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Unveiled diversity: Amazonian Campinaranas harbor twice the number of bryophyte species recorded in the last century

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ABSTRACT

Campinaranas are unique vegetation patches in the Amazonian biome, characterized by white-sand soils with relatively low nutrient content and subject to periodic flooding coupled with fluctuating groundwater levels. This study aimed to produce a synopsis of the bryophyte flora in Campinarana habitats by combining information from the literature with new collections made in the Uatumã Sustainable Development Reserve (Balbina, Central Amazonia), and areas of the middle Uaupés river (São Gabriel da Cachoeira, upper Rio Negro). One hundred and forty-three species were identified among mosses and liverworts, of which 68 are reported for the first time in Campinaranas. The species *Frullania rio-janeirensis*, *Ceratolejeunea filaria*, *Diplasiolejeunea cobrensis* and *Bazzania diversicuspis* are new records for the state of Amazonas. These results reveal high species richness for Campinaranas and indicate the need for continued study in this underexplored Amazonian habitat. This study emphasizes the importance of carrying out floristic inventories in poorly known environments and of further studies with different approaches, such as ecological, phytogeographic and genetic efforts.

Keywords: Amazon, bryophytes, Campinarana, rainforest, tropics

Introduction

Despite appearing homogeneous, Amazonia houses a wide variety of habitats favoring a vast diversity of life forms (Pires & Prance 1985) which is increasingly subject to contemporary threats (Ellwanger *et al.* 2020).

Campinaranas are unique vegetation patches in the Amazonian biome, characterized by white-sand soils with relatively low nutrient content subject to periodic flooding coupled with fluctuating groundwater levels (Reichardt *et al.* 1975; Anderson 1981; Adeney *et al.* 2016).

White-sand ecosystems (including Campinaranas) covers approximately 5 % of the Amazon (Anderson 1981; Adeney *et al.* 2016). In Brazil, Campinaranas form vast areas on the upper Rio Negro and across the state of Roraima, but occur as fragmented patches or vegetation islands surrounded by Terra Firme forest in the Central and Lower Amazonia (Anderson 1981; Adeney *et al.* 2016).

Campinaranas, as opposed to Terra Firme forests, are composed by vegetation with a high degree of sclerophylly, low canopy and low productivity (Coomes & Grubb 1996). Their species composition and distribution patterns have been the focus of several recent ecological studies,

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particularly analyzing the woody component such as trees and shrubs (García-Villacorta *et al.* 2016; Guevara *et al.* 2016), or vascular epiphytes, especially orchids (Braga 1978; Prance 1996; Klein & Piedade 2019). These studies support the idea that Campinaranas harbor a typical assemblage of species related to the peculiarities of these environments. When compared to other vegetation types, they are less diverse but show a relatively high number of endemic, *i.e*. restricted, species. However, bryophytes (avascular plants) have not received the same attention as the other groups, being registered in these environments only in a few specific studies.

The first survey of bryophytes in Amazonian Campinarana was conducted by Lisboa (1976) in an area of Campina (a term used as a synonym for Campinarana) located at the km 62 of the Manaus-Caracaraí road. This author considered the bryophytes, with 34 species, a well-represented group in comparison with the 45 species of woody plants reported by Anderson *et al.* (1975) for the same area. Earlier references of bryophytes in Amazonian Campinarana included only the genus *Sphagnum* (Ducke 1922; Ducke & Black 1954; Egler 1960).

Griffin (1979) presented an annotated list of 147 bryophyte species collected in the greater Manaus region within a radius of 150 km of the capital of Amazonas State. Among the different vegetation types encompassed within his study area, Campinas harbored a bryophyte flora made up of 19 species with wide geographic distribution.

More recently, Sierra *et al.* (2018) presented a list of 150 species from different habitats in the Jaú National Park, Amazonas State, of which 34 occurred in Campinarana as well as other vegetation types, such as Terra Firme (upland) and Igapó forests (seasonally inundated blackwater forests).

Although commonly associated with preserved, humid and shaded places, bryophytes are also found in extreme environments such as deserts, pole regions and alpine elevations (Vittoz *et al.* 2010; Bramley-Alves *et al.* 2014; Smith & Stark 2014). Bryophytes are avascular plants composed of species assemblages sensitive to environmental gradients. It is therefore expected that bryophyte assemblages in Campinaranas should also show specific patterns when compared to those of the relatively well-known Terra Firme forest. However, there is a deep gap in the knowledge that prevents such analysis. Among the 576 species of bryophytes listed for the Amazonia in the records of the repository Flora do Brasil 2020 (BFG 2018), only 15 are reported to occur in Campinaranas. After almost half a century from the first inventories, the number of bryophytes species from Amazonian Campinaranas in BFG (2018) is lower than the number of records provided by the literature, which highlights not only the need for more studies, but also the importance of a synthesis of the knowledge in this ecosystem type.

The fragmented nature of Campinaranas, the small area of their patches, and their susceptibility to anthropic disturbance place this vegetation type as one of the most threatened in the Amazonia (Silveira 2017). The lack of connectivity between these small patches hinders the recovery of locally extinct species (Álvarez-Alonso *et al.* 2013). The increasing threat in Amazonia forest calls attention to the need to protect this fragile ecosystem (Adeney *et al.* 2016).

Vascular plants depend on numerous factors for their establishment, but soil plays a predominant role. Bryophyte distribution, on the other hand, is mainly determined by niche and dispersal potential (Lönnel *et al.* 2012; Mota-de-Oliveira & ter Steege 2015; Barbé *et al.* 2016; Garcia *et al.* 2020). Considering the richness recorded in the surrounding habitats, the low number of bryophyte species currently registered in Campinaranas is possibly a reflection of the lack of studies. In view of the bioindicator potential of these plants and the vulnerability of this type of ecosystem in Amazonia, assessing the bryophyte flora in these environments may contribute to the conservation of this biota.

The term Campinarana is associated with different phytophysiognomies called Campinarana Florestada (forested Campinarana), Campinarana Arborizada (wooded Campinarana), Campinarana Arbustiva (shrubby Campinarana) and Campinarana Gramíneo-lenhosa (grassy-woody Campinarana or Campina) (IBGE 2012).

This study aimed to produce a synopsis of the bryophyte flora in Campinaranas, merging information from the literature and new collections in the Uatumã Sustainable Development Reserve (Balbina, Central Amazonia) and the vicinity of the Uaupés river (São Gabriel da Cachoeira, Upper Rio Negro).

Materials and methods

Literature review

The species list was based on previously published checklists, floristic inventories, ecological studies and taxonomic monographs in Amazonia, from which the information specifically related to species occurring in Campinaranas was filtered (Spruce 1884; Griffin 1975; Lisboa 1976; Reese 1993; Gradstein 1994; Gradstein & Costa 2003; Sierra *et al.* 2018; Pereira 2019). Species specifically occurring in Campinaranas cited in BFG (2018) were also included.

Sampling area

Collections were carried out in two areas: the Uatumã Sustainable Development Reserve (USDR hereafter) and in the vicinity of the Uaupés river in São Gabriel da Cachoeira (SGC hereafter). Both areas are located in the state of Amazonas (Fig. 1).

The USDR is located in the municipalities of Itapiranga and São Sebastião do Uatumã, Central Amazonia, comprising an area of 4,244 km^2 along the Uatumã river basin. The reserve harbors four types of forests: Terra Firme, Várzea and Igapó, and Campinarana (Koury *et al.* 2012). Collections were made in areas of Campinarana Arbustiva, in which herbs and shrubs predominate distributed among low trees up to 7 m tall and a clean and sometimes open understory; Campinarana Arborizada, which is a non-forested formation but with some trees that reach 12 m; and Campinarana Florestada with trees over 20 m high and an understory with the presence of palm trees (Fig. 2). The study area in SGC comprised trails along the Uaupés river, covering approximately 191.1 km of Campinarana Florestada.

Bryophyte collections

In the USDR, collections were performed in the vertical and horizontal gradient of the forest, covering a distance of approximately 2.18 km, including all Campinaranas.

In the vicinity of the Uaupés river in SGC, collections were made along trails in an opportunistic manner, including only the understory and maximizing the number of species sampled. Although canopy samples were not included, bryophytes growing on recently fallen branches were collected.

In the two study areas, all available substrates were explored, namely, living tree trunks, logs, rocks, soil and leaves (Fig. 3). The collection followed the techniques described by Yano (1984) and the specimens were sun dried.

Identification and classification

The identification was based on specialized literature (Yano 1992; Ireland & Buck 1994; He 1999; Ilkiu-Borges 2006; Gradstein *et al.* 2001; Buck 2003; Dauphin 2003; Gradstein & Costa 2003; Ilkiu-Borges & Lisboa 2004; Gradstein & Ilkiu-Borges 2009, 2015; Bastos 2012; Pócs *et al.* 2014; Shi & Zhu 2015; Bastos *et al.* 2016; Gradstein 2016; 2017; Bastos & Zartman 2017; Lima *et al.* 2018; Oliveira-da-Silva & Ilkiu-Borges 2018; Bastos & Gradstein 2020) and/or on the analysis by specialists. The classification system adopted was the one of Crandall-Stotler *et al.* (2009) for Marchantiophyta and Goffinet *et al.* (2009) for Bryophyta, with updates by Carvalho-Silva *et al.* (2017) for Sematophyllaceae and Shi *et al.* (2015) for the genus *Dibrachiella*.

The specimens were classified according to the substrate from which they were collected: corticolous – on barks of

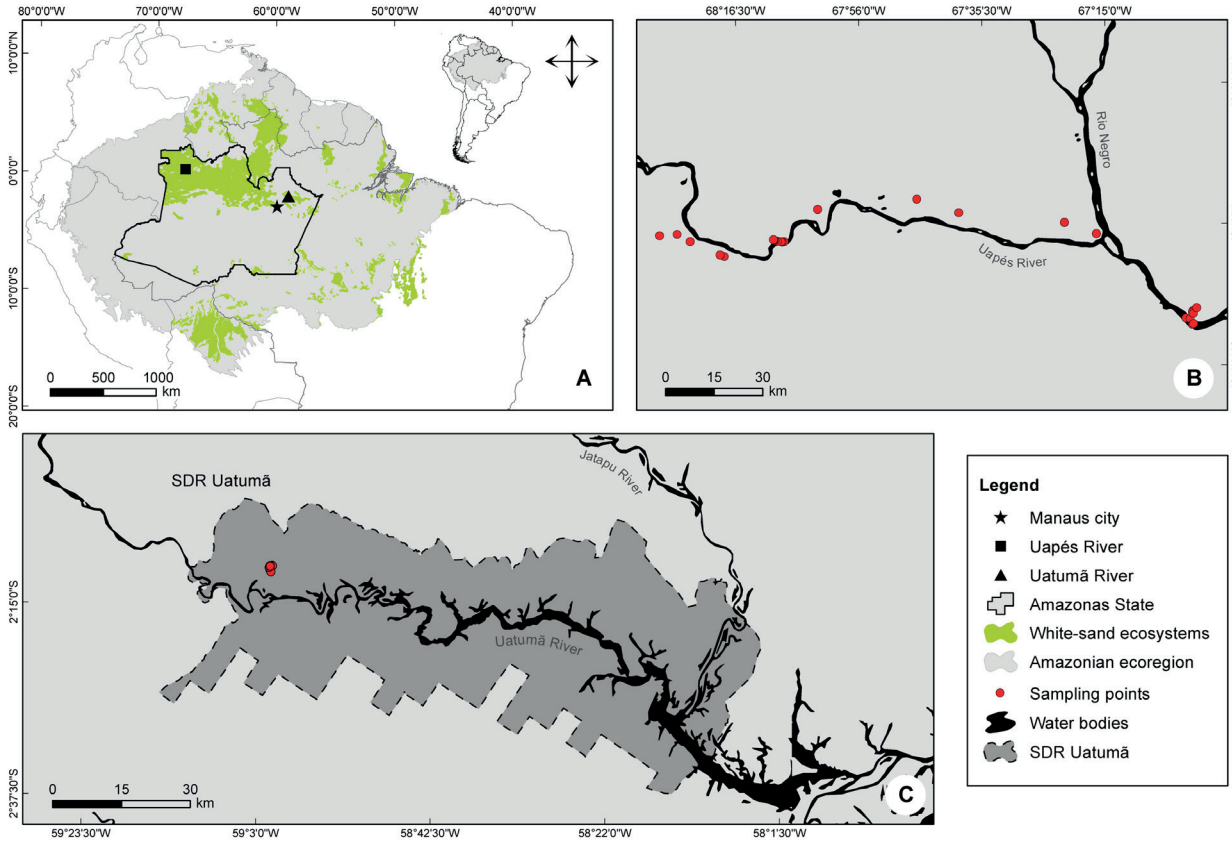

Figure 1. Map of the two study areas. **A.** Location of the two study areas in the Amazonas State and identification of Campinarana; **B.** Collection points along of the Uaupés river, municipality of São Gabriel da Cachoeira; **C.** Collection points in the Uatumã Sustainable Development Reserve, municipality of São Sebastião do Uatumã.

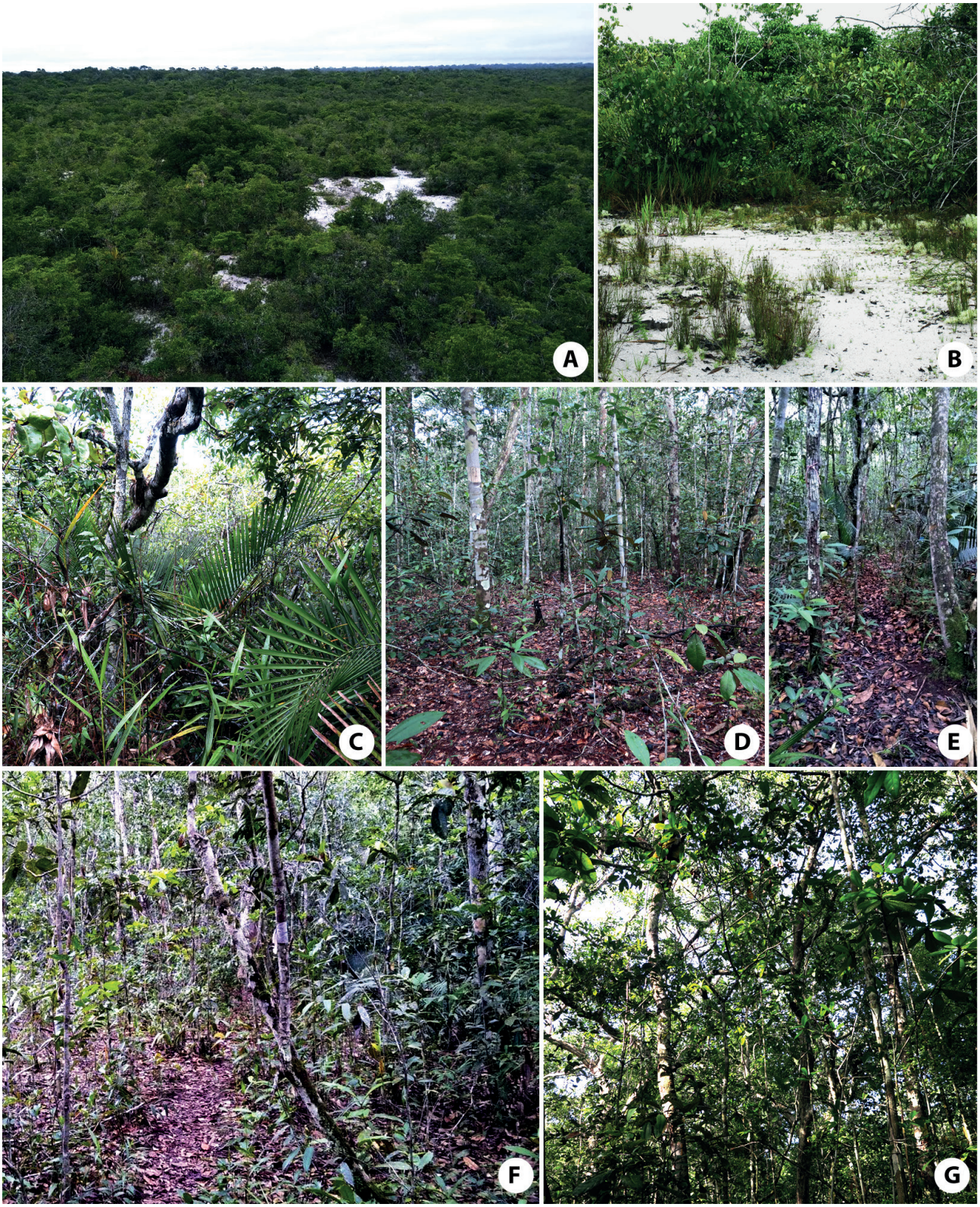

Figure 2. Field images of the collection areas in different physiognomies of Campinarana in the Amazonia. Campinarana arbustiva in aerial (**A**) and understory (**B** and **C**) view. Campinarana arborizada seen from the understory (**D** and **E**) and general (**F**) view. Campinarana florestada in general view (**G**). Photos: Antônio Huxley Melo do Nascimento (**A**) and Charles E. Zartman (**B**-**G**).

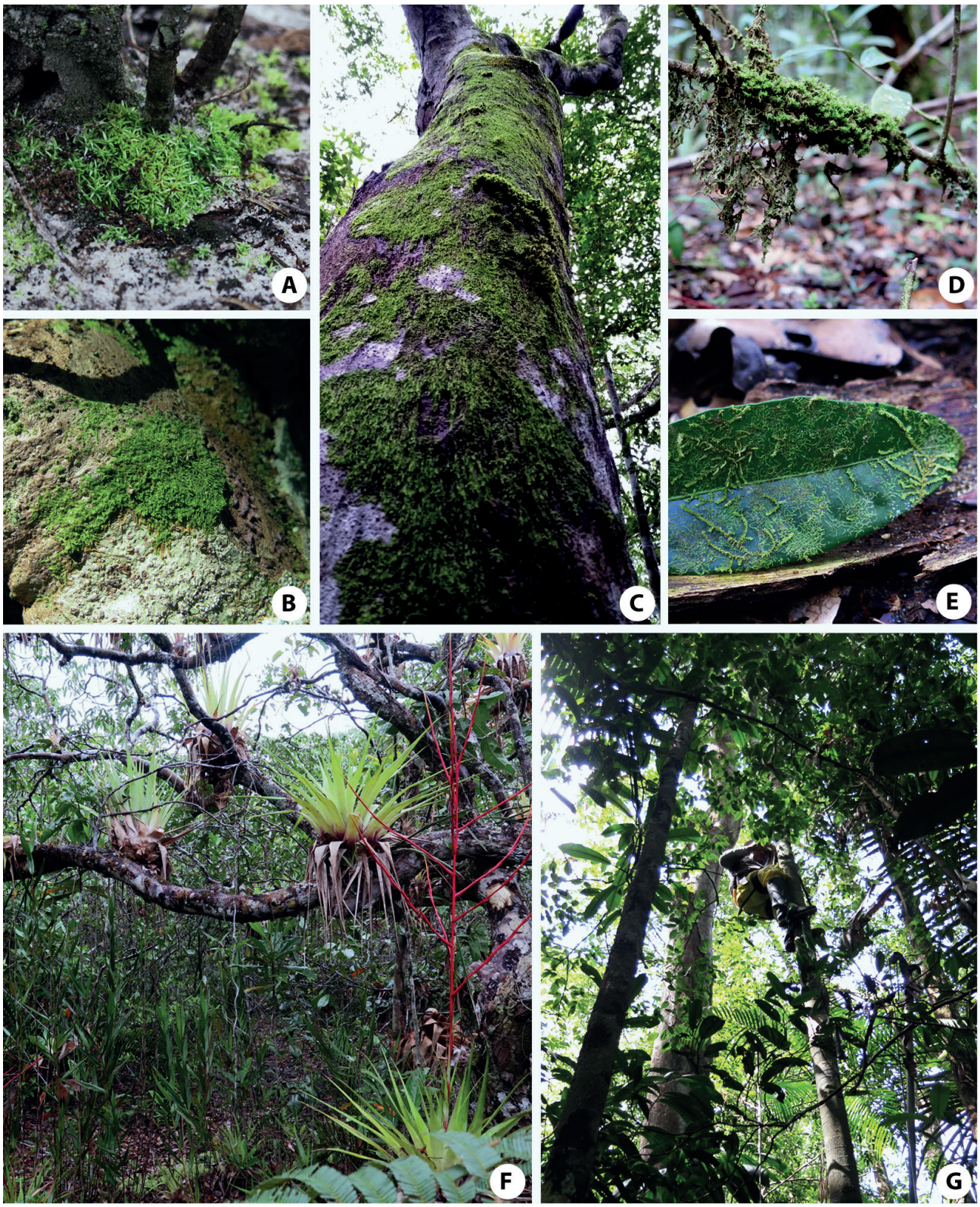

Figure 3. Substrates colonized by bryophytes in the study area. **A.** Soil in Campinarana arbustiva; **B.** Termite mound; **C.** Tree trunk; **D.** Tree branch; **E**. Living leaf; **F.** Understory of a Campinarana arbustiva; **G.** Tree climber collecting samples in the canopy in a Campinarana florestada. All photos by Charles E. Zartman.

living trees; epixylous – on decaying wood; epiphyllous – on leaves; saxicolous – on rocks; and terricolous – on soil (Robbins 1952). As for the world distribution patterns, the species were classified as Pantropical, Neotropical, Afro-american, Amazonia, Amazonia-Guianas, Endemic in Brazil, Holartic regions, Madagascar, S Europe, SW Asia, Tropical South-American, and Trinidad (Fulford 1966; Reese 1993; Gradstein & Costa 2003; Santos & Costa 2010; Gradstein & Uribe 2011; Santos *et al.* 2011; Gradstein 2013; Heirinchs *et al.* 2015; Carmo & Peralta 2016; Pócs 2016; Gradstein 2017; BFG 2018; Pereira 2019).

Exsiccates will be deposited in the INPA herbarium from the Instituto Nacional de Pesquisas da Amazônia.

Results and discussion

Collections from the USDR, margins of the Uaupés river in SGC, and different Amazonian Campinaranas reported by Lisboa (1976), Griffin (1979), Sierra *et al.* (2018) and BFG (2018) resulted in a list of 143 species, of which 68 % are liverworts (97 spp., 42 genera, 10 families) and 32 % mosses (46 spp., 24 genera, 13 families) (Tab. 1).

A total of 116 species were identified in the 1273 specimens collected in Campinaranas of the USDR and SGC, and 68 of them are reported for the first time in this vegetation. *Frullania rio-janeirensis*, *Ceratolejeunea filaria*, *Diplasiolejeunea cobrensis* and *Bazzania diversicuspis* are new records for the state of Amazonas. These results reveal a high richness of species in Campinaranas and indicate the need for systematized sampling effort in this yet unexplored ecosystem.

Of the total of 143 species found in Campinaranas, 46 were recorded during the new collections and in the literature, whereas 20 are found in literature records only. Six species were solely reported by Lisboa (1976), seven by Griffin (1979), six by Sierra *et al.* (2018) and eight were exclusive to the list of BFG (2018). Some species were taxonomically updated, such as *Cheilolejeunea clausa* (cited as *Eusmolejeunea suaveolens* Spruce in Lisboa 1976), *Frullania kunzei* and *Frullania intumescens* (cited as *Frullania neesi* Lindb. and *Frullania montagnei* Gottsche in Griffin 1979, respectively).

In relation to the species registered in BFG (2018) for Amazonian Campinaranas (15 spp.), our list represents an addition of 128 species. In comparison with the current number of species registered by BFG (2018) for Terra Firme forest, the most investigated Amazonian vegetation type, Campinaranas harbor ca. 32 % of the total richness of this environment. An early study on bryophytes in different Amazonian vegetation types in Colombia already indicated that species richness in white sand forests was not much lower than in other environments (Benavides *et al.* 2006). Using comparable sampling effort, the authors registered 32 species in the white-sand areas and 45 species in terra firme forests. According to Adeney *et al.* (2016), Campinaranas patches are usually overlooked because they are embedded in Terra Firme forests and therefore hardly detected in satellite images. Consequently, the number of species that occur in this vegetation type across the Amazon is also likely to be underestimated, especially of plant groups such as bryophytes.

Our results showed Lejeuneaceae as the most species rich family (64 spp.), followed by Calymperaceae (20 spp.), Lepidoziaceae (14 spp.), Sematophyllaceae (6 spp.) and Frullaniaceae (7 spp.) (Fig. 4). Lejeuneaceae is among the largest liverwort families and has a wide distribution, with a range of occurrence from rainforests to open formations, from lowlands to mountain ecosystems (Gradstein 1994; Gradstein *et al.* 2001; Carmo & Peralta 2016; Oliveira-da-Silva & Ilkiu-Borges 2018). Lepidoziaceae is also a widely worldwide distributed family and in Brazil has been reported in the majority of the phytogeographic domains (Amazonia, Caatinga, Cerrado and Atlantic Forest) (Gradstein & Costa 2003; BFG 2018). In turn, Frullaniaceae is a well-represented family in open vegetation types such as restinga, savanna, as well as in the understory and canopy of dense forest (Gradstein & Costa 2003). These liverwort families were expected to occur in our study in view of the many types of Campinarana present in the USDR, varying from a grassy-woody Campinaranas with high luminosity and open understory to shaded forested Campinaranas with a species-rich understory and greater variety of substrates, including living leaves and decaying branches.

Among acrocarpous mosses, Calymperaceae was the most representative family with 20 species and *Syrrhopodon* Schwägr. was the genus with the largest number of species (10 spp.). The same result was recorded by PHM Sobreira (2018 unpubl. res.), who investigated the richness and composition of bryophyte and fern species in Campinarana and Terra Firme forest from two sites in Central Amazonia. Calymperaceae has high ecological and taxonomic importance in the Neotropics. More than half of its species reported to the Neotropics occur in the Brazilian Amazonia, where it is well represented in many of its ecosystems, including Campinaranas (Lisboa 1976; Gradstein *et al.* 2001; Pereira 2019). This family has a high rate of endemism and successfully colonizes different habitats, which is reflected on its high morphological variation (Reese 1993; Pereira 2019).

Corticolous bryophytes predominated in Amazonian Campinaranas. In this study, 116 were found on living tree trunks, 28 on decaying trunks, 18 on living leaves, 28 on rocks, and 26 on soil (Fig. 5). Some species were collected on more than one type of substrate, such as *Calypogeia tenax,* found growing on both decaying logs in SGC and rocks in the Jaú National Park (Sierra *et al.* 2018), and *Ceratolejeunea coarina* collected on both living trunks and living leaves in the USDR. The high colonization of living trunks by bryophytes can be explained by the great availability of

Table 1. List of bryophyte species in the Amazonian Campinarana, with an indication of world distribution, Brazilian phytogeographic domains, substrates, voucher of the collections, and references consulted. AM: Amazonia. CA: Caatinga. CE: Cerrado. AF: Atlantic Forest. PA: Pampa. PN: Pantanal. C: Corticolous. Ep: Epiphyllous. Ex: Epixylic. S: Saxicolous. T: Terricolous. USDR: Uatumã Sustainable Development Reserve. SGC: São Gabriel da Cachoeira. *New occurrence for the state of Amazonas. ** First record in Campinarana in Central Amazonia.

Taxa	World distribution	Phytogeographic domain	Substrate	Voucher collections USDR and SGC	Reference (occurrence in Campinarana)
MARCHANTIOPHYTA (Liverworts)					
Aneuraceae H.Klinggr.					
Riccardia regnellii (Ångstr.) K.G.Hell	Tropical South-American	AM, CE, AF	Ex	Cerqueira 1201	Sierra *et al.* (2018)
Calypogeiaceae Arnell					
Calypogeia tenax (Spruce) Steph.	Amazonian	AM	Ex, T	Sierra 5018	Sierra *et al.* (2018)
Mnioloma parallelogramum (Spruce) R.M.Schust.	Amazonian	AM, AF	Ex, S, T	Sierra 4851	Sierra *et al.* (2018)
***M. caespitosa* (Spruce) R.M.Schust.**	Tropical South-American	AM	C	Cerqueira 943	-
Cephaloziaceae Mig.					
Odontoschisma brasiliense Steph.	Endemic to Brazil	AM, AF	C, Ex, S	-	Griffin (1979)
O. variabile (Lindenb. & Gottsche) Trevis.	Afro-American (also in S Europe and SW Asia)	AM, CE, AF	C, Ex	Cerqueira 839, 845	Griffin (1979) Sierra *et al.* (2018)
Frullaniaceae Lorch.					
Frullania caulisequa (Nees) Mont.	Neotropical	AM, CA, CE, AF, PA	C	Cerqueira 929	Sierra *et al.* (2018)
***F. exilis* Taylor**	Neotropical	AM, CE, AF	C	Cerqueira 874, 899	-
F. gibbosa Nees	Neotropical	AM, CA, CE, AF, PN	C, S	-	Griffin (1979)
F. intumescens (Lehm. & Lindenb.) Lehm. & Lindenb.	Neotropical	AM, AF	C	-	Griffin (1979)
F. kunzei (Lehm. & Lindenb.) Lehm. & Lindenb.	Neotropical	AM, CE, AF, PN	C	Cerqueira 934	Griffin (1979)
F. nodulosa (Reinw. *et al.*) Nees	Pantropical	AM, AF	C, Ex, T	Cerqueira 901	Lisboa (1976) Griffin (1979)
F. rio-janeirensis* (Raddi) Ångstr.	Pantropical	AM, CE, AF, PN	C	Sierra 5081	-
Lejeuneaceae Cas. -Gil					
Acrolejeunea torulosa (Lehm. & Lindenb.) Schiffn.	Neotropical	AM, CE, AF, PN	C	Cerqueira 841 Sierra 5036	Lisboa (1976) Sierra *et al.* (2018)
Archilejeunea badia (Spruce) Steph.	Amazonian	AM, AF	C	Sierra 4830	Sierra *et al.* (2018)
A. crispistipula (Spruce) Steph.	Amazonian (and Guyana)	AM	C	Cerqueira 839	Sierra *et al.* (2018) BFG (2018)
A. juliformis (Nees) Gradst.	Amazonian endemic	AM, AF	C	Cerqueira 934	Sierra *et al.* (2018)
***A. ludoviciana* (Lehm.) P.Geissler & Gradst.**	Neotropical	AM	C	Sierra 4650	-
***Caudalejeunea lehmanniana* (Gottsche) A.Evans**	Afro-American	AM, CE, AF, PA	C	Cerqueira 981,994 Sierra 4877	-
Ceratolejeunea coarina (Gottsche) Schiffn.	Afro-American	AM, CE, AF	C, Ep	Cerqueira 847	Sierra *et al.* (2018)
***C. confusa* R.M.Schust.**	Neotropical	AM, AF	C	Cerqueira 855, 905	
C. cornuta (Lindenb.) Steph.	Afro-American	AM, AF	C, Ex, Ep, S	Cerqueira 919, 937	Lisboa (1976)
C. cubensis (Mont.) Schiffn.	Neotropical	AM, AF	C, Ex	Cerqueira 842	Sierra *et al.* (2018)
***C. desciscens* (Sande Lac.) Schiffn.**	Amazonian (and Guyanas)	AM	C	Cerqueira 878 Sierra 5038	-
C. filaria* (Lehm.) Steph.	Neotropical	AM, AF	C	Zartman 10192	-
C. rubiginosa Steph.	Neotropical	AM, AF	C, Ep, Ex	-	Sierra *et al.* (2018)
***Cheilolejeunea acutangula* (Nees) Grolle**	Neotropical	AM, CE, AF	C, Ex	Cerqueira 860	-

Table 1. Cont.

Taxa	World distribution	Phytogeographic domain	Substrate	Voucher collections USDR and SGC	Reference (occurrence in Campinarana)
**C. adnata* (Lehm.) Grolle	Neotropical	AM, AF, PN	C	Cerqueira 844	-
C. aneogyna (Spruce) A.Evans	Amazonia-Guianas	AM, AF	C	Cerqueira 842	Sierra *et al.* (2018)
C. asperifolia (Spruce) Gradst. & Ilk.-Borg.	Amazonian	AM	C	Cerqueira 915; Sierra 4665	Sierra *et al.* (2018)
C. clausa (Nees & Mont.) R.M.Schust.	Neotropical	AM, CE, AF, PN	C, Ex, S, T	-	Lisboa (1976)
**C. fragrantissima* (Spruce) R.M.Schust.	South-American	AM	C	Sierra 4821	-
C. neblinensis Ilk.-Borg. & Gradst.	Amazonian (and Bahia)	AM	C	Cerqueira 839; Sierra 4649	Sierra *et al.* (2018)
**C. oncophylla* (Ångstr.) Grolle & M.E.Reiner	Neotropical	AM, AF	C	Sierra 4827	-
**C. papulosa* Schiffn.	Amazonian	AM	C	Cerqueira 914; Sierra 4651	-
C. rigidula (Mont.) R.M.Schust.	Afro-American	AM, CA, CE, AF, PN	C, Ep	Cerqueira 919	Sierra *et al.* (2018)
**C. trifaria* (Reinw. *et al.*) Mizut.	Pantropical	AM, CE, AF, PN	C	Zartman 10205	-
**Cololejeunea appressa* (A.Evans) Benedix	Pantropical	AM	Ep	Sierra 5027	-
**C. camillii* (Lehm.) A.Evans	Neotropical	AM, AF	Ep	Sierra 4834	-
**C. obliqua* (Nees & Mont.) Schiffn.	Pantropical	AM, AF	C	Sierra 5033	-
**C. surinamensis* Tixier	South-American	AM, CE, AF	Ep	Sierra 5016	-
**Colura tortifolia* (Nees & Mont.) Trevis.	Neotropical	AM, AF	C, Ep	Sierra 5033	
**Cyclolejeunea convexistipa* (Lehm. & Lindenb.) A.Evans	Neotropical	AM, AF	C, Ep	Cerqueira 1045, 1046	-
**C. luteola* (Spruce) Grolle	Neotropical	AM, CE, AF	C, Ex, S	Sierra 4805	-
**C. peruviana* (Lehm. & Lindenb.) A.Evans	Neotropical	AM, AF	C, Ep	Zartman 10206	-
**Dibrachiella parviflora* (Nees) X.Q.Shi, R.L.Zhu & Gradst.	Neotropical	AM, AF	C	Cerqueira 847	-
**Diplasiolejeunea brunnea* Steph.	Neotropical	AM, CE, AF	C	Cerqueira 846; Zartman 10203	-
**D. buckii* Grolle	Amazonian	AM	C	Cerqueira 906, 909	-
**D. cobrensis* Steph.	Neotropical	AM, CE, AF	C	Cerqueira 901, 903	-
Drepanolejeunea palmifolia (Nees) Schiffn.	Amazonian	AM, CE, AF, PN	C, Ep	Sierra 4821 Zartman 10198	Sierra *et al.* (2018)
**D. polyrhiza* (Nees) Grolle & R.-L. Zhu	Amazonian (and Guyanas)	AM	Ep	Sierra 5066	-
**Lejeunea cerina* (Lehm. & Lindenb.) Lehm. & Lindenb.	Neotropical	AM, AF	C	Zartman 10217	-
**L. flava* (Sw.) Nees	Pantropical	AM, CA, CE, AF, PA, PN	C	Sierra 4877	-
**L. immersa* Spruce	Amazonian (and Bahia)	AM, AF	C	Sierra 4655	-
**L. reflexistipula* (Lehm. & Lindenb.) Spruce	Neotropical	AM, CE, AF	C	Sierra 4836	-
**Lepidolejeunea involuta* (Gottsche) Grolle	Neotropical	AM, AF	C, Ep, S, T	Sierra 4833	-
**Leptolejeunea elliptica* (Lehm. & Lindenb.) Besch.	Neotropical	AM, CA, CE, AF	C	Cerqueira 846	-
**L. moniliata* Steph.	Amazonian (and Guyanas)	AM, AF	Ep	Sierra 5066, 5070, 5071	-
**Lopholejeunea subfusca* (Nees) Schiffn.	Pantropical	AM, AF, CA, CE, PN	C	Cerqueira 938	-
L. eulopha (Taylor) Schiffn.	Pantropical	AM	C	Cerqueira 1200	BFG (2018)
Macrocolura sagittistipula (Spruce) R.M.Schust.	Neotropical	AM	C	Sierra 4820	BFG (2018)
**Microlejeunea bullata* (Taylor) Steph.	Neotropical	AM, CA, CE, AF, PA, PN	C	Sierra 4820	-
**Neurolejeunea seminervis* (Spruce) Schiffn.	Neotropical	AM	C	Sierra 4845	-

Table 1. Cont.

Taxa	World distribution	Phytogeographic domain	Substrate	Voucher collections USDR and SGC	Reference (occurrence in Campinarana)
Odontolejeunea lunulata (F.Weber) Schiffn.	Pantropical	AM, CE, AF	C, Ep	Zartman 10206	Lisboa (1976)
Pictolejeunea sprucei Grolle	Amazonian	AM, AF	Ex, S	Sierra 4864	Sierra et al. (2018)
**Prionolejeunea denticulata* (F.Weber) Schiffn.	Neotropical	AM, AF	C	Sierra 4827	-
**Pycnolejeunea contigua* (Nees) Grolle	Pantropical	AM, AF	C	Cerqueira 876, 904 Sierra 4657	-
P. macroloba (Nees & Mont.) Schiffn.	Neotropical	AM, AF	C, Ex	Cerqueira 856, 908 Sierra 4780	Lisboa (1976) Sierra *et al.* (2018)
**P. remotistipula* C.J.Bastos & Zartman	Amazonian	AM	C	Cerqueira 860, 867,910	-
Schiffneriolejeunea amazonica Gradst.	Amazonian	AM	C	Cerqueira 918,939	BFG (2018)
**Symbiezidium barbiflorum* (Lindenb. & Gottsche) A.Evans	Afro-american	AM, AF	C	Cerqueira 1202, 1203	-
**S. transversale* (Sw.) Trevis.	Neotropical	AM, AF	C, Ex	Sierra 5027	-
Thysananthus amazonicus (Spruce) Schiffn.	Neotropical	AM, CE, AF	C, Ex	Cerqueira 841, 912	Lisboa (1976)
**Verdoornianthus marsupiifolius* (Spruce) Gradst.	Amazonian	AM	C	Cerqueira 874, 877	-
**V. griffinii* Gradst.	Amazonian (and French Guyana)	AM, AF	C, Ep	Cerqueira 910, 916	-
Vitalianthus aphanellus (Spruce) Bechteler, G.E.Lee, Schäf.-Verw. & Heinrichs	Tropical South American	AM, AF	C	Sierra 5064	Sierra *et al.* (2018)
Xylolejeunea crenata (Nees & Mont.) X.-L.He & Grolle	Neotropical	AM, AF	Ex, S	Cerqueira 1047 Sierra 4818	Sierra *et al.* (2018) BFG (2018)
Lepidoziaceae Limpr.					
**Bazzania diversicuspis* Spruce	Tropical South American (and Trinidad)	AM	C	Cerqueira 854, 857	-
B. hookeri (Lindenb.) Trevis.	Neotropical	AM, AF	C	Cerqueira 842	Sierra et al. (2018)
B. longistipula (Lindenb.) Trevis.	Neotropical	AM, AF	C	-	Sierra *et al.* (2018)
B. pallidevirens (Steph.) Fulford	Tropical South American	AM, CE, AF	C, Ex	-	Lisboa (1976) Sierra *et al.* (2018)
Micropterygium leiophyllum Spruce	Amazonian (+ Costa Rica)	AM, CE, AF	C, S, T	Sierra 5035	Sierra *et al.* (2018)
**M. parvistipulum* Spruce	Amazonian-Guianas	AM	T	Zartman 10194	-
**M. pterygophyllum* (Nees) Trevis.	Amazonian	AM, CE, AF	C, Ex, S, T	Zartman 10198	-
M. trachyphyllum Reimers	Neotropical	AM, CE, AF	C, Ex, S, T	Cerqueira 863	Lisboa (1976) Sierra *et al.* (2018)
Monodactylopsis monodactyla (Spruce) R.M.Schust.	Neotropical	AM, AF	T	-	Sierra *et al.* (2018)
**Pteropsiella frondiformis* Spruce	Amazonian	AM	T	Sierra 4814	-
P. metzgeriiformis R.M.Schust.	South-American	AM, AF	T	Sierra 4781	Lisboa (1976)
Telaranea nematodes (Gottsche ex Austin) M.A.Howe	Afro-American	AM, CE, AF	T	-	Lisboa (1976)
**T. pecten* (Spruce) J.J.Engel & G.L.Merr.	Amazonian (and Guyanas and West Indies)	AM	T	Sierra 4870	-
Zoopsidella integrifolia (Spruce) R.M.Schust.	Neotropical	AM, CE, AF	T	Sierra 4825	Sierra *et al.* (2018)
Pallaviciniaceae Mig.					
Symphyogyna brasiliensis (Nees) Nees & Mont.	Afro-American	AM, CE, AF	Ex, S, T	-	Sierra *et al.* (2018)
Plagiochilaceae (Joerg.) K. Müll.					

Table 1. Cont.

Taxa	World distribution	Phytogeographic domain	Substrate	Voucher collections USDR and SGC	Reference (occurrence in Campinarana)
Plagiochila disticha (Lehm. & Lindenb.) Lindenb.	Neotropical	AM, CA, CE, AF PN	C, S	Sierra 4838	Sierra *et al.* (2018)
P. montagnei Nees	Neotropical	AM, AF	C, S	-	Lisboa (1976) Sierra *et al.* (2018)
Radulaceae K. Müll.					
***Radula flaccida* Lindenb. & Gottsche	Afro-American	AM, AF	C, Ep	Cerqueira 1204	-
***R. javanica* Gottsche	Pantropical	AM, CE, AF, PN	C	Zartman 10211	-
Ricciaceae L.					
Riccia vitalii Jovet-Ast	Neotropical	AM, CA, CE, AF, PA, PN	S, T	-	BFG (2018)
BRYOPHYTA (Mosses)					
Calymperaceae Kindb.					
***Calymperes bartramii* W.D.Reese	South-American	AM	C	Zartman 10215	-
***C. mitrafugax* Florsch.	South-American	AM	C	Cerqueira 949	-
***C. nicaraguense* Renauld & Cardot	Neotropical	AM, AF	C	Cerqueira 1205	-
Octoblepharum albidum Hedw.	Pantropical	AM, CA, CE, AF, PA, PN	C	Cerqueira 982	Griffin (1979) BFG (2018)
O. ampullaceum Mitt.	South-American	AM	-	-	Griffin (1979)
O. cocuiense Mitt.	Neotropical	AM, CE, AF	C, Ex	Cerqueira 839 Sierra 4785	Griffin (1979)
O. cylindricum Mont.	Neotropical	AM, CA, CE, AF	C, Ex, T	Cerqueira 911	Lisboa (1976) Griffin (1979)
O. leucobryoides O.Yano	Endemic to Brazil	AM, AF	C, T, S	Cerqueira 1206	Sierra *et al.* (2018)
O. pulvinatum (Dozy & Molk.) Mitt.	Neotropical	AM, CA, CE, AF, PN	C, T	Cerqueira 1207	Lisboa (1976) Griffin (1979)
O. stramineum Mitt.	Neotropical	AM	C, T	Cerqueira 893 Sierra 4666	Lisboa (1976) Griffin (1979)
Syrrhopodon annotinus W.D.Reese & D.G.Griffin	Amazonian	AM	C	Sierra 4662	Sierra *et al.* (2018)
***S. cryptocarpus* Dozy & Molk.	Neotropical	AM, AF	C	Cerqueira 846	-
S. fimbriatus Mitt.	South-American	AM	C	-	Lisboa (1976)
***S. flexifolius* Mitt.	Neotropical	AM	C	Cerqueira 1208	-
S. helicophyllus Mitt.	South-American	AM, AF	C	Cerqueira 866 Sierra 4653	Lisboa (1976)
***S. hornschuchii* Mart.	South-American	AM, AF	C	Sierra 4811	-
***S. leprieurii* Mont.	Neotropical	AM, AF	C	Cerqueira 845	-
S. parasiticus (Brid.) Besch.	Pantropical	AM, CE, AF, PN	C	-	Lisboa (1976)
S. simmondsii Steere	Neotropical	AM	C	Cerqueira 839 Sierra 4864	Sierra *et al.* (2018)
S. xanthophyllus Mitt.	Neotropical	AM	C	Sierra 4861	Sierra *et al.* (2018)
Hypnaceae Schimp.					
***Phyllodon truncatulus* (Müll. Hal.) W.R.Buck	Neotropical	AM, CE, AF	C	Sierra 4819	-
Hookeriaceae Schimp.					
***Crossomitrium Epyllum* (Mitt.) Müll. Hal.	Neotropical	AM, AF	Ep	Sierra 5080	-

Table 1. Cont.

Taxa	World distribution	Phytogeographic domain	Substrate	Voucher collections USDR and SGC	Reference (occurrence in Campinarana)
***Hookeria acutifolia* Hook. & Grev.	Neotropical	AM, AF	C	Sierra 5085	-
Leucobryaceae Schimp.					
***Campylopus savannarum* (Müll. Hal.) Mitt.	Pantropical	AM, AF, CA, CE, PN	S	Cerqueira 1210	-
***C. surinamensis* Müll. Hal.	Neotropical	AM, AF, CE, PN	S	Cerqueira 1209	-
Leucobryum albicans (Schwägr.) Lindb.	Neotropical	AM, CA, CE, AF	S, T	-	BFG (2018)
L. crispum Müll. Hal.	Neotropical	AM, CE, AF	S, T	-	Griffin (1979)
L. martianum (Hornsch.) Müll. Hal.	Neotropical	AM, CA, CE, AF, PN	C, Ex, T	Cerqueira 839	Griffin (1979) Sierra *et al.* (2018)
Ochrobryum gardneri (Müll. Hal.) Lindb.	Afro-American	AM, CE, AF, PN	C, S	-	BFG (2018)
Neckeraceae Schimp.					
Neckeropsis undulata (Hedw.) Reichardt	Neotropical	AM, CA, CE, AF, PN	C, S	-	BFG (2018)
Orthotrichaceae Arn.					
***Schlotheimia rugifolia* (Hook.) Schwägr.	Neotropical	AM, CE, AF	C	Cerqueira 938	-
Pilotrichaceae Kindb.					
***Cyclodictyon varians* (Sull.) Kuntze	Neotropical	AM, CE, AF	C	Sierra 4840	-
***Hypnella pallescens* (Hook.) A.Jaeger	Neotropical	AM, CE, AF	Ex	Sierra 10212	-
Phyllodrepaniaceae Crosby					
***Mniomalia viridis* (Mitt.) Müll. Hal.	South-American	AM, CE	C	Sierra 4829	-
Pottiaceae Schimp.					
Trichostomum tenuirostre (Hook. & Taylor) Lindb.	Neotropical	AM, CA, CE, AF	C, T	-	BFG (2018)
Pterobryaceae Kindb.					
Henicodium geniculatum (Mitt.) W.R.Buck	Neotropical	AM, CE, AF, PN	C	-	Lisboa (1976)
Pireella pohlii (Schwägr.) Cardot	Neotropical	AM, CE, AF	C	-	BFG (2018)
Pylaisiadelphaceae Goffinet & W.R.Buck					
Isopterygium tenerum (Sw.) Mitt.	Neotropical	AM, CA, CE, AF, PA, PN	C, S	-	BFG (2018)
Taxithelium planum (Brid.) Mitt.	Afro-American	AM, CE, AF, PN	C	-	Sierra *et al.* (2018)
Sematophyllaceae Broth.					
Brittonodoxa subpinnata (Brid.) W.R. Buck, P.E.A.S.Câmara & Carv.-Silva	Pantropical	AM, CA, CE, AF, PA, PN	C, Ex, S	-	Griffin (1979)
Meiothecium revolubile Mitt.	South-American	AM, CE, AF	C	-	Lisboa (1976)
Microcalpe subsimplex (Hedw.) W.R.Buck	Neotropical	AM, AF, CA, CE, PN	C, Ex, T	Cerqueira 881	Lisboa (1976) Griffin (1979)
Trichosteleum. papillosum (Hornsch.) A.Jaeger	South-American	AM, CE, AF	C	Cerqueira 1211	Griffin (1979)
***T. subdemissum* (Besch.) A.Jaeger	South-American	AM, CE, AF	C, S	Sierra 4857	-
T. vicentinum (Mitt.) A.Jaeger	Neotropical	AM	C	-	Sierra *et al.* (2018)
Sphagnaceae Dumort.					
Sphagnum atroligneum H.A.Crum	Endemic to Brazil	AM, AF	S, T	-	BFG (2018)

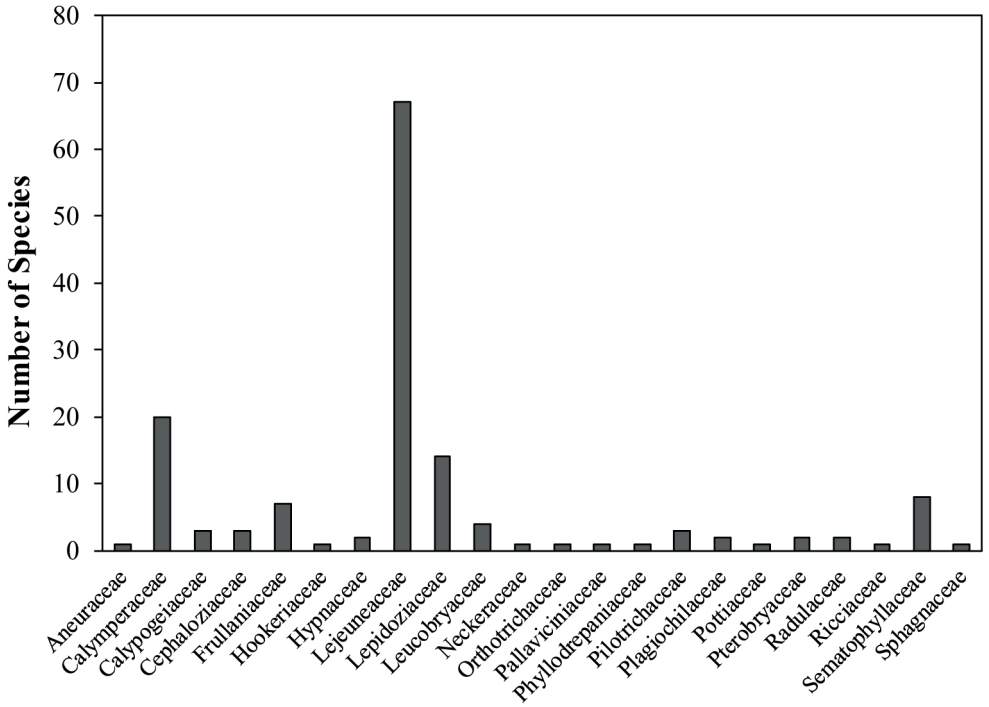

Figure 4. Species richness of bryophyte families in Amazonian Campinaranas.

this substrate in tropical forests (Richards 1984). Favored by high humidity of tropical environments, this substrate provides ideal microclimatic conditions for the development of bryophytes (Frahm 2003).

The bryophytes listed in this study present predominantly Neotropical distribution pattern (70 spp.), but also South American (13 spp.), Pantropical (15 spp.), Amazonian (14 spp.), Endemic to Brazil (03 spp.), Afroamerican (11 spp.), distribution in Amazonian-Guyanas (6 spp.), Tropical South American (5 spp.), Amazonian (+ Bahia) (2 spp.), and Amazonian (+ Costa Rica), S Europe, SW Asia and Trinidad (one species each).

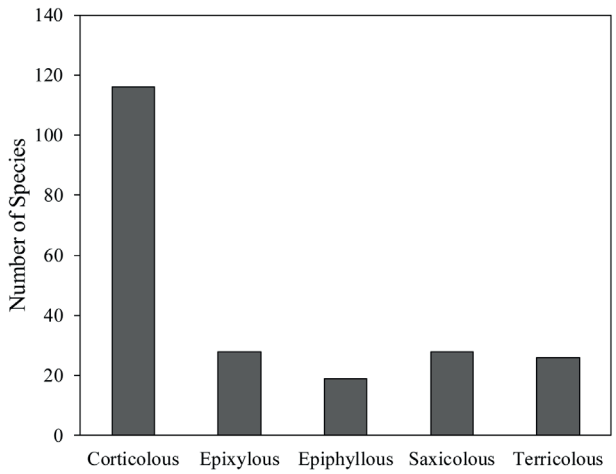

Figure 5. Distribution of species according to the substrates that they were collected in Amazonian Campinaranas.

Twenty-nine species are in Brazil exclusive to the Amazonian domain. Among them, the species *Calypogeia tenax*, *Mnioloma caespitosa*, *Archilejeunea ludoviciana*, *Cheilolejeunea asperifolia*, *C. fragrantíssima*, *C. neblinensis*, *C. papulosa*, *Diplasiolejeunea buckii*, *Drepanolejeunea polyrhiza*, *Pycnolejeunea remotistipula*, *Verdoornianthus marsupiifolius*, *Micropterygium parvistipulum*, *Pteropsiella frondiformis*, *Telaranea pecten*, *Calymperes bartramii*, *Octoblepharum stramineum*, *Syrrhopodon annotinus*, *S. fimbriatus* and *S. flexifolius* were thus far known from Terra Firme forest only, and had, therefore, their range of distribution extended to Campinarana vegetation with the present work.

This study emphasizes the importance of carrying out floristic inventories in poorly known environments and of further studies with different approaches, such as ecological, phytogeographic and genetic.

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