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ABSTRACT
The Martírios-Andorinhas Mountain Ridge, in southeastern Pará, is located in a transition zone between two important biomes in Tropical America, Amazonia and the Brazilian Cerrado. The aim of this study was to inventory the bryophyte flora in different vegetation formations of the Martírios-Andorinhas Mountain Ridge, as a contribution to the evaluation of the environmental conservation status of the area. A total of 1784 specimens (1093 of mosses, 691 of liverworts) were gathered, with a prevalence of mosses over liverworts. In terms of species richness, however, liverworts (65 spp.) were as diverse as mosses (65). The number of specimens was higher in secondary forest (799), followed by gallery forest (670), riparian forest (208), and savanna (107). In turn, in number of species, gallery forest (88 spp./25 exclusive) surpassed secondary forest (75/17), riparian forest (64/8), and savanna (32/1). Bryophyte composition and richness reflects the environmental conditions in each vegetation type. Six species are new occurrences for the state of Pará, four for the northern region, and one for Brazil. The great majority (95 %) of the species were already recorded from the Amazonian domain, while 76 % were known from the Cerrado domain. The high percentage of species recorded from Amazonia can be explained by the presence of humid lowland forests in the study area, promoting the establishment of Amazonian species including many Lejeuneaceae.

KEY WORDS
Mosses, liverworts, conservation unit, Amazonia, Brazilian Planalto.

RÉSUMÉ

Bryophytes de la crête de la montagne Martírios-Andorinhas, une zone de transition Amazonie-Cerrado fortement impactée dans le sud-est du Pará, Brésil.

La crête de la montagne Martírios-Andorinhas, dans le sud-est du Pará, est située dans une zone de transition entre deux biomes importants d'Amérique tropicale : l'Amazonie et le Cerrado brésilien. Le but de cette étude était d'étudier la flore des bryophytes dans différentes formations végétales de la crête de Martírios-Andorinhas, afin de contribuer à l'évaluation de l'état de conservation environnementale de la zone. Un total de 1784 spécimens (1093 de mousses, 691 d'hépatiques) ont été collectés, avec une prévalence des mousses sur les hépatiques. En terme de richesse spécifique, cependant, les hépatiques (65 spp.) étaient aussi diverses que les mousses (65). Le nombre de spécimens était plus élevé dans la forêt secondaire (799), suivie de la forêt galerie (670), de la forêt riveraine (208) et de la savane (107). À son tour, en nombre d'espèces, la forêt galerie (88 spp./25 exclusives) a dépassé la forêt secondaire (75/17), la forêt riveraine (64/8) et la savane (32/1). La composition et la richesse des bryophytes reflètent les conditions environnementales de chaque type de végétation. Six espèces sont de nouvelles occurrences pour l'état du Pará, quatre pour la région du nord et une pour le Brésil. La grande majorité (95 %) des espèces étaient déjà répertoriées dans le domaine amazonien, tandis que 76 % étaient connues dans le domaine du Cerrado. Le pourcentage élevé d'espèces enregistrées en Amazonie peut s'expliquer par la présence de forêts humides de plaine dans la zone d'étude, favorisant l'établissement d'espèces amazoniennes dont de nombreuses Lejeuneaceae.

MOTS CLÉS
Mousses,
hépatiques,
unité de conservation,
Amazonie,
Planalto brésilien.

INTRODUCTION

The Martírios-Andorinhas Mountain Ridge, southeastern Pará state, is located in a transition zone between the Amazonian and Brazilian Planalto regions, being two of ten main phytogeographic regions recognized in Tropical America (Gradstein *et al*. 2001). These two regions represent two important neotropical biomes, Amazonia and the Brazilian Cerrado. The Martírios-Andorinhas Mountain Ridge, moreover, is situated within two conservation units, the Martírios-Andorinhas Mountain Ridge State Park (MAMRSP) and the São Geraldo do Araguaia Environmental Protection Area (Araguaia EPA) (Sectam 2006).

The creation of these conservation units was motivated by the location of the Martírios-Andorinhas Mountain Ridge within a highly impacted area of Amazonia, called the "Arc of Deforestation". This area, which extends from Acre to western Maranhão, undergoes a continuous process of deforestation leading fragmentation of vegetation and significant losses of biodiversity (Vieira *et al*. 2008). The most important vegetation formations of the Martírios-Andorinhas Mountain Ridge are humid Amazonian forest and Cerrado, the latter including gallery forests, grasslands and rocky fields (Sectam 2006; Gorayeb *et al*. 2008).

First lists of plant species from the Martírios-Andorinhas Mountain Ridge focused on orchids (Atzingen *et al*. 1996) and vascular plants (Amaral *et al*. 2008), amounting to about 225 species. Most recently, Alves (2020) reported 72 species of Cyperaceae Juss., of which seven were new to Pará. Despite being located in a highly impacted area in an enclave between two important biomes, no other floristic or phytotaxonomic studies have been carried out in the two conservation units and bryophytes remain completely unexplored.

Hitherto, bryophyte studies in southeastern Pará were conducted only in two localities: the Tucuruí hydroelectric dam region (Ilkiu-Borges *et al*. 2004; Garcia *et al*. 2014) and the Carajás Mountain Ridge (Lisboa & Ilkiu-Borges 1996; Moraes & Lisboa 2006; Oliveira-da-Silva & Ilkiu-Borges 2018). In the latter locality, Oliveira-da-Silva & Ilkiu-Borges (2018) reported 89 bryophyte species from canga vegetation (vegetation on iron rocks). Taking into account other vegetation formations of Carajás, the number of bryophyte species is likely to be at least two-fold higher.

The Martírios-Andorinhas Mountain Ridge includes a high range of vegetation formations and landscapes across different elevations (to maximally 600 m), favoring bryophyte richness (Santos & Costa 2010). It is therefore an area with potentially high bryophyte diversity.

The aim of this study was to investigate the bryophyte flora in different vegetation formations of the Martírios-Andorinhas Mountain Ridge, as a contribution to the evaluation of the conservation status of the area.

MATERIAL AND METHODS

The Martírios-Andorinhas Mountain Ridge, encompassing the MAMRASP and the Araguaia EPA conservation units, is located in the municipality of São Geraldo do Araguaia, southeastern Pará, 6°12'48.2"S, 48°31'19.8"W (Fig. 1). MAMRASP is an integral protection conservation unit of about 25 000 hectares created with the aim of safeguarding natural ecosystems, permitting scientific, cultural, educational and entertainment activities (Pará 1996). Araguaia EPA, in turn, is a sustainable use conservation unit of 26 702 hectares aimed at reconciling the preservation of biodiversity with human activities and land occupation (Pará 1996; Sectam

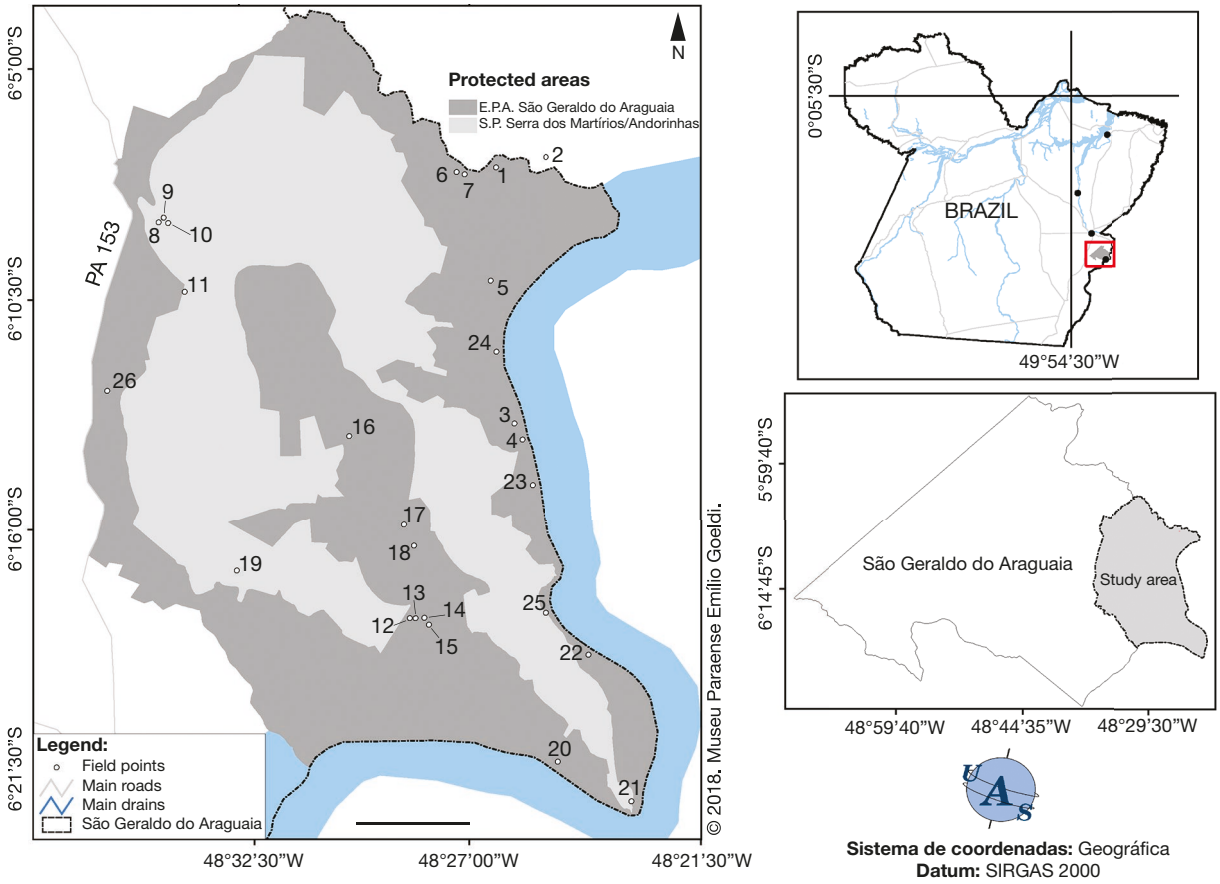

Fig. 1. — Maps showing the location of the Martírios-Andorinhas Mountain Ridge. Source: Museu Paraense Emílio Goeldi – UAS.

2006). It acts as a buffer zone mitigating environmental impacts affecting MAMRASP.

The Martírios-Andorinhas Mountain Ridge is part of the Amazon region but exhibits environments typical of the transition zone between Amazonia and the Brazilian Cerrado including forests, areas of ecological tension, Cerrado vegetation, fields and secondary vegetation (Sectam 2006; Gorayeb *et al.* 2008).

The climate is tropical with a prolonged dry season (Aw type; Köppen classification), an average temperature of 28°C and annual precipitation of 1639 mm (Sectam 2006). The relief is characterized by a very rugged topography with a maximum altitude of 600 meters. The soils are classified as Argisols, Oxisols and Neossols, the latter being the dominant (Sectam 2006; Gorayeb *et al.* 2008).

The vegetation of the Martírios-Andorinhas Mountain Ridge is composed of five main types, of which four were explored in this study: gallery forest, riparian forest, secondary forest and savanna (Fig. 2A-F). In addition, semi-deciduous (dry) forest occurs in the area. Savanna predominates and is characterized by the presence of rocky outcrops and herbaceous, shrub and tree-like layers, the latter consisting of small trees with tortuous branches, exhibiting fire-adapted traits (Ribeiro & Walter 1998; Gorayeb *et al.* 2008). Gallery forests occur on the banks of small streams and rivers, forming a canopy cover across the entire watercourse. They are composed of evergreen species (which do not drop their leaves during the dry season) surrounded by savanna and grass formations (Ribeiro & Walter 1998; Gorayeb *et al.* 2008).

Riparian forests border medium-sized and large rivers do not form a canopy over the entire watercourse. They include tree species with different degrees of deciduousness and differ from deciduous forests by being associated with watercourses and higher and denser vegetation. In the study area, riparian forests were observed on the banks of the Araguaia and Sucupira rivers (Ribeiro & Walter 1998; Gorayeb *et al.* 2008). Secondary forests are forests in the process of regeneration after anthropogenic disturbance. Semi-deciduous forests, finally, occur on mountain slopes, not being dependent on watercourses, and develop on fertile soils enriched by forest biomass (Ribeiro & Walter 1998; Gorayeb *et al.* 2008).

Bryophytes were collected during two excursions, from 14 to 18 December 2007 and from 25 to 30 August 2018, through free walks (Filgueiras *et al.* 1994) across all main local vegetation types except semi-deciduous forests. The collecting methodology was based on Yano (1984) with adaptations and included all substrates colonized by bryophytes.

Bryophyte identification was done using Florschütz-De Waard (1996), Buck (1998, 2003), Reiner-Drehwald (1998, 2000), He (1999), Dauphin (2003), Gradstein & Costa (2003), Gradstein & Ilkiu-Borges (2009, 2015), Bordin &

Fig. 2. — Vegetation types and substrates of bryophytes of the Martírios-Andorinhas Mountain Ridge: **A**-**C**, savanna; **D**, secondary forest; **E**, gallery forest; **F**, riparian forest; **G**, soil; **H**, decaying wood; **I**, living tree trunk; **J**-**L**, rock.

Yano (2013), Pócs *et al.* (2014), Bastos & Gradstein (2020a, b), and Oliveira-da-Silva *et al.* (2021). The classification of the Bryophyta follows Goffinet *et al.* (2009) with adaptations for Sematophyllaceae (Carvalho-Silva *et al.* 2017); that of Marchantiophyta follows Crandall-Stotler *et al.* (2009) with adaptations for *Dibrachiella* (Spruce) X.Q.Shi, R.L.Zhu & Gradst. (Shi *et al.* 2015) and *Thysananthus* Lindenb. (Sukkharak & Gradstein 2017). Vouchers were deposited in herbarium MG.

Data on the geographic distribution of the species in Brazil and world range were based on Yano (1992, 2006, 2011), Reese (1993), Gradstein (1994), Churchill (1998), He (1999), Dauphin (2003), Gradstein & Costa (2003), Reiner-Drehwald & Schäfer-Verwimp (2008), Costa *et al.* (2011), Peralta *et al.* (2011), Oliveira & Bastos (2014), Gradstein & Ilkiu-Borges (2015), Bastos & Gradstein (2020a, b), Flora do Brasil (2020), Wynns (2020), and Silva *et al.* (2021). Substrate classification followed Robbins (1952) with adaptations for termite mounds and living leaves.

RESULTS

A total of 1784 bryophyte specimens were collected in the Martírios-Andorinhas Mountain Ridge, including 130 species, 63 genera and 26 families (Table 1). Moss collections (1093 specimens) were more numerous than liverworts (691 specimens) but species richness of the two groups was equal, and include 65 species of mosses (in 34 genera and 17 families) and 65 of liverworts (in 29 genera and nine families).

The largest number of collections was made in secondary forest (799 specimens), followed by gallery forest (670), riparian forest (208) and savanna (107). However, the highest number of bryophyte species was found in gallery forest (88 spp. of which 25 exclusive), followed by secondary forest (75/17), riparian forest (64/8) and savanna (32/1). The number of shared and exclusive species in the vegetation types is presented in a Venn diagram (Fig. 3).

Secondary forest harboured more mosses (524 specimens/39 spp.) than liverworts (275/36); the same trend was observed in riparian forest (mosses: 118/33; liverworts: 90/31), and savanna (mosses: 76/23; liverworts: 31/9). In gallery forest, however, liverworts (45 spp.) were more diverse than mosses (43) even though the number of collections of liverworts (295 specimens) from gallery forest was lower than that of mosses (375) (Fig. 4).

The most speciose families of mosses were Calymperaceae Kindb. (13 spp.), Fissidentaceae Schimp. (10 spp.) and Sematophyllaceae Broth. (9 spp.). Among liverworts, they were Lejeuneaceae Rostovzev (46 spp.), Frullaniaceae Lorch (4 spp.) and Plagiochilaceae (Jörg.) Müll.Frib. & Herzog (4 spp.).

Six families (Aneuraceae H.Klinggr., Cephaloziellaceae Douin, Bartramiaceae Schwägr., Brachytheciaceae Schimp., Dicranaceae Schimp., Pterigynandraceae Schimp.) were represented by only one species, each with more than one occurrence. Only two families (Cephaloziaceae Mig. and Pottiaceae Hampe) were represented by a single species, each found only once in the study area.

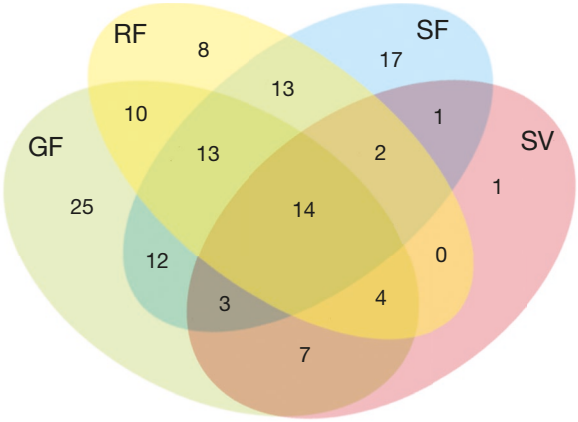

FIG. 3. — Exclusive and shared species in the vegetation types of the Martírios-Andorinhas Mountain Ridge. Abbreviations: **GF**, gallery forest; **RF**, riparian forest; **SF**, secondary forest; **SV**, savanna.

Aneuraceae (1 sp.), Cephaloziaceae (1 sp.), Cephaloziellaceae (1 sp.), Lepidoziaceae Limpr. (4 spp.), and Pterigynandraceae (1 sp.) were exclusive to gallery forest. Radulaceae Müll.Frib. (3 spp.) and Pottiaceae (1 sp.) were exclusive to secondary forests. No family was found to occur exclusively in the riparian forest or in savanna.

Taxithelium planum (Brid.) Mitt. was the most abundant moss species in the Martírios-Andorinhas Mountain Ridge, with 105 occurrences, followed by *Microcalpe subsimplex* (Hedw.) W.R.Buck (98 occurrences) and *Octoblepharum albidum* Hedw. (72 occurrences). Among liverworts, *Ceratolejeunea cubensis* (Mont.) Schiffn. and *Acrolejeunea emergens* (Mitt.) Steph. were the most frequently found, with 58 and 56 occurrences, respectively.

Six species were new occurrences for the state of Pará: *Calymperes tenerum* Müll.Hal., *Cylindrocolea planifolia* (Steph.) R.M.Schust., *Eulacophyllum cultelliforme* (Sull.) W.R.Buck & Ireland, *Taxiphyllum laevifolium* (Mitt.) W.R.Buck, *Syrrhopodon flexifolius* Mitt. and *Trichosteleum vincentinum* (Mitt.) A.Jaeger. *Bryum limbatum* Müll. Hal., *Lejeunea cancellata* Nees & Mont., *Lophocolea platensis* C.Massal. and *Trachyphyllum dusenii* (Broth.) Broth. are being recorded for the first time in the northern region of Brazil and *Trichosteleum cyparissoides* (Hornsch.) H.Rob. is new to the country of Brazil.

Regarding substrates, 52.0 % (928) of the specimens were corticolous, 29.3 % (523) rupicolous, 14.4 % (257) epixylous, 3.9 % (70) terrestrial, 0.2 % (4) occurred on termite mounds, and only 0.1 % (2) were epiphyllous (Fig. 2G, H). The predominant pattern of geographic distribution was Neotropical (78 spp.), followed by Pantropical (31), widely distributed (7), South American (6), Afro-American (5) and endemic to Brazil (2). The latter two species included *Cheilolejeunea savannae* L.P.C.Macedo, Ilk.-Borg. & C.J.Bastos and *Lejeunea oligoclada* Spruce. *Schusterolejeunea inundata* (Spruce) Grolle has peri-Amazonian distribution, being restricted to the edges of Amazonia and the Guianas.

TABLE 1. — Bryophytes of the Martírios-Andorinhas Mountain Ridge. Abbreviations: **LT**, living trunks; **DT**, decaying trunks; **R**, rock; **S**, soil; **TM**; termite mounds; **LL**, living leaves; **GF**, gallery forest; **RF**, riparian forest; **SV**, savanna; **SF**, secondary forest; *, new to Pará state; **, new to the northern region of Brazil; ***, new to Brazil.

Family/Species	Occurrence Number	Substrate						Vegetation type				World distribution	Voucher
		LT	DT	R	S	TM	LL	GF	RF	SV	SF		
MARCHANTIOPHYTA	–	–	–	–	–	–	–	–	–	–	–	–	–
Aneuraceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Riccardia regnellii (Ångstr.) K.G.Hell	2	–	1	1	–	–	–	2	–	–	–	Neotropical	J.C.S. Santos 790
Cephaloziaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Odontoschisma variabile (Lindenb. & Gottsche) Trevis.	1	–	–	1	–	–	–	1	–	–	–	Afro-American	J.C.S. Santos 789
Cephaloziellaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
**Cylindrocolea planifolia* (Steph.) R.M.Schust.	2	–	–	2	–	–	–	2	–	–	–	Neotropical	J.C.S. Santos 767
Frullaniaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Frullania ericoides (Nees) Mont.	2	2	–	–	–	–	–	–	–	–	2	Pantropical	J.C.S. Santos 873
F. gibbosa Nees	8	5	2	1	–	–	–	2	2	4	–	Neotropical	J.C.S. Santos 674
F. intumescens (Lehm. & Lindenb.) Lehm. & Lindenb.	4	1	–	3	–	–	–	2	–	2	–	Neotropical	J.C.S. Santos 718
Frullania sp.	6	2	–	4	–	–	–	–	–	–	6	–	J.C.S. Santos 908
Lejeuneaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Acrolejeunea emergens (Mitt.) Steph.	56	42	4	10	–	–	–	27	18	7	4	Pantropical	J.C.S. Santos 941
A. torulosa (Lehm. & Lindenb.) Schiffn.	15	7	2	6	–	–	–	8	–	5	2	Neotropical	J.C.S. Santos 915
Archilejeunea badia (Spruce) Steph.	1	1	–	–	–	–	–	–	–	–	1	South American	P.L.B. Lisboa 5779
A. fuscescens (Lehm.) Fulford	3	3	–	–	–	–	–	1	2	–	–	Neotropical	J.C.S. Santos 952
Ceratolejeunea coarina (Gottsche) Schiffn.	12	9	–	3	–	–	–	3	–	–	9	Neotropical	J.C.S. Santos 1027
C. confusa R.M. Schust.	4	–	–	3	1	–	–	4	–	–	–	Neotropical	J.C.S. Santos 746
C. cornuta (Lindenb.) Steph.	9	3	–	6	–	–	–	7	–	1	1	Neotropical	J.C.S. Santos 642
C. cubensis (Mont.) Schiffn.	58	27	1	30	–	–	–	35	–	–	23	Neotropical	J.C.S. Santos 636
C. guianensis (Nees & Mont.) Steph.	22	7	–	15	–	–	–	16	1	1	4	Neotropical	J.C.S. Santos 753
Cheilolejeunea acutangula (Nees) Grolle	5	3	–	1	1	–	–	5	–	–	–	Neotropical	J.C.S. Santos 766
C. adnata (Lehm.) Grolle	26	25	1	–	–	–	–	–	1	1	24	Neotropical	P.L.B. Lisboa 5651
C. aneogyna (Spruce) A.Evans	3	1	1	1	–	–	–	–	2	–	1	Neotropical	P.L.B. Lisboa 5781
C. comans (Spruce) R.M.Schust.	9	8	1	–	–	–	–	5	3	–	1	South American	J.C.S. Santos 837
C. lobulata (Lindenb.) Gradst. & C.J.Bastos	31	20	–	11	–	–	–	22	3	2	4	Neotropical	J.C.S. Santos 765
C. rigidula (Mont.) R.M.Schust.	15	6	–	9	–	–	–	6	1	8	–	Pantropical	P.L.B. Lisboa 5570
C. savannae L.P.C.Macedo, Ilk.-Borg. & C.J.Bastos	10	5	–	5	–	–	–	10	–	–	–	Endemic	J.C.S. Santos 638
C. trifaria var. *clausa* (Nees & Mont.) C.J.Bastos & Gradst.	3	2	–	1	–	–	–	3	–	–	–	Neotropical	J.C.S. Santos 841
Cololejeunea contractiloba A. Evans	1	–	1	–	–	–	–	1	–	–	–	Neotropical	J.C.S. Santos 868
C. diaphana A. Evans	2	2	–	–	–	–	–	1	1	–	–	Neotropical	J.C.S. Santos 960
C. subcardiocarpa Tixier	2	–	1	–	–	–	1	1	1	–	–	Neotropical	J.C.S. Santos 1056
Dibrachiella auberiana (Mont.) X.Q.Shi, R.L.Zhu & Gradst.	2	2	–	–	–	–	–	–	–	–	2	Neotropical	P.L.B. Lisboa 5850
D. parviflora (Nees) X.Q.Shi, R.L.Zhu & Gradst.	35	27	3	2	3	–	–	–	26	–	9	Neotropical	J.C.S. Santos 890
Frullanoides corticalis (Lehm. & Lindenb.) van Slageren	1	1	–	–	–	–	–	1	–	–	–	Neotropical	J.C.S. Santos 995
Lejeunea adpressa Nees	24	19	4	1	–	–	–	4	1	–	19	Neotropical	J.C.S. Santos 964
L. bermudiana (A.Evans) R.M.Schust.	8	6	1	1	–	–	–	1	–	–	7	Neotropical	J.C.S. Santos 1032
***L. cancellata* Nees & Mont.	5	1	1	1	1	1	–	3	2	–	–	Neotropical	J.C.S. Santos 884
L. cerina (Lehm. & Lindenb.) Lehm. & Lindenb.	8	6	–	2	–	–	–	3	–	–	5	Neotropical	J.C.S. Santos 851
L. controversa Gottsche	4	1	–	3	–	–	–	2	1	–	1	Neotropical	P.L.B. Lisboa 5653
L. flava (Sw.) Nees	19	16	–	3	–	–	–	19	–	–	–	Pantropical	J.C.S. Santos 1023
L. glaucescens Gottsche	25	13	7	4	1	–	–	11	5	–	9	Neotropical	J.C.S. Santos 893
L. oligoclada Spruce	19	16	2	1	–	–	–	17	1	–	1	Endemic	J.C.S. Santos 851
L. phyllobola Nees & Mont.	3	2	1	–	–	–	–	1	1	–	1	Neotropical	J.C.S. Santos 899
L. setiloba Spruce	2	2	–	–	–	–	–	–	2	–	–	Neotropical	J.C.S. Santos 970
L. trinitensis Lindenb.	3	3	–	–	–	–	–	–	2	–	1	Neotropical	J.C.S. Santos 939
Leptolejeunea elliptica (Lehm. & Lindenb.) Besch.	1	–	–	–	–	–	1	–	1	–	–	Pantropical	P.L.B. Lisboa 5654
Lopholejeunea subfusca (Nees) Schiffn.	5	4	–	1	–	–	–	2	1	–	2	Pantropical	J.C.S. Santos 962
Microlejeunea epiphylla Bischl.	7	6	1	–	–	–	–	5	1	–	1	Neotropical	J.C.S. Santos 791
Myriocoleopsis minutissima subsp. *myriocarpa* (Nees & Mont.) R.L.Zhu, Y.Yu & Pócs	1	1	–	–	–	–	–	–	1	–	–	Pantropical	J.C.S. Santos 962
Prionolejeunea denticulata (F. Weber) Schiffn.	2	–	–	2	–	–	–	1	1	–	–	Neotropical	J.C.S. Santos 634
Pycnolejeunea contigua (Nees) Grolle	10	10	–	–	–	–	–	9	1	–	–	Pantropical	J.C.S. Santos 740
P. papillosa X.L.He	1	1	–	–	–	–	–	1	–	–	–	Neotropical	J.C.S. Santos 721
Schusterolejeunea inundata (Spruce) Grolle	1	1	–	–	–	–	–	–	1	–	–	Amazonia and Guianas	J.C.S. Santos 961
Stictolejeunea balfourii (Mitt.) E.W.Jones	2	1	1	–	–	–	–	–	–	–	2	Pantropical	P.L.B. Lisboa 5682
Symbiezidium transversale (Sw.) Trevis.	6	6	–	–	–	–	–	–	1	–	5	Pantropical	J.C.S. Santos 888
Thysananthus auriculatus (Wilson & Hook.) Sukkharak & Gradst.	18	13	3	2	–	–	–	7	4	–	7	Pantropical	J.C.S. Santos 837
Xylolejeunea crenata (Nees & Mont.) X.L.He & Grolle	3	–	–	2	1	–	–	3	–	–	–	Neotropical	J.C.S. Santos 1074

Table 1. — Continuation.

Family/Species	Occurrence Number	Substrate						Vegetation type				World distribution	Voucher
		LT	DT	R	S	TM	LL	GF	RF	SV	SF		
Lepidoziaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Micropterygium leiophyllum Spruce	12	–	–	10	2	–	–	12	–	–	–	Neotropical	J.C.S. Santos 642
Monodactylopsis monodactyla (Spruce) R.M.Schust.	1	–	1	–	–	–	–	1	–	–	–	Neotropical	J.C.S. Santos 643
Zoopsidella integrifolia (Spruce) R.M.Schust.	21	–	–	10	11	–	–	21	–	–	–	Neotropical	J.C.S. Santos 732
Lophocoleaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Lophocolea liebmanniana Gottsche	1	–	1	–	–	–	–	–	–	–	1	Neotropical	P.L.B. Lisboa 5776
***L. platensis* C.Massal.	3	–	–	3	–	–	–	3	–	–	–	South American	J.C.S. Santos 632
Plagiochilaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Plagiochila disticha (Lehm. & Lindenb.) Lehm. & Lindenb.	40	39	1	–	–	–	–	–	1	–	39	Neotropical	P.L.B. Lisboa 5648
P. martiana (Nees) Lindenb.	12	12	–	–	–	–	–	–	1	–	11	Neotropical	P.L.B. Lisboa 5652
P. montagnei Nees	17	14	2	1	–	–	–	1	–	–	16	Neotropical	J.C.S. Santos 853
P. raddiana Lindenb.	14	12	–	2	–	–	–	3	–	–	11	Neotropical	J.C.S. Santos 866
Radulaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Radula flaccida Lindenb. & Gottsche	3	3	–	–	–	–	–	–	–	–	3	Afro-American	P.L.B. Lisboa 5844
R. javanica Gottsche	39	39	–	–	–	–	–	–	–	–	39	Pantropical	P.L.B. Lisboa 5717
R. mammosa Spruce	1	1	–	–	–	–	–	–	–	–	1	Neotropical	P.L.B. Lisboa 5703
BRYOPHYTA	–	–	–	–	–	–	–	–	–	–	–	–	–
Bartramiaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Philonotis hastata (Duby) Wijk & Margad.	5	1	–	4	–	–	–	4	1	–	–	Wide	J.C.S. Santos 864
Brachytheciaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Zelometeorium patulum (Hedw.) Manuel	2	2	–	–	–	–	–	–	1	–	1	Neotropical	P.L.B. Lisboa 5648
Bryaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Bryum coronatum Schwägr.	3	–	–	2	–	1	–	1	–	2	–	Wide	J.C.S. Santos 835
***B. limbatum* Müll. Hal.	1	–	–	1	–	–	–	1	–	–	–	Neotropical	J.C.S. Santos 1057
Rhodobryum subverticillatum Broth.	1	–	–	1	–	–	–	1	–	–	–	South American	P.L.B. Lisboa 5665
Calymperaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Calymperes afzelii Sw.	24	21	3	–	–	–	–	–	–	–	24	Pantropical	J.C.S. Santos 921
C. erosum Müll. Hal.	25	15	4	6	–	–	–	9	2	1	13	Pantropical	J.C.S. Santos 743
C. palisotii Schwägr.	9	6	1	2	–	–	–	5	–	–	4	Wide	J.C.S. Santos 855
**C. tenerum* Müll. Hal.	1	–	–	1	–	–	–	–	1	–	–	Pantropical	J.C.S. Santos 973
Octoblepharum albidum Hedw.	72	49	8	13	2	–	–	21	7	8	36	Pantropical	J.C.S. Santos 983
O. cylindricum Mont.	11	6	–	4	1	–	–	5	4	2	–	Neotropical	J.C.S. Santos 667
O. pulvinatum (Dozy & Molk.) Mitt.	5	1	–	1	3	–	–	5	–	–	–	Neotropical	J.C.S. Santos 726
Syrrhopodon cryptocarpus Dozy & Molk.	16	16	–	–	–	–	–	–	4	–	12	Pantropical	J.C.S. Santos 882
**S. flexifolius* Mitt.	1	–	1	–	–	–	–	–	–	–	1	Neotropical	P.L.B. Lisboa 5916
S. gardneri (Hook.) Schwägr.	1	–	–	1	–	–	–	–	–	–	1	Pantropical	J.C.S. Santos 919
S. incompletus Schwägr.	39	33	5	–	–	1	–	–	–	1	38	Afro-American	P.L.B. Lisboa 5560
S. ligulatus Mont.	2	2	–	–	–	–	–	2	–	–	–	Neotropical	J.C.S. Santos 999
S. prolifer Schwägr.	48	4	–	40	4	–	–	38	1	9	–	Pantropical	J.C.S. Santos 703
Dicranaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Leucoloma tortellum (Mitt.) A.Jaeger	6	–	–	6	–	–	–	5	–	1	–	Neotropical	J.C.S. Santos 644
Fissidentaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Fissidens angustelimbatus Mitt.	1	–	–	1	–	–	–	–	1	–	–	Neotropical	J.C.S. Santos 898
F. angustifolius Sull.	2	1	–	–	1	–	–	–	1	–	1	Pantropical	J.C.S. Santos 943
F. elegans Brid.	22	4	1	16	1	–	–	16	2	–	4	Neotropical	J.C.S. Santos 631
F. guianensis Mont.	23	12	4	6	1	–	–	2	1	2	18	Neotropical	J.C.S. Santos 651
F. pallidinervis Mitt.	8	6	–	2	–	–	–	2	–	–	6	Neotropical	P.L.B. Lisboa 5594
F. pellucidus Hornsch.	7	1	–	5	1	–	–	6	–	1	–	Pantropical	J.C.S. Santos 767
F. perfalcatus Broth.	3	2	–	1	–	–	–	2	1	–	–	Pantropical	J.C.S. Santos 805
F. radicans Mont.	1	–	1	–	–	–	–	–	–	–	1	Pantropical	P.L.B. Lisboa 5914
F. submarginatus Bruch	3	–	–	–	2	1	–	1	–	2	–	Pantropical	J.C.S. Santos 1049
F. zollingeri Mont.	7	2	1	–	4	–	–	–	2	1	4	Pantropical	J.C.S. Santos 885
Hypnaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Chrysohypnum diminutivum (Hampe) W.R.Buck	25	11	13	1	–	–	–	–	1	–	24	Wide	J.C.S. Santos 928
Ectropothecium leptochaeton (Schwägr.) W.R.Buck	6	–	–	6	–	–	–	5	–	–	1	Neotropical	J.C.S. Santos 646
Phyllodon truncatulus (Müll. Hal.) W.R.Buck	1	–	–	1	–	–	–	1	–	–	–	Neotropical	P.L.B. Lisboa 5663
**Taxiphyllum laevifolium* (Mitt.) W.R.Buck	6	5	–	–	1	–	–	–	6	–	–	Neotropical	J.C.S. Santos 954
Vesicularia vesicularis (Schwägr.) Broth.	9	–	5	2	2	–	–	–	3	–	6	Neotropical	J.C.S. Santos 892
Leucobryaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Campylopus pilifer Brid.	1	–	–	1	–	–	–	1	–	–	–	Neotropical	J.C.S. Santos 729
C. surinamensis Müll. Hal.	32	1	–	27	4	–	–	20	–	12	–	Neotropical	J.C.S. Santos 661
Leucobryum martianum (Hornsch.) Müll. Hal.	31	5	5	15	6	–	–	26	1	2	2	Neotropical	J.C.S. Santos 677
Ochrobryum subulatum Hampe	3	–	2	1	–	–	–	3	–	–	–	South American	J.C.S. Santos 1038
Neckeraceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Neckeropsis disticha (Hedw.) Kindb.	11	9	–	2	–	–	–	–	–	–	11	Pantropical	P.L.B. Lisboa 5739
N. undulata (Hedw.) Reichardt	32	30	2	–	–	–	–	–	1	–	31	Neotropical	P.L.B. Lisboa 5648

Table 1. — Continuation.

Family/Species	Occurrence Number	Substrate						Vegetation type				World distribution	Voucher
		LT	DT	R	S	TM	LL	GF	RF	SV	SF		
Pilotrichaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Callicostella pallida (Hornsch.) Ångstr.	38	6	9	22	1	–	–	14	8	4	12	Neotropical	J.C.S. Santos 893
C. rufescens (Mitt.) A.Jaeger	1	–	–	1	–	–	–	–	1	–	–	Neotropical	J.C.S. Santos 898
Pottiaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Hyophila involuta (Hook.) A.Jaeger	1	–	–	1	–	–	–	–	–	–	1	Wide	J.C.S. Santos 930
Pterigynandraceae	–	–	–	–	–	–	–	–	–	–	–	–	–
******Trachyphyllum dusenii* (Broth.) Broth.	4	1	–	3	–	–	–	4	–	–	–	Afro-American	J.C.S. Santos 864
Pterobryaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Henicodium geniculatum (Mitt.) W.R.Buck	2	2	–	–	–	–	–	1	–	–	1	Pantropical	J.C.S. Santos 878
Jaegerina scariosa (Lorentz) Arzeni	3	3	–	–	–	–	–	1	2	–	–	Pantropical	J.C.S. Santos 899
Pylaisiadelphaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Isopterygium subbrevisetum (Hampe) Broth.	16	9	6	1	–	–	–	1	–	–	15	Neotropical	P.L.B. Lisboa 5670
I. tenerifolium Mitt.	7	2	–	5	–	–	–	6	1	–	–	Neotropical	J.C.S. Santos 612
I. tenerum (Sw.) Mitt.	46	17	7	20	2	–	–	22	7	6	11	Wide	J.C.S. Santos 706
Taxithelium planum (Brid.) Mitt.	105	52	35	17	1	–	–	6	24	3	72	Pantropical	J.C.S. Santos 984
T. pluripunctatum (Renauld & Cardot) W.R.Buck	2	–	–	1	1	–	–	2	–	–	–	Neotropical	J.C.S. Santos 1001
Sematophyllaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Acroporium pungens (Hedw.) Broth.	3	–	3	–	–	–	–	–	–	–	3	Neotropical	P.L.B. Lisboa 5775
Brittonodoxa subpinnata (Brid.) W.R.Buck, P.E.A.S.Câmara & Carv.-Silva	7	2	2	3	–	–	–	4	1	1	1	Pantropical	J.C.S. Santos 857
Microcalpe subsimplex (Hedw.) W.R.Buck	98	33	23	38	4	–	–	61	4	7	26	Neotropical	J.C.S. Santos 760
*******Trichosteleum cyparissoides* (Hornsch.) H.Rob.	1	1	–	–	–	–	–	–	–	1	–	Neotropical	P.L.B. Lisboa 5569
T. papillosum (Hornsch.) A.Jaeger	5	3	1	1	–	–	–	1	–	1	3	Neotropical	J.C.S. Santos 844
T. subdemissum (Besch.) A.Jaeger	45	10	9	19	7	–	–	32	7	2	4	Pantropical	J.C.S. Santos 725
**T. vincentinum* (Mitt.) A. Jaeger	8	1	6	1	–	–	–	1	1	–	6	Neotropical	P.L.B. Lisboa 5650
Vitalia cuspidifera (Mitt.) P.E.A.S.Câmara, Carv.-Silva & W.R.Buck	14	–	1	13	–	–	–	12	–	2	–	Neotropical	J.C.S. Santos 630
Stereophyllaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Entodontopsis leucostega (Brid.) W.R.Buck & Ireland	48	16	3	29	–	–	–	14	18	5	11	Wide	J.C.S. Santos 662
**Eulacophyllum cultelliforme* (Sull.) W.R.Buck & Ireland	8	–	–	8	–	–	–	3	1	–	4	Neotropical	J.C.S. Santos 904
Pilosium chlorophyllum (Hornsch.) Broth.	31	11	15	5	–	–	–	6	1	–	24	Neotropical	J.C.S. Santos 624
Thuidiaceae	–	–	–	–	–	–	–	–	–	–	–	–	–
Pelekium involvens (Hedw.) Touw	9	1	8	–	–	–	–	–	–	–	9	Afro-American	P.L.B. Lisboa 5582
P. scabrosulum (Mitt.) Touw	71	44	27	–	–	–	–	–	1	–	70	Neotropical	J.C.S. Santos 921
P. schistocalyx (Müll. Hal.) Touw	14	10	2	2	–	–	–	2	–	–	12	Neotropical	J.C.S. Santos 838
Total	1784	928	257	523	70	4	2	670	208	107	799	–	–

DISCUSSION

The results showed a clear prevalence of mosses over liverworts, confirming that mosses are better equipped against desiccation (Goffinet *et al*. 2009) and predominate in dryer and more exposed environments (Lisboa & Ilkiu-Borges 1996; Yano & Peralta 2009, 2011; Luizi-Ponzo *et al*. 2013; Silva *et al*. 2014; Carmo & Peralta 2016; Peñaloza-Bocajá *et al*. 2017; Valente *et al*. 2017; Oliveira-da-Silva & Ilkiu-Borges 2018). However, despite the large difference in abundance, the representation of the two groups in terms of number of species was equal, due possibly to the ample presence of humid, shaded microhabitats in the gallery forests – associated with water courses and shading of trees – favoring the growth of liverworts.

Sixteen species of liverworts occurred exclusively in this environment. A similar correlation between environmental conditions and species richness and composition was observed by Valente *et al*. (2013), suggesting that bryophyte diversity is triggered by availability of moisture and light.

The family composition of mosses and liverworts is similar to that found elsewhere in the region (Brito & Ilkiu-Borges 2013; Pantoja *et al*. 2015; Fagundes *et al*. 2016; Oliveira-da-Silva & Ilkiu-Borges 2018; Ilkiu-Borges *et al*. 2020) and reflects the composition of neotropical lowland forests (Gradstein & Pócs 1989; Gradstein *et al*. 2001).

Families represented by one single species are more or less common in lowland forests and open environments (Gradstein *et al*. 2001), but the species occur at low frequencies. The two families represented by one specimen (Cephaloziaceae: *Odontoschisma variable* (Lindenb. & Gottsche) Trevis.; Pottiaceae: *Hyophila involuta* (Hook.) A.Jaeger.) have already been recorded in other areas of Pará. *Odontoschisma variable* was also recorded in the Cachimbo Mountain Ridge and Carajás Mountain Ridge (Gradstein & Ilkiu-Borges 2015; Ilkiu-Borges & Oliveira-da-Silva 2017), whereas *Hyophila involuta* is a very common species on rock in wet sites and on concrete in ruderal areas, being the most frequent species recorded by Lisboa & Ilkiu-Borges (1995) in the city of Belém, the capital of Pará.

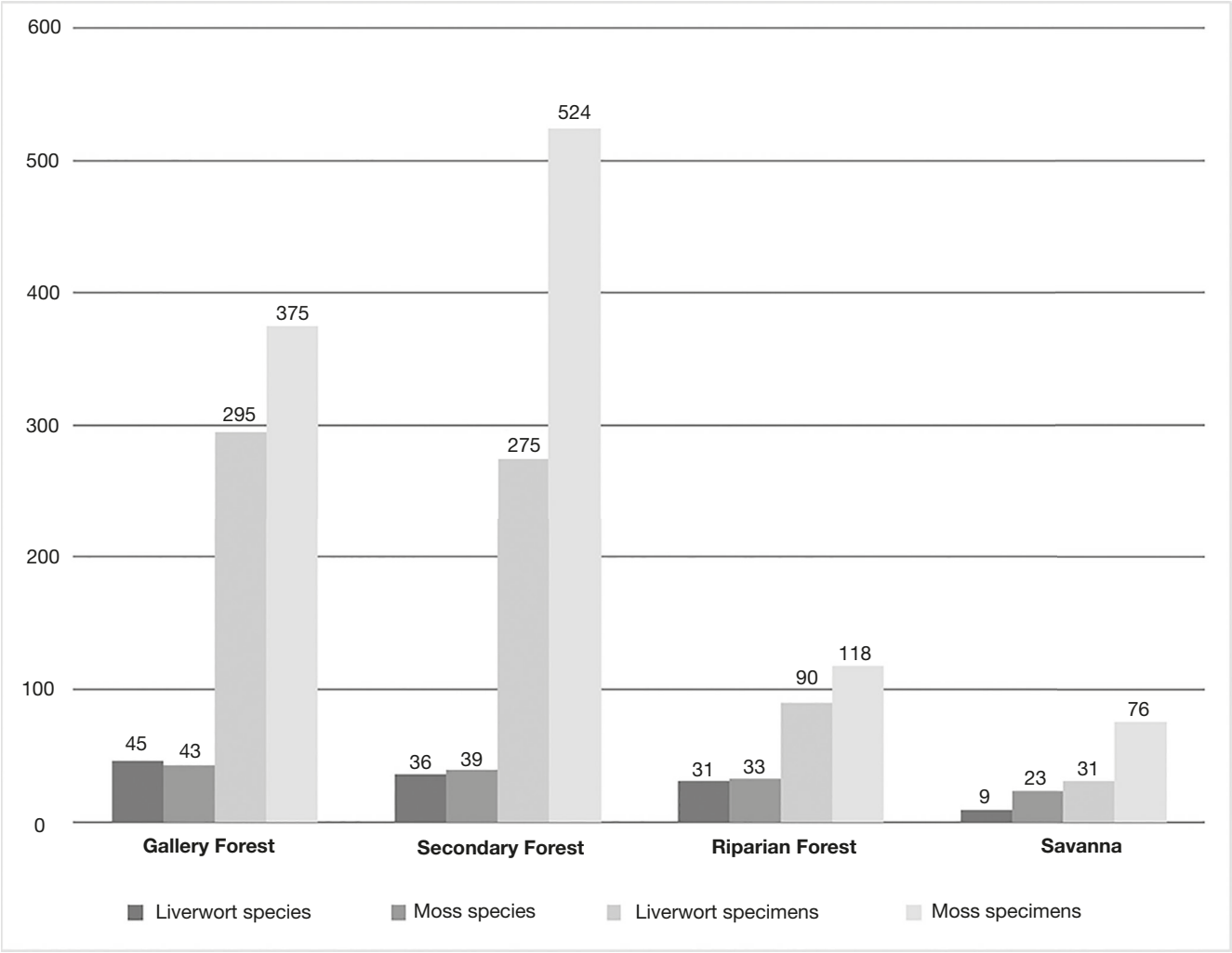

Fig. 4. — Distribution of species and specimens of bryophytes in vegetation types of the Martírios-Andorinhas Mountain Ridge.

The exclusive occurrence of several liverworts to gallery forest (e.g. *Riccardia regnellii* (Ångstr.) K.G.Hell, *Cylindrocolea planifolia*, many species of Lejeuneaceae, all species of Lepidoziaceae, *Lophocolea platensis*) reflects their preference for natural or more humid environments (Gradstein *et al*. 2001). Radulaceae and Pottiaceae were exclusive to secondary forest where they included the most common species, but were usually adapted to moist habitats. Oliveira-da-Silva *et al*. (2021) found that secondary forests harbored a relatively poor flora of *Radula* Dumort. but in our study all species of this genus were gathered in secondary forest and were absent in natural environments.

The mosses most frequently collected in the Martírios-Andorinhas Mountain Ridge (*Taxithelium planum*, *Microcalpe subsimplex*, *Octoblepharum albidum*) are widely distributed in the Neotropics, where they occur in different vegetation types and colonize a wide variety of substrates (Yano 1992; Florschütz-De Waard 1996; Câmara 2011). In Pará, these species have been found to be common in urban areas (Lisboa & Ilkiu-Borges 1995), but also in natural primary or secondary forests (Moraes & Lisboa 2006; Brito & Ilkiu-Borges 2013; Pantoja *et al*. 2015; Fagundes *et al*. 2016; Oliveira-da-Silva & Ilkiu-Borges 2018; Ilkiu-Borges *et al*. 2020).

As to the most common liverworts in the study area, *Ceratolejeunea cubensis* was collected in gallery forest and secondary forest mainly colonizing rocks and living trunks, while *Acrolejeunea emergens* occurred in all vegetation types, colonizing living trunks, rocks and, occasionally, decaying trunks. *Ceratolejeunea cubensis* is a Neotropical species commonly found on rocks, living and decomposing trunks (Gradstein & Costa 2003), in humid forests, seasonal forests, and open places in primary and secondary vegetation (Dauphin 2003). *Acrolejeunea emergens* is usually found on barks in scrubby secondary vegetation, restinga, and on isolated trees in cultivated areas (Gradstein 1994; Gradstein & Costa 2003).

Among the new occurrences for the state of Pará, *Cylindrocolea planifolia*, *Eulacophyllum cultelliforme* and *Taxiphyllum laevifolium* were known in all regions of Brazil (Flora do Brasil 2020), *Calymperes tenerum* was previously registered in the southeastern region and Tocantins (Flora do Brasil 2020), *Syrrhopodon flexifolius* was registered in Amazonas (Flora do

Brasil 2020), and *Trichosteleum vincentinum* was reported for Amazonas and Bahia (Flora do Brasil 2020).

Bryum limbatum, *Lejeunea cancellata*, and *Lophocolea platensis* were already registered from the other four regions of Brazil and are being recorded here for the first time in the northern region. Likewise, *Trachyphyllum dusenii* was only known in Maranhão, Distrito Federal, Goiás, Mato Grosso and Minas Gerais. *Trichosteleum cyparissoides* (formerly known as *Trichosteleum bolivarense* H.Rob.), the species found new to the country of Brazil in this study, had been formerly reported as *Trichosteleum bolivarense* from different localities in Brazil, but these records were recently excluded from Brazil (Flora do Brasil 2020).

Regarding substrate preferences of species, the results of this study met the expectations. The high diversity of tropical trees and shrubs coupled with relatively high air humidity and shade (Richards 1984) favored the development of corticolous bryophyte species, which predominated in the study area. As rocky outcrops are also prominent in the area, rocks were the second most frequently colonized substrate, especially along streams and waterfalls.

The scarcity of epiphyllous species, which were only found in forests associated with watercourses, reflects the dryer condition of the environment in the Martírios-Andorinhas Mountain Ridge. The rather open or low forest structure resulted in relatively low atmospheric humidity, despite a relatively high annual precipitation (1639 mm), causing increased temperature and evapo-transpiration, and ultimately negatively affecting the establishment and growth of epiphyllous bryophytes (Olarinmoye 1974). Although the two parks are protected areas, land use – characterized by the conversion of large portions of the area into agricultural lands and pasture – is a major threat to the epiphyllous flora and the whole vegetation (Pócs 1996).

The phytogeographical make-up of the flora of the study area was also similar to that found in other studies conducted in the region (Brito & Ilkiu-Borges 2013; Tavares-Martins *et al*. 2014; Ilkiu-Borges *et al*. 2020). As to the three endemic species recorded in this study, *Cheilolejeunea savannae* was recently described by Macedo *et al*. (2020) from Amazonian savannas in the eastern Amazon (Amapá, Pará, Maranhão), but also occurs in different forest types. *Lejeunea oligoclada* was known from Amazonia and the Brazilian Atlantic coast, where it is widespread and rather common (Reiner-Drehwald & Schäfer-Verwimp 2008; Bastos & Gradstein 2020b). It was found in canga vegetation at the Carajás Mountain Ridge (Ilkiu-Borges & Oliveira-da-Silva 2018), the nearest mountain ridge to the study area. *Schusterolejeunea inundata*, known from Colombia, Venezuela, Peru, Brazil and the Guianas (Gradstein 2021), was previously recorded from the states of Amazonas, Pará, and Maranhão (Lisboa & Ilkiu-Borges 2001; Gradstein & Costa 2003; Peralta *et al*. 2011), where it is uncommon.

Approximately 95 % of the bryophyte species from the Martírios-Andorinhas Mountain Ridge were already registered from Amazonia and 76 % from the Cerrado domain. The higher representation of Amazonian species may be due to the common occurrence of forests in the study area, promoting the establishment of species typical of Amazonian forests including many members of Lejeuneaceae. On the other hand, this may as well reflect the insufficient knowledge of the bryophyte flora of the Cerrado region, being still one of the lesser studied regions of Brazil.

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