Head with white and black bands .... ***Erythrolamprus aesculapii***
   Head with red and black bands .... ***Oxyrhopus guibei***
3. Scales on the top of the head with black edges.................. .... ***Leptophis marginatus***
   Scales on the top of the head of another pattern 4
4. Apical pits on the dorsal scales present 5
   Apical pits on the dorsal scales absent 6
5. Post-orbital black line present .... ***Philodryas olfersii***
   Post-orbital black line absent .... ***Xenodon merremii***
6. Longitudinal stripes along the body absent ... ***Dipsas mikanii***
   Longitudinal stripes along the body present 7
7. Longitudinal stripes along the entire body starting just after the head .... ***Dryophylax hypoconia***
   Longitudinal stripes starting at the final third of the body..... .... ***Erythrolamprus macrossomus***

Supplementary Material

The following online material is available for this article:

Appendix - List of specimens from Refúgio Biológico Bela Vista deposited in the Herpetological Collection of Bertha Lutz of the

Universidade Federal da Integração Latino-Americana, Foz do Iguaçu, Paraná.

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Denise de Cerqueira Rossa-Feres

Author Contributions

Gabriel S. Vicente-Ferreira: contributed to data collection; contribution to data analysis and interpretation; contribution to manuscript preparation.

Eloize F. do Nascimento: contributed to the concept and design of the study; contribution to data collection; contribution to critical revision, adding intellectual content.

Camila S. Batista: contributed to the concept and design of the study; contribution to data collection.

Tarik A. Kardush: contributed to the concept and design of the study; contribution to data collection.

Kathia Luz Burdiles Reyes: contributed to data collection.

Michel V. Garey: contributed to the concept and design of the study; contribution to manuscript preparation; contribution to critical revision, adding intellectual content.

Conflicts of Interest

The authors declare no conflict of interest related to this manuscript.

Data availability

Supporting data are available at https://doi.org/10.48331/scielodata.NCQEPO.

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Article

Mite fauna (Acari) associated with apple orchards (*Malus domestica*) and spontaneous vegetation as reservoir for predatory mites

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Abstract: The aim of this study was to recognize the mite fauna associated with apple orchards in southern Brazil and present a dichotomous key of the species sampled and those already reported in apple trees in southern Brazil. The studies were carried out in the 2020/2021 harvest in seven apple orchards of the Eva, Fuji and Gala cultivars located in the municipalities of Muitos Capões, Antônio Prado (Rio Grande do Sul state) and São Joaquim (Santa Catarina state). The orchards were divided into quadrants and sampling was carried out monthly. In each orchard, 40 plants were sampled, with three leaves of each plant collected in apical, median and basal regions of a median branch. In addition, monthly five species of spontaneous plants per orchard were sampled. A total of 8,425 mites were found, with the greatest abundance in Antônio Prado (50%), followed by Muitos Capões (35.5%) and São Joaquim (14.5%). The specimens found belong to 29 families, 64 genera and 99 species, in addition to mites of the order Oribatida. The greatest diversity was found in spontaneous vegetation (59 species), being 19 exclusives to apple trees and 21 species common to apple trees and spontaneous vegetation. Phytoseiidae was the family that presented the greatest richness, with 16 species, of which seven were common in apple trees and spontaneous plants. The most abundant species was *Aculus schlechtendali* Nalepa (Eriophyidae) (39.5%), followed by *Panonychus ulmi* (Koch) (Tetranychidae) (14.6%), *Polyphagotarsonemus latus* (Banks) (Tarsonemidae) (9.4%) and *Neoseiulus californicus* (McGregor) (Phytoseiidae) (7.4%). These results suggest that the mite fauna present in apple orchards in different landscapes and management are distinct, with a greater diversity of phytoseiid mites present in organic areas. Therefore, to maintain a greater diversity of predatory mites in these orchards, organic management seems to be the most appropriate. Furthermore, the high acarine diversity found in spontaneous vegetation demonstrates the importance of maintaining these plants in orchards that serve as refuges and reservoirs, favoring the permanence of natural enemies in these environments.
Keywords: *Aculus schlechtendali; Eva; Fuji; Gala; Neoseiulus californicus; Panonychus ulmi.*

Acarofauna (Acari) associada a pomares de maçã (*Malus domestica*) e vegetação espontânea como reservatório de ácaros predadores

Resumo: O objetivo deste estudo foi reconhecer a acarofauna associada a pomares de macieira no sul do Brasil e apresentar uma chave dicotômica das espécies amostradas e daquelas já relatadas em macieiras no sul do Brasil. Os estudos foram realizados na safra 2020/2021 em sete pomares de macieiras das cultivares Eva, Fuji e Gala localizados nos municípios de Muitos Capões, Antônio Prado (RS) e São Joaquim (SC). Os pomares foram divididos em quadrantes e a amostragem foi realizada mensalmente. Em cada pomar foram amostradas 40 plantas, sendo três folhas de cada planta coletadas nas regiões apical, mediana e basal de um ramo mediano. Além disso, mensalmente foram amostradas cinco espécies de vegetação espontânea por pomar. Foram encontrados 8.425 ácaros, com maior abundância em Antônio Prado (50%), seguido por Muitos Capões (35,5%) e São Joaquim (14,5%). Os exemplares encontrados pertencem a 29 famílias, 64 gêneros e 99 espécies, além de ácaros da ordem Oribatida. A maior abundância foi encontrada em vegetação espontânea (59 espécies), sendo 19 exclusivas de macieiras e 21 espécies comuns a macieiras e vegetação espontânea. Phytoseiidae foi a família que apresentou maior riqueza, com 16 espécies, das quais sete eram comuns em macieiras e vegetação espontânea. A espécie mais abundante foi *Aculus schlechtendali* Nalepa (Eriophyidae) (39,5%), seguida por *Panonychus ulmi* (Koch) (Tetranychidae) (14,6%), *Polyphagotarsonemus latus* (Banks) (Tarsonemidae) (9,4%) e *Neoseiulus californicus* (McGregor) (Phytoseiidae) (7,4%). Esses resultados sugerem que a acarofauna presente em pomares de macieira em diferentes paisagens e manejos são distintas, com maior diversidade de ácaros fitoseídeos presentes em áreas orgânicas. Portanto, para manter uma maior diversidade de ácaros predadores nesses pomares, o manejo orgânico parece ser o mais adequado. Além disso, a elevada diversidade de ácaros encontrada na vegetação espontânea demonstra a importância da manutenção destas plantas em pomares que servem como refúgios e reservatórios, favorecendo a permanência de inimigos naturais nestes ambientes.

Palavras-chave: *Aculus schlechtendali; Eva; Fuji; Gala; Neoseiulus californicus; Panonychus ulmi.*

Introduction

Brazil is among the largest apple producers (*Malus domestica* Borkh: Rosaceae) in the world (Kist et al. 2019), with cultivation concentrated in the highest regions of the states of Santa Catarina and Rio Grande do Sul, largest producers, followed by Paraná (Kist et al. 2019). There is a significant number of apple cultivars, with Gala and Fuji being the most important, but more recent cultivars, such as Eva, have achieved relevance in national production (Kist et al. 2019).

Conventional agriculture is widely used in several cultures due to its high productivity, but it presents risks that include loss of biodiversity, environmental pollution and risk to human health (Gomiero et al. 2011, Campbell et al. 2017). Aiming at sustainable development and better use of natural resources (Walker et al. 2017, Zhu et al. 2018, Willet et al. 2019) the organic agriculture system has stood out in several countries (Gomiero et al. 2011, Smith-Spangler et al. 2012, Caprio et al. 2015, Gomiero 2018). Pesticide spraying has been the main criterion used to differentiate organic from conventional management (Sumberg & Giller 2022). Another alternative to conventional agriculture is regenerative agriculture, which seeks to improve soil protection, not using machinery and maintaining cover with spontaneous or non-spontaneous vegetation (The Soil Association, 2021), if necessary, this system allows the use of pesticides for pest control in the Integrated Pest Management.

Landscape management can contribute to the sustainable control of pest species, as the composition of the environment can directly affect the abundance of a herbivore, affecting its dispersal, mortality or reproduction, or indirectly, affecting its natural enemies (Veres et al. 2013). Spontaneous growth vegetation occurs associated with orchards, usually between the rows of trees and can be native or exotic, with natural germination and rapid growth (Lykouressis et al. 2008, Diehl et al. 2012). The morphology of some of these plants consists of trichomes, domatia and nectaries, which are beneficial structures for the plant and offer refuge, a safe place for oviposition and provide alternative foods such as pollen and nectar to mite species (Agrawal & Karban 1997, Ferla & Moraes 2002, Prischmann & James 2003, Matos et al. 2006, Duso et al. 2010). Certain plants, associated with orchards, play an important ecological role as they host species that help in the biological control of agricultural pests, as they naturally migrate from this spontaneous vegetation to the main crop of the orchard (Tixier et al. 2000, Altieri 2002, Kreiter et al. 2003, Lykouressis et al. 2008, Ji et al. 2022).

The indiscriminate use of pesticides in orchards can lead to a reduction in natural enemies and, consequently, to an increase in the population of phytophagous mites, causing economic losses (Van Leeuwen & Dermauw 2016, Walker et al. 2017, Schmidt-Jeffris & Beers 2018). Mites of the suborders Prostigmata and Mesostigmata are of greatest agricultural economic importance (Evans 1992). Among the Prostigmata they were the phytophagous of the families Eriophyidae, Tarsonemidae, Tenuipalpidae and Tetranychidae, and the predators Stigmaeidae (Jeppson et al. 1975), respect to Mesostigmata, Phytoseiidae stood out (McMurtry et al. 2013, 2015, Demite et al. 2014). Eriophyidae and Tetranychidae are phytophagous mites found associated with apple orchards (Ferla et al. 2018, Nascimento et al. 2020). Among these stand out *Panonychus ulmi* (Koch), *Tetranychus urticae* Koch (Tetranychidae) and *Aculus schlechtendali* Nalepa (Eriophyidae) (Ferla et al. 2018, Nascimento et al. 2020, Kasap & Atlihan 2021, Corrêa et al. 2021, Silva et al. 2022). The record of the presence of *A. schlechtendali* in southern Brazil serves as a warning for the apple production chain, as it is a species of quarantine importance present in Brazil (Ferla et al. 2018, Nascimento et al. 2020, Corrêa et al. 2021, Silva et al. 2022).

The study of the diversity and seasonality of mite populations associated with plants is of great importance for the advancement of biological control methods for pests in agroecosystems and for the assessment of damage caused and biological changes in these habitats. The aim of this study was to recognize the mite fauna associated with apple orchards, in southern Brazil as well as to perform a dichotomous key with the species associated with these orchards and those already reported in previous works carried out in the same region.

Materials and Methods

1. *Study area*

The studies were carried out in the 2020/2021 season in seven apple orchards of the Eva, Fuji and Gala cultivars located in the municipalities of Muitos Capões (28°23'23"S 51°15'12"W) and Antônio Prado (28°22 '44"S 49°56'12"W), state of Rio Grande do Sul and São Joaquim (28°53'23"S 51°23'06"W), state of Santa Catarina (Figure 1).

1.1. Antônio Prado

Three organic orchards of Eva, Fuji and Gala cultivars were evaluated. To control herbivores, Bordeaux mixture, lime sulfur, neem oil and Cera Trap® attractant were used. Spontaneous vegetation was maintained, and mowing was only carried out when there was a need to move. In these orchards, the soil cover was preserved, with the presence of spontaneous vegetation, such as grasses and weeds, in association with litter maintained in the area.

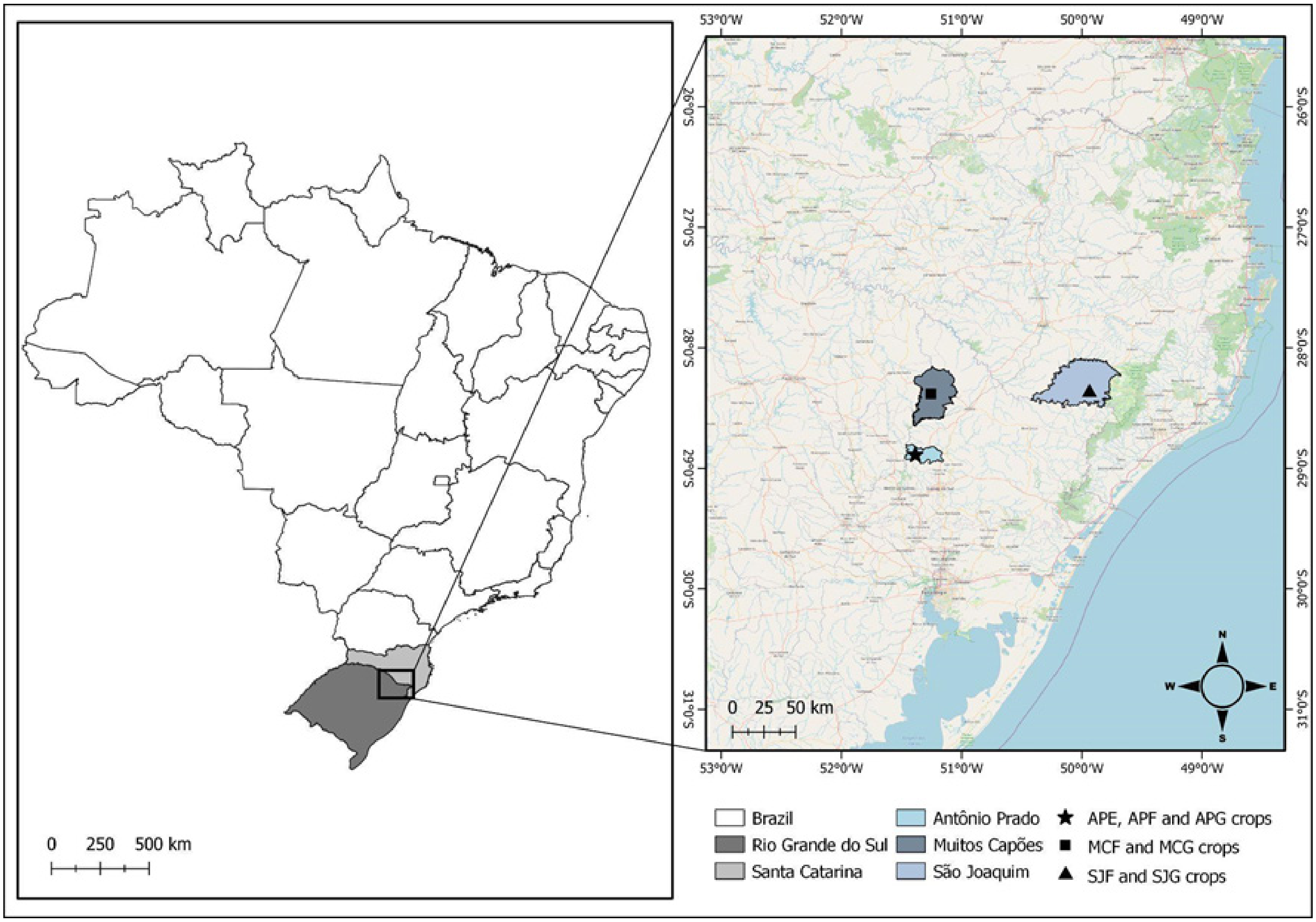

Figure 1. Collection points in apple-producing regions in the municipalities of Antônio Prado and Muitos Capões, Rio Grande do Sul, and São Joaquim, Santa Catarina, Brazil. Authorship: Castro, I. S.

1.2. Muitos Capões

Two conventional orchards were evaluated, one Fuji and the other Gala. In both orchards, the soil was kept unprotected with the use of herbicides and weeding to control pests in the orchards, as well as the spraying of pesticides to control pests.

1.3. São Joaquim

Two orchards with regenerative agriculture were evaluated, one Fuji and the other Gala. In these orchards, the soil was kept covered by spontaneous vegetation, grasses, in association with litter. Weeding was not carried out. Pigs, sheep and chickens were kept grazing throughout the area, feeding on weeds and aborted apple tree fruits. In these areas, when necessary, producers spray pesticides to control pests.

2. Sampling procedures

2.1. Apple tree plants

Samplings were carried out monthly from September 2020 to August 2021. The orchards were divided into quadrants and the sampled trees were marked to identify the origin of the sampled leaves. In each orchard, 40 plants were sampled, selected from the fifth row, counting from the edge, from which three leaves of a median branch of each plant in the apical, median and basal regions of the branch were detached, totaling 120 leaves/area. In the senescence period, branches were collected from the middle part of the plant and three buds selected from the apical, median and basal regions, totaling 120 buds/area. The material was individually packed in previously identified transparent plastic bags, kept at low temperature and taken to the Laboratory of Acarology (Labacari) of the University of Vale do Taquari – Univates, Lajeado, RS.

2.2. Spontaneous vegetation

Five species of spontaneous vegetation most frequent in each month, in the evaluated orchards, were collected in sufficient quantity for a sampling effort of one hour of screening (Diehl et al. 2012). The collected vegetation was packed separately in plastic bags identified with the name of the respective cultivar and the municipality of origin, stored in a styrofoam box with artificial ice (Gelox®) and immediately transported to Labacari.

3. Identification

3.1. Mite species

The material was examined with Leica S6E stereoscopic microscope, with a fine-tipped brush. The mites were mounted on microscope slides using Hoyer's medium (Jeppson et al. 1975) and kept in a stove at a temperature between 50 and 60 °C for approximately eight days, for medium drying, fixation and clarification of the specimens. Morphological identification was made with Zeiss Axio Scope A1 phase contrast optical microscope and proper bibliography (Baker & Tuttle 1994, Chant & McMurtry 1994, 2007, Amrine & Stasny 1994, Amrine et al. 2003, Fan & Zhang 2005, Johann et al. 2013, Skvarla et al. 2014, Silva et al. 2016). The species found in the study were deposited in the Reference Collection of Mites of the Museum of Science Univates (Sisgen: A8302CB and Sisgen: A05CB2A).

3.2. Spontaneous vegetation species

After sampling, a sample of each vegetation sampled was mounted on a specimen sheet for identification with specific bibliography (Moreira & Bragança 2011, Lorenzi 2014). Family determination was based on Angiosperm Phylogeny Group IV systems (APG IV, 2016).

4. Dichotomous key

A dichotomous key was performed with species sampled in this work and those already reported on apple trees (*Malus* spp.) from Brazil (Figueiredo 1950, Flechtmann 1966, Lorenzato et al. 1986, Lorenzato 1987, Lorenzato & Sechi 1993, Flechtmann 1996, Ferla & Moraes 1998, Lin & Zhang 2002, Monteiro 2002, Moraes & Flechtmann 2007, Ferla & Botton 2008, Oliveira et al. 2010, Mineiro et al. 2015, Ferla et al. 2018). The key was based partially on Muma (1963), André (1980), Denmark (1982), Baker (1990), Baker and Tuttle (1994), Lofego (1998), Krantz and Walter (2009), Walter et al. (2009), Johann et al. (2013), Rocha et al. (2014), Beard et al. (2015), Rezende et al. (2015), Demite et al. (2016), Fan et al. (2016), Paktinat-Saeij et al. (2016), Silva et al. (2016), Johann et al. (2017), Silva et al. (2020) and Sousa et al. (2020).

Results

A total of 8,425 mites were found, of which 1,908 were present in spontaneous vegetation. The highest abundance was found in Antônio Prado (50%), followed by Muitos Capões (35.5%) and São Joaquim (14.5%). 26 families with 67 species of spontaneous vegetation were collected. Among the plant families, eight had mites (Table 1).

The mite specimens found belong to 29 families, 64 genera and 99 species. In addition, 684 mites belonging to the suborder Oribatida were found. The greatest diversity of mite species was found in spontaneous vegetation (59 species). 19 species were exclusive from apple trees, and

Table 1. Spontaneous vegetation in apple orchards in the municipalities of Muitos Capões, Antônio Prado, state of Rio Grande do Sul and São Joaquim, state of Santa Catarina, Brazil, assessed between August 2020 and September 2021. Eating habits: P = Predator, G = Generalist and F = Phytophagous.

Botanical family	Botanical species	Abundance of mites
AMARANTHACEAE	*Amaranthus deflexus*	–
	Iresine diffusa	–
APIACEAE	*Centella asiatica*	–
	Conium maculatum	–
	Daucus pusillus	–
APOCYNACEAE	*Oxypetalum* sp.	–
ARALIACEAE	*Hydrocotyle leucocephala*	–
ASTERACEAE	*Baccharis anomala*	17
	Baccharis dracunculifolia	–
	Baccharis sp.	–
	Baccharis trimera	–
	Bidens pilosa	50
	Chromolaena laevigata	69
	Conyza bonariensis	–
	Conyza canadensis	1
	Elephantopus mollis	154
	Gamochaeta americana	–
	Hypochaeris sp.	9
	Koanophyllon sp.	–
	Senecio brasiliensis	–
	Sonchus oleraceus	1
	Taraxacum officinale	4
	Vernonanthura sp.	1
	Vernonanthura tweediana	322

Continue...

Continuation

Botanical family	Botanical species	Abundance of mites
BRASSICACEAE	*Raphanus sativus*	8
CARYOPHYLLACEAE	*Stellaria media*	–
COMMELINACEAE	*Commelina erecta*	–
CONVOLVULACEAE	*Ipomoea alba*	–
	Ipomoea indivisa	–
	Ipomoea sp.	–
CUCURBITACEAE	*Sicyos* sp.	–
EUPHORBIACEAE	*Euphorbia heterophylla*	26
FABACEAE	*Trifolium pratense*	6
	Trifolium repens	42
	Vicia cracca	1
HYPERICACEAE	*Hypericum caprifoliatum*	–
LAMIACEAE	*Cantinoa mutabilis*	12
	Leonurus japonicus	–
MALVACEAE	*Sida* sp.	–
	Sida rhombifolia	6
OXALIDACEAE	*Oxalis* sp.	–
PLANTAGINACEAE	*Plantago australis*	624
POACEAE	*Axonopus affinis*	–
	Bromus catharticus	–
	Bromus unioloides	12
	Eragrostis plana	–
	Holcus lanatus	73
	Lolium multiflorum	190
	Paspalum dilatatum	17
	Paspalum pumilum	12
	Paspalum urvillei	20
	Sporobolus indicus	1
	Steinchisma hians	8
	Urochloa plantaginea	34
POLYGONACEAE	*Rumex obtusifolius*	–
PTERIDACEAE	*Adiantopsis chlorophylla*	45
ROSACEAE	*Acaena eupatoria*	42
RUBIACEAE	*Richardia brasiliensis*	10
	Richardia sp.1	–
	Richardia sp.2	–
SCROPHULARIACEAE	*Scoparia* sp.	1
	Veronica persica	8
SOLANACEAE	*Solanum americanum*	–
	Solanum pseudocapsicum	2
TALINACEAE	*Talinum paniculatum*	73
VERBENACEAE	*Lantana camara*	–
	Verbena litoralis	7
		1.908

21 species were common to apple trees and spontaneous vegetation. Phytoseiidae was the family with the greatest diversity, with 16 species, seven of them common in both apple trees and spontaneous vegetation. Tarsonemidae was the second-diversity family with 12 species, followed by Cunaxidae with seven species and Ologamasidae, Stigmaeidae, Tetranychidae and Tydeidae, with six species each. The most abundant species was *A. schlechtendali* (39.5%), followed by *P. ulmi* (14.6%), *P. latus* (9.4%) and *Neoseiulus californicus* (McGregor) (7.4%). Of these, *A. schlechtendali* was exclusive from apple trees and the other species were found both in apple trees and spontaneous vegetation. Among the spontaneous vegetation, *Plantago australis* Lam. (Plantaginaceae) was the species with the highest mite abundance (32.7%), with 56.9% generalists and 41.7% predators. The second species was *Vernonanthura tweediana* (Baker) H. Rob. (Asteraceae) (16.9%). Among the mites recorded, the highest abundance of predatory mites was on *V. tweediana* (51.9%).

Below, the mite species and its respective host plants, the municipality of origin of the samples, apple tree cultivar that was being cultivated in the orchard, month and year of collection and the number of specimens collected in parentheses.

Mesostigmata

Ascidae

Asca sp.1

Antônio Prado: EVA – *Elephantopus mollis* Kunth (Asteraceae) – I-2021 (1), IV-2021 (2), *Vernonanthura tweediana* (Baker) H. Rob. (Asteraceae) – IV-2021 (3). FUJI – *Elephantopus mollis* – II-2021 (1), III-2021 (2). GALA – *Hypochaeris* sp. (Asteraceae) – IX-2020 (1). Muitos Capões: FUJI – *Trifolium repens* L. (Fabaceae) – III-2021 (4). GALA – *Plantago australis* Lam. (Plantaginaceae) – V-2021 (2), *Vernonanthura tweediana* – V-2021 (2). São Joaquim: FUJI – *Lolium multiflorum* L. (Poaceae) – XI-2020 (5), *Plantago australis* – I-2021 (2), IV-2021 (2), V-2021 (8), VIII-2021 (1), *Verbena litoralis* Kunth (Verbenaceae) – IV-2021 (2). GALA – *Plantago australis* – I-2021 (10), III-2021 (1), VI-2021 (3).

Asca sp.2

Antônio Prado: EVA – *Vernonanthura tweediana* – V-2021 (1).

Asca sp.3

Antônio Prado: FUJI – *Malus domestica* Borkh (Rosaceae) – X–2020 (1).

Blattisociidae

Lasioseius sp.

Antônio Prado: FUJI – *Plantago australis* – IV-2021 (2). GALA – *Elephantopus mollis* – V-2021 (3), *Paspalum urvillei* Steud. (Poaceae) – I-2021 (1). Muitos Capões: FUJI – *Vernonanthura tweediana* – IV-2021 (2). GALA – *Plantago australis* – V-2021 (1). São Joaquim: FUJI – *Plantago australis* – XII-2020 (3), II-2021 (1), IV-2021 (1), *Trifolium repens* – XII-2020 (1), *Verbena litoralis* – IV-2021 (1). GALA – *Holcus lanatus* L. (Poaceae) – II-2021 (1).

Digamasellidae

Dendrolaelaps sp.

Antônio Prado: FUJI – *Plantago australis* – III-2021 (1). São Joaquim: FUJI – *Acaena eupatoria* Cham. & Schltdl. (Rosaceae) – V-2021 (2), *Lolium multiflorum* – III-2021 (1), *Plantago australis* – IV-2021 (2). GALA – *Plantago australis* – IV-2021 (3).

Laelapidae

Cosmolaelaps sp.1

Antônio Prado: EVA – *Elephantopus mollis* – III-2021 (1). FUJI – *Elephantopus mollis* – XII-2020 (2), *Lolium multiflorum* – XII-2020 (1), *Paspalum dilatatum* Poir. (Poaceae) – XI-2020 (1).

Cosmolaelaps sp.2

Antônio Prado: EVA – *Elephantopus mollis* – III-2021 (1). FUJI – *Steinchisma hians* (Elliott) Nash. (Poaceae) – V-2021 (1).

Gaeolaelaps aculeiferoides (Teng, 1982)

Hypoaspis (*Gaeolaelaps*) *aculeiferoides* Teng, 1982: 161.

Muitos Capões: GALA – *Urochloa plantaginea* (Link) R. D. Webster (Poaceae) – I-2021 (1).

Pseudoparasitus sp.

Muitos Capões: FUJI – *Lolium multiflorum* – IX-2020 (1).

Macrochelidae

Macrocheles sp.1

Antônio Prado: FUJI – *Plantago australis* – III-2021 (2). GALA – *Plantago australis* – III-2021 (1), VIII-2021 (1). Muitos Capões: GALA – *Urochloa plantaginea* – I-2021 (3).

Macrocheles sp.2

São Joaquim: FUJI – *Plantago australis* – V-2021 (1).

Macrocheles subbadius (Berlese, 1904)

Holostaspis subbadius Berlese, 1904: 264.

São Joaquim: FUJI – *Plantago australis* – V-2021 (1), GALA – III-2021 (1).

Melicharidae

Orolaelaps sp.1

Antônio Prado: EVA – *Adiantopsis chlorophylla* (Sw.) Fée (Pteridaceae) – VII-2021 (3), *Elephantopus mollis* – I-2021 (1), *Plantago australis* – IV-2021 (1). FUJI – *Elephantopus mollis* – III-2021 (1), *Lolium multiflorum* – VI-2021 (2), *Trifolium repens* – VI-2021 (1). GALA – *Elephantopus mollis* – V-2021 (4), *Lolium multiflorum* – X-2020 (4), *Paspalum pumilum* Nees. (Poaceae) – IX-2020 (3).

Orolaelaps sp.2

Antônio Prado: EVA – *Adiantopsis chlorophylla* – VII-2021 (1). FUJI – *Paspalum dilatatum* – XI-2020 (2).

Ologamasidae

Gamasiphis sp.

Antônio Prado: EVA – *Elephantopus mollis* – III-2021 (1). FUJI – *Elephantopus mollis* – III-2021 (1), *Paspalum dilatatum* – XI-2020 (2). GALA – *Lolium multiflorum* – IX–2020 (1). São Joaquim: FUJI – *Plantago australis* – VII-2021 (2).

Neogamasellevans ammonis Karg & Schorlemmer, 2009

Neogamasellevans ammonis Karg & Schorlemmer, 2009: 71–72

Antônio Prado: EVA – *Solanum pseudocapsicum* L. (Solanaceae) – IX-2020 (1). FUJI – *Conyza canadensis* (L.) Cronquist (Asteraceae) – X-2020 (1). GALA – *Paspalum urvillei* – II-2021 (1). Muitos Capões: GALA – *Bidens pilosa* L. (Asteraceae) – VI-2021 (1). São Joaquim: FUJI – *Lolium multiflorum* – III-2021 (1).

Neogamasellevans preendopodalis Loots & Ryke, 1967

Neogamasellevans preendopodalis Loots & Ryke, 1967: 14.

Muitos Capões: FUJI – *Lolium multiflorum* – X-2020 (1).

Ologamasus postpilus Karg & Schorlemmer, 2009

Ologamasus postpilus Karg & Schorlemmer, 2009: 77–78.

Antônio Prado: EVA – *Plantago australis* – VIII-2021 (1). FUJI – *Plantago australis* – VI-2021 (1). GALA – *Elephantopus mollis* – V-2021 (1).

Ologamasus margaridae Bizarro & Rode, 2023

Ologamasus margaridae Bizarro & Rode, 2023: 495–514.

Antônio Prado: FUJI – *Cantinoa mutabilis* (Rich.) Harley & J. F. B. Pastore (Lamiaceae) – VII-2021 (6), *Elephantopus mollis* – III-2021 (1), *Steinchisma hians* – V-2021 (1), *Plantago australis* – VI-2021 (2), *Paspalum dilatatum* – XI-2020 (8). GALA – *Elephantopus mollis* – V-2021 (1), *Hypochaeris* sp. – XII-2020 (2), *Lolium multiflorum* – X-2020 (1), *Paspalum dilatatum* – IX-2020 (1), III-2021 (4), *Trifolium repens* – VI-2021 (1), *Veronica persica* Poir. (Scrophulariaceae) – VIII-2021 (1). São Joaquim: GALA – *Holcus lanatus* – X-2020 (1), *Lolium multiflorum* – X-2020 (7), *Plantago australis* – X-2020 (1), VIII-2021 (2). FUJI – *Lolium multiflorum* – III-2021 (1), *Plantago australis* – I-2021 (1), III-2021 (1), V-2021 (2), VIII-2021 (1).

Ologamasus tuberculatus Bizarro & Rode, 2023

Ologamasus tuberculatus Bizarro & Rode, 2023: 495–514.

Antônio Prado: EVA – *Plantago australis* – III-2021 (2), IV-2021 (3). FUJI – *Elephantopus mollis* – III-2021 (3), *Lolium multiflorum* – VI-2021 (1), *Talinum paniculatum* (Jacq.) Gaertn. (Talinaceae) – VI-2021 (1). GALA – *Lolium multiflorum* – III-2021 (2), *Plantago australis* – VII-2021 (4), VIII-2021 (1), *Paspalum urvillei* – III-2021 (1), *Richardia brasiliensis* Gomes (Rubiaceae) – IV-2021 (1). Muitos Capões: FUJI – *Lolium multiflorum* – X-2020 (1). GALA – *Lolium multiflorum* – X-2020 (1), *Plantago australis* – V-2021 (1).

Pachylaelapidae

Zygoseius sp.

Antônio Prado: FUJI – *Plantago australis* – III-2021 (2).

Zygoseius furciger (Berlese, 1916)

Lasioseius (*Zygoseius*) *furciger* Berlese, 1916: 12: 19–67.

Antônio Prado: FUJI – *Cantinoa mutabilis* – VII-2021 (2). GALA – *Richardia brasiliensis* – IV-2021 (2). São Joaquim: FUJI – *Raphanus sativus* L. (Brassicaceae) – IX-2020 (1). GALA – *Holcus lanatus* – XII-2020 (1), *Plantago australis* – II-2021 (1), III-2021 (1). Muitos Capões: FUJI – *Lolium multiflorum* – VIII-2021 (1), *Plantago australis* – VIII-2021 (4).

Parasitidae

Eugamasus sp.1

Antônio Prado: GALA – *Hypochaeris* sp. – IX-2020 (2), *Paspalum pumilum* – IX-2020 (1). Muitos Capões: FUJI – *Trifolium repens* – III-2021 (1). São Joaquim: FUJI – *Plantago australis* – XII-2020 (1), III-2021 (1). GALA – *Plantago australis* – III-2021 (1).

Eugamasus sp.2

Antônio Prado: EVA – *Adiantopsis chlorophylla* – VII-2021 (1). FUJI – *Paspalum dilatatum* – XI-2020 (1).

Phytoseiidae

Amblyseius chiapensis De Leon, 1961

Amblyseius chiapensis De Leon, 1961: 85.

Antônio Prado: EVA – *Malus domestica* – III-2021 (1).

Amblyseius nicola Chant & Hansell, 1971

Amblyseius nicola Chant & Hansell, 1971: 714.

São Joaquim: FUJI – *Acaena eupatoria* – IX-2020 (1), *Lolium multiflorum* – I-2021 (3), *Plantago australis* – I-2021 (12). GALA – *Acaena eupatoria* – VIII-2021 (1), *Lolium multiflorum* – X-2020 (6), *Plantago australis* – I-2021 (16), II-2021 (1), IV-2021 (3).

Amblyseius vitis Ferla & Silva, 2009

Amblyseius vitis Ferla & Silva, 2009: 509–10.

Antônio Prado: EVA – *Taraxacum officinale* F. H. Wigg. (Asteraceae) – IX-2020 (2). FUJI – *Elephantopus mollis* – XII-2020 (1), *Paspalum dilatatum* – XI-2020 (1). GALA – *Lolium multiflorum* – X-2020 (1).

Arrenoseius gaucho Ferla, Silva & Moraes, 2010

Arrenoseius gaucho Ferla, Silva & Moraes, 2010: 15.

Antônio Prado: EVA – *Adiantopsis chlorophylla* – VII-2021 (6), *Elephantopus mollis* – I-2021 (2), II-2021 (1), III-2021 (8), IV-2021 (1), *Plantago australis* – IV-2021 (38), VIII-2021 (4), *Vernonanthura tweediana* – XII-2020 (2). FUJI – *Elephantopus mollis* – XII-2020 (11), II-2021 (1), III-2021 (6), *Lolium multiflorum* – XII-2020 (4), VI-2021 (4), *Plantago australis* – III-2021 (2), IV-2021 (3), *Paspalum urvillei* – I-2021 (1), *Talinum paniculatum* – VI-2021 (2), *Vernonanthura* sp. – XI-2020 (1). GALA – *Elephantopus mollis* – V-2021 (1), *Hypochaeris* sp. – XII-2020 (2), *Lolium multiflorum* – X-2020 (1), *Plantago australis* – VII-2021 (5), VIII-2021 (5), *Paspalum urvillei* – I-2021 (1), *Veronica persica* – VIII-2021 (1). São Joaquim: FUJI – *Bromus unioloides* H.B.K. (Poaceae) – X-2020 (2), *Holcus lanatus* – XII-2020 (1), *Plantago australis* – I-2021 (3), II-2021 (2), III-2021 (6), V-2021 (6), VI-2021 (2). GALA – *Acaena eupatoria* - XI-2020 (2), *Holcus lanatus* – XI-2020 (1), II-2021 (1), *Lolium multiflorum* – IX-2020 (1), I-2021 (2), III-2021 (2), *Plantago australis* – XII-2020 (1), I-2021 (3), II-2021 (2), III-2021 (2), *Raphanus sativus* – IX-2020 (6). Muitos Capões: FUJI – *Vernonanthura tweediana* – IV-2021 (2).

Arrenoseius sp.

Antônio Prado: EVA – *Adiantopsis chlorophylla* – VII-2021 (2), *Malus domestica* – IV-2021 (1), *Vernonanthura tweediana* – V-2021 (1). FUJI – *Elephantopus mollis* – III-2021 (1), *Lolium multiflorum* – VI-2021 (2), *Plantago australis* – III-2021 (2), IV-2021 (1), *Steinchisma hians* – V-2021 (1).

Euseius inouei (Ehara & Moraes, 1998)

Amblyseius (*Euseius*) *inouei* Ehara & Moraes, 1998: 59.

Antônio Prado: EVA – *Chromolaena laevigata* (Lam.) R. M. King & H. Rob. (Asteraceae) – III-2021 (3), *Malus domestica* – XI-2020 (6), XII-2020 (1), II-2021 (4), III-2021 (13), IV-2021 (12), V-2021 (1). FUJI – *Malus domestica* - XI-2020 (1). GALA - *Malus domestica* – XI-2020 (1).

Euseius mesembrinus (Dean, 1957)

Typhlodromus mesembrinus Dean, 1957: 165.

Antônio Prado: EVA – *Chromolaena laevigata* – I-2021 (1), II-2021 (1), III-2021 (28), *Malus domestica* – XII-2020 (3), I-2021 (14), II-2021 (3), III-2021 (4), IV-2021 (23), V-2021 (2).

Galendromus (*Galendromus*) *annectens* (De Leon, 1958)

Typhlodromus annectens De Leon, 1958: 75.

Antônio Prado: EVA – *Malus domestica* – I-2021 (1). GALA – *Malus domestica* – II-2021 (4), III-2021 (1), IV-2021 (4).

Metaseiulus (*Metaseiulus*) *eiko* (El-Banhawy, 1984)

Typhlodromus eiko El-Banhawy, 1984: 138.

Antônio Prado: EVA – *Malus domestica* – XII-2020 (3), I-2021 (1), II-2021 (4), V-2021 (3), *Vernonanthura tweediana* – III-2021 (4).

FUJI – *Malus domestica* – XII-2020 (1), I-2021 (1), III-2021 (2), IV-2021 (2). GALA – *Malus domestica* – I-2021 (4), II-2021 (10), III-2021 (1), VI-2021 (2), VIII-2021 (1).

Neoseiulus sp.

São Joaquim: GALA – *Plantago australis* – VIII-2021 (1).

Neoseiulus californicus (McGregor, 1954)

Neoseiulus californicus McGregor, 1954: 89.

Antônio Prado: EVA – *Malus domestica* – X-2020 (1), XII-2020 (3), II-2021 (3), FUJI – *Malus domestica* – X-2020 (1), I-2021 (3), III-2021 (1). GALA – *Malus domestica* – XII-2020 (1), I-2021 (7), II-2021 (3). Muitos Capões: FUJI – *Lolium multiflorum* – XI-2020 (1), *Malus domestica* – XII-2020 (6), I-2021 (27), II-2021 (31), III-2021 (66), IV-2021 (14), V-2021 (7), VI-2021 (10), *Plantago australis* – II-2021 (1), VI-2021 (1), V-2021 (1), *Vernonanthura tweediana* – V-2021 (16). GALA – *Bidens pilosa* – V-2021 (1), *Malus domestica* – XI-2020 (2), XII-2020 (8), I-2021 (85), II-2021 (37), III-2021 (36), IV-2021 (10), V-2021 (8), VI-2021 (7), *Vernonanthura tweediana* – IX-2020 (1), XII-2020 (12), V-2021 (1). São Joaquim: FUJI – *Lolium multiflorum* – III-2021 (6), *Malus domestica* – I-2021 (11), II-2021 (5), III-2021 (32), IV-2021 (7), V-2021 (8), *Plantago australis* – I-2021 (1), IV-2021 (4), V-2021 (1), *Verbena litoralis* – IV-2021 (1). GALA – *Acaena eupatoria* – IV-2021 (2), V-2021 (1), *Holcus lanatus* – II-2021 (1), *Lolium multiflorum* – III-2021 (21), V-2021 (1), *Malus domestica* – XII-2020 (1), II-2021 (18), III-2021 (47), IV-2021 (26), V-2021 (14), *Plantago australis* – IV-2021 (3), V-2021 (1).

Neoseiulus fallacis (Garman, 1948)

Iphidulus fallacis Garman, 1948: 13.

Antônio Prado: FUJI – *Malus domestica* – X-2020 (1).

Neoseiulus mumai (Denmark, 1965)

Cydnodromus mumai Denmark, 1965: 91.

Antônio Prado: FUJI – *Lolium multiflorum* – XI-2020 (1).

Neoseiulus tunus (De Leon, 1967)

Typhlodromips tunus De Leon, 1967: 29.

Antônio Prado: EVA – *Baccharis anomala* DC. (Asteraceae) – I-2021 (2), *Malus domestica* – I-2021 (1), II-2021 (2), III-2021 (3), IV-2021 (4). FUJI – *Malus domestica* – VI-2021 (1).

Phytoseius sp.

São Joaquim: GALA – *Plantago australis* – II-2021 (1).

Proprioseiopsis ovatus (Garman, 1958)

Amblyseius ovatus Garman, 1958: 78.

Antônio Prado: EVA – *Sporobolus indicus* (L.) R. Br. (Poaceae) – IV-2021 (1). FUJI – *Veronica persica* – VIII-2021 (1). Muitos Capões: FUJI – *Malus domestica* – XI-2020 (1). GALA – *Malus domestica* – I-2021 (1), *Plantago australis* – XII-2020 (1), V-2021 (2), *Vernonanthura tweediana* – XI-2020 (1), V-2021 (1). São Joaquim: FUJI – *Holcus lanatus* – II-2021 (3), *Plantago australis* – I-2021 (9), II-2021 (1). GALA – *Acaena eupatoria* – IV-2021 (1), V-2021 (1), *Lolium multiflorum* – III-2021 (1), *Plantago australis* – I-2021 (3).

Uropodina

Antônio Prado: GALA – *Lolium multiflorum* – X-2020 (1). Muitos Capões: GALA – *Urochloa plantaginea* – I-2021 (1).

Veigaiidae

Antônio Prado: GALA – *Paspalum pumilum* – IX-2020 (1).

Trombidiformes

Alycidae

Amphialycus (*Amphialycus*) *pentophthalmus* Zachvatkin, 1949

Amphialycus pentophthalmus Zachvatkin, 1949: 30: 292–97

Antônio Prado: FUJI – *Paspalum urvillei* – I-2021 (1).

Laminamichaelia sp.

Antônio Prado: FUJI – *Lolium multiflorum* – XII-2020 (1).

Cunaxidae

Armascirus sp.

Antônio Prado: GALA – *Elephantopus mollis* – V-2021 (1), *Plantago australis* – VII-2021 (1).

Cunaxoides lajeadensis Wurlitzer & Monjarás-Barrera, 2020.

Cunaxoides lajeadensis Wurlitzer et al. 2020: 402–07.

Antônio Prado: EVA – *Baccharis anomala* – I-2021 (1), *Vernonanthura tweediana* – X-2020 (1), III-2021 (4), IV-2021 (1).

Dactyloscirus sp.

Antônio Prado: FUJI – *Elephantopus mollis* – III-2021 (1).

Neocunaxoides ovatus Lin, 2003

Neocunaxoides ovatus Lin, Zhang & Ji, 2003: 103–05.

Antônio Prado: EVA – *Adiantopsis chlorophylla* – VII-2021 (1). FUJI – *Elephantopus mollis* – II-2021 (1), III-2021 (2), *Plantago australis* – V-2021 (3). GALA – *Elephantopus mollis* – V-2021 (1), *Plantago australis* – VII-2021 (2). Muitos Capões: FUJI – *Bidens pilosa* – V-2021 (1). GALA – *Vernonanthura tweediana* – V-2021 (2).

Pulaeus mormacensis Wurlitzer & Silva, 2021

Pulaeus mormacensis Wurlitzer et al. 2021: 1255–60.

Antônio Prado: FUJI – *Plantago australis* – IV-2021 (1). Muitos Capões: GALA – *Plantago australis* – V-2021 (1).

Rubroscirus grilloi Wurlitzer & Ferla, 2020

Rubroscirus grilloi Wurlitzer et al. 2020: 2228–33.

Muitos Capões: GALA – *Plantago australis* – XII-2020 (1).

Scutopalus tomentosus Rocha, Skvarla & Ferla, 2013

Scutopalus tomentosus Rocha et al. 2013: 39–42.

Antônio Prado: EVA – *Vernonanthura tweediana* V-2021 (1). FUJI – *Talinum paniculatum* – VI-2021 (1). GALA – *Elephantopus mollis* – V-2021 (1).

Eriophyidae

Aculus schlechtendali (Nalepa, 1890)

Phyllocoptes schlechtendali Nalepa, 1890: 99: 40–69.

Antônio Prado: EVA – *Malus domestica* – X-2020 (13), XI-2020 (457), XII-2020 (898), I-2021 (2), VIII-2021 (1). FUJI – *Malus domestica* – XII-2020 (46), I-2021 (36), II-2021 (3), VIII-2021 (1). GALA – *Malus domestica* – XII-2020 (17), I-2021 (206), II-2021 (100), VI-2021 (56). Muitos Capões: FUJI – *Malus domestica* – X-2020 (24), XI-2020 (12), XII-2020 (154), I-2021 (4), II-2021 (1), IV-2021 (24), VIII-2021 (5). GALA – *Malus domestica* – X-2020 (124), XI-2020 (424), XII-2020 (656), I-2021 (1), VIII-2021 (2). São Joaquim: FUJI – *Malus domestica* – I-2021 (1), III-2021 (4). GALA – *Malus domestica* – I-2021 (56), VI-2021 (1), VIII-2021 (1).

Erythraeidae

Leptus sp.

Antônio Prado: FUJI – *Plantago australis* – IV-2021 (2).

Eupodidae

Benoinyssus sp.1

Antônio Prado: EVA – *Elephantopus mollis* – III-2021 (3). FUJI – III-2021 (4), *Plantago australis* – III-2021 (1), *Richardia brasiliensis* – IV-2021 (1). GALA – *Euphorbia heterophylla* – III-2021 (2), *Plantago australis* – VII-2021 (1), VIII-2021 (1). Muitos Capões: FUJI – *Euphorbia heterophylla* – V-2021 (1), *Plantago australis* – VIII-2021 (1), *Trifolium repens* – IV-2021 (2). GALA – *Vernonanthura tweediana* – V-2021 (2). São Joaquim: GALA – *Plantago australis* – XI-2020 (1), IV-2021 (1).

Benoinyssus sp.2

Antônio Prado: GALA – *Malus domestica* – IV-2021 (1), VIII-2021 (1), *Paspalum urvillei* – III-2021 (1).

Eupodes sp.

Muitos Capões: GALA – *Bidens pilosa* – VI-2021 (1), *Plantago australis* – V-2021 (1).

Iolinidae

Pseudopronematulus sp.

Antônio Prado: EVA – *Baccharis anomala* – I-2021 (8), *Chromolaena laevigata* – III-2021 (1), *Malus domestica* – XI-2020 (2), XII-2020 (8), I-2021 (12), II-2021 (10), III-2021 (5), IV-2021 (3), *Paspalum urvillei* – II-2021 (1), *Vernonanthura tweediana* – III-2021 (3), IV-2021 (5). FUJI – *Malus domestica* – XI-2020 (3), IV-2021 (1), *Steinchisma hians* – V-2021 (2), *Talinum paniculatum* – VI-2021 (1). GALA – *Euphorbia heterophylla* – III-2021 (1), *Malus domestica* – XI-2020 (2), XII-2020 (1), I-2021 (1), II-2021 (2), III-2021 (2) – VI-2021 (1). Muitos Capões: FUJI – *Vernonanthura tweediana* – IV-2021 (1). GALA – *Bidens pilosa* – IV-2021 (4), *Euphorbia heterophylla* – IV-2021 (10), *Malus domestica* – I-2021 (1), III-2021 (1).

Scutacaridae

Scutacarus sp.

Antônio Prado: EVA – *Adiantopsis chlorophylla* – VII-2021 (1). São Joaquim: FUJI – *Plantago australis* – IV-2021 (1).

Stigmaeidae

Agistemus brasiliensis Matioli, Ueckermann & Oliveira, 2002

Agistemus brasiliensis Matioli, Ueckermann & Oliveira, 2002: 106.

Antônio Prado: EVA – *Baccharis anomala* – I-2021 (1), *Chromolaena laevigata* – I-2021 (1), III-2021 (3), *Malus domestica* – XI-2020 (3), XII-2020 (10), I-2021 (69), II-2021 (40), IV-2021 (50), V-2021 (3), *Vernonanthura tweediana* – III-2021 (29), IV-2021 (31), V-2021 (24). FUJI – *Malus domestica* – XI-2020 (1), XII-2020 (1), I-2021 (2), II-2021 (4), IV-2021 (2). GALA – *Elephantopus mollis* – V-2021 (1), *Malus domestica* – XII-2020 (1), IV-2021 (2), VI-2021 (12). Muitos Capões: FUJI – *Bidens pilosa* – IV-2021 (1), *Malus domestica* – II-2021 (1), IV-2021 (1), V-2021 (1), VI-2021 (10), *Plantago australis* – VI-2021 (17), *Vernonanthura tweediana* – IV-2021 (7). GALA – *Bidens pilosa* – IV-2021 (1), *Malus domestica* – II-2021 (1), III-2021 (3), IV-2021 (1), V-2021 (2), VI-2021 (17). São Joaquim: GALA – *Malus domestica* – III-2021 (1).

Agistemus floridanus Gonzalez, 1965

Agistemus floridanus Gonzalez, 1965: 42.

Antônio Prado: FUJI – *Malus domestica* – VI-2021 (3). GALA – *Malus domestica* – II-2021 (4). São Joaquim: FUJI – *Malus domestica* – I-2021 (1). GALA – *Malus domestica* – II-2021 (1).

Agistemus riograndensis Johann & Ferla, 2013

Agistemus riograndensis Johann et al. 2013: 247.

Antônio Prado: EVA – *Chromolaena laevigata* – II-2021 (2), *Elephantopus mollis* – IV-2021 (5), *Malus domestica* – II-2021 (30), III-2021 (123), IV-2021 (49), V-2021 (8). FUJI – *Malus domestica* – III-2021 (1), IV-2021 (5), V-2021 (1). GALA – *Malus domestica* – II-2021 (6), III-2021 (5), IV-2021 (6), V-2021 (10). Muitos Capões: FUJI – *Malus domestica* - III-2021 (2), V-2021 (3). GALA – *Euphorbia heterophylla* – V-2021 (4), *Malus domestica* – III-2021 (2), IV-2021 (9), *Plantago australis* – V-2021 (1), *Vernonanthura tweediana* – V-2021 (6). São Joaquim: FUJI – *Malus domestica* – III-2021 (3), IV-2021 (4), V-2021 (9). GALA – *Malus domestica* – III-2021 (4), IV-2021 (15), V-2021 (23), *Plantago australis* – IV-2021 (1), V-2021 (2).

Agistemus sp.

Antônio Prado: FUJI – *Malus domestica* – V-2021 (1).

Eustigmaeus segnis (Koch, 1836)

Caligonus segnis Koch, 1836: 5(10).

São Joaquim: FUJI – *Acaena eupatoria* – IV-2021 (1), V-2021 (1), *Plantago australis* – V-2021 (5). GALA – *Plantago australis* – V-2021 (1), VI-2021 (4). Muitos Capões: GALA – *Vernonanthura tweediana* – V-2021 (2).

Ledermuelleriopsis punctata Soliman, 1975

Ledermuelleriopsis punctata Soliman, 1975: 244.

Muitos Capões: FUJI – *Plantago australis* – IX-2020 (1).

Tarsonemidae

Daidalotarsonemus esalqi Rezende, Lofego & Ochoa, 2015

Daidalotarsonemus esalqi Rezende, Lofego & Ochoa, 2015: 436–41.

Antônio Prado: EVA – *Malus domestica* – III-2021 (1). Muitos Capões: GALA – *Malus domestica* – XI-2020 (1).

Daidalotarsonemus savanicus Rezende, Lofego & Ochoa, 2015

Daidalotarsonemus savanicus Rezende, Lofego & Ochoa, 2015: 441–46.

Antônio Prado: EVA – *Chromolaena laevigata* – III-2021 (4), *Malus domestica* – I-2021 (1), III-2021 (2), IV-2021 (6), *Vernonanthura tweediana* – IV-2021 (1).

Fungitarsonemus sp.

São Joaquim: FUJI – *Malus domestica* – V-2021 (1).

Polyphagotarsonemus latus (Banks, 1904)

Tarsonemus latus Banks, 1904: 55.

Antônio Prado: EVA – *Baccharis anomala* – I-2021 (1), *Malus domestica* – I-2021 (1), II-2021 (16). FUJI – *Malus domestica* – XII-2020 (62), I-2021 (72), II-2021 (54). GALA – *Malus domestica* – XII-2020 (2), I-2021 (302), II-2021 (278).

Rhynchotarsonemus sp.

Antônio Prado: EVA – *Malus domestica* – III-2021 (1).

Tarsonemus confusus Ewing, 1939

Tarsonemus confusus Ewing, 1939: 26.

Antônio Prado: EVA – *Malus domestica* – IV-2021 (5). Muitos Capões: FUJI – *Vernonanthura tweediana* – IV-2021 (10). São Joaquim: FUJI – *Malus domestica* – II-2021 (2).

Tarsonemus merus Lin & Zhang, 2002

Tarsonemus merus Lin & Zhang, 2002: 248.

Antônio Prado: EVA – *Malus domestica* – XI-2020 (1), XII-2020 (1), II-2021 (1), III-2021 (10), IV-2021 (3). FUJI – *Malus domestica* – VIII-2021 (9). GALA – *Malus domestica* – II-2021 (3), IV-2021 (4), VI-2021 (3), VIII-2021 (7). Muitos Capões: FUJI – *Lolium multiflorum* – IX-2020 (1), *Malus domestica* – III-2021 (1), *Plantago australis* – II-2021 (1), *Vernonanthura tweediana* – V-2021 (16). GALA – *Malus domestica* – IX-2020 (2), XI-2020 (1), II-2021 (1), III-2021 (2), VIII-2021 (1), *Sida rhombifolia* – VIII-2021 (2), *Vernonanthura tweediana* – XII-2020 (1). São Joaquim: FUJI – *Malus domestica* – IX-2020 (11), III-2021 (12), V-2021 (1), VI-2021 (10), VII-2021 (8), VIII-2021 (2). GALA – *Malus domestica* – IX-2020 (3), II-2021 (3), III-2021 (7), IV-2021 (9), V-2021 (3), VI-2021 (17), VII-2021 (7).

Tarsonemus waitei Banks, 1912

Tarsonemus waitei Banks, 1912: 96.

Antônio Prado: EVA – *Malus domestica* – XI-2020 (3), XII-2020 (25), I-2021 (3), III-2021 (2), IV-2021 (5). FUJI – *Malus domestica* – IV-2021 (3), VII-2021 (9), VIII-2021 (1). GALA – *Adiantopsis chlorophylla* – V-2021 (1), *Malus domestica* – XII-2020 (1), I-2021 (1), II-2021 (5), IV-2021 (2), VII-2021 (4), VIII-2021 (3). Muitos Capões: FUJI – *Malus domestica* – IX-2020 (1), XI-2020 (2), XII-2020 (3), IV-2021 (4), VII-2021 (1), VIII-2021 (2), *Scoparia* sp. – IX-2020 (1). GALA – *Malus domestica* – IX-2020 (1), X-2020 (1), XI-2020 (3), XII-2020 (1), II-2021 (4), VI-2021 (2), VIII-2021 (13). São Joaquim: FUJI – *Malus domestica* – IX-2020 (2), IV-2021 (3), VIII-2021 (1). GALA – *Malus domestica* – I-2021 (2), II-2021 (6), III-2021 (2), IV-2021 (3), VII-2021 (3).

Xenotarsonemus sp.1

Muitos Capões: FUJI – *Malus domestica* – IX-2020 (1), VIII-2021 (12).

Xenotarsonemus sp.2

Antônio Prado: EVA – *Vernonanthura tweediana* – III-2021 (1). FUJI – *Talinum paniculatum* – VI-2021 (25). Muitos Capões: FUJI – *Bidens pilosa* – V-2021 (3), *Lolium multiflorum* – XI-2020 (1), *Plantago australis* – IX-2020 (3), VIII-2021 (2), *Trifolium pratense* L. (Fabaceae) – VI-2021 (5), *Vernonanthura tweediana* – IV-2021 (18), V-2021 (2). GALA – *Plantago australis* – V-2021 (43), *Vernonanthura tweediana* – V-2021 (17). São Joaquim: FUJI – *Plantago australis* – II-2021 (2), IV-2021 (2), *Verbena litoralis* – IV-2021 (1), GALA – *Acaena eupatoria* – IV-2021 (1), *Lolium multiflorum* – III-2021 (1).

Xenotarsonemus sp.3

Antônio Prado: EVA – *Elephantopus mollis* – IV-2021 (1). Muitos Capões: GALA – *Plantago australis* – V-2021 (15), *Vernonanthura tweediana* – V-2021 (33).

Xenotarsonemus sp.4

Antônio Prado: EVA – *Elephantopus mollis* – IV-2021 (1), *Plantago australis* – IV-2021 (26), *Vernonanthura tweediana* – IV-2021 (2). GALA – *Plantago australis* – VII-2021 (2). São Joaquim: FUJI – *Acaena eupatoria* – VIII-2021 (1), *Plantago australis* – I-2021 (1), II-2021 (1), VI-2021 (7), *Verbena litoralis* – VII-2021 (2). GALA – *Plantago australis* – IV-2021 (2), V-2021 (1).

Tenuipalpidae

Brevipalpus sp.1

Antônio Prado: EVA – *Malus domestica* – I-2021 (1), III-2021 (2), IV-2021 (1). FUJI – *Malus domestica* – III-2021 (7), V-2021 (2). GALA – *Malus domestica* – XII-2020 (1), I-2021 (1), IV-2021 (4), V-2021 (1), VI-2021 (1). Muitos Capões: FUJI – *Malus domestica* – III-2021 (1). GALA – *Malus domestica* – V-2021 (1).

Brevipalpus sp.2

Antônio Prado: EVA – *Elephantopus mollis* – IV-2021 (1). Muitos Capões: FUJI – *Trifolium repens* – VI-2021 (2). GALA – *Bidens pilosa* – IV-2021 (33).

Tenuipalpus sp.

Antônio Prado: EVA – *Malus domestica* – I-2021 (1).

Tetranychidae

Aponychus mauritianum Ferla & Ferla, 2020

Aponychus mauritianum Ferla et al. 2020: 1069–73.

Muitos Capões: FUJI – *Plantago australis* – VI-2021 (9).

Mononychellus planki (McGregor, 1950)

Tetranychus planki McGregor, 1950: 300.

Antônio Prado: EVA – *Sida rhombifolia* – I-2021 (1).

Panonychus ulmi (Koch, 1836)

Tetranychus ulmi Koch, 1836: 11.

Antônio Prado: EVA – *Malus domestica* – I-2021 (1). FUJI – *Malus domestica* – XI-2020 (2), II-2021 (1), III-2021 (8), IV-2021 (4), V-2021 (3), VI-2021 (1). GALA – *Malus domestica* – III-2021 (8), IV-2021 (11), VI-2021 (2). Muitos Capões: FUJI – *Malus domestica* – XI-2020 (2), XII-2020 (13), I-2021 (33), II-2021 (10), III-2021 (36), IV-2021 (227), V-2021 (143), VI-2021 (42). GALA – *Malus domestica* – IX-2020 (2), X-2020 (1), XI-2020 (5), XII-2020 (11), I-2021 (40), II-2021 (58), III-2021 (11), IV-2021 (30), V-2021 (26), VI-2021 (11), *Trifolium repens* – V-2021 (1). São Joaquim: FUJI – *Malus domestica* – IX-2020 (1), XI-2020 (4), XII-2020 (5), I-2021 (326), II-2021 (2), III-2021 (1), V-2021 (1), VIII-2021 (5). GALA – *Acaena eupatoria* – I-2021 (1), *Malus domestica* – XI-2020 (2), XII-2020 (17), I-2021 (105), II-2021 (2), III-2021 (5), IV-2021 (1), V-2021 (1), VIII-2021 (2).

Tetranychus sp.1

Antônio Prado: EVA – *Chromolaena laevigata* – II-2021 (6), *Elephantopus mollis* – IV-2021 (1). GALA – *Trifolium pratense* – VI-2021 (1). Muitos Capões: FUJI – *Bidens pilosa* – IV-2021 (2).

Tetranychus urticae Koch, 1836

Tetranychus urticae Koch, 1836.

Antônio Prado: EVA – *Malus domestica* – XII-2020 (4), I-2021 (1), III-2021 (1). FUJI – *Malus domestica* – X-2020 (3), XII-2020 (6), I-2021 (3), II-2021 (1). GALA – *Malus domestica* – XII-2020 (1). Muitos Capões: GALA – *Malus domestica* – XII-2020 (1).

Triophtydeidae

Triophtydeus sp.

Antônio Prado: EVA – *Malus domestica* – I-2021 (1). GALA – *Malus domestica* – VIII-2021 (1).

Trombidiidae

Antônio Prado: FUJI – *Lolium multiflorum* – VI-2021 (1).

Tydeidae

Lorryia aberrans (Oudemans, 1932)

Tydeus aberrans Oudemans, 1932: 350.

São Joaquim: FUJI – *Malus domestica* – IX-2020 (2).

Lorrya parvireticuli Mondin, Nuvoloni & Feres, 2016

Lorrya parvireticuli Mondin, Nuvoloni & Feres, 2016: 475.

São Joaquim: FUJI – *Plantago australis* – I-2021 (1).

Pretydeus henriandrei Kaźmierski, 1996

Pretydeus henriandrei Kaźmierski, 1996: 173.

Antônio Prado: FUJI – *Malus domestica* – VIII-2021 (1).

Quasitydeus sp.

Antônio Prado: FUJI – *Malus domestica* – II-2021 (1), III-2021 (1).

Tydeus californicus (Banks, 1904)

Tetranychoides californicus Banks, 1904: 54.

Antônio Prado: EVA – *Baccharis anomala* – I-2021 (2), *Chromolaena laevigata* – II-2021 (1), III-2021 (17), *Malus domestica* – X-2020 (1), XI-2020 (1), I-2021 (23), II-2021 (12), III-2021 (31), IV-2021 (31), V-2021 (5), VII-2021 (1), *Plantago australis* – IV-2021 (2), *Sida rhombifolia* – I-2021 (1), *Vernonanthura tweediana* – X-2020 (1), III-2021 (4). FUJI – *Malus domestica* – IV-2021 (2), V-2021 (1), VI-2021 (2). GALA – *Malus domestica* – II-2021 (1), III-2021 (1), V-2021 (3), VI-2021 (2), VIII-2021 (2).

São Joaquim: FUJI – *Malus domestica* - III-2021 (1), IV-2021 (2), *Plantago australis* – V-2021 (1). GALA – *Malus domestica* – IV-2021 (1).

Tydeus manoi Silva, Rocha & Ferla, 2014

Tydeus manoi Silva et al. 2014: 504–06.

São Joaquim: FUJI – *Acaena eupatoria* – IX-2020 (1), V-2021 (5), VIII-2021 (2), *Plantago australis* – VI-2021 (8). GALA – *Acaena eupatoria* – VI-2021 (5), *Plantago australis* – VI-2021 (4).

Sarcoptiformes

Acaridae

Tyrophagus putrescentiae (Schrank, 1781)

Acarus putrescentiae Schrank, 1781: 552.

Antônio Prado: EVA – *Malus domestica* – IX-2020 (1), X-2020 (1), VII-2021 (5). FUJI – *Lolium multiflorum* – VI-2021 (1), *Malus domestica* – IX-2020 (1). Muitos Capões: FUJI – *Bidens pilosa* - IV-2021 (1), *Lolium multiflorum* – IX-2020 (1), *Malus domestica* – IX-2020 (4), XI-2020 (1), *Plantago australis* – VIII-2021 (1), *Trifolium repens* – X-2020 (2), IV-2021 (3). GALA – *Lolium multiflorum* – X-2020 (2), XII-2020 (3), *Malus domestica* – XI -2020 (1), *Vernonanthura tweediana* – XII -2020 (1). São Joaquim: FUJI – *Lolium multiflorum* – III-2021 (6), *Plantago australis* – I-2021 (1). GALA – *Holcus lanatus* – X-2020 (1), *Lolium multiflorum* – III-2021 (2), *Malus domestica* – VIII-2021 (2), *Plantago australis* – XI-2020 (1).

Histiostomatidae

Histiostoma sp.

São Joaquim: FUJI – *Plantago australis* – V-2021 (2).

Oribatida

Antônio Prado: EVA – *Adiantopsis chlorophylla* – VII-2021 (16), *Baccharis anomala* – I-2021 (2), *Elephantopus mollis* – I-2021 (5), II-2021 (2), III-2021 (17), IV-2021 (10), *Plantago australis* – IV-2021 (8), VIII-2021 (8), *Solanum pseudocapsicum* – IX-2020 (1), *Sida rhombifolia* – I-2021 (2), *Taraxacum officinale* – IX-2020 (2), *Vernonanthura tweediana* – X-2020 (1), XII-2020 (5). FUJI – *Cantinoa mutabilis* – VII-2021 (4), *Elephantopus mollis* – II-2021 (1), III-2021 (18), *Lolium multiflorum* – X-2020 (4), XI-2020 (1), XII-2020 (10), VI-2021 (14), *Plantago australis* – III-2021 (7), IV-2021 (6), VI-2021 (2), *Paspalum dilatatum* – XI-2020 (2), I-2021 (2), *Richardia brasiliensis* – IV-2021 (3), *Steinchisma hians* – V-2021 (3), *Talinum paniculatum* – VI-2021 (43), *Urochloa plantaginea* – V-2021 (1), *Veronica persica* – VIII-2021 (1). GALA – *Adiantopsis chlorophylla* – V-2021 (13), *Euphorbia heterophylla* – III-2021 (1), *Elephantopus mollis* – V-2021 (18), *Hypochaeris* sp. – IX-2020 (1), XII-2020 (1), *Lolium multiflorum* – IX-2020 (1), X-2020 (10), *Plantago australis* – VII-2021 (18), VIII-2021 (3), *Paspalum dilatatum* – III-2021 (2), *Trifolium repens* – I-2021 (3), *Richardia brasiliensis* – IV-2021 (3), *Urochloa plantaginea* – I-2021 (28), *Veronica persica* – VIII-2021 (2). Muitos Capões: FUJI – *Bidens pilosa* – V-2021 (1), *Euphorbia heterophylla* – V-2021 (3), *Lolium multiflorum* – X-2020 (16), *Plantago australis* – IX-2020 (2), XII-2020 (1), II-2021 (2), V-2021 (10), VIII-2021 (1), *Sonchus oleraceus* – I-2021 (1), *Trifolium repens* – X-2020 (1), IV-2021 (12), VI-2021 (1), VII-2021 (5), *Veronica persica* – IX-2020 (2), *Vernonanthura tweediana* – V-2021 (1), IV-2021 (8). GALA – *Euphorbia heterophylla* – I-2021 (2), IV-2021 (1), V-2021 (1), *Lolium multiflorum* – X-2020 (3), *Plantago australis* – X-2020 (2), XII-2020 (1), V-2021 (26), VII-2021 (3), VIII-2021 (3), *Paspalum dilatatum* – IX-2020 (6), II-2021 (3), *V. cracca* – VI-2021 (1), *Vernonanthura tweediana* – II-2021 (1), V-2021 (25). São Joaquim: FUJI – *Acaena eupatoria* – V-2021 (7), VI-2021 (2), *Bromus unioloides* – X-2020 (10), *Holcus lanatus* – X-2020 (9), XII-2020 (1), II-2021 (19), *Lolium multiflorum* – XI-2020 (1), III-2021 (8), *Malus domestica* – IX-2020 (9), X-2020 (1), III-2021 (1), IV-2021 (2), VII-2021 (2), *Plantago australis* – XII-2020 (2), I-2021 (4), II-2021 (10), III-2021 (12), IV-2021 (1), V-2021 (20), VIII-2021 (2), *Raphanus sativus* – IX-2020 (1). GALA – *Acaena eupatoria* – IX-2020 (1), XI-2020 (1), IV-2021 (1), V-2021 (2), *Holcus lanatus* – X-2020 (7), XII-2020 (7), II-2021 (19), *Lolium multiflorum* – IX-2020 (1), X-2020 (5), III-2021 (9), *Malus domestica* – IX-2020 (1), VI-2021 (3), VII-2021 (5), VIII-2021 (1), *Plantago australis* – XI-2020 (9), XII-2020 (1), II-2021 (12), III-2021 (11), IV-2021 (3), V-2021 (5), VII-2021 (3), VIII-2021 (1), *Trifolium repens* – X-2020 (1), XII-2020 (1).

Winterschmitiidae

Czenskinspia transversostriata (Oudemans, 1931)

Donndorffia transversostriata Oudemans, 1931: 203.

Antônio Prado: EVA – *Chromolaena laevigata* – III-2021 (1), *Malus domestica* – IV-2021 (3), *Vernonanthura tweediana* – III-2021 (4), IV-2021 (3). GALA – *Malus domestica* – VI-2021 (1). Muitos Capões: FUJI – *Plantago australis* – II-2021 (1). GALA – *Vernonanthura tweediana* – V-2021 (1). São Joaquim: FUJI – *Malus domestica* – III-2021 (6), V-2021 (2). GALA – *Malus domestica* – IV-2021 (1), V-2021 (3).

Dichotomous key for the identification of the mite fauna associated with apple plants in Brazil

1. Chelicerae stylet shaped, curved blades or toothed chelae. Palp with a thumb-claw complex or simple and with 1-5 segments; Stigma, when present, at the base or between bases of chelicerae, at base of gnathosoma, on the anterior margin of the propodosoma or laterally to coxal region between legs III and IV……2

– Chelicerae ending in toothed chelae; Simple palpus; Opening of the tracheas absent or indistinct……54

2. With stigma laterally, between legs III and IV region……Order Mesostigmata……3

– Stigma, when present, at the base or between bases of chelicerae, at the base of gnathosoma, on the anterior margin of the propodosoma……Order Trombidiforme……26

3. Adults with more than 20 pairs of dorsal shield setae……Ascidae……*Asca*

Adults with less than 20 pairs of dorsal shield setae……Phytoseiidae……4

4. Podonotal region of dorsal shield with 5 or 6 pairs of lateral setae……5

– Podonotal region of dorsal shield with 4 pairs of lateral setae……Amblyseiinae……9

5. Setae *Z1*, *S2*, *S4* and *S5* absent; Setae *r3* usually inserted into the dorsal shield……Phytoseiinae……*Phytoseius guianensis* De Leon

– At least one of the following setae present: *Z1*, *S2*, *S4* or *S5*; Setae *r3* usually inserted into the body cuticle……Subfamily Typhlodrominae……6

6. Setae *R1* absent and *S2* present……*Galendromus* (*G.*) *annectens* (De Leon)

– Setae *R1* present and *S2* usually absent……7

7. Setae long on the margin of dorsal shield; Setae *R1* much smaller than *s6*……*Typhlodromina tropica* (Chant)

– Setae short on the margin of the dorsal shield; Setae *R1* and *s6* with similar length……8

8. Sternal shield with 2 pairs of setae……*Metaseiulus* (*M.*) *camelliae* (Chant & Yoshida-Shaul)

– Sternal shield with 3 pairs of setae……*Metaseiulus* (*M.*) *eiko* (El-Banhawy)

9. Sternal shield with median posterior projection……10

– Sternal shield without median posterior projection……17

10. Chelicerae of normal size and shape, with prominent teeth distributed evenly along the fixed digit; peritreme usually extending to *j1* level……*Typhlodromalus*……11

– Chelicerae reduced in size, with small teeth at the distal tip of the fixed digit; peritreme usually not extending to *j3* level……*Euseius*……13

11 Spermatheca with visible ductus major, swollen bifid atrium and thick cervix……*T. marmoreus* (El-Banhawy)

– Spermatheca not as above……12

12 Setae *z4* at most 20% longer than *z2*……*T. peregrinus* (Muma)

– Setae *z4* about twice longer than *z2*……*T. aripo* De Leon

13. Dorsal shield smooth……14

Dorsal shield reticulated……15

14. Setae *z4* as long or longer than the distance between their bases and bases of setae *z2*……*E. concordis* (Chant)

– Setae *z4* approximately half the distance between their bases and the bases of setae *z2*……*E. mesembrinus* (Dean)

15. Genu III without macroseta……*E. sibelius* (De Leon)

– Genu III with macroseta……16

16. Setae *r3* inserted on unsclerotised cuticle and *R1* on dorsal shield……*E. alatus* De Leon

– Setae *r3* and *R1* inserted on unsclerotised cuticle……*E. inouei* (Ehara & Moraes)

17. Setae *S4* absent……*Phytoseiulus macropilis* (Banks)

– Setae *S4* present……18

18. Proportion of setae size *s4*:*Z1*>3.1……19

– Proportion of setae size *s4*:*Z1*<3.1……23

19. Setae *J2* present or if absent then *j5* also absent……20

Setae *J2* absent and setae *j5* present……*Proprioseiopsis ovatus* (Garman)

20. Sternal shield usually as long as wide; all shields lightly sclerotized……*Amblyseius chiapensis* De Leon

– Sternal shield usually wider than long; all shield heavily sclerotinized……21

21. Leg I with macrosseta……*Iphiseiodes*……22

– Leg I without macrosseta……*Arrenoseius*

22 Ventri-anal shield with 4 pairs of preanal setae……………………………………………… *I. metapodalis* (El-Banhawy)
– Ventri-anal shield with 3 pairs of preanal setae……………………………………………*I. zuluagai* Denmark & Muma
23. Genus of leg II without and of leg III rarely with macrosseta…………………*Neoseiulus*……………………………24
– Genus of leg II and III rarely without macrosseta………………………………………*Typhlodromips mangleae* De Leon
24. Spermathecal calyx about truncate near atrium……………………………………………*N. tunus* (De Leon)
– Spermathecal calyx with rounded end near atrium…………………………………………………………………25
25 Most dorsal setae long, frequently exceeding the bases of nearby setae……………………………………………
………………………………………………………………………………………*N. californicus* (McGregor)
– Most dorsal setae short, not reaching the bases of nearby setae…………………………………… *N. fallacis* (Garman)
26. Adults with two pairs of legs; body vermiform……………………………………………………………………
Eriophyidae………………………………………………………………………*Aculus schlechtendali* (Nalepa)
– Adults with four pairs of legs; body oval to rounded……………………………………………………………27
27. Palpus with thumb-claw complex ……………………………………………………………………………28
– Palpus without thumb-claw complex……………………………………………………………………………36
28. Palp tarsus with comb-like setae……………………………Cheyletidae……………………………*Cheletomorpha*
– Palp tarsus without comb like setae…………………………………………………………………………29
29. With long recurved whip like chelicera……………………………Tetranychidae……………………………30
– With short needle like chelicerae……………………………Stigmaeidae…………………*Agistemus*………………34
30. Empodium with tenent hairs. With prominent projections over rostrum……………………………………………
……………………………………………………………………………………………*Bryobia praetiosa* Koch
– Empodium without tenent hairs. Without prominent projections over rostrum……………………………………31
31. Empodium clawlike. With three pairs of para-anal setae……………………………………*Panonychus ulmi* (Koch)
– Empodium split distally. With two pairs of para-anal setae……………………………*Tetranychus*…………………32
32. Empodia I - II with spur…………………………………………………………………………………………33
– Empodia I - II without spur…………………………………………………………………………*T. urticae* Koch
33. Aedeagus with large knob, posterior and anterior projections pointed, dorsal margin convex………………………
……………………………………………………………………………………………*T. mexicanus* (McGregor)
– Aedeagus head curved hook, with pointed tip………………………………………………………*T. ludeni* Zacher
34. Length of setae *c1* between 45–60µm………………………………………………………*A. floridanus* Gonzalez
– Length of setae *c1* between 60–80µm…………………………………………………………………………35
35. Ratios of setae ve/ve-ve 2.5, e1/e1-e1 1.9, and h1/h1-h1 2.4 ……………………………………………………
A. brasiliensis Matioli, Ueckermann & Oliveira
– Ratios of setae ve/ve-ve 3.7, e1/e1-e1: 2.3, and h1/h1-h1: 2.0……………………………………………………
……………………………………………………………………………………*A. riograndensis* Johann & Ferla
36. Gnatosoma with quadrangular or circular contour; Leg IV slender without pretarsus and claws in females, but, usually with a sessile single claw in males, leg IV with three-segmented in females with femurgenu and tibiotarsus fused, in male with three or four segments with tibia and tarsus usually separate……………………………Tarsonemidae ……………………………… 37
– Gnatosoma with variable contour; Leg IV not like this ……………………………………………………………… 45
37. Metapodosomal venter with 3 or 4 pairs of setae; leg I without pulvillus……………………………………………
………………………………………………………………………………*Polyphagotarsonemus latus* (Banks)
– Metapodosomal venter with 2 pairs of setae; Leg I with pulvillus…………………………………………………38
38. Some of the dorsal idiossomal setae enlarged…………………………*Daidalotarsonemus*……………………39
– Dorsal idiossomal setae not enlarged……………………………………………………………………………40
39 Setae *e* thin (± 3 µm); palp long (± 18 µm)……………………………………*D. esalqi* Rezende, Lofego & Ochoa
– Setae *e* broad (± 17 µm); palp short (± 10 µm)…………………………………*D. savanicus* Rezende, Lofego & Ochoa
40 Gnathosornal palpi markedly elongated………………………………………………………*Rhynchotarsonemus*
– Gnathosornal palpi not markedly elongated……………………………………………………………………41
41 Tegula enlogated……………………………………………………………………………………*Xenotarsonemus*
– Tegula not elongated………………………………………………………………………………………………42
42 Tarsi I-III relatively long………………………………………………………………………*Fungitarsonemus*
– Tarsi I-III normal……………………………………*Tarsonemus*……………………………………………43
43. Setae *sc2* at least 1.5 times longer than the distance between their bases………………………………*T. waitei* Banks
Setae *sc2* about as long as or shorter than distance between their bases……………………………………………44
44. Poststernal apodeme not bifurcated anteriorly at the level of setae *3a* ………………………………………………
……………………………………………………………………………………………*T. merus* Lin & Zhang
Poststernal apodeme bifurcated anteriorly at the level of setae *3a*……………………………………*T. confusus* Ewing

45. Posterior part of opistho dorsum with setae *f1* as a trichobothrium…… Eupodidae……*Benoinyssus*

– Setae *f1* not like this……46

46. Chelicerae fused at base and with movable digit further modified into an elongate stylet…… 47

– Chelicerae not fused at base and capable of moving scissor-like over gnathosoma…… Cunaxidae……*Cunaxoides*

47. Prodorsum without trichobothria……Tenuipalpidae…… 48

Prodorsum with trichobothria……49

48. Setae *h2* elongate, much longer than other dorsal setae……*Tenuipalpus*

– Setae *h2* not elongate, similar in shape and length of other dorsal setae……*Brevipalpus*

49. Adults with 1 pair of genital papillae or papillae absent……Iolinidae……*Pseudopronematulus*

– Adults with 2 pairs of genital papillae……50

50. Leg I with vestigial or no apotele……Triophtydeidae……*Triophtydeu*s

– Leg I with apotele ……Tydeidae……51

51. Up to three seta on genu II……52

– No setae on genu II……*Pretydeus henriandrei* Kaźmierski

52. Femur III with two setae……*Lorryia aberrans* (Oudemans)

– Femur III with no setae……53

53. Femur II with three setae……*Quasitydeus*

– Femur II with two setae ……*Tydeus californicus* (Banks)

54. Prodorsum without specialized sensory organs other than setiform setae; adult idiosoma weakly sclerotized…… Suborder Oribatida, Cohort Astigmatina……55

– Prodorsum usually with a pair of specialized setae arising from sensory pits or bothridia (pseudostigmatic organs); adult idiosoma usually well sclerotized…… Suborder Oribatida (excluding Astigmatina)

55. One pair of short and strong condilophores……Acaridae……*Tyrophagus putrescentiae* (Schrank)

– Condilophores fused into v-shaped sclerites……Winterschmidtiidae …… *Czenspinskia transversostriata* (Oud.)

Discussion

After a long period of absence of studies on mites in apple cultivation (Lorenzato et al. 1986, Ferla & Moraes 1998, Monteiro 2002, Monteiro et al. 2006, 2008), this study presents relevant results on the mite fauna, especially after the recent record of *A. schlechtendali* in culture (Ferla et al. 2018, Nascimento et al. 2020). Understanding the predators and prey species associated with this crop would facilitate management practices, aiming to improve the apple production. In addition, this is also the first study that evaluates the mite fauna in producing organic apple orchards in Brazil.

The data presented here show the mite fauna associated with apple orchards in southern Brazil. The greatest acarine abundance was observed in the municipality of Antônio Prado, possibly because one more orchard was sampled than in the other municipalities. However, it is worth noting that greater diversity was presented in organic orchards, in addition to low populations of phytophagous mites, suggesting that native predatory mites have the capacity to control *P. ulmi* and *A. schlechtendali*, two exotic phytophagous species.

Aculus schlechtendali was the most abundant phytophagous species, suggesting that it is a species with the potential to cause economic damage to the crop. Recent records of the species in the country (Ferla et al. 2018, Nascimento et al. 2020), together with the findings of this study, warn about the possibility of this species reaching the status of a pest in culture. According to a study predicting the potential distribution of *A. schlechtendali*, in addition to the states in the southern region of the country, other areas in the state of São Paulo and possibly in Minas Gerais were shown to be potentially suitable for its occurrence (Corrêa et al. 2021). This species is considered an important pest of apple trees in several countries (Duso et al. 2010), mainly in nurseries and orchards, where it can be found feeding on flowers, fruits and leaves, affecting the plants physiological activity, quality and aesthetics of plants (Easterbrook & Palmer 1996, Walde et al. 1997, Spieser et al. 1998, Duso et al. 2010).

Spontaneous vegetation present in the orchards showed high acarine diversity, with emphasis on predatory species. Thus, it can be stated that the maintenance of spontaneous vegetation in orchards favors the permanence of predators, acting as a refuge and reservoir for these natural enemies (Altieri 1999, 2002, Prischmann & James 2003). Certain plants associated with orchards play an important ecological role as they are hosts of species that help in the biological control of agricultural pests, as they naturally migrate from this spontaneous vegetation to the main crop of the orchard (Tixier et al. 2000, Lykouressis et al. 2008, Ji et al. 2022). These plants can provide shelter and food, such as pollen, for predatory mites, keeping them in these areas even in periods with unfavorable abiotic conditions or when there is a shortage of prey (Landis et al. 2000, Tixier et al. 2000, Demite & Feres 2005), assisting in the colonization of these areas through aerial dispersal (Tixier et al. 2000, Jung & Croft 2001). *Plantago australis* and *V. tweediana* harbored a greater abundance of mites and presented a higher proportion of predators, demonstrating that they are species with the potential to be maintained in orchards. Faoro (2022) cites *Plantago major* L. (Plantaginaceae), plantain, a species of the same genus as the main species found in the orchards of this study, as a plant with the potential to harbor predatory mites and recommends its maintenance in orchards. However, further studies on the potential of these plants as reservoirs of natural enemies of phytophagous mites must be carried out.

Phytoseiidae is an important family for apple cultivation (Monteiro et al. 2008, Silva et al. 2022), this study presented the greatest diversity, with species that may be migrating from spontaneous vegetation to apple trees. This mite family can feed on phytophagous mites and have other alternative food sources, such as pollen, fungi, plant exudate and insects (McMurtry et al. 1970, McMurtry & Rodriguez 1987). The most abundant predator species observed in the orchards evaluated was *N. californicus*, a species that occasionally uses pollen as food (Pascua et al. 2020). In Antônio Prado orchards, maintained under organic management, *N. californicus* was found only on apple plants, however in these orchards there was a greater diversity of predatory mite species. In orchards in the municipalities of Muitos Capões and São Joaquim, under conventional and regenerative management, *N. californicus* was present both in apple trees and in spontaneous vegetation, however, these orchards showed lower diversity of Phytoseiidae. While 13 species of Phytoseiidae were found in Antônio Prado, in São Joaquim there were only five and in Muitos Capões three. As the last two areas use pesticide spraying to control pests, more frequently in conventional than in regenerative areas, it is likely that the low acarine diversity in these areas compared to organic management areas is related to the use of pesticides. According to Maeyer et al. (1992), less intensive agricultural management allows greater conservation of the diversity of natural enemies. The spraying of pesticides is one of the main factors responsible for reducing the diversity of arthropods, especially natural enemies (Kropczyn & Tuovinen 1988, Meyer et al. 2009).

The findings of this study indicate that the different management systems used in orchards influence the occurrence of predatory species, mainly Phytoseiidae, with greater diversity being found in organic orchards. Therefore, to maintain a greater diversity of phytoseiid mites in apple orchards, organic management appears to be the most appropriate to be used. Furthermore, the high acarine diversity, mainly predators, found in the spontaneous vegetation, demonstrated the importance of maintaining these plants in orchards serving as a refuge and reservoir, favoring the permanence of natural enemies in these environments.

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Authors Contributions

Priscila de Andrade Rode: substantial contribution in the concept and design of the study, contribution to data collection, contribution to data analysis and interpretation, and contribution to manuscript preparation.

Júlia Jantsch Ferla: contribution to dichotomous key confection, to critical revision, and adding intellectual content.

Gabriel Lima Bizarro: contribution to data collection, mite identification, to critical revision, and adding intellectual content.

Matheus Schussler: contribution to data collection, and to mite identification.

Noeli Juarez Ferla: substantial contribution in the concept and design of the study, contribution to critical revision, and to adding intellectual content.

Conflicts of Interest

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

Data Availability

Supporting data are available at <https://doi.org/10.48331/scielodata.JBIZS9>.

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Traits of the host trees, not community diversity, drive epiphytes abundance in tropical seasonal forests

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Abstract: Epiphytes are considered indicators of forest ecological integrity, but the factors that explain their abundance are still not well understood. We here evaluated tree colonization by epiphytes in old-growth monospecific reforestation stands of *Astronium urundeuva* (M.Allemão) Engl. (Anacardiaceae) and *Eucalyptus saligna* Sm. (Myrtaceae), in comparison to a neighbor seasonal tropical forest fragment under similar environmental conditions. In each forest type, we identified and measured all trees (planted and colonizers) from 5-cm stem diameter in five 200 m² plots and quantified all vascular epiphytes per tree. Tree species were categorized by bark roughness, canopy deciduousness and growth rate. The abundance of epiphytes and the frequency of host trees were higher in the *A. urundeuva* plantation than in the native forest, with the *E. saligna* stand in an intermediate position. Also, we found that host traits influenced the abundance of epiphytes in their trunks. Host trees had average stem perimeter and height both higher than non-hosts, which indicates that colonization is more likely to occur in older trees. The average abundance of epiphytes per tree was higher in species with rough bark, but no relationship was found with canopy deciduousness or tree growth rate. We evidenced, therefore, that forest plantations, even if monospecific, can provide habitat for epiphytes. However, at community level, colonization success, either in native or restored forest, depends on the relative abundance of species whose bark type favors epiphytes establishment.

Keywords: *Non-Tree Life Forms; Forest Restoration; Tropical Seasonal Forest; Epiphytism; Host Preference.*

Atributos das árvores hospedeiras, e não a diversidade da comunidade, conduzem a abundância de epífitas em florestas tropicais sazonais

Resumo: Epífitas são consideradas indicadores de integridade ecológica em florestas, mas os fatores que explicam sua abundância ainda não são bem compreendidos. Neste estudo, avaliamos a colonização por epífitas em antigos talhões monoespecíficos de *Astronium urundeuva* (M.Allemão) Engl. (Anacardiaceae) e *Eucalyptus saligna* Sm. (Myrtaceae), em comparação com um fragmento vizinho de floresta estacional semidecidual sob condições ambientais semelhantes. Em cada tipologia florestal, identificamos e medimos todas as árvores (plantadas e que colonizaram os locais) a partir de 5 cm de diâmetro à altura padrão, em cinco parcelas de 200 m². Nelas, também quantificamos todas as epífitas vasculares por árvore. Em busca de uma explicação funcional para as diferenças entre espécies, utilizamos rugosidade da casca, deciduidade da copa e taxa de crescimento como atributos potencialmente relevantes. A abundância das epífitas e a frequência de forófitos foi maior no talhão de *A. urundeuva* do que na floresta nativa, com o talhão de *E. saligna* ocupando uma posição intermediária. Encontramos evidências, também, de que os atributos dos forófitos influenciaram a abundância de epífitas em seus troncos. Os forófitos apresentaram maior perímetro médio e altura que as árvores não hospedeiras, o que indica que a colonização é mais provável de ocorrer em árvores mais velhas. A abundância média de epífitas por árvore foi maior em espécies com casca rugosa, mas nem a deciduidade da copa, nem a velocidade de crescimento exerceram efeito neste aspecto. Evidenciamos, portanto que, plantações florestais, ainda que monoespecíficas, podem prover habitat para epífitas. Contudo, em nível de comunidade, o sucesso da colonização, seja em florestas nativas ou restauradas, depende da abundância relativa de espécies cujo tipo de casca favorece o estabelecimento de epífitas.

Palavras-chave: *Formas de Vida Não-Arbóreas; Restauração Florestal; Epifitismo; Preferência de Hospedeiro.*

Introduction

When tropical forests recover from disturbances (either naturally or via active restoration), it is well known that epiphytes are the latest plant group to colonize and re-establish in that ecosystem (Lisboa et al., 1991, Kanowski et al., 2003, Martin et al., 2013, Novais et al., 2020, Parra-Sanchez & Banks-Leite 2020). Intrinsic characteristics of the group, such as slow growth and requirements for specific substrate and humidity in the canopy (Zotz 1995, Hietz 1999), besides dispersal limitations due to low landscape permeability, affect their arrival and establishment (Reid et al., 2016). For these reasons, epiphytes presence may be a good indicator of forest ecosystem health (Hietz 1999) and thus to assess forest restoration success or guiding adaptive management interventions.

Studies have shown low abundance of epiphytes in secondary and restored tropical forests (Suganuma & Durigan 2015, Garcia et al., 2016), and the viability of increasing epiphyte presence in forest ecosystems undergoing restoration has been recently investigated. Different attempts to restore epiphyte community include reintroducing them on planted trees (Duarte & Gandolfi 2017, Domene 2018, Benavides et al., 2023, Sasamori et al., 2023) or stimulating natural colonization by tree planting in different spatial arrangements (Reid et al., 2016). Despite limited evidence of success provided by those studies, re-introduction of these plants in forest restoration projects has been recommended, whenever budget restrictions allow (Duarte & Gandolfi 2017). Little scientific research has been done, however, to evaluate whether spontaneous colonization of planted trees by epiphytes could be enhanced by the selection of a particular group of tree species. Host tree characteristics that favor the colonization and perpetuation of epiphytes might be crucial to assist in planning and decision-making of forest restoration projects, since species' conservation is utterly dependent on environmental recovery (Reid et al., 2016).

Epiphytes are plants which use other plants (phorophytes or hosts) as support in some part of their life cycle, with no soil connection nor using nutrients from the hosts directly (Madison 1977, Kress 1986). Epiphytes form a synusiae whose abundance can be related to microclimatic conditions and successional stage, with higher abundance being expected in wetter habitats and mature forests (Richards 1996, Novais et al., 2020). There is scientific evidence for epiphyte preference for certain species of phorophytes (Kersten 2010, Couto et al., 2022), which indicates a relationship between colonization success and traits of host trees. Bark roughness of the host tree has been considered a relevant trait (Kernan & Fowler 1995, Carlsen 2000, Callaway et al., 2002, Hernandez-Garcia 2021), as it determines water retention capacity, which is important in the epiphyte establishment phase (Kersten 2010). However, a recent review at global scale (Tay et al., 2023) showed that it is not just about bark roughness, with how an epiphyte attaches itself to the substrate being a crucial issue.

In this study, we assessed three distinct types of forests located in similar environmental conditions: one homogeneous forest plantation of an exotic species (*Eucalyptus saligna* Sm., Myrtaceae), another of a Brazilian native species (*Astronium urundeuva* (M.Allemão) Engl., Anacardiaceae), and a native tropical seasonal forest fragment with no evidence of recent disturbance. We aimed at verifying whether epiphyte abundance differs between forest types and between host species as related to their traits. At community level, we expected that epiphyte abundance would be higher in the native forest, given previous studies showing low abundance in monospecific plantations (Hietz 2005; Boelter et al., 2011). Our hypothesis was that tree species diversity permits a higher diversity of organisms that depend on them (Barthlott et al., 2001, Thomsen et al., 2018, Wagner & Zots 2020). To investigate whether the success of epiphyte colonization can be explained by the traits of the host tree, we explored size (height and stem perimeter), growth rate, canopy deciduousness, and bark roughness as predictors of epiphytes' presence and abundance. We expected to find a positive relationship of epiphyte colonization with host tree size (Malizia 2003, Burns & Dawson 2005, Hirata et al., 2008), because it is a proxy for the substrate surface to be colonized. By favouring epiphyte fixation and water retention, bark roughness (Malizia 2003, Wagner et al., 2021) should have a positive effect. Moreover, we expected more epiphytes on slow-growing trees, provided that fast growth could hamper epiphytes' fixation on the stems (Hirata et al., 2008). Because hosts with seasonal deciduous canopy due to seasonal droughts have been reported to have less colonization by epiphytes (Einzmann et al., 2015), we expected that deciduous trees would have lower epiphyte abundance in the studied forests.

Material and Methods

1. *Study site*

The three forest types studied form a continuous patch of about 8 ha, located around the stream of a small tributary of the Paranapanema river, between the municipalities of Assis and Tarumã (São Paulo, Brazil), at an average elevation of 520 meters above sea level (Figure 1). Regional climate is Köppen's Cfa, which is humid subtropical with hot summer (Alvares et al., 2013). The average annual rainfall is 1450 mm, concentrated during summer (December to March), with an average annual temperature of 21.8°C (Durigan & Leitão-Filho 1995). Soil type is a clayish and fertile Haplic Lixisol according to WRB (2006) (Durigan & Leitão-Filho 1995). The original vegetation of the region is Seasonal Semideciduous Forest (IBGE 2012).

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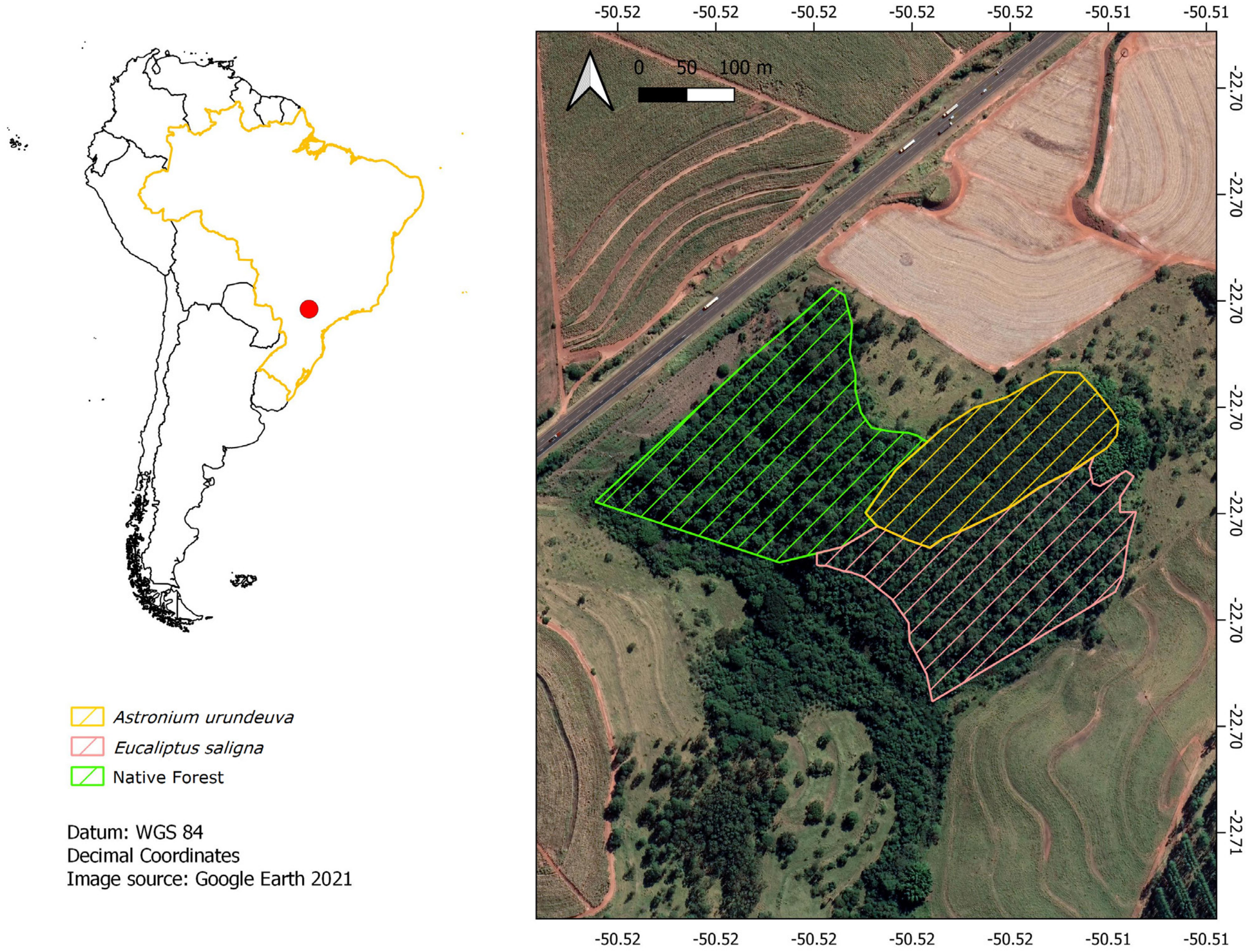

Figure 1. Location of the study site in Brazil, and position of the three forest stands studied, forming a continuous forest fragment, between Assis and Tarumã municipalities.

The forest types assessed were: (i) a monospecific plantation of aroeira (*Astronium urundeuva*), with an area of 2.5 ha (central coordinates 22º42'05"S and 50º30'54"W), with native plants colonizing the understory; (ii) a monospecific plantation of eucalyptus (*Eucalyptus saligna*) with an approximate area of 2.5 ha (central coordinates 22º42'10"S and 50º30'53"W), with abundant regeneration of native plants in its understory; (iii) an old-growth forest remnant, with an area of 3.0 ha (central coordinates 22º42'05"S and 50º31'04"W). *E. saligna* (henceforth *Eucalyptus*) is an exotic species widely cultivated in Brazil. *A. urundeuva* (henceforth *Astronium*), despite native in the seasonal Atlantic Forest (Souza et al., 2019), has not been recorded in the study region (Durigan et al., 2004).

The precise age of the planted stands could not be rescued, but both were planted simultaneously more than 40 years before sampling. No anthropogenic disturbances have been recorded in the native remnant at least for the last 40 years (Figure 2).

2. *Sampling design and data collection*

In each forest type, we sampled five plots of 25 × 8 m (200 m²), 20 m apart from each other, at least 50 m away from the stream margin. In each plot, we identified and measured the stem diameter of all tree individuals with diameter at breast height (DBH) ≥ 5 cm and visually estimated the total height. We measured each stem individually and, to represent tree size in the analyses, we decided to convert the measure of stem diameter into perimeter, summing up them in cases of multi-stemmed trees. Epiphytes rely on bark surface available to be colonized. Therefore, we considered that perimeter would be a more suitable predictor variable to represent substrate surface than the mean diameter, the squared diameter, or the basal area. Should we have used basal area as predictor, for example, we could have risked underestimating available colonizing surface in multi-stemmed trees with similar basal area to single-stemmed trees. Within each forest type we considered all sampled trees as potential hosts, including native species that colonized the understory of the monospecific plantations.

The tree species recorded were functionally classified according to three traits: i) bark roughness (smooth or rough); ii) leaf phenology (deciduous or evergreen), and iii) growth rhythm (fast, moderate, or slow). For bark roughness we used the images from Ramos et al., (2015); for leaf phenology, we consulted Backes and Irgang (2002) and the database from Universidade Estadual do Centro Oeste – Unicentro (https://sites.unicentro.br/wp/manejoflorestal/). To categorize the native species by growth rate, we used data taken from the permanent

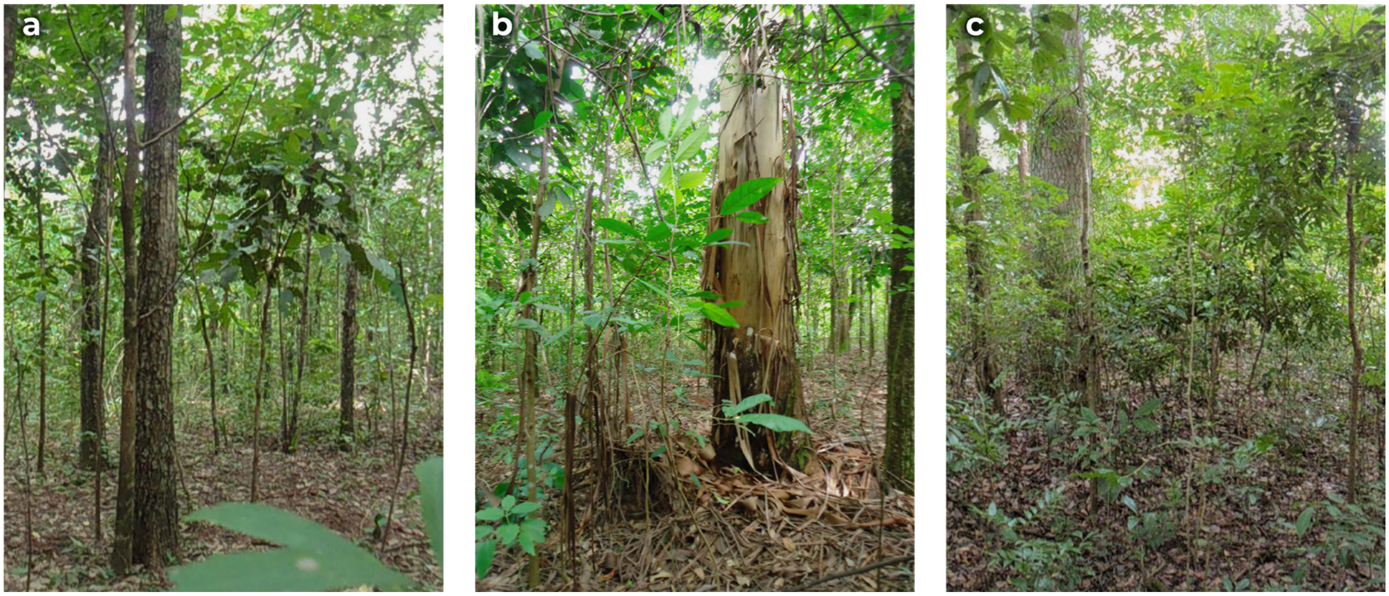

Figure 2. The three forest types studied: (a) Planted stand of aroeira (*Astronium urundeuva*); (b) Planted stand of eucalypt (*Eucalyptus saligna*); (c) Native Forest.

plot network installed since 1992 in the sampled native forest fragment (Giampietro 2005, data available at the BioTime data base Dornelas et al., 2018). For *Eucalyptus* and *Astronium*, we estimated the mean annual increase in diameter from data obtained in the sampling plots and the approximate age of the stands. Based on the distribution of values among species, we established the categories as: slow growth = annual diameter increment <1.5 mm/yr; moderate growth = 1.5–2.5 mm/yr; and fast growth ≥2.5 mm/yr.

For each sampled tree, we recorded the presence or absence of epiphytes to obtain the percentage of host trees in each forest type. In each host tree, we counted all individuals of established vascular epiphytes. To properly separate individual epiphytes growing in clusters, we considered any clearly delimited group as one single individual, following previous studies (Sanford 1968, Wagner & Zots 2020). When analyzing rhizomatous epiphyte species (creeping habit), rhizome interruption was used as criterium to differentiate individuals. Although we aimed at epiphytes abundance and not composition, we roughly categorized the species in taxonomic groups, to provide an overall characterization of the epiphyte community present in the study areas. As in other studies (Wagner et al., 2015), all Pteridophyte species were considered as a single group and the other groups refer to the families recorded.

3. *Data analysis*

For each forest type, we calculated the mean values of basal area, host tree density and epiphyte density per hectare. We calculated the frequency (%) of host trees in relation to the total number of individuals sampled in each plot. To compare these variables among forest types, we used analysis of variance (ANOVA), followed by Tukey test.

To explore the relationships between epiphytes and traits of individual trees, we also performed analysis of variance (ANOVA) followed by Tukey test. Data were log-transformed for specific models to meet normality assumptions and to reduce the influence of outliers, the variables transformed were: tree height, stem perimeter and number of epiphytes per tree. For the models assessing the tree height and stem perimeter (response variables) of host and non-host trees (predictor variable) we performed only the log transformation (Quinn & Keough 2002). For the bark roughness model, we applied log+1 transformation in the response variable number of epiphytes per tree, due to the presence of zero values. To verify whether the abundance of epiphytes was associated with host tree traits, we carried out the analyses of variance (ANOVA) at host species level, to avoid bias due to the large differences in number of host individuals among species. We thus obtained the average number of epiphytes per tree for each host species. We then compared the epiphytes abundance between trait groups as follows: i) slow vs. moderate vs. fast growing, vi) deciduous vs. evergreen, and vii) rough vs. smooth bark.

We checked the assumptions for all models by graphical analyses and performed Levene's test for homogeneity of variance across groups from car package (Fox & Weisberg 2019). All analyses were performed using the R program version 4.1.1 (R Core Team 2021), for the Tukey post-hoc test we used the agricolae package (Mendiburu 2021).

Results

In the whole area sampled, we recorded a total of 469 trees, from 56 species. Out of these, 197 trees (104 planted and 23 native colonizing species) were sampled in the *Astronium* stand, 187 trees (43 planted 25 native colonizing species) in the *Eucalyptus* stand, and 85 trees (31 species) in the native forest. Among the sampled trees, 254 (54%) were hosts, with a total of 3,394 epiphytes counted (see Table 1).

When the forest stands were compared, we found no differences in basal area [Figure 3(a), P = 0.12, with an average of 47.61 m^2 ha^{-1} in the native forest, 35.57 m^2 ha^{-1} in the *Astronium* stand, and 24.70 m^2 ha^{-1} in the *Eucalyptus* stand. However, we found differences in epiphyte occurrence. Frequency [Figure 3(b), P = 0.0123], and density [Figure 3(c), P = 0.0059] of trees with epiphytes were both higher in the *Astronium* stand than in the native forest, not differing from the *Eucalyptus* stand,

Table 1. Tree species, traits, and average number of epiphytes found in all three forest stands.

Species	Growth rhythm of the species	Deciduousness	Bark texture	Average epiphythes/tree	Bromeliaceae	Pteridophyta	Cactaceae	Piperaceae	Orchidaceae	Araceae	Total epiphytes
Aegiphila integrifolia (Jacq.) Moldenke	Fast	Deciduous	Rough	0.0	0	0	0	0	0	0	0
Albizia niopoides (Spruce ex Benth) Burkart	Fast	Deciduous	Smooth	0.0	0	0	0	0	0	0	0
Alchornea glandulosa Poepp. & Endl.	Fast	Evergreen	Smooth	1.8	12	8	0	0	0	0	20
Aloysia virgata Ruiz & Pav.) Juss.	Moderate	Deciduous	Rough	8.0	2	6	0	0	0	0	8
Annona cacans Warm.	Fast	Deciduous	Rough	0.0	0	0	0	0	0	0	0
Annona sylvatica A.St.-Hil.	Fast	Evergreen	Smooth	0.5	0	1	0	0	0	0	1
Aspidosperma polyneuron Müll.Arg.	Moderate	Evergreen	Rough	0.0	0	0	0	0	0	0	0
Astronium graveolens Jacq.	Moderate	Deciduous	Smooth	6.0	0	0	6	0	0	0	6
Astronium urundeuva (M.Allemão) Engl.	Slow	Deciduous	Rough	20.4	1569	537	8	2	1	0	2117
Campomanesia xanthocarpa (Mart.) O.Berg	Slow	Evergreen	Rough	0.5	0	0	0	1	0	0	1
Casearia gossypiosperma Briq.	Fast	Deciduous	Smooth	5.0	25	0	0	0	0	0	25
Casearia sylvestris Sw.	Moderate	Evergreen	Rough	64.0	2	62	0	0	0	0	64
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	Slow	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Colubrina glandulosa Perkins	Moderate	Deciduous	Rough	1.5	0	0	5	1	0	0	6
Cordia superba Cham.	Fast	Deciduous	Rough	3.0	0	0	2	1	0	0	3
Croton floribundus Spreng.	Fast	Evergreen	Smooth	2.0	2	0	0	0	0	0	2
Cupania vernalis Cambess.	Fast	Evergreen	Rough	1.7	1	4	0	0	0	0	5
Cytharexylum myrianthum Cham.	Fast	Deciduous	Rough	7.5	1	29	0	0	0	0	30
Eucalyptus saligna Smith	Fast	Evergreen	Smooth	2.0	80	3	1	0	0	0	84
Eugenia blastanta (O.Berg) D.Legrand	Slow	Evergreen	Rough	3.0	0	0	5	1	0	0	6
Eugenia uniflora L.	Slow	Evergreen	Smooth	3.0	3	0	0	0	0	0	3
Ficus eximia Schott.	Fast	Deciduous	Smooth	3.5	1	4	2	0	0	0	7
Gallesia integrifolia Spreng. Harms	Moderate	Evergreen	Smooth	0.6	0	0	1	2	0	0	3
Guarea guidonia (L.) Sleumer	Fast	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Guarea kunthiana A.Juss.	Moderate	Evergreen	Smooth	3.9	17	86	0	2	0	0	105
Inga vera Willd.	Fast	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Jacaranda micrantha Cham.	Moderate	Deciduous	Rough	4.0	0	4	0	0	0	0	4
Lacistema hasslerianum Chodat	Moderate	Evergreen	Smooth	2.5	3	2	0	0	0	0	5
Machaerium paraguariense Hassl.	Fast	Deciduous	Smooth	2.0	0	0	2	0	0	0	2
Margaritaria nobilis L.f.	Moderate	Deciduous	Smooth	2.0	0	2	0	0	0	0	2

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Species	Growth rhythm of the species	Deciduousness	Bark texture	Average epiphythes/tree	Bromeliaceae	Pteridophyta	Cactaceae	Piperaceae	Orchidaceae	Araceae	Total epiphytes
Metrodorea nigra A.St.-Hil.	Slow	Evergreen	Smooth	0.3	0	1	0	1	0	0	2
Moquiniastrum polymorphum (Less.) G.Sancho	Fast	Evergreen	Rough	11.0	9	13	0	0	0	0	22
Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	Fast	Evergreen	Smooth	1.3	26	0	0	0	0	0	26
Myrsine umbellata Mart.	Moderate	Evergreen	Smooth	5.0	161	17	0	1	0	0	179
Nectandra cuspidata Nees	Fast	Evergreen	Smooth	0.1	2	0	0	0	0	0	2
Nectandra megapotamica (Spreng.) Mez	Fast	Evergreen	Smooth	0.7	0	3	0	1	0	0	4
Nectandra oppositifolia Nees & Mart.	Moderate	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Ocotea diospyrifolia (Meisn.) Mez	Moderate	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Ocotea indecora (Schott) Mez	Moderate	Evergreen	Smooth	1.4	0	12	2	0	0	0	14
Ocotea puberula (Rich.) Nees	Moderate	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Peltophorum dubium (Spreng.) Taub.	Fast	Deciduous	Rough	0.0	0	0	0	0	0	0	0
Picramnia ramiflora Planch.	Slow	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Piptadenia gonoacantha (Mart.) J.F.Macbr.	Fast	Deciduous	Rough	1.0	0	0	0	1	0	0	1
Prockia crucis P.Browne ex L.	Moderate	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Prunus myrtifolia (L.) Urb.	Slow	Evergreen	Smooth	10.0	5	35	0	0	0	0	40
Psidium guajava L.	Slow	Evergreen	Smooth	2.1	19	0	0	0	0	0	19
Sapium glandulosum (L.) Morong	Fast	Deciduous	Smooth	0.0	0	0	0	0	0	0	0
Siparuna guianensis Aubl.	Moderate	Evergreen	Smooth	2.7	19	24	0	0	0	0	43
Sorocea bonplandii (Baill.) W.C.Burger et al.	Slow	Evergreen	Smooth	0.3	0	0	0	1	0	0	1
Syagrus romanzoffiana (Cham.) Glassman	Slow	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Tabernaemontana catharinensis A.DC.	Fast	Deciduous	Smooth	11.3	38	6	0	0	0	1	45
Terminalia glabrescens Mart.	Moderate	Deciduous	Rough	46.0	25	21	0	0	0	0	46
Trichilia catigua A.Juss.	Moderate	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Trichilia clausseni C.DC.	Fast	Deciduous	Smooth	0.7	0	0	0	8	0	0	8
Trichilia pallida Sw.	Moderate	Evergreen	Smooth	6.8	93	326	0	3	0	0	422
Zanthoxylum caribaeum Lam.	Fast	Deciduous	Smooth	5.5	5	6	0	0	0	0	11

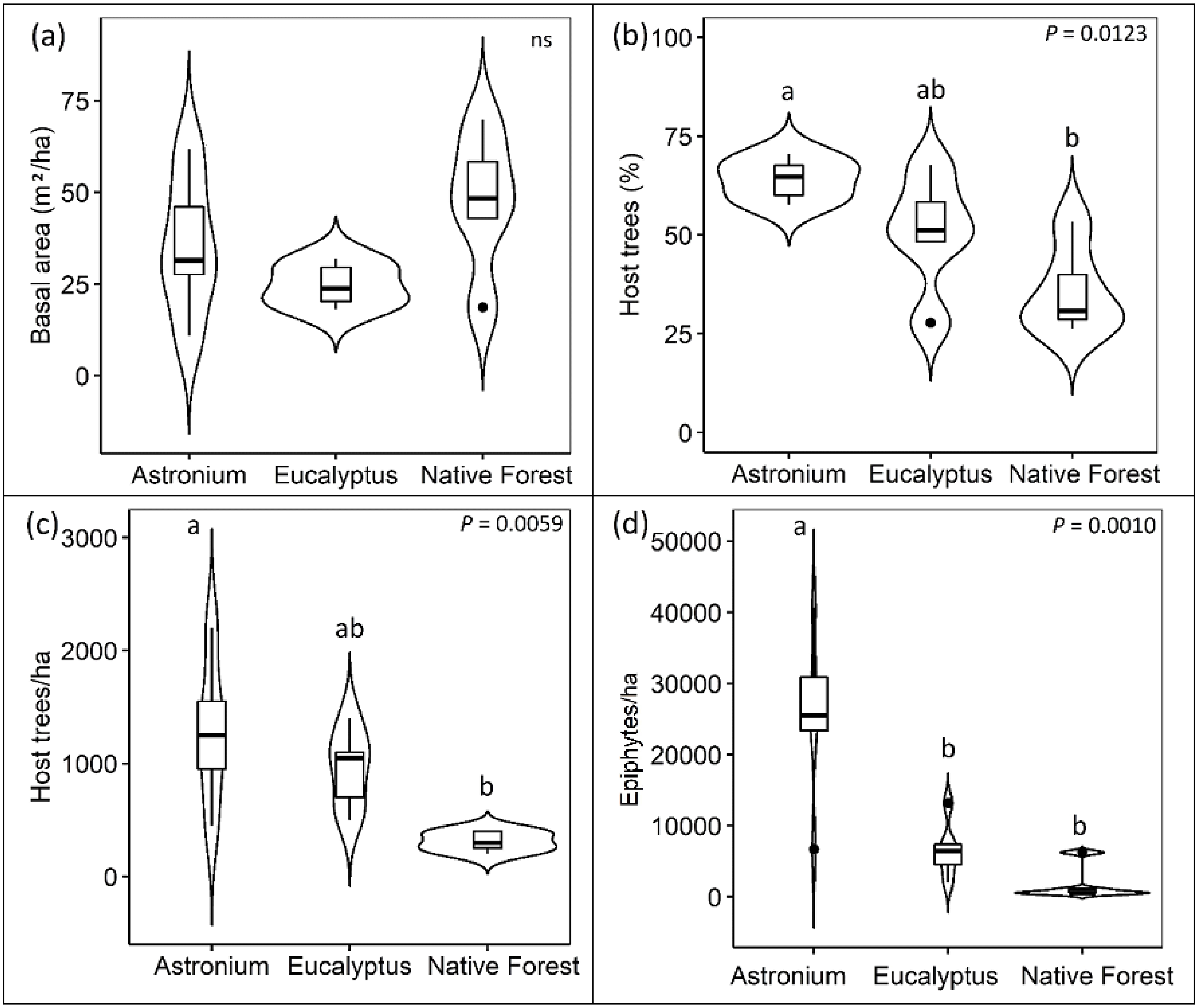

Figure 3. Comparison between forest types (stand of *Astronium urundeuva*, *Eucalyptus saligna* and native forest) based on tree basal area (a), frequency of host trees per hectare (b), density of host trees (c), and epiphyte density (number of epiphytes per hectare) (d). Box plots show median and quartiles from the raw data. Violin plots show the data distribution (density curves). The same letter on top of the shapes indicates the values do not differ by Tukey's test (P values are <0.05; α = 0.05); ns: non-significant differences.

which stayed in an intermediate position. The average abundance of epiphytes per hectare in the *Astronium* stand was higher than in the other two forest types, which did not differ [Figure 3(d), P = 0.0010].

When host and non-host trees were compared (Figure 4), we found significant differences in their size. Average stem perimeter of host trees (51 cm), as a proxy for the substrate area to be colonized, was 46% greater than that of non-host trees (35 cm) [Figure 4(a), P < 0.0001]. Host trees, with average height of 15.2 m, were 50% taller than non-host trees (10.1 m) [Figure 4(b), P < 0.0001].

When we compared the abundance of epiphytes between groups of host species by their traits (Figure 5), we found differences only related to bark roughness. While species with rough bark had an average of 17 epiphytes per tree, those with smooth bark had only 3 epiphytes per tree [Figure 5(a)]. No significant differences were found related to leaf phenology [Figure 5(b), P = 0.67] or growth rhythm [Figure 5(c), P = 1.44] of the host species.

As a rough characterization of the epiphyte community composition, we found, in decreasing order of frequency: Bromeliaceae (in 42% of trees, recorded in all forest types), Pteridophytes (in 34% of trees, in all forest types), Piperaceae (4% of trees, absent in the *Eucalyptus* stand), Cactaceae (3% of trees, all forest types), and, at last, Orchidaceae and Araceae, both recorded only in the *Astronium* stand, each one in a single tree sampled (Table 1).

Discussion

Epiphytes presence has been considered a good indicator of forest ecosystem health worldwide (Benzing 1998, Hietz 1999), but whether

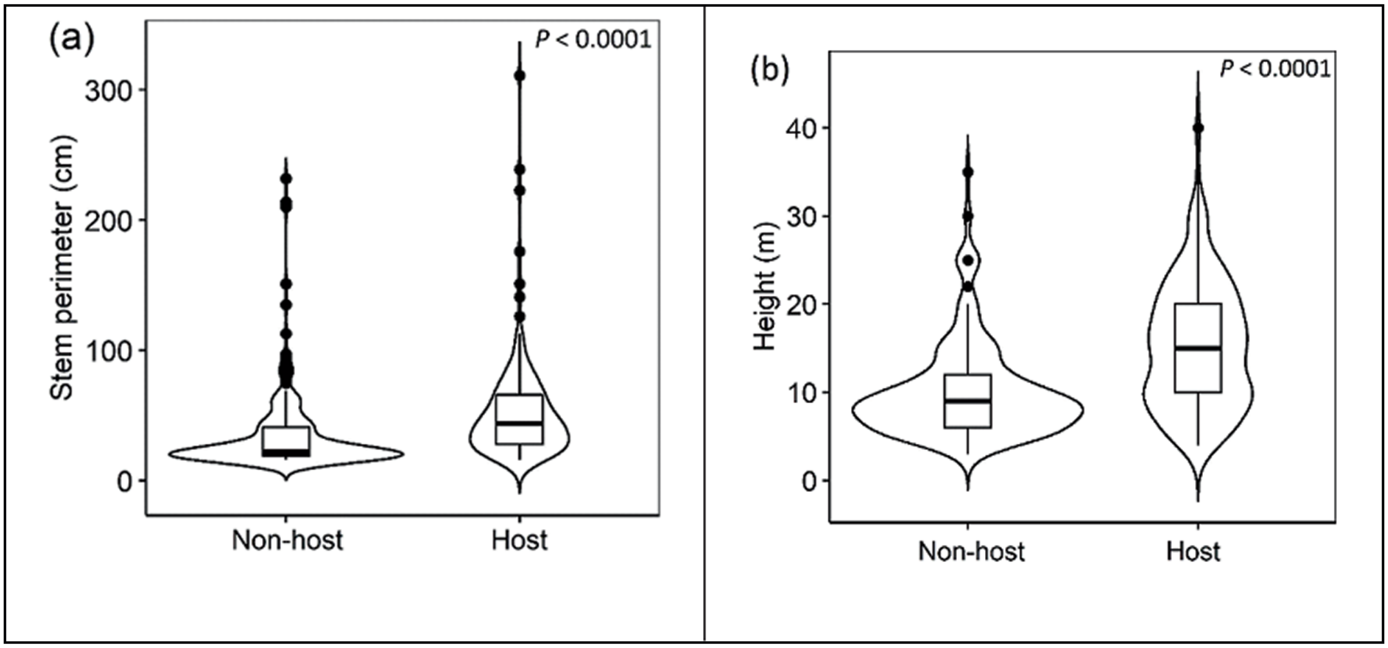

Figure 4. Comparison of tree size between host (n = 254) and non-host (n = 215) trees, by average values of (a) Stem Perimeter, and (b) Tree height. Box plots showing the median and quartiles, combined with violin plots showing the shape of data distribution. Box plots show median and quartiles from the raw data. Violin plots show the data distribution (density curves).

epiphyte abundance depends on the host tree traits, and therefore on community composition, is still controversial (Tay et al., 2023). Besides the importance of this issue for plant community ecology, it has practical implications for the real world, since restoring forests became a global challenge (Verdone & Seidl 2017). By exploring the epiphyte abundance in a native undisturbed forest in comparison with planted forest stands, our study contributes to the debate within the restoration context. The species diversity to be reintroduced has been an issue in forest restoration for a long time, considered by researchers to be essential for the success of restoration (Ruiz-Jaen & Aide 2005, Rodrigues et al., 2009, Rodrigues et al., 2011). From our results we can infer that selecting the tree species matters, because different species provide different contributions in triggering colonization by epiphytes. Planting a high number of tree species, however, may not assure epiphyte abundance, if the species planted do not have the right traits to be a welcoming host.

1. *Can monospecific forest plantations catalyze colonization by epiphytes?*

Several studies have shown that monospecific plantations catalyse colonization by tree species from the regional pool (Parrota et al., 1997, Brockerhoff et al., 2008, Viani et al., 2010, Guerin et al., 2021), partially corroborating the Field of Dreams hypothesis (Palmer et al., 1997, Suganuma & Durigan 2021). However, this issue has not been explored for life forms other than trees. The only known study for the Atlantic Forest region addressing this issue concluded that monospecific plantations do not favor epiphyte colonization, and monospecific plantations with exotic species tend to be even worse as catalysts for epiphyte colonization (Boelter et al., 2011).However, we achieved very different results from those found by the cited author. . Refuting our first hypothesis, we found lower frequency of trees with epiphytes and lower abundance of epiphytes per host tree or per hectare in the native forest remnant compared to *Astronium* plantation (native species). The *Eucalyptus* stand (exotic species) did not differ from the native forest. We therefore concluded that monospecific stands can be as efficient or even more than the diverse native forest in catalysing epiphytes colonization. The low tree diversity of planted stands, which even after 40 years have lower tree species richness than the native forest, did not result in the expected low abundance of epiphytes. We did not assess epiphyte diversity, however, which could have been affected by tree species richness (Barthlott et al., 2001).

2. *Does host tree size matter?*

Our results support the positive correlation between epiphyte abundance and host size, as found by Malizia (2003), Burns & Dawson (2005), (Laube & Zots 2006), Hirata et al., (2008), and Shen et al., (2022). However, other studies have failed to prove this relationship (Bennet 1986; Zimmerman & Olmstead 1992, Vergara-Torres et al., 2010).When comparing the average size between host and non-host trees, we found a large difference, with an advantage for trees with epiphytes both in height (50% larger) and in stem perimeter (46% larger). We used the stem perimeter as the predictor variable because it is more directly correlated to substrate surface than stem diameter or basal area, especially in the cases of multi-stemmed trees. Our result can be explained, therefore, simply by the greater surface available for colonization or by taller trees providing higher light incidence on their trunks (Sillet 1999). However, it can also be indirectly associated with the age of the trees, as larger trees tend to be older within a population, so they had more chances of being colonized, as they were exposed to the colonization process for a longer time. In our study, however, all trees planted within a stand were the same age, restricting this explanation to hosts in the native forest or to those growing in the understory of planted stands, for which differences in size could be related to differences in age.

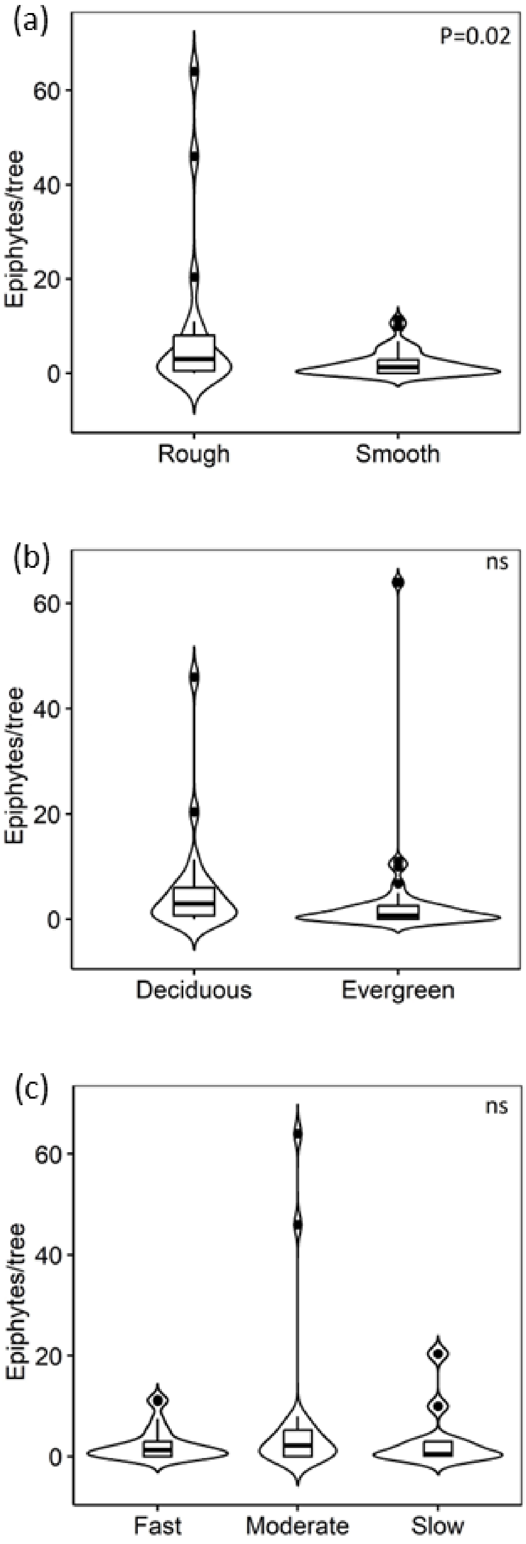

Figure 5. Comparison of epiphytes abundance (average number of epiphytes per tree) between host species, grouped by their traits. (a) Rough (n = 17) vs. Smooth bark (n = 39); (b) Deciduous (n = 21) vs. Evergreen (n = 35); and (c) Fast (n = 25) vs. Moderate (n = 20) vs. Slow growth (n = 11). Box plots show median and quartiles from the raw data. Violin plots show the data distribution (density curves).

3. *Are there traits of the host tree favoring epiphytes colonization?*

Studies have shown the existence of “functional specificity” (Malizia 2003, Wagner et al., 2021, Couto et al., 2022), with certain traits of the host tree species turning them into preferred or limiting hosts (Hernandez-Perez et al., 2018). In studies addressing plant-plant interactions, it is not uncommon that host specificity is not proven at the species level, but that hosts show some functional pattern related to the demands of plants that depend on them (Norton & Carpenter 1998, Campos et al., 2021). Our study supports the existence of traits favoring epiphytes colonization, with bark roughness standing out, as previously demonstrated by Benzing (1990), Malizia (2003), and Wagner et al., (2021). The tridimensional structures in rough bark can give the species a better performance as host (Benzing 1990, Brown 1990, Kersten et al., 2009, Sáyago et al., 2013). Water retention by rough, porous bark favors the anchorage of bromeliad seeds, promoting their survival and protecting them from drought at early stages (Reyes-Garcia et al., 2008, Hietz & Hietz-Seifert 1995, Castro-Hernandez et al., 1999, Wolf & Konings 2001, Winkler et al., 2005, Geraldino et al., 2010). Bark traits, therefore, explain the high abundance of epiphytes in the *Astronium* stand, because this planted species, with its rough bark, corresponds to more than half the trees in the community.

Contrary to our expectations, however, neither tree growth rate nor leaf phenology explained differences in epiphytes abundance among host species. Rasmussem & Rasmussem (2018), in a review about epiphyte habitat, suggested that these plants face the challenge of adapting to a constantly changing environment, so that slow growth could be favorable, but this was also not proven by Hirata et al., (2008). Deciduous canopy is reported to exert a negative influence due to exposing epiphytes to drought conditions in seasonal climates, impairing their establishment and growth (Einzmann et al., 2015). Despite the long dry season in our study sites, deciduousness seemed not to be a relevant trait, since the fully deciduous *A. urundeuva* was among the most favorable host species.

Conclusion

Comparing old monospecific plantations and an old-growth forest in the same landscape, under the same soil and climate conditions, provided us a unique opportunity to investigate the relationship between epiphyte abundance and the tree community diversity and composition, which are, ultimately, driven by the size and traits of individual trees. We concluded that the abundance of epiphytes per tree in the studied forests is primarily determined by the bark traits, with rough bark favoring colonization by epiphytes, supporting the hypothesis of “functional specificity”. Since bark roughness is an evolutionary trait of the species, it is the proportion of species with smooth or rough bark in the community that will determine the abundance of epiphytes in the forest. The attribute is especially advantageous in seasonal forests, where there is water restriction for part of the year. This finding has relevant implications for management interventions or ecological restoration, in cases where restoring epiphyte populations is among the project’s goals. The expected negative influence of deciduousness on epiphyte abundance was not confirmed in our study, although it may occur in other forests under more stressful climatic conditions.

Although we found a positive correlation between tree size and the number of epiphytes, this correlation is likely more related to the age of the phorophyte than to the intrinsic growth rate of the species, because the abundance of epiphytes per host tree did not differ between slow, moderate, or fast-growing species. It is reasonable to expect, therefore, that the abundance of epiphytes within a forest, whether secondary or restored, will increase over time, until it reaches levels compatible with old-growth forests under similar climatic conditions, with higher abundance being expected in wetter habitats.

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Associate Editor

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Author Contributions

Dimitrio Fernandes Schievenin: collected and analyzed the data, and led the writing of the manuscript.

Camila Alonso Santos: collected the data, contributed to the draft and gave final approval for publication.

Karina de Lima: collected the data, contributed to the draft and gave final approval for publication.

Antônio Carlos Galvão de Melo: designed the methodology, contributed to the draft and gave final approval for publication.

Vera Lex Engel: designed the methodology, contributed to the draft and gave final approval for publication.

Giselda Durigan: conceived the idea, designed the methodology, and contributed to the draft and final version of the manuscript.

Conflicts of Interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Data Availability

All data collected and used to base our analysis, and therefore, this study, are available in the Dataverse at https://doi.org/10.48331/scielodata.5E2RBE.

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