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Bryophytes from Caviana and Mexiana islands, archipelago of Marajó, Brazil

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ABSTRACT
The archipelago of Marajó (Pará State, Brazil) in the mouth of the Amazon river is the largest fluvial-marine complex worldwide, comprising about 2500 islands. The aim of this study was to investigate floristic and ecological attributes of the bryophyte flora of two major islands of the archipelago, Caviana and Mexiana, as a contribution to environmental conservation. In total, 572 samples were studied. The bryoflora of Caviana was represented by 89 species (39 mosses, 50 liverworts) and Mexiana by 50 species (28 mosses, 22 liverworts). Together, the two islands harbored 100 species (46 mosses and 54 liverworts). No statistical similarity was observed in the species composition between the two islands and 50 species were exclusive to Caviana while 11 species were only found on Mexiana. The latter island harbored a greater richness of mosses while liverworts were more diverse on Caviana. Epiphyllous bryophytes were exclusively found on Caviana. The floristic differences between the two islands are explained by differences in environmental conditions and vegetation cover. *Drepanolejeunea lichenicola* (Spruce) Steph., *Eulacophyllum cultelliforme* (Sull.) W.R.Buck & Ireland and *Meteoridium remotifolium* (Müll.Hal.) Manuel are new to the state of Pará and 31 species are recorded for the first time from Marajó.

KEY WORDS
Amazonia,
Bryophyta,
continental island,
floristics,
Marchantiophyta,
tropical rainforest.

RÉSUMÉ
Bryophytes des îles Caviana et Mexiana, archipel de Marajó, Brésil.
L'archipel de Marajó (État du Pará) à l'embouchure du fleuve Amazone est le plus grand complexe fluvial-marin du monde, comprenant environ 2500 îles. L'objectif de cette étude est d'étudier les caractéristiques floristiques et écologiques de la flore des bryophytes de deux grandes îles de l'archipel, Caviana et Mexiana, comme contribution à la conservation de l'environnement. Au total, 572 échantillons ont été étudiés. La bryoflore de Caviana est représentée par 89 espèces (39 mousses, 50 hépatiques) et Mexiana par 50 espèces (28 mousses, 22 hépatiques). Ensemble, les deux îles abritent 100 espèces (46 mousses et 54 hépatiques). Aucune similitude statistique n'est observée dans la composition des espèces entre les deux îles et 50 espèces sont exclusives à Caviana tandis que 11 espèces ne sont trouvées que sur Mexiana. Cette dernière île abrite une plus grande richesse de mousses tandis que les hépatiques sont plus diversifiées sur Caviana. Les bryophytes épiphylles sont trouvés exclusivement sur Caviana. Les différences floristiques entre les deux îles s'expliquent par des différences de conditions environnementales et de couvert végétal. *Drepanolejeunea lichenicola* (Spruce) Steph., *Eulacophyllum cultelliforme* (Sull.) W.R.Buck & Ireland et *Meteoridium remotifolium* (Müll.Hal.) Manuel sont nouveaux dans l'état du Pará et 31 espèces sont enregistrées pour la première fois à Marajó.

MOTS CLÉS
Amazonie,
Bryophyta,
île continentale,
floristique,
Marchantiophyta,
forêt tropicale humide.

INTRODUCTION

There are two kinds of islands, continental and oceanic, each differing in plant composition (Tan & Pócs 2000). The former ones are part of a continental shelf and their proximity to the continent should have freely allowed the past migration of plant species. Oceanic islands, instead, are more distant from the continent and not part of a continental shelf; they originated from the bottom of the ocean and their flora emerged from diaspores transported over long distances (Tan & Pócs 2000).

Brazil has a great number of islands, the majority of them being continental. São Paulo State, for instance, encompasses 106 continental islands (Ângelo 1989). Numerous continental (fluvial) islands are located in Amazonia, especially in the archipelago of Marajó (Pará State), located in the mouth of the Amazon river and being the largest fluvial-marine complex worldwide comprising about 2500 islands. The main island, Marajó, encompasses an area of *c.* 49 606 km^2 and comprises 12 municipalities (Cruz 1987; Amaral *et al.* 2007).

Bryophyte studies on Brazilian islands have been carried out on most of the (few) oceanic islands of the country, including on Fernando de Noronha Island, Trindade Island, and Martim Vaz Archipelago (Gepp 1890; Vital *et al.* 1991; Yano 1998; Faria *et al.* 2012). Continental islands have been studied in the states of São Paulo and Rio de Janeiro (Yano 1990; Oliveira-e-Silva & Yano 2000; Visnadi & Vital 2001; Oliveira-e-Silva *et al.* 2002; Yano *et al.* 2003; Joyce *et al.* 2006; Yano & Peralta 2007, 2008; Peralta & Yano 2008), in Roraima (Milliken & Ratter 1989; Yano 1992) and in the state of Pará (Lisboa *et al.* 1993, 1998, 1999; Lisboa & Maciel 1994; Ilkiu-Borges *et al.* 2004, 2009; Souza & Lisboa 2005; Brito & Ilkiu-Borges 2013; Moura *et al.* 2013; Garcia *et al.* 2014). The results of these studies have shown the importance of Brazilian islands as environments of high bryophyte diversity and have indicated the need for further work on the subject.

The present paper deals with the bryoflora of the archipelago of Marajó (Pará State). The islands of the Marajó archipelago are isolated environments within the confluence of the Atlantic ocean with the Amazonas and Tocantins river basins and are covered by grasslands, savannas or cerrado vegetation, "restinga" (woodland on sand), mangroves, Teso vegetation, "várzea" forest (periodically flooded forests), terra firme forest (upland forests), and secondary vegetation (Lisboa *et al.* 1993, Amaral *et al.* 2007, Lisboa 2012). Besides the largest island, Marajó, the archipelago includes two broad islands, Caviana (4968 km^2) and Mexiana (1543 km^2). Hitherto, 116 bryophyte species have been reported from the archipelago, all of them from Marajó (Lisboa & Maciel 1994; Lisboa *et al.* 1993, 1998, 1999; Garcia *et al.* 2014; Brito & Ilkiu-Borges 2012, 2013). The latter authors (Brito & Ilkiu-Borges 2012, 2013) recorded two species new to the state of Pará, one new to Brazil, and one new to South America.

The aim of the present study was to analyze the bryophyte floras of Caviana and Mexiana, Pará State, as a contribution to the evaluation of the importance of the islands for environmental conservation.

MATERIAL AND METHODS

The studied islands, Caviana (0°41'N-0°07'N and 49°37'W-50°20'W) and Mexiana (0°01'N-0°13'S and 50°10'W-50°40'W), are located in the mouth of the Amazon river, being part of the Marajó archipelago and belonging to the municipality of Chaves (Lima *et al.* 2005; Fig. 1). The name Caviana refers to two different, neighboring islands, "Caviana de Dentro" and "Caviana de Fora", the first one is being five times smaller than the second. The present study deals with Caviana de Fora. Caviana and Mexiana are situated north of Chaves, being separated from the island of Marajó by the Norte channel and from each other by the Perigoso channel. Average annual temperature in Chaves is 25-26°C,

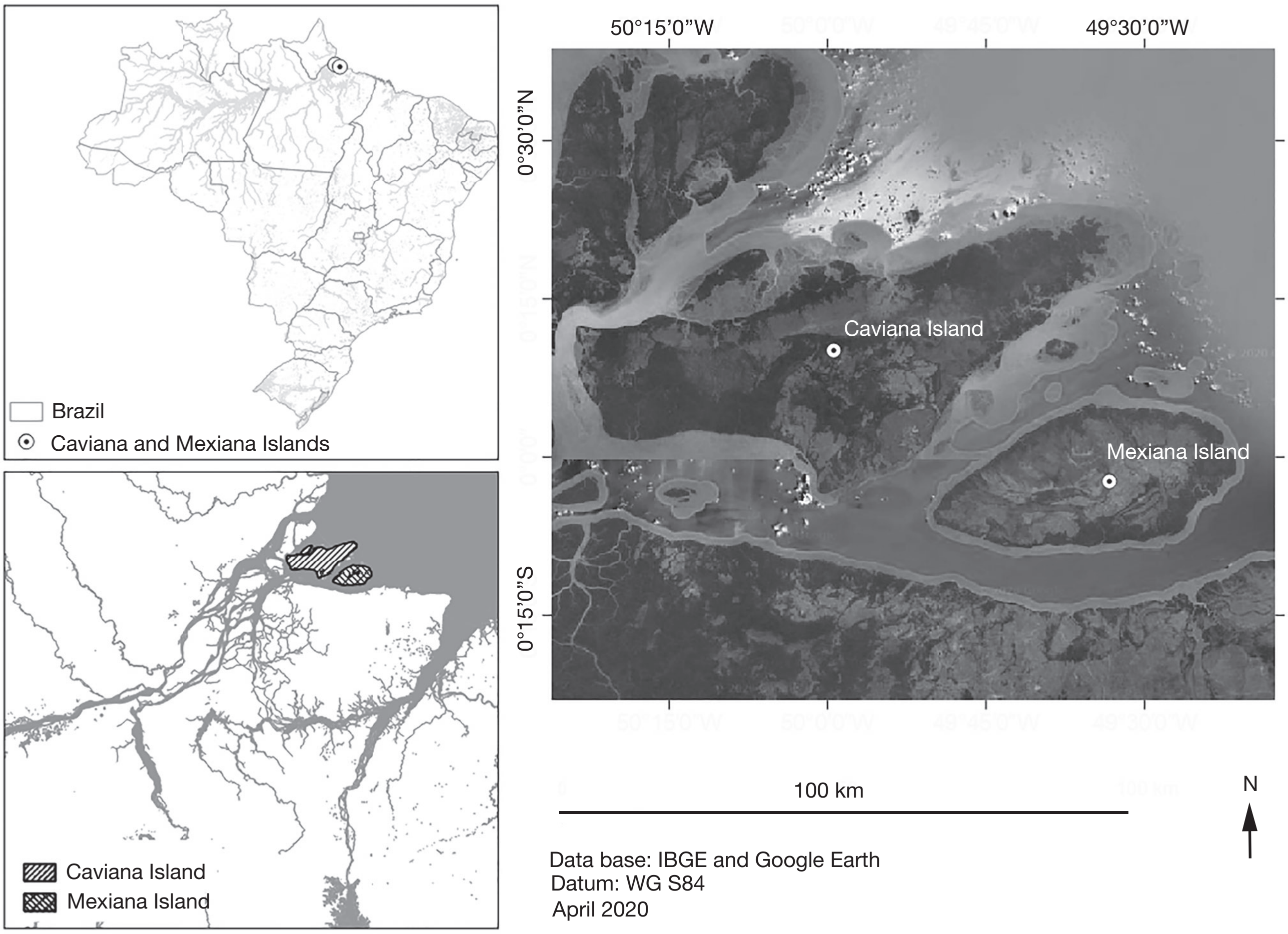

Fig. 1. — Location of Caviana and Mexiana islands, Marajó archipelago, Brazil.

relative air humidity more than 80%, and annual rainfall around 2500 mm (SEPOF 2011).

The two islands differ in vegetation cover (Lisboa *et al.*, unpubl. fieldwork report). In Caviana, "várzea" forests form a narrow to broad marginal strips along watercourses and the remaining area is covered by "terra firme" forests and grasslands (savanna). The same vegetation types occur on Mexiana but the "várzea" forests on the latter island are mixed with mangrove and larger areas are covered by grassland. During fieldwork, fewer bryophytes were observed in Mexiana than in Caviana.

Bryophyte collecting was done in the framework of the project "Estudos de briófitas em áreas de conservação da biodiversidade na Amazônia Oriental, Pará, Brasil" (process n° 477512/2006-2), coordinated by Dr Regina Célia Lobato Lisboa (former researcher at Museu Paraense Emílio Goeldi - MPEG). The collections were made haphazardly by Dr Pedro Lisboa, Valéria Pereira, and Marinaldo Cardoso during July-August 2007. In total, 572 samples were collected according to the method described by Yano (1984); vouchers are deposited in MG.

The specimens were identified using Gradstein (1994), Reiner-Drehwald (2000), Buck (2003), Gradstein & Costa (2003), Zartman & Ilkiu-Borges (2007), Dauphin (2009), and Gradstein & Ilkiu-Borges (2009). Classification of the species follows Crandall-Stotler *et al.* (2009) for liverworts (Marchantiophyta) and Goffinet *et al.* (2009) for mosses (Bryophyta), updated by Carvalho-Silva *et al.* (2017) for Sematophyllaceae.

Ordination of groups, formed by the composition of species in each island, was calculated by Non-metric Multidimensional Scaling Method (NMDS) based on a distance binary matrix in which the figure seeks to find the data points in two or more dimensions, considering the Similarity Index by Jaccard (Legendre & Legendre 2012), followed by ANOSIM similarity analysis of groups, with 10 000 permutations (Clarke 1993). Both analyzes were performed using the Past 3.24 software (Hammer *et al.* 2013).

For analysis of substrate preference, the species were classified into four categories: corticolous, epixylic, epiphyllous, and terrestrial (Robbins 1952); for phytogeographical analysis into seven categories: Pantropical, Neotropical, Afro-American, Wide, Tropical and Subtropical America, and Brazilian Amazon (Gradstein & Costa 2003; Santos & Costa 2010; Santos *et al.* 2011; Gradstein 2013). The sets of colonized substrates were visualized using an UpSet diagram (Lex *et al.* 2014) in the software R v. 3.5.1 (R Core Team 2018) through the UpSetR package (Conway *et al.* 2017).

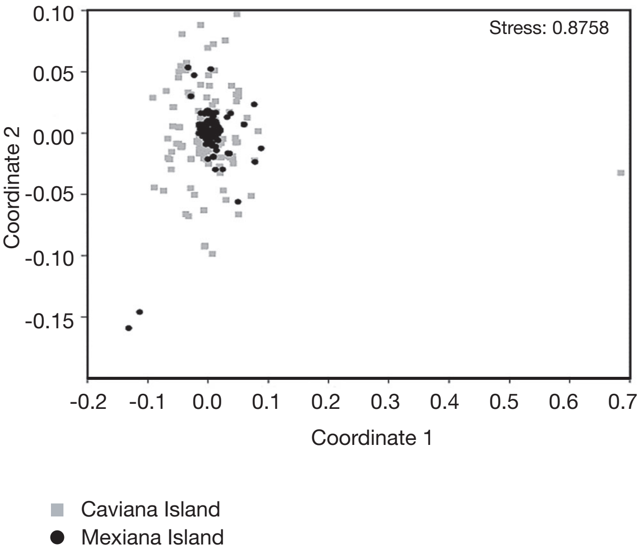

FIG. 2. — NMDS ordination of floristic data from Caviana and Mexiana islands.

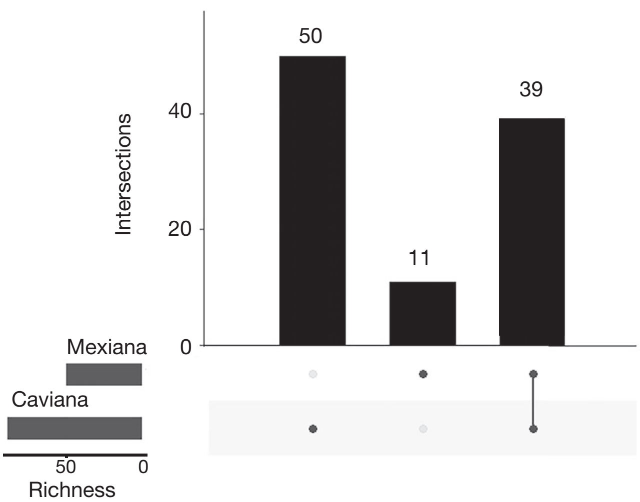

FIG. 3. — Species richness of bryophytes on Caviana and Mexiana islands.

RESULTS

The inventory of Caviana yielded 89 bryophyte species (39 of mosses, 50 of liverworts) in 47 genera and 18 families, that of Mexiana 50 species (28 mosses, 22 liverworts) in 29 genera and 10 families. Together, the two islands harbored 100 bryophyte species (46 mosses, 54 liverworts) in 51 genera and 19 families.

Statistically significant similarity was not observed in the species composition between Caviana and Mexiana islands and two significantly different groups were formed according to the ANOSIM analysis ($R = 0.08$; $p = 0.0001$). Although the two groups were not visible in the NMDS ordination (Fig. 2), with high stress value in repeating attempts, the two islands shared only 39% (39 spp.) of the registered species (Fig. 3). A total of 61 species (61%) were found on only one island, including 50 spp. (50%) exclusive to Caviana and 11 spp. (11%) to Mexiana.

Richness of liverworts was highest on Caviana with 50 species (56%), while mosses showed greater percent richness on Mexiana with 28 species (56%). Lejeuneaceae was the richest and most abundant family on both islands with 42 species (512 occurrences) on Caviana and 21 species (106 occurrences) on Mexiana. At the genus level, *Lejeunea* was richest on Caviana (10 spp.), whereas *Calymperes* (7 spp.) was richest on Mexiana. At the species level, *Dibrachiella parviflora* (78 occurrences) and *Stictolejeunea squamata* (72 occurrences) were most common on Caviana, while *Taxithelium planum* (35 occurrences) followed by *Dibrachiella parviflora* (24 occurrences) were most abundant on Mexiana.

Drepanolejeunea lichenicola (Spruce) Steph., *Eulacophyllum cultelliforme* (Sull.) W.R.Buck & Ireland and *Meteoridium remotifolium* (Müll.Hal.) Manuel are new to the state of Pará, and 38 species and one family (Radulaceae) are recorded for the first time from the archipelago of Marajó.

The majority of the species (68) had a Neotropical distribution pattern. The remaining distribution patterns were Pantropical (20 spp.), Wide (6 spp.), Afro-American (4 spp.), Tropical and subtropical America (1 sp.), and Brazilian Amazon (1 sp.). The latter pattern concerned *Lejeunea obidensis* Spruce, a species endemic to Brazil.

Regarding substrate preference, corticolous species predominated (91 spp.), with 37 species exclusively recorded from living trees (Fig. 4). Epixylic taxa included 55 species, 17 species were epiphyllous and 5 species were found terrestrial. Epiphylls were only collected on Caviana and six of them (*Cololejeunea obliqua, Crossomitrium patrisiae* (Brid.) C.Müll., *Crossomitrium epiphyllum* (Mitt.) Müll.Hal., *Drepanolejeunea lichenicola* and *Leptolejeunea elliptica* (Lehm. & Lindenb.) Besch., *Odontolejeunea lunulata* (F.Weber) Schiffn.) were exclusively found on leaves. Three species (*Ceratolejeunea laetefusca* (Austin) R.M.Schust., *Pilosium chlorophyllum* (Hornsch.) Broth., *Xylolejeunea crenata* (Nees & Mont.) X.L.He & Grolle) were only found on dead wood (fallen trees and branches) and none of the terrestrial species showed exclusivity in substrate colonization.

DISCUSSION

RICHNESS AND FLORISTIC COMPOSITION

The detected differences in species richness and frequency (as expressed by the number of occurrences) between Caviana and Mexiana corroborate the field observation that Caviana harbored more bryophytes than Mexiana. These results may be explained by differences in vegetation cover of the two islands, notably the greater surface area of grassland on Mexiana and the common occurrence of mangrove species within the *várzea* forests of the island, indicating higher salinity. As shown in the literature, bryophyte development may be negatively influenced by salt water (Hart *et al.* 1991; Sabovljević & Sabovljević 2007) and by drought (Richards 1984; Cornelissen & ter Steege 1989; Acebey *et al.* 2003;

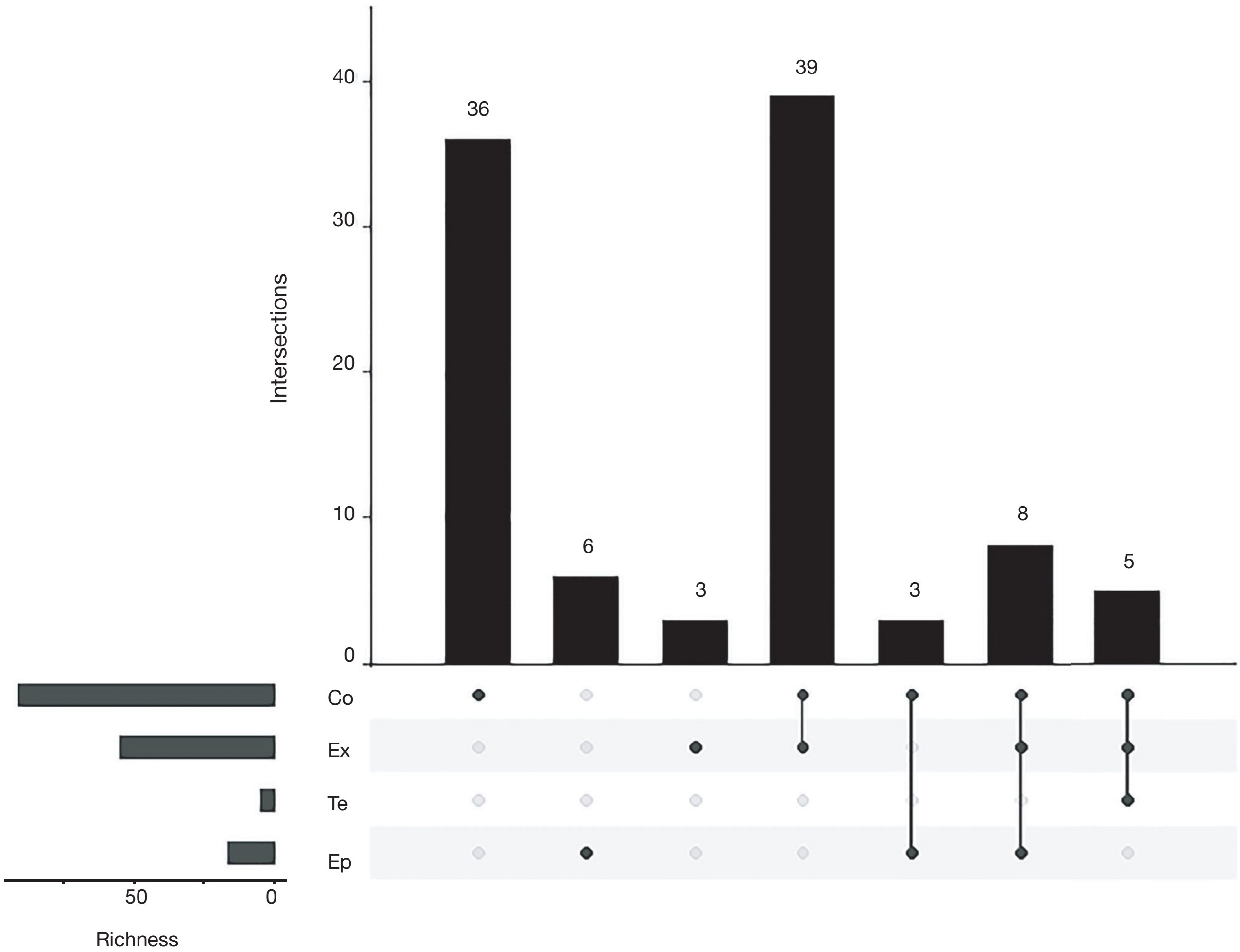

Fig. 4. — Substrate preference of bryophytes on Caviana and Mexiana islands.

Gradstein 2008; Gradstein & Sporn 2010; Benítez *et al.* 2015; Mota-de-Oliveira 2018).

The dissimilarity in species composition of Caviana and Mexiana may be due to the large number of unique species recorded in each location (50 spp. and 11 spp., respectively), favoring the formation of two distinct groups in the ordination analysis even when not graphically visible. Although flooded forests predominate on Caviana and Mexiana, the relative surface area covered by várzea forests is different on the two islands and this may have caused different environmental conditions on the islands and thus have influenced bryophyte richness and composition (see Glime 2017). In addition, differences in microhabitat complexity on the two islands might have played a role (Braga 1979; Ferreira *et al.* 2011).

Earlier studies on the bryoflora of Marajó archipelago have focused on mosses and this has rendered the impression that mosses were more common than liverworts in the area (Lisboa *et al.* 1993, 1998, 1999; Lisboa & Maciel 1994; Brito & Ilkiu-Borges 2013; Garcia *et al.* 2014). The present study, however, shows that both mosses and liverworts can prevail in the archipelago. Several studies have indicated that mosses may more common in open environments due to their greater capacity for desiccation tolerance (Watson 1914; Proctor & Tuba 2002; Glime 2017), while liverworts prefer more shady and humid environments (Pócs 1982; Gradstein *et al.* 2001). We suggest, therefore, that the higher diversity of liverworts on Caviana may be related to the greater extension of *terra firme* forests on Caviana and the greater homogeneity of its *várzea* forests (unmixed with mangrove species), creating a larger area of humid forest environment than on Mexiana. The greater surface area of open vegetation and the heterogeneity of mixed *várzea*–mangrove forest on Mexiana, on the other hand, may have caused higher diversity of mosses on this island.

Predominance of mosses was also found by Garcia *et al.* (2014) in Reserva Bacurizal on Marajó (Salvaterra municipality), an area including *restinga*, mangrove and forest dominated by *Platonia insignis* Mart. and *Parahancornia amapa* (Huber) Ducke. Brito & Ilkiu-Borges (2013), on the other hand, observed the prevalence of liverworts in an area of *várzea* forest, *teso* vegetation, grassland, mangrove and secondary vegetation on Marajó (municipalities of Cachoeira do Arari and Soure).

Lejeuneaceae was the most speciose and abundant bryophyte family on both islands, representing 42% of total bryophyte

Table 1. — Bryophytes recorded from Caviana and Mexiana islands, Marajó archipelago. Abbreviations: **Cav**., Caviana; **Mex**. = Mexiana; **Co** = corticolous; **Ep** = epiphyllous; **Ex** = epixylic; **Te** = Terrestrial. * New to Marajó Archipelago. ** New to Pará state. Numbers for locations and substrate types are the number of occurrences of species.

	Oc.		Substract					
Family/species	**Cav.**	**Mex.**	**Ep**	**Te**	**Ex**	**Co**	**Distribution**	**Voucher**
BRYOPHYTA	–	–	–	–	–	–	–	–
Bartramiaceae	–	–	–	–	–	–	–	–
Philonotis uncinata var. *glaucescens* (Hornsch.) Florsch.	–	2	–	–	1	1	Wide	5503
Philonotis hastata (Duby) Wijk & Margad.*	–	1	–	–	–	1	Wide	5491
Brachytheciaceae	–	–	–	–	–	–	–	–
Meteoridium remotifolium (Müll.Hal.) Manuel**	1	–	–	–	–	1	Neotropical	5286
Zelometeorium patulum (Hedw.) Manuel	30	–	1	–	17	12	Neotropical	5012
Calymperaceae	–	–	–	–	–	–	–	–
Calymperes afzelii Sw.	23	6	–	–	2	27	Pantropical	4997
Calymperes erosum Müll.Hal.	11	15	–	–	7	19	Pantropical	5159
Calymperes lonchophyllum Schwägr.	6	1	–	–	2	5	Pantropical	5014
Calymperes levyanum Besch.	3	4	–	–	1	6	Neotropical	5163
Calymperes nicaraguense Renauld & Cardot	9	19	–	–	2	26	Neotropical	5157
Calymperes palisotii Schwägr.	3	9	–	–	1	11	Wide	5335
Calymperes pallidum Mitt.*	1	1	–	–	–	2	Neotropical	5230
Octoblepharum albidum Hedw.	37	14	–	–	7	44	Pantropical	5018
Octoblepharum pulvinatum (Dozy & Molk.) Mitt.	3	–	–	–	1	2	Neotropical	5224
Syrrhopodon incompletus Schwägr.	5	12	–	–	1	16	Afro-American	5125
Syrrhopodon prolifer Schwägr.*	5	–	–	–	1	4	Neotropical	5164
Fissidentaceae	–	–	–	–	–	–	–	–
Fissidens angustifolius Sull.*	1	–	–	–	–	1	Pantropical	5312
Fissidens guianensis Mont.	55	17	–	–	11	61	Neotropical	4995
Fissidens inaequalis Mitt.	1	–	–	–	–	1	Neotropical	5339
Fissidens intramarginatus (Hampe) A.Jaeger	4	12	–	–	2	14	Neotropical	5016
Fissidens pellucidus Hornsch.	1	2	–	–	–	3	Neotropical	5102
Fissidens steerei Grout*	–	1	–	–	–	1	Pantropical	5395
Fissidens zollingeri Mont.	–	3	–	–	–	3	Pantropical	5420
Hookeriaceae	–	–	–	–	–	–	–	–
Crossomitrium epiphyllum (Mitt.) Müll.Hal.*	1	–	1	–	–	–	Pantropical	5120
Crossomitrium patrisiae (Brid.) C.Müll.	4	–	4	–	–	–	Neotropical	5120
Hypnaceae	–	–	–	–	–	–	–	–
Chryso-hypnum diminutivum (Hampe) W.R.Buck	1	–	–	–	–	1	Wide	5237
Leucomiaceae	–	–	–	–	–	–	–	–
Leucomium strumosum (Hornsch.) Mitt.	19	–	–	–	7	12	Pantropical	5023
Neckeraceae	–	–	–	–	–	–	–	–
Neckeropsis disticha (Hedw.) Kindb.*	16	–	–	–	4	12	Pantropical	4999
Neckeropsis undulata (Hedw.) Reichardt	56	1	1	–	11	45	Pantropical	4998
Phyllodrepaniaceae	–	–	–	–	–	–	–	–
*Mniomalia viridis (*Mitt.) Müll.Hal.*	3	–	–	–	2	1	Neotropical	5163
Pilotrichaceae	–	–	–	–	–	–	–	–
Callicostella pallida (Hornsch.) Ångstr.	59	10	–	3	38	28	Neotropical	5021
Lepidopilum scabrisetum (Schwägr.) Steere*	3	–	–	–	–	3	Neotropical	5206
Lepidopilum surinamense Müll.Hal.	27	1	–	–	11	17	Neotropical	4998
Pilotrichum evanescens (Müll.Hal.) Crosby*	2	–	–	–	1	1	Neotropical	5272
Pterobryaceae	–	–	–	–	–	–	–	–
Henicodium geniculatum (Mitt.) W.R.Buck	2	–	–	–	1	1	Pantropical	5277
Orthostichopsis tetragona (Hedw.) Broth.	8	–	–	2	4	2	Neotropical	5150
Pylaisiadelphaceae	–	–	–	–	–	–	–	–
Isopterygium tenerum (Sw.) Mitt.	26	14	–	–	16	24	Neotropical	5166
Pterogonidium pulchellum (Hook.) Müll.Hal.	–	2	–	–	–	2	Neotropical	5386
Taxithelium planum (Brid.) Mitt.	52	35	–	2	27	58	Wide	5001
Sematophyllaceae	–	–	–	–	–	–	–	–
Brittonodoxa subpinnata (Brid.) W.R.Buck	4	2	–	–	2	4	Pantropical	5105
Microcalpe subsimplex (Hedw.) W.R.Buck	12	9	–	–	5	16	Pantropical	5126
Trichosteleum bolivarense H. Rob.*	–	1	–	–	–	1	Neotropical	5414
Trichosteleum papillosum (Hornsch.) A.Jaeger	10	11	–	–	12	9	Neotropical	5121
Trichosteleum subdemissum (Besch.) A.Jaeger	–	4	–	–	1	3	Pantropical	5383
Stereophyllaceae	–	–	–	–	–	–	–	–
Eulacophyllum cultelliforme (Sull.) W.R.Buck & Ireland**	2	–	–	–	–	2	Neotropical	5174
Pilosium chlorophyllum (Hornsch.) Broth.	2	–	–	–	2	–	Neotropical	5126
Thuidiaceae	–	–	–	–	–	–	–	–
Pelekium scabrosulum (Mitt.) Touw*	38	13	–	–	10	41	Neotropical	4997
MARCHANTIOPHYTA	–	–	–	–	–	–	–	–
Frullaniaceae	–	–	–	–	–	–	–	–
Frullania nodulosa (Reinw., Blume & Nees) Nees*	1	–	–	–	–	1	Pantropical	5168
Lejeuneaceae	–	–	–	–	–	–	–	–
Acrolejeunea torulosa (Lehm. & Lindenb.) Schiffn.	–	3	–	–	–	3	Neotropical	5417

Table 1. — Continuation

Family/species	Oc.		Substract				Distribution	Voucher
	Cav.	Mex.	Ep	Te	Ex	Co		
Archilejeunea fuscescens (Lehm.) Fulford	–	2	–	–	–	2	Neotropical	5415
Ceratolejeunea cubensis (Mont.) Schiffn.	25	–	2	–	8	15	Neotropical	4998
Ceratolejeunea cornuta (Lindenb.) Steph.	7	3	–	–	1	9	Afro-American	5070
Ceratolejeunea guianensis (Nees & Mont.) Steph.*	2	–	1	–	–	1	Neotropical	5041
Ceratolejeunea laetefusca (Austin) R.M.Schust.	1	–	–	–	1	–	Neotropical	5231
Ceratolejeunea minuta G.Dauphin*	6	–	–	–	1	5	Neotropical	5010
*Cheilolejeunea adnata (*Lehm.) Grolle	8	–	–	–	1	7	Neotropical	5083
Cheilolejeunea comans (Spruce) R.M.Schust.	4	8	–	–	5	7	Neotropical	5017
Cheilolejeunea sp.	–	2	–	–	–	2	Neotropical	5515
Cheilolejeunea oncophylla (Ångstr.) Grolle & M.E.Reiner	7	3	–	–	–	10	Neotropical	5211
Cheilolejeunea rigidula (Mont.) R.M.Schust.	4	6	–	–	–	10	Pantropical	5341
Cololejeunea camillii (Lehm.) A. Evans*	3	1	2	–	–	2	Neotropical	5118
Cololejeunea contractiloba A. Evans*	1	–	–	–	–	1	Tropical and Subtropical America	5087
Cololejeunea obliqua (Nees & Mont.) Schiffn.*	7	–	7	–	–	–	Neotropical	5035
Cololejeunea subcardiocarpa Tixier	1	–	–	–	–	1	Neotropical	5311
Dibrachiella auberiana (Mont.) X.Q.Shi, R.L.Zhu & Gradst.	2	–	–	–	–	2	Neotropical	5029
Dibrachiella parviflora (Nees) X.Q.Shi, R.L.Zhu & Gradst.	78	24	–	1	19	82	Neotropical	4995
Diplasiolejeunea brunnea Steph.*	1	–	–	–	–	1	Neotropical	5311
Drepanolejeunea lichenicola (Spruce) Steph.**	1	–	1	–	–	–	Neotropical	5118
Lejeunea adpressa Nees	13	2	1	–	3	11	Neotropical	5074
Lejeunea asperrima Spruce*	2	–	–	–	–	2	Neotropical	5109
Lejeunea cerina (Lehm. & Lindenb.) Lehm. & Lindenb.*	55	–	–	–	5	50	Neotropical	4996
Lejeunea controversa Gottsche*	21	–	–	–	4	17	Neotropical	5002
Lejeunea glaucescens Gottsche*	26	3	–	1	8	20	Neotropical	5023
Lejeunea immersa Spruce*	6	1	–	–	5	2	Neotropical	5059
Lejeunea laetevirens Nees & Mont.	5	1	–	–	–	6	Neotropical	5042
Lejeunea obidensis Spruce*	2	–	–	–	1	1	Brazilian Amazon	5279
Lejeunea phyllobola Nees & Mont.	2	–	–	–	–	2	Neotropical	5209
Lejeunea tapajosensis Spruce*	1	–	–	–	–	1	Neotropical	5198
Leptolejeunea elliptica (Lehm. & Lindenb.) Besch.	4	–	4	–	–	–	Neotropical	5000
Lopholejeunea subfusca (Nees) Schiffn.	8	7	–	–	4	11	Pantropical	5028
Microlejeunea bullata (Taylor) Steph.	1	2	1	–	–	2	Neotropical	5140
Microlejeunea epiphylla Bischl.	–	3	–	–	–	3	Neotropical	5489
Odontolejeunea lunulata (F.Weber) Schiffn.*	2	–	2	–	–	–	Afro-American	5151
Otigoniolejeunea huctumalcensis (Lindenb. & Gottsche) Y.M.Wei, R.L.Zhu & Gradst.*	6	–	1	–	1	4	Neotropical	5066
Pictolejeunea picta (Steph.) Grolle*	5	–	–	–	–	5	Neotropical	5054
Prionolejeunea denticulata (F.Weber) Schiffn.	1	–	–	–	–	1	Neotropical	5271
Prionolejeunea muricatoserrulata (Spruce) Steph.*	26	–	–	–	–	26	Neotropical	5003
Rectolejeunea versifolia (Schiffn.) L.Söderstr. & A.Hagborg	2	1	–	–	1	2	Neotropical	5007
Stictolejeunea balfourii (Mitt.) E.W.Jones*	9	13	–	–	3	19	Wide	5009
Stictolejeunea squamata (F.Weber) Schiffn.	72	5	–	–	9	68	Neotropical	4995
Symbiezidium transversale (Sw.) Trevis.	66	14	2	–	3	75	Neotropical	4995
Taxilejeunea obtusangula (Spruce) A.Evans*	13	–	1	–	1	11	Neotropical	5032
Thysananthus auriculatus (Wilson & Hook.) Sukkharak & Gradst.	2	2	–	–	1	3	Pantropical	5343
Xylolejeunea crenata (Nees & Mont.) X.L.He & Grolle*	4	–	–	–	4	–	Neotropical	5126
Plagiochilaceae	–	–	–	–	–	–	–	–
Plagiochila disticha (Lehm. & Lindenb.) Lehm. & Lindenb.*	2	–	–	–	–	2	Neotropical	5080
Plagiochila gymnocalycina (Lehm. & Lindenb.) Mont. & Nees*	2	–	–	–	–	2	Neotropical	5197
Plagiochila montagnei Nees	10	–	–	–	3	7	Neotropical	5146
Plagiochila raddiana Lindenb.*	1	1	–	–	–	2	Neotropical	5349
Radulaceae	–	–	–	–	–	–	–	–
Radula flaccida Lindenb. & Gottsche*	17	–	4	–	2	11	Afro-American	5000
Radula javanica Gottsche*	8	–	–	–	–	8	Pantropical	4999
Radula kegelii Steph.*	3	–	–	–	–	3	Neotropical	5112
Total Caviana (89 ssp.)	1102	-	36	7	249	810	–	–
Total Mexiana (50 ssp.)	–	329	–	2	55	272	–	–

diversity on Mexiana and 46% on Caviana. The family is the most diverse liverwort family in Brazil with 285 species (Costa & Peralta 2015) and may account for 70% of total liverwort diversity in tropical lowland rainforests (Gradstein *et al.* 2001). The high diversity of the genus *Lejeunea* on Caviana (10 spp.) concurs with its commonness in humid tropical lowland forests of Brazil (Costa & Peralta 2015), whereas the high diversity of *Calymperes* (Calymperaceae) on Mexiana coincides with its commonness in the Amaton basin. Here, Calymperaceae together with Sematophyllaceae, Fissidentaceae and Pilotrichaceae account for nearly 50% of the moss diversity (Gradstein *et al.* 2001). In addition, many other bryophyte species of Caviana and Mexiana are widely distributed in the forests of Amazonia (Santos & Lisboa 2008; Brito & Ilkiu-Borges 2013) and the common *Stictolejeunea squamata* and *Taxithelium planum* are very frequent species in *várzea* forests of the Eastern Amazon (Brito & Ilkiu-Borges 2013; Moura *et al.* 2013; Garcia *et al.* 2014).

New occurences and distribution patterns

The large number of new records for Marajó archipelago shows the importance of continuing the exploration of non-studied area in Amazonia. The newly recorded *Drepanolejeunea lichenicola* is a typical epiphyll known from montane to submontane environments in Mata Atlantica Forest (Bahia, Rio de Janeiro, São Paulo, Paraná). In addition, the species has been found at lowland elevation (below 500 m) in northern Amazonia (Costa *et al.* 2017). Although never collected in Pará state, the species has been recorded from submontane cloud forest of adjacent French Guiana (Gradstein & Ilkiu-Borges 2009). Its occurrence on Caviana, where it was growing on living leaves, is therefore not fully unexpected. *Eulacophyllum cultelliforme* and *Meteoridium remotifolium* had been reported for all Brazilian regions, but in the Northern region were known from Amazonas, Tocantins and Roraima (Costa & Peralta 2015).

The predominance of Neotropical species have been commonly reported in bryophyte surveys in Pará state (Garcia *et al.* 2014; Tavares-Martins *et al.* 2014; Fagundes *et al.* 2016). It was an expected result since the majority of the bryophytes of tropical America are distributed throughout the Neotropical region (Gradstein *et al.* 2001). Indeed, bryophytes have been shown to have a high capacity for dispersion over long distances even though community assembly is restricted by ecological filters rather than by dispersion limitation (Mota de Oliveira *et al.* 2009; Patiño & Vanderpoorten 2018).

As shown by Santos & Costa (2010) and others, most bryophytes of lowland and submontane rainforests are widely distributed. The very low endemism on Caviana and Mexiana, represented by a single endemic species, *Lejeunea obidensis*, could therefore be expected. Even so, the occurrence of this endemic species on the islands is important and underlines the necessity for conservation of the endangered ecosystems of the Marajó archipelago (Loyola *et al.* 2018).

Substrate preference

High diversity of substrates at the landscape level may explains up to 44% of the bryophyte richness (Lõhmus *et al.* 2007). In this study we found that about 90% of the bryophyte species were corticolous, with 37 species exclusively occurring on bark. High richness of corticolous epiphytes is characteristic of humid tropical forests and concurs with the high diversity of tree species in these habitats (Pócs 1982; Richards 1984). Recent studies have shown that these epiphytic communities are highly sensitive to environmental variation and disturbance (Gradstein 1992; Gradstein & Sporn 2010), showing the necessity of conservation of their habitats.

The occurrence of bryophytes on living leaves is a further characteristic of humid tropical forests (Richards 1984). Epiphyllous species are sensitive to local environmental conditions (Monge-Najera 1989; Zartman 2003); many of them are shade specialists and are the first to disappear when the vegetal cover of a forest is altered (Gradstein 1992, 1997). In this study, epiphyllous bryophytes exclusively occurred on Caviana island and were not seen on Mexiana. The restriction of epiphylls to Caviana together with the higher species diversity and exclusive occurrence of many species on this island (e.g. *Cololejeunea* spp., *Lejeunea* spp., *Fissidens* spp., *Pictolejeunea picta*, *Prionolejeunea* spp., *Radula* spp., *Zelometeorium patulum*) seems to indicate that habitat conditions on Caviana were more suitable for the establishment of bryophytes than on Mexiana. Future studies on the bryophyte diversity of these islands should include measurement of microclimatic conditions and other abiotic factors such as salinity.

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