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in different forests in the eastern Amazonia

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Exploring the diversity of bryophytes in different forests in the eastern Amazonia

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ABSTRACT

The Lower Tocantins region, which includes the municipality of Abaetetuba, is located in the north-eastern of Pará state, in Eastern Amazonia, Brazil, presenting a heterogeneous set of forests, among which Terra Firme, Várzea, and Freshwater Beach forests stand out for their floristic, economic, and ecological significance. However, the bryophyte flora is poorly known in the Lower Tocantins, with only 51 moss species reported for the region. This study aimed to investigate the richness and composition of bryophytes in different types of forests in Abaetetuba, Lower Tocantins River basin, Pará state, to contribute to the floristic knowledge of bryophytes in the region. Species diversity and exploratory analyses were conducted to understand the bryophyte communities in Terra Firme, Várzea, and Freshwater Beach forests. The bryophyte flora recorded in Abaetetuba comprises 103 species (36 mosses and 67 liverworts), including widely distributed species in the three forest types and species restricted mainly to Terra Firme forests. There were two new records, one for South America (*Cololejeunea setiloba* A. Evans) and another for the state of Pará (*Leptolejeunea radicata* (Mont.) Grolle). The richness and composition of species in Terra Firme and Freshwater Beach forests align with what has been reported in studies conducted in the Lower Amazon, but yielded discrepant results from previous studies in Várzea forests. Regarding the colonization of substrates, the complexity of the structure of the communities increased from Freshwater Beach forests to Várzea and Terra Firme forests, in this order, with the appearance of terricolous species in Várzea forests and of species colonizing termite mounds in Terra Firme forests. These findings indicate that Amazonian environments, their biodiversity, and the distribution pattern of species can be better understood through the exploration of new areas.

KEY WORDS

Brazil,
Freshwater Beach forest,
Terra Firme forest,
Várzea forest,
liverworts,
mosses.

RÉSUMÉ

Explorer la diversité des bryophytes dans différentes forêts de l'est de l'Amazonie.

La région du Bas Tocantins, qui comprend la municipalité d'Abaetetuba, est située au nord-est de l'état de Pará, en Amazonie orientale, au Brésil. Elle présente un ensemble hétérogène de forêts, parmi lesquelles les forêts de Terra Firme, Várzea et Freshwater Beach se distinguent par leur importance floristique, économique et écologique. Cependant, la flore bryophytique est mal connue dans le Bas Tocantins, avec seulement 51 espèces de mousses signalées pour la région. Cette étude visait à étudier la richesse et la composition des bryophytes dans différents types de forêts d'Abaetetuba, bassin du fleuve Tocantins inférieur, état du Pará, afin de contribuer à la connaissance floristique des bryophytes dans la région. La diversité des espèces a été étudiée et des analyses exploratoires ont été menées pour comprendre les communautés de bryophytes dans les forêts de Terra Firme, Várzea et Freshwater Beach. La flore bryophytique enregistrée à Abaetetuba comprend 103 espèces (36 mousses et 67 hépatiques), y compris des espèces largement réparties dans les trois types forestiers et des espèces limitées principalement aux forêts de Terra Firme. Il y a deux nouveaux signalements, un pour l'Amérique du Sud (*Cololejeunea setiloba* A.Evans) et un autre pour l'état du Pará (*Leptolejeunea radicata* (Mont.) Grolle). La richesse et la composition des espèces des forêts de Terra Firme et de Freshwater Beach sont compatibles avec ce qui a été rapporté dans les études menées dans la basse Amazonie, mais ont donné des résultats divergents par rapport aux études précédentes dans les forêts de Várzea. En ce qui concerne la colonisation des substrats, la complexité de la structure des communautés a augmenté depuis les forêts de Freshwater Beach jusqu'aux forêts de Várzea et Terra Firme, dans cet ordre, avec l'apparition d'espèces terricoles dans les forêts de Várzea et d'espèces colonisant les termitières dans les forêts de Terra Firme. Ces résultats indiquent que les environnements amazoniens, leur biodiversité et le modèle de répartition des espèces peuvent être mieux compris grâce à l'exploration de nouvelles zones.

MOTS CLÉS
Brésil,
Freshwater Beach,
forêt de Terra Firme,
forêt de Várzea,
hépatiques,
mousses.

INTRODUCTION

The Lower Tocantins region, one of the earliest areas colonized in Pará state, encompasses 11 municipalities. It is part of the Tocantins-Araguaia Basin, one of the most significant river basins in Brazil, second only to the Amazon River basin (Almeida 2010). The vegetation in the Lower Tocantins region comprises a diverse array of forests, including Terra Firme (upland) forests, Várzea (flooded) forests, and Freshwater Beach forests (Amaral *et al.* 2002).

Terra Firme forests constitute approximately 85% of the Amazonia (Pires 1973; IBGE 2012). This ecosystem is characterized by the prevalence of tall trees (over 25 m in height), closed canopy, open understory, and high biomass. It is distinguished by diverse flora, featuring medium to large leafy species in areas unaffected by flooding during rains or periodic river floods (Pires 1973; IBGE 2012). Comparatively, Terra Firme forests exhibit a high richness of bryophyte species when contrasted with other types of Amazonian forests, ranging from 99 to 133 species (Tavares-Martins *et al.* 2014; Takashima-Oliveira *et al.* 2020). This discrepancy is attributed to high humidity, shading, and high substrate variety, which collectively favor the establishment of bryophytes (Souza & Lisboa 2005).

Várzea forests are located on the banks of rivers in the Amazon estuary, where they are flooded daily due to the influence of river fluctuations and tidal dynamics. This forest type holds significant economic potential through the extraction of valu-

able plant resources such as açai (*Euterpe oleracea* Mart.), rubber tree (*Hevea brasiliensis* (A.Juss.) Müll. Arg.), andiroba (*Carapa guianensis* Aubl.), and timber (Anderson & Jardim 1989). Várzea forests also exhibit a notable richness of bryophytes, ranging from 33 to 72 species (Brito & Ilkiu-Borges 2013; Moura *et al.* 2013), second only to the Terra Firme forests (Souza & Lisboa 2005, 2006). The flood dynamics favor the occurrence of morphologically specialized taxa, such as *Lejeunea combuensis* O.S.Moura, Ilk.-Borg. & Reiner-Drehwald, an endemic species from Pará, only known from this type of vegetation (Moura *et al.* 2012; Bastos & Gradstein 2020a).

Freshwater Beaches, also located on the banks of rivers, have pioneer vegetation in short, narrow areas, adapted to constant sand deposition (Amaral *et al.* 2002). Studies on the bryophyte flora in Freshwater Beaches solely focused on mosses (18 species) and are limited to the municipality of Barcarena in Pará state (Souza & Lisboa 2005, 2006).

Few studies on the diversity of bryophytes have been conducted in the Lower Tocantins region. There are records of only 51 mosses in the municipality of Barcarena by Souza & Lisboa (2005, 2006) in addition to sparse records made by Reimers (1933) and samples deposited in herbaria of the region, such as the João Murça Pires Herbarium (MG) in Museu Paraense Emílio Goeldi and the Herbarium of the Federal Institute of Pará (HIFPA) – Abaetetuba campus. This corresponds to 18.7% of the known bryophytes in Pará. Surveys on the biodiversity in the region are, therefore, sorely needed to support conservation strategies.

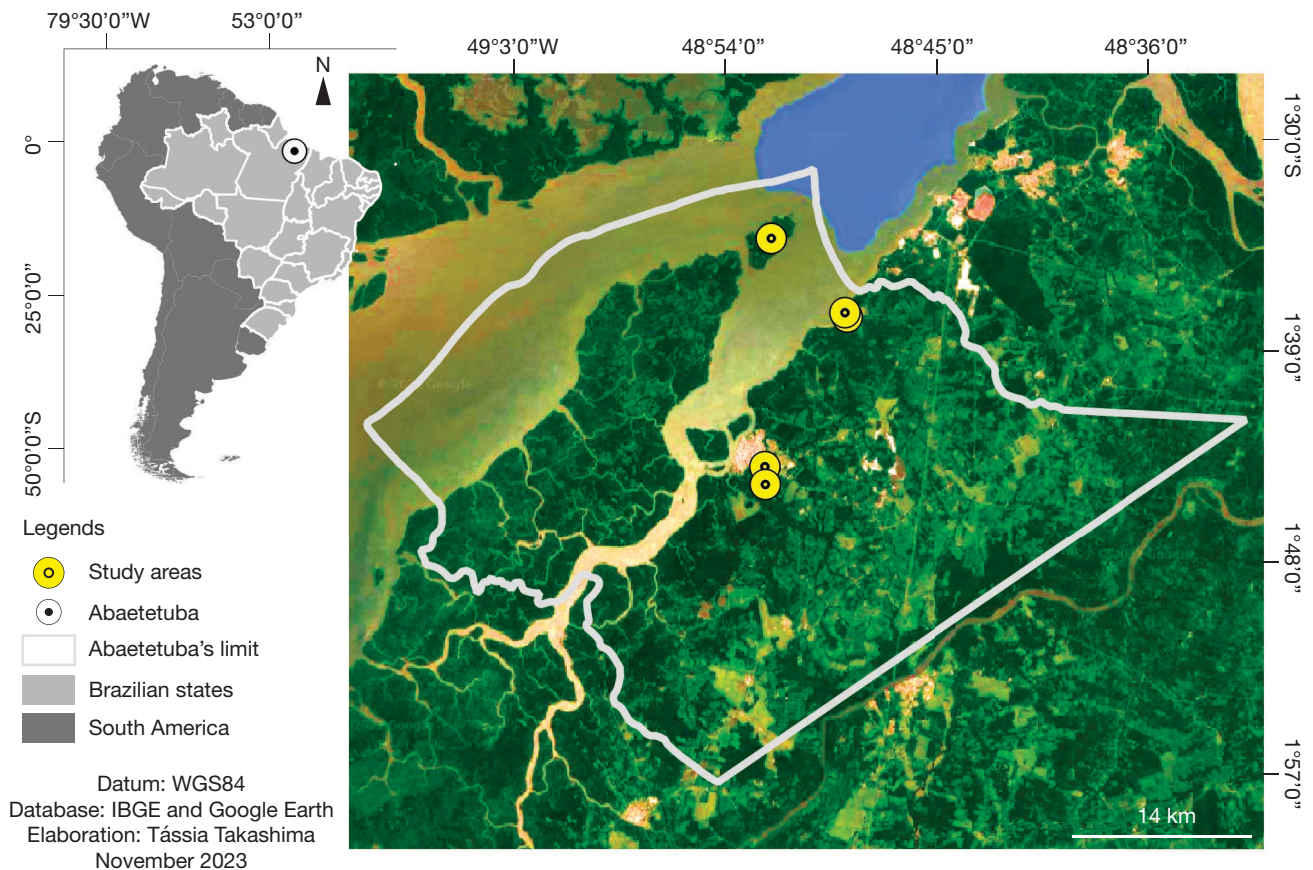


FIG. 1. — Location map of collection points in the municipality of Abaetetuba, Lower Tocantins.

This study aimed to investigate the richness and composition of bryophytes in different types of forests in Abaetetuba, Lower Tocantins River basin, Pará state, to contribute to the floristic knowledge of bryophytes in the region.

MATERIAL AND METHODS

The municipality of Abaetetuba covers an area of 1 610 652 km² and is located in the northeast of the state of Pará (FAPESPA 2022) (Fig. 1). Abaetetuba has a super-humid equatorial climate with an annual rainfall of around 2000 mm, with the rainy season running from January to June, and the drier season during the last few months of the year (FAPESPA 2022). The region is composed of Terra Firme, Várzea (daily flooded), Igapó (seasonally flooded), mangrove, and Freshwater Beach forests (FAPESPA 2022). Because of their abundance and ecological importance to the region, three types of forests were selected for the study in the municipality of Abaetetuba: Terra Firme forest (TF), located in Laranjal Environmental Reserve, Sororocando no Mato Private Reserve of Natural Heritage, and Capim Island; Várzea forest (VF), located in Vila de Beja Environmental Forest and Capim Island; and Freshwater Beach forest (FB), in Beja Beach.

The Terra Firme forest studied has a prevalence of medium to large broad-leaved species, such as *Astrocaryum gynacanthum*

Mart. and *Dinizia excelsa* Ducke (Fig. 2A), with stratified vegetation in the understory, canopy, and emergent trees.

The Várzea forest studied covered formations established along the tributaries at the mouth of the Tocantins River, in the plains of the Amazon estuary, thus being subject to daily flooding due to the influence of tidal dynamics (Lima 1956). In this specific forest, there was a frequent presence of *Hilairanthus schauerianus* (Moldenke) Cornejo, a typical mangrove species, and *Euterpe oleracea* (Fig. 2C, D). Although açai (*E. oleracea*) is a common palm tree in Várzea forest, it was intensively managed in the study area with > 200 clumps/ha (Freitas *et al.* 2021).

Freshwater Beach had herbaceous stratum in areas formations established on the banks of the mouth of the Tocantins River (Souza & Lisboa 2006; IBGE 2012), with species adapted to soils with continuous sand deposition, such as *Mauritia flexuosa* L. and *Prunus domestica* L. (Fig. 2B).

According to the structure of the vegetation (plant stratification and biomass), TF presents the highest degree of structural complexity of the forest, followed by VF and FB.

Bryophytes were collected between October 12 and 16, 2020, by the free-walking method. This method involves following imaginary transects and collecting all the species found along the lines covered (Filgueiras *et al.* 1994). The collection effort engaged four people, walking for approximately 9 hours and covering an average area of 20 hectares

in each forest. Bryophytes were collected up to 1.5 m from the ground in each forest type. Samples from all possible substrates colonized by bryophytes were collected. The collection and herborization procedures followed the methodology described by Glime (2017).

The species were classified in accordance to the colonized substrate into corticolous (growing on living trunk), epixylic (growing on dead trunk), terricolous (growing on soil), rupicolous (growing on rocks), epiphyllous (growing on living leaves) and species growing on termite mounds (Robbins 1952; Brito & Ilkiu-Borges 2013).

Species were identified using specialized literature (Buck 2003; Gradstein & Costa 2003; Gradstein & Ilkiu-Borges 2009; Bordin & Yano 2013; Bastos & Gradstein 2020a, 2020b; Gradstein 2021; Oliveira-da-Silva *et al.* 2021). The taxonomic classification follows Goffinet *et al.* (2009) for mosses (Bryophyta), with updates for Sematophyllaceae (Carvalho-Silva *et al.* 2017), and Crandall-Stotler *et al.* (2009) for liverworts (Marchantiophyta), with adaptations for *Dibrachiella* (Spruce) X.Q.Shi, R.L.Zhu & Gradst. (Shi & Zhu 2015) and *Thysananthus* Lindenb. (Sukkharak & Gradstein 2017). The identified material was herborized and incorporated into the MG Herbarium (acronym based on the Index Herbariorum).

The species diversity in each forest (TF, VF, and FB) was analyzed considering three distinct indices, expressed according to Hill's numbers collectively as q -values (Hill 1973; Chao *et al.* 2014). The first metric used was species richness ($q = 0$), representing the count of unique species in each forest. The second metric applied was Shannon diversity ($q = 1$), a widely used metric that explores the relationship between species richness and evenness, placing less weight on dominant species (Zhang *et al.* 2012; Schang *et al.* 2022). The third metric used was inverse Simpson ($q = 2$), which simultaneously considers species richness and evenness while incorporating weighting for dominant species.

The q -values and corresponding indices were graphically depicted as diversity profile curves, including Hill's numbers as a function of order q (Chao *et al.* 2014). The slope of the resulting curve means the unevenness of species relative abundances; a steeper decline indicates a more uneven distribution of relative abundances. Conversely, a constant curve at the species richness level implies complete evenness in relative abundances (Chao *et al.* 2014).

Exploratory analyses to visualize the species richness of each forest and substrate were carried out using the Venn diagrams, as implemented in the packages *Vennuler*, and *UpSetR* packages in R v. 4.3.1 software (R Core Team 2023).

RESULTS

A total of 2388 occurrences of 103 species distributed in 42 genera and 14 families were identified, with one species being endemic to Brazil (*Cheilolejeunea savannae* L.P.C.Macedo, Ilk.-Borg. & C.J.Bastos) (Table 1). The species diversity profile curves plotted for the three forest types (Fig. 3) illustrate that TF exhibited the highest richness (89 species) with 85% of the

total number of occurrences (2041 specimens), followed by VF (42 species/262 specimens) and FB (27 species/85 specimens).

TF exhibited the highest species diversity profile as measured by Hill numbers, followed by VF and FB (Fig. 3). However, TF displayed the steepest slope in the species diversity profile, reflecting a more uneven distribution of relative abundance among species. In VF and FB, the slope of the curve showed a more linear pattern, indicating an increased uniformity in the relative abundances of species in these communities.

About 14% (15 spp.) of the recorded species occurred concomitantly in the three types of forests, while about 24% (25 spp.) occurred in two types of forests (Fig. 4). TF and VF shared the higher number of species (18 spp.). TF forest presented the highest number of restricted species (51 spp.), that is, species occurring only in this type of forest (Fig. 4). *Cheilolejeunea rigidula* (Mont.) R.M.Schust. and *Lejeunea laetevirens* Nees & Mont. stood out with more than five occurrences in each studied forest. Among the restricted species, *Microcalpe subsimplex* (Hedw.) W.R.Buck stood out with 106 occurrences in TF and the genus *Radula* Dumort. was recorded only in TF. Seven and five species were restricted to VF and FB, respectively (Fig. 4).

Liverworts were more representative in the number of species and occurrences (68 spp./1721 specimens) compared to mosses (36 spp./667 specimens). The same pattern was observed in terms of number of occurrences: TF presented 1431 specimens of liverworts and 610 of mosses. In all forests, the richness of liverworts exceeded that of mosses by nine to 21 species; most significant difference was observed in TF (55 spp. of liverworts/34 spp. of mosses) and the lowest in FB (18 spp. of liverworts/9 spp. of mosses).

Lejeuneaceae was most species-rich and most abundant family in TF (49 spp./1399 specimens) and VF (28 spp./227 specimens) and the only family of liverworts recorded in FB, with 18 species and 56 occurrences. Six families – Leucobryaceae, Leucomiaceae, Pilotrichaceae, Thuidiaceae, Calypogeiaceae, and Radulaceae – were registered only in TF. No family was exclusive to VF and FB.

Cololejeunea (Spruce) Steph. was the genus with the highest number of species (8 spp./268 specimens), while *Ceratolejeunea* (Spruce) J.B.Jack & Steph. was the most abundant (7 spp./353 specimens) in TF. In VF, *Ceratolejeunea* and *Lejeunea* Lib. were the species-richest and most abundant genera with four species in 37 occurrences each. *Cheilolejeunea* (Spruce) Steph. stood out in FB with three species and 26 occurrences.

Cheilolejeunea rigidula was the most abundant liverwort species in all studied forests (TF: 210 specimens; VF: 34 specimens; FB: 19 specimens) and, among mosses, *Calymperes erosum* Müll. Hall. was the most abundant in TF (110 specimens) and VF (11 specimens), and *Calymperes palisotii* Schwägr. in FB (7 specimens).

Two new occurrences were found in this study: *Cololejeunea setiloba* A.Evans is being reported for the first time in South America, collected in TF (one specimen) and VF (two specimens); *Leptolejeunea radicosa* (Mont.) Grolle is a new record for the state of Pará, recorded only in TF (29 specimens) (Fig. 5). Both species were colonizing living tree trunk and leaf.



FIG. 2. — Types of forests and substrates of bryophytes in the municipality of Abaetetuba, Lower Tocantins: **A**, Terra Firme forest; **B**, Freshwater Beach; **C, D**, Várzea forest; **E**, bryophytes on the trunk of a living tree; **F**, liverwort on decaying wood; **G**, *Radula flaccida* Lindenb. & Gottsche on a leaf.

TABLE 1. — Bryophytes from the forests of Terra Firme (TF), Várzea (VF), and Freshwater Beach (FB) in Abaetetuba, Lower Tocantins. Abbreviations: **Co**, corticolous; **Ep**, epiphyllous; **Ex**, epixylic; **Ru**, rupicolous; **Te**, terricolous; **Tm**, termite mound; **P**, A. K. Sousa-Pereira. Symbols: *, new to Pará state; **, new to South America.

Taxa	Occurrences	Environment			Substrat						Voucher
		TF	VF	FB	Co	Ex	Ep	Te	Tm	Ru	
BRYOPHYTA											
Calymperaceae											
<i>Calymperes erosum</i> Müll. Hal.	124	110	11	3	90	34	–	–	–	–	P98
<i>C. lonchophyllum</i> Schwägr.	24	23	1	–	24	–	–	–	–	–	P119
<i>C. palisotii</i> Schwägr.	13	2	4	7	9	4	–	–	–	–	P166
<i>C. rubiginosum</i> (Mitt.) W.D.Reese	9	9	–	–	9	–	–	–	–	–	P176
<i>Octoblepharum albidum</i> Hedw.	69	62	2	5	52	16	–	–	1	–	P787
<i>O. cocuiense</i> Mitt.	3	3	–	–	2	1	–	–	–	–	P443
<i>O. cylindricum</i> Mont.	20	20	–	–	19	–	–	1	–	–	P245
<i>O. pulvinatum</i> (Dozy & Molk.) Mitt.	8	8	–	–	8	–	–	–	–	–	P107
<i>Syrrhopodon africanus</i> (Mitt.) Paris subsp. <i>graminicola</i> (R.S.Williams) W.D.Reese	13	13	–	–	8	5	–	–	–	–	P299
<i>S. cryptocarpus</i> Dozy & Molk.	15	15	–	–	12	3	–	–	–	–	P394
<i>S. elatus</i> Mont.	14	14	–	–	12	2	–	–	–	–	P651
<i>S. hornsuschii</i> Mart.	2	1	1	–	1	1	–	–	–	–	P240
<i>S. ligulatus</i> Mont.	3	2	1	–	2	1	–	–	–	–	P274
Fissidentaceae											
<i>Fissidens elegans</i> Brid.	7	7	–	–	7	–	–	–	–	–	P625
<i>F. flaccidus</i> Mitt.	1	–	1	–	–	–	–	1	–	–	P772
<i>F. hornsuschii</i> Mont.	1	1	–	–	1	–	–	–	–	–	P120
<i>F. ornatus</i> Herzog	4	4	–	–	3	1	–	–	–	–	P112
<i>F. pellucidus</i> Hornsch.	11	9	2	–	7	2	–	2	–	–	P176
<i>F. zollingeri</i> Mont.	1	–	–	1	–	–	–	–	–	1	P764
Leucobryaceae											
<i>Campylopus savannarum</i> (Müll. Hal.) Mitt.	1	1	–	–	–	–	–	1	–	–	P761
Leucomiaceae											
<i>Leucomium strumosum</i> (Hornsch.) Mitt.	28	28	–	–	18	10	–	–	–	–	P181
Pilotrichaceae											
<i>Callicostella pallida</i> (Hornsch.) Ångstr.	2	2	–	–	–	2	–	–	–	–	P268
<i>C. rufescens</i> (Mitt.) A.Jaeger	3	3	–	–	1	2	–	–	–	–	P92
Pylaisiadelphaceae											
<i>Isopterygium subbrevisetum</i> (Hampe) Broth.	12	12	–	–	10	2	–	–	–	–	P625
<i>I. tenerifolium</i> Mitt.	9	9	–	–	4	5	–	–	–	–	P148
<i>I. tenerum</i> (Sw.) Mitt.	7	7	–	–	4	3	–	–	–	–	P140
<i>Pterogonidium pulchellum</i> (Hook.) Broth.	18	14	–	4	11	7	–	–	–	–	P138
<i>Taxithelium planum</i> (Brid.) Mitt.	32	31	1	–	22	9	–	1	–	–	P281
<i>T. pluripunctatum</i> (Renauld & Cardot) W.R.Buck	8	7	1	–	4	3	–	1	–	–	P428
Sematophyllaceae											
<i>Brittonodoxa subpinnata</i> (Brid.) W.R.Buck, P.E.A.S.Câmara & Carv.-Silva	19	13	–	6	16	3	–	–	–	–	P160
<i>Microcalpe subsimplex</i> (Hedw.) W.R.Buck	106	106	–	–	59	47	–	–	–	–	P107
<i>Meiothecium boryanum</i> (Müll. Hal.) Mitt.	1	1	–	–	–	1	–	–	–	–	P299
<i>Trichosteleum papillosum</i> (Hornsch.) A.Jaeger	29	25	3	1	9	20	–	–	–	–	P545
<i>T. subdemissum</i> (Besch.) A.Jaeger	20	19	–	1	10	10	–	–	–	–	P167
Stereophyllaceae											
<i>Pilosium chlorophyllum</i> (Hornsch.) Broth.	25	24	–	1	8	16	–	–	–	1	P123
Thuidiaceae											
<i>Pelekium scabrosulum</i> (Mitt.) Touw	5	5	–	–	4	1	–	–	–	–	P119
MARCHANTIOPHYTA											
Calypogeiaceae											
<i>Calypogeia miquelii</i> Gottsche, Lindenb. & Nees	1	1	–	–	–	–	–	1	–	–	P230
Frullaniaceae											
<i>Frullania cuencensis</i> Taylor	1	–	1	–	1	–	–	–	–	–	P561
<i>F. gibbosa</i> Nees	1	–	1	–	–	1	–	–	–	–	P617
<i>F. riojaneirensis</i> (Raddi) Ångstr.	2	2	–	–	–	2	–	–	–	–	P416
<i>F. subtilissima</i> (Mont.) Lindenb.	1	1	–	–	–	1	–	–	–	–	P395
Lejeuneaceae											
<i>Acrolejeunea torulosa</i> (Lehm. & Lindenb.) Schiffn.	1	–	–	1	1	–	–	–	–	–	P801
<i>Archilejeunea badia</i> (Spruce) Steph.	1	–	1	–	1	–	–	–	–	–	P594
<i>A. juliformis</i> (Nees) Gradst.	24	24	–	–	21	3	–	–	–	–	P109
<i>Ceratolejeunea coarina</i> (Gottsche) Schiffn.	113	104	8	1	76	14	23	–	–	–	P143
<i>C. confusa</i> R.M.Schust.	26	26	–	–	20	6	–	–	–	–	P319
<i>C. cornuta</i> (Lindenb.) Steph.	183	156	26	1	133	29	21	–	–	–	P817
<i>C. cubensis</i> (Mont.) Schiffn.	5	5	–	–	3	1	1	–	–	–	P108
<i>C. guianensis</i> (Nees & Mont.) Steph.	17	15	2	–	9	7	1	–	–	–	P113
<i>C. laetefusca</i> (Austin) R.M.Schust.	1	1	–	–	1	–	–	–	–	–	P237
<i>C. minuta</i> G.Dauphin	47	46	1	–	41	4	2	–	–	–	P226

Table 1. — Continuation.

Taxa	Occurrences	Environment			Substrat						Voucher
		TF	VF	FB	Co	Ex	Ep	Te	Tm	Ru	
<i>Cheilolejeunea acutangula</i> (Nees) Grolle	1	1	–	–	1	–	–	–	–	–	P259
<i>C. adnata</i> (Lehm.) Grolle	21	21	–	–	17	3	1	–	–	–	P143
<i>C. adnata</i> var. <i>autoica</i> Gradst. & Ilk.-Borg.	4	4	–	–	2	2	–	–	–	–	P115
<i>C. aneogyna</i> (Spruce) A.Evans	7	7	–	–	7	–	–	–	–	–	P463
<i>C. holostipa</i> (Spruce) Grolle & R.L.Zhu	4	4	–	–	3	1	–	–	–	–	P439
<i>C. lobulata</i> (Lindenb.) C.J.Bastos & Gradst.	1	1	–	–	1	–	–	–	–	–	463
<i>C. rigidula</i> (Mont.) R.M.Schust.	263	210	34	19	205	44	14	–	–	–	P274
<i>C. savannae</i> L.P.Macedo, Ilk.-Borg. & C.J.Bastos	4	–	–	4	4	–	–	–	–	–	P789
<i>C. trifaria</i> (Reinw., Blume & Nees) Mizut.	3	–	–	3	3	–	–	–	–	–	P814
<i>C. uncioloba</i> (Lindenb.) Malombe	2	–	2	–	–	2	–	–	–	–	P575
<i>Cololejeunea camillei</i> (Lehm.) A.Evans	38	38	–	–	3	1	34	–	–	–	P177
<i>C. cardiocarpa</i> (Mont.) A.Evans	71	69	1	1	4	1	66	–	–	–	P91
<i>C. crenata</i> (A.Evans) Pócs	4	4	–	–	–	–	4	–	–	–	P634
<i>C. diaphana</i> A.Evans	23	23	–	–	1	1	21	–	–	–	P672
<i>C. panamensis</i> G.Dauphin & Pócs	15	15	–	–	1	2	12	–	–	–	P673
<i>C. setiloba</i> A.Evans**	3	1	2	–	1	–	2	–	–	–	P756
<i>C. subcardiocarpa</i> Tixier	70	68	1	1	3	–	67	–	–	–	P99
<i>C. surinamensis</i> Tixier	50	50	–	–	4	1	45	–	–	–	P104
<i>Cyclolejeunea convexistipa</i> (Lehm. & Lindenb.) A.Evans	3	3	–	–	–	–	3	–	–	–	P288
<i>Dibrachiella auberiana</i> (Mont.) X.Q.Shi, R.L.Zhu & Gradst.	3	1	2	–	–	2	1	–	–	–	P568
<i>Diplasiolejeunea brunnea</i> Steph.	2	2	–	–	–	–	2	–	–	–	P431
<i>D. unidentata</i> (Lehm. & Lindenb.) Schiffn.	1	–	–	1	–	1	–	–	–	–	P807
<i>Drepanolejeunea fragilis</i> L. Söderstr., A.Hagborg & von Konrat	27	25	1	1	13	6	8	–	–	–	P455
<i>Harpalejeunea oxyphylla</i> (Nees & Mont.) Steph.	9	9	–	–	7	2	–	–	–	–	P213
<i>H. stricta</i> (Lindenb. & Gottsche) Steph.	7	7	–	–	4	–	3	–	–	–	P366
<i>Lejeunea adpressa</i> Nees	11	5	6	–	8	2	1	–	–	–	P430
<i>L. boryana</i> Mont.	6	6	–	–	6	–	–	–	–	–	P176
<i>L. controversa</i> Gottsche	2	2	–	–	1	1	–	–	–	–	P189
<i>L. flava</i> (Sw.) Nees	55	55	–	–	38	7	10	–	–	–	P295
<i>L. glaucescens</i> Gottsche	49	36	12	1	10	36	2	1	–	–	P371
<i>L. laetevirens</i> Nees & Mont.	109	80	18	11	94	9	6	–	–	–	P370
<i>L. phyllobola</i> Nees & Mont.	4	3	1	–	3	1	–	–	–	–	P642
<i>Leptolejeunea elliptica</i> (Lehm. & Lindenb.) Besch.	11	9	1	1	1	–	10	–	–	–	P455
<i>L. radicata</i> (Mont.) Grolle*	22	22	–	–	–	–	22	–	–	–	P178
<i>Lopholejeunea nigricans</i> (Lindenb.) Schiffn.	22	–	21	1	22	–	–	–	–	–	P563
<i>L. subfusca</i> (Nees) Schiffn.	32	13	14	5	21	11	–	–	–	–	P184
<i>Microlejeunea epiphylla</i> Bischl.	9	6	1	2	7	–	2	–	–	–	P302
<i>Myriocoleopsis minutissima</i> subsp. <i>myriocarpa</i> (Nees & Mont.) R.L.Zhu, Y.Yu & Pócs	2	1	–	1	1	–	1	–	–	–	P830
<i>Otigonolejeunea huctumalcensis</i> (Lindenb. & Gottsche) Y.M.Wei, R.L.Zhu & Gradst.	39	39	–	–	37	1	1	–	–	–	P97
<i>Prionolejeunea denticulata</i> (F.Weber) Schiffn.	15	15	–	–	15	–	–	–	–	–	P119
<i>Pycnolejeunea contigua</i> (Nees) Grolle	6	5	1	–	4	2	–	–	–	–	P396
<i>P. macroloba</i> (Nees & Mont.) Schiffn.	2	2	–	–	–	2	–	–	–	–	P308
<i>Rectolejeunea emarginuliflora</i> (Schiffn.) A.Evans	83	64	19	–	64	9	10	–	–	–	P548
<i>R. flagelliformis</i> A.Evans	32	29	3	–	23	3	6	–	–	–	P273
<i>Stictolejeunea balfourii</i> (Mitt.) E.W.Jones	15	–	14	1	10	3	–	1	–	1	P589
<i>S. squamata</i> (F.Weber) Schiffn.	17	–	17	–	14	3	–	–	–	–	P544
<i>Symbiezidium barbiflorum</i> (Lindenb. & Gottsche) A.Evans	25	14	11	–	24	1	–	–	–	–	P98
<i>Thysananthus plicatiflorus</i> (Spruce) Sukkharak & Gradst.	4	–	4	–	3	1	–	–	–	–	P572
<i>Xylolejeunea crenata</i> (Nees & Mont.) X.L.He & Grolle	56	53	3	–	17	39	–	–	–	–	P95
Plagiochilaceae											
<i>Plagiochila disticha</i> (Lehm. & Lindenb.) Lehm. & Lindenb.	8	3	5	–	7	1	–	–	–	–	P453
Radulaceae											
<i>Radula flaccida</i> Lindenb. & Gottsche	17	17	–	–	3	–	14	–	–	–	P447
<i>R. javanica</i> Gottsche	8	8	–	–	7	1	–	–	–	–	P447
Total specimens	2388	2041	262	85	1477	481	416	10	1	3	–
Total species	103	89	42	27	87	70	32	9	1	3	–

Regarding substrates, corticolous species were more representative in terms of the total number of species (87 spp.) and number of exclusive species (17 spp.), that is, species that occurred exclusively on one type of substrate (Fig. 6A). However, a substantial proportion (c. 33%) of the total number

of species occurring in soil and rocks were exclusive on these substrates. The only species recorded on termite mounds (*Octoblepharum albidum* Hedw.) was also recorded on living and decaying trunks, and thus there were no exclusive species on termite mounds. A higher number of species shared

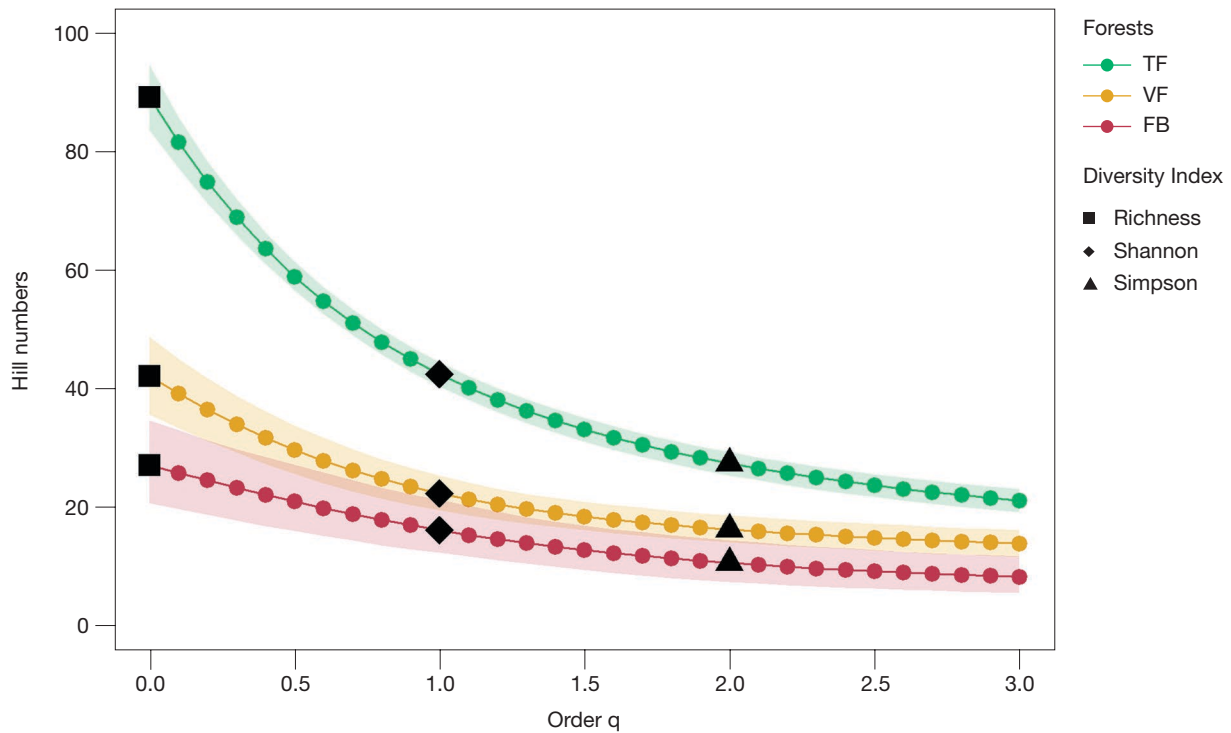


FIG. 3. — Diversity profile curves plotting the species diversity of Terra Firme (TF), Várzea (VF), and Freshwater Beach (FB) forests as a function of q -order values. **Coloured dots** represent Hill numbers: species richness ($q=0$), Shannon diversity ($q=1$), and inverse Simpson diversity ($q=2$). The slope of the curve reflects the uniformity of relative species abundances (e.g. a steeper curve indicates a more uneven distribution of relative abundances).

among different substrates was on living and decaying trunks (35 spp.), followed by living and decaying trunks, and living leaves (19 spp.) (Fig. 6A).

Lejeunea glaucescens Gottsche and *Stictolejeunea balfourii* (Mitt.) E.W.Jones colonized the greatest diversity of substrates, growing on four types of substrates (Fig. 6B). However, the former showed a preference for decaying trunk and the latter for living trunk.

The complexity of the structure of the communities based on substrate types colonized increased in this order: FB, VF, and TF (Fig. 6C). In FB, the species colonized four types of substrates, with predominance of corticolous species over epixylic, epiphyllous and rupicolous species. In VF, terricolous species were already recorded, and the epixylic community became richer and similar to the corticolous community. Species colonizing termite mounds were only observed in TF, where the terrestrial community was reduced, and the epixylic community became even more pronounced and similar to the corticolous community. The epiphyllous community was more representative in TF and showed some similarity with the corticolous community in all forests (Fig. 6C).

DISCUSSION

SPECIES RICHNESS AND ABUNDANCE

The structure of the vegetation and the availability of substrates were likely the most relevant factors determining the high diversity of bryophytes in TF and the lower frequency

of species records in VF and FB (Holz *et al.* 2002; Souza & Lisboa 2005). In TF, medium to large tree species prevail, promoting shading, higher humidity, and greater availability of substrates colonized by bryophytes. These factors may explain the pattern of higher richness observed in TF in this study and among others carried out in the Amazonian region (e.g. Souza & Lisboa 2005; Fagundes *et al.* 2016). We observed that bryophyte communities in TF follow the floristic pattern observed for vascular plants reported in the Amazonian Terra Firme forest, exhibiting high species richness with abundant rare species (Leitão Filho 1987).

In addition to the lower structural complexity when compared to TF, a factor that influences the availability of substrate for bryophyte colonization, the VF studied also exhibited a predominance of *Euterpe oleracea* (açai), a common palm tree in the Amazon estuary's floodplain areas that is extensively managed for fruit consumption and commercialization in the region (Arima *et al.* 1998; Freitas *et al.* 2021). The stem of this species is practically smooth, which results in lower water retention and, consequently, a less favorable surface for bryophyte propagules to establish and grow (Frahm *et al.* 2003). The small stem diameter (12 to 18 cm; Oliveira *et al.* 2000) is also a factor that may have influenced the richness and composition of the epiphytic bryophyte community (Holz *et al.* 2002). Other possible contributing factors are the flood dynamics in VF associated with the exploitation of açai fruit. Therefore, the richness found in the present study area does not correspond to that reported in other VF areas in Amazonia (e.g. Souza & Lisboa 2005; Moura *et al.* 2013; Ilkiu-Borges *et al.* 2020).

In FB, we observed the forest with the most open vegetation in this study. It is likely that some factors, such as low humidity, exposure to air currents, high intensity of sunlight, and high temperatures, further limited the colonization of bryophytes (Vitt & Belland 1997; Souza & Lisboa 2005; Tng *et al.* 2009).

About 14% of the recorded species showed wide ecological amplitude, growing in areas with extreme and hostile forest characteristics (e.g. high light intensity in FB, very shaded area in TF, flood dynamics in VF). However, only *Cheilolejeunea rigidula* and *Lejeunea laetevirens* showed greater ability to establish and form populations in the three forests, considering a minimum occurrence of five records in each forest. Both species have high phenotypic plasticity and morphological adaptations (e.g. well-developed lobules and vegetative reproduction, respectively) (Ilkiu-Borges 2000; Gradstein 2021), improving their ability to colonize various types of forests and substrates.

Terra Firme and Várzea forests share more similar microclimatic conditions such as high humidity and low to moderate intensity of sunlight, which may have favored the greater sharing of species between these two forests (Moura *et al.* 2013; Fagundes *et al.* 2016). The higher number of species restricted to TF confirms that bryophytes preferably inhabit humid and shaded forests (Gradstein *et al.* 2001; Holz *et al.* 2002; Tng *et al.* 2009) without the stress imposed by floods.

Many authors consider *Microcalpe subsimplex* as a generalist species (e.g. Fagundes *et al.* 2016; Takashima-Oliveira *et al.* 2020). In this study, however, *M. subsimplex* had a preference for TF and occurred only on living (59 occurrences) or decaying (47 occurrences) trunks. Most representatives of the genus *Radula* were mostly epiphyllous in humid and shaded forests (Oliveira-da-Silva *et al.* 2021). *Radula flaccida* Lindenb. & Gottsche is a species indicator of primary forests in the Brazilian Amazonia (Takashima-Oliveira *et al.* 2020), which explains the occurrence of the genus *Radula* only in TF in the present study.

The predominance of liverworts over mosses, observed in the three forests studied, is common in floristic inventories of bryophytes in the neotropical region (e.g. Gradstein & Pócs 1989; Gradstein *et al.* 2001) and Amazonian lowland forests (e.g. Moura *et al.* 2013; Ilkiu-Borges *et al.* 2020).

Lejeuneaceae is one of the most diverse families of bryophytes in Amazonia (Gradstein *et al.* 2001) and it is constantly reported as the most well-represented in surveys of bryophytes in the state of Pará (e.g. Takashima-Oliveira *et al.* 2020; Souza *et al.* 2021). The wide ecological range of Lejeuneaceae (Mota-de-Oliveira 2018) can be attributed to the high diversity of species (about 1900 species estimated worldwide; Söderström *et al.* 2016). Accordingly, Lejeuneaceae was the most species rich and most diverse family in all forests in this study.

Except for Radulaceae, all other families (Leucobryaceae, Leucomiaceae, Pilotrichaceae, Thuidiaceae, and Calypogeiaceae) that occurred exclusively in TF were represented by species common to Amazonian lowland forests (Gradstein *et al.* 2001). However, most of these families were represented by locally rare species, with up to five occurrences

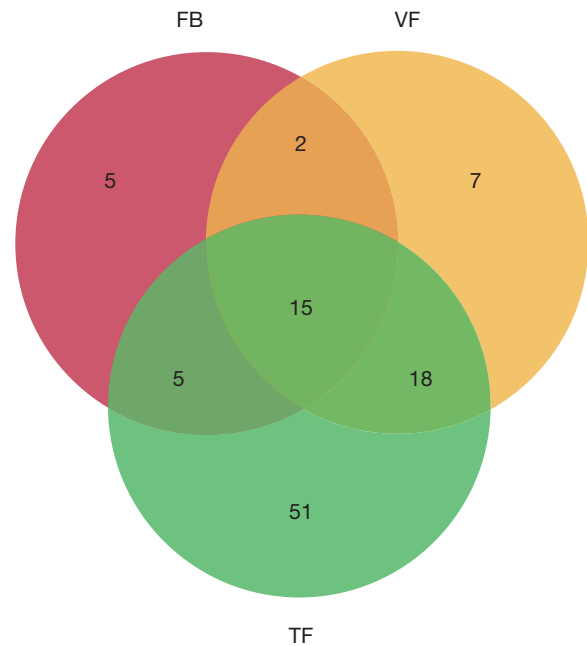


FIG. 4. — Exclusive and shared species in the forests of Abaetetuba. Abbreviations: **FB**, Freshwater Beach; **TF**, Terra Firme forest; **VF**, Várzea forest.

(Oliveira-da-Silva & Ilkiu-Borges 2018; Macedo *et al.* 2022). Among them, Leucobryaceae and Calypogeiaceae presented only one record each: *Campylopus savannarum* (Müll. Hal.) Mitt. and *Calypogeia miquelii* Gottsche, Lindenb. & Nees, respectively, both species usually found in sandy and clayey soils (Gradstein 2021).

The preference of *Cololejeunea* species for humid forests of lowland tropical forests in Amazonia may have favored the greater species richness of this genus in TF (Pócs *et al.* 2014). In turn, FB is a forest exposed to high-intensity sunlight and low air humidity, characteristics that may have favored tolerant species such as those of the genus *Cheilolejeunea* (*C. rigidula*, *C. savannae*, and *C. trifaria* (Reinw., Blume & Nees) Mizut.) (Bastos & Gradstein 2020a; Macedo *et al.* 2022).

The most frequent liverworts and mosses in each forest (*Cheilolejeunea rigidula*, *Calymperes erosum*, and *C. palisotii*) are generalist species that occur in several types of substrates and forests in Tropical America (Buck 2003; Bastos & Gradstein 2020a; Souza *et al.* 2021). Both *C. erosum* and *C. palisotii* present papillose cells throughout the leaf, a trait associated with the ability to rapidly absorb and retain water (Reese 1961; Frahm *et al.* 2003), providing advantages for colonization of hostile environments with high exposure to sunlight (Souza *et al.* 2021; Macedo *et al.* 2022).

NEW RECORDS

Cololejeunea setiloba (Fig. 5A-D) is being recorded for the first time in South America in this study. This species had previously been recorded in Costa Rica and the United States (Eggers 2001; Stotler & Crandall-Stotler 2017) in floodplain forest and swamp forest, on damp logs without bark, smooth bark, or on tree roots (Breil 1970). With these new occurrences in South America, *C. setiloba* now exhibits a wider American

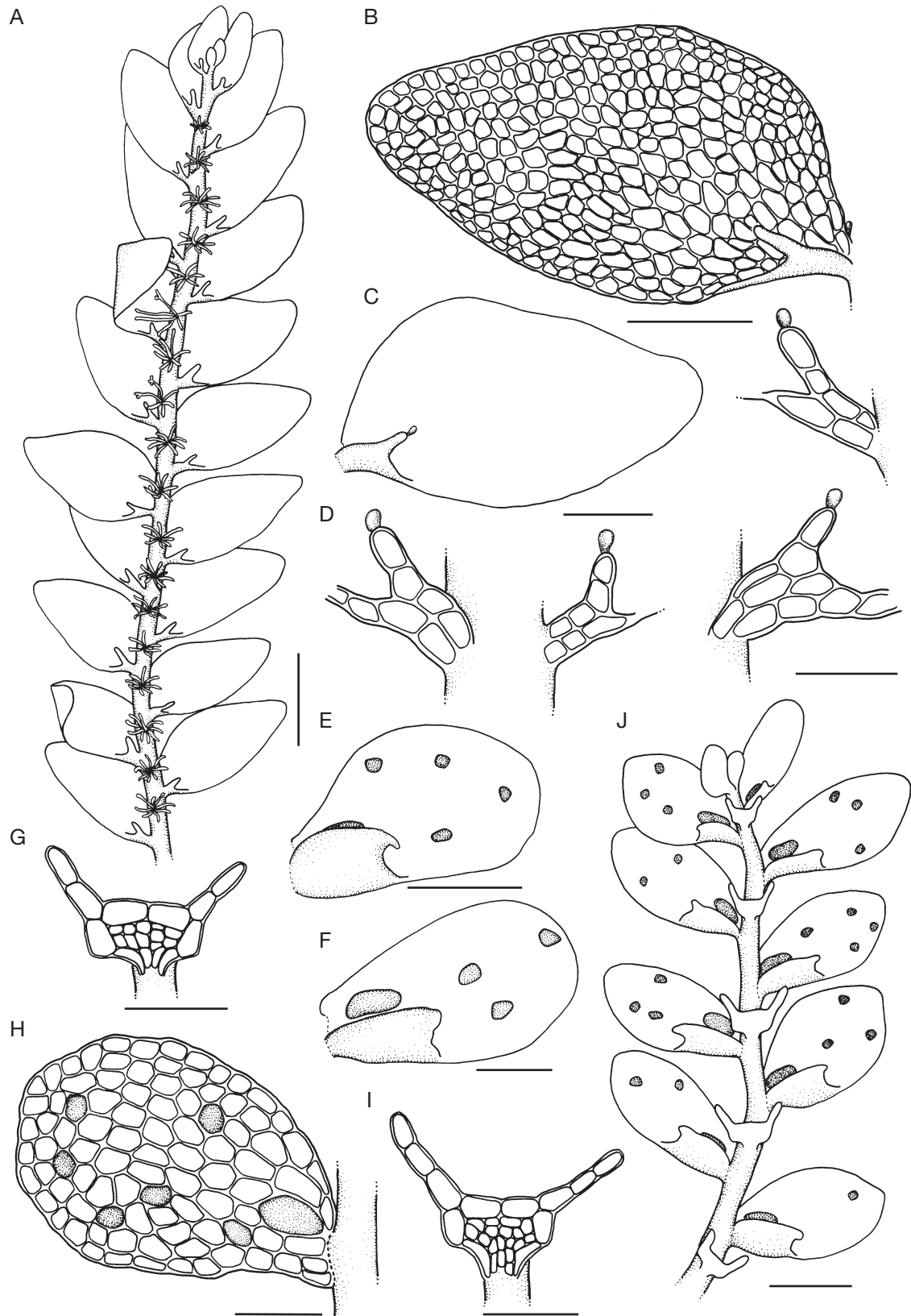


FIG. 5. — **A-D**, *Cololejeunea setiloba* A.Evans (from A. K. Sousa-Pereira 608): **A**, sector of a stem, ventral view; **B, C**, leaves, ventral view; **D**, lobules. **E-J**, *Leptolejeunea radicata* (Mont.) Grolle (from A. K. Sousa-Pereira 202): **E, F**, leaves, ventral view; **G, I**, underleaves; **H**, leaf, dorsal view; **J**, sector of a stem. Scale bars: A, 250 μ m; B, C, E, J, 100 μ m; D, F-I, 50 μ m.

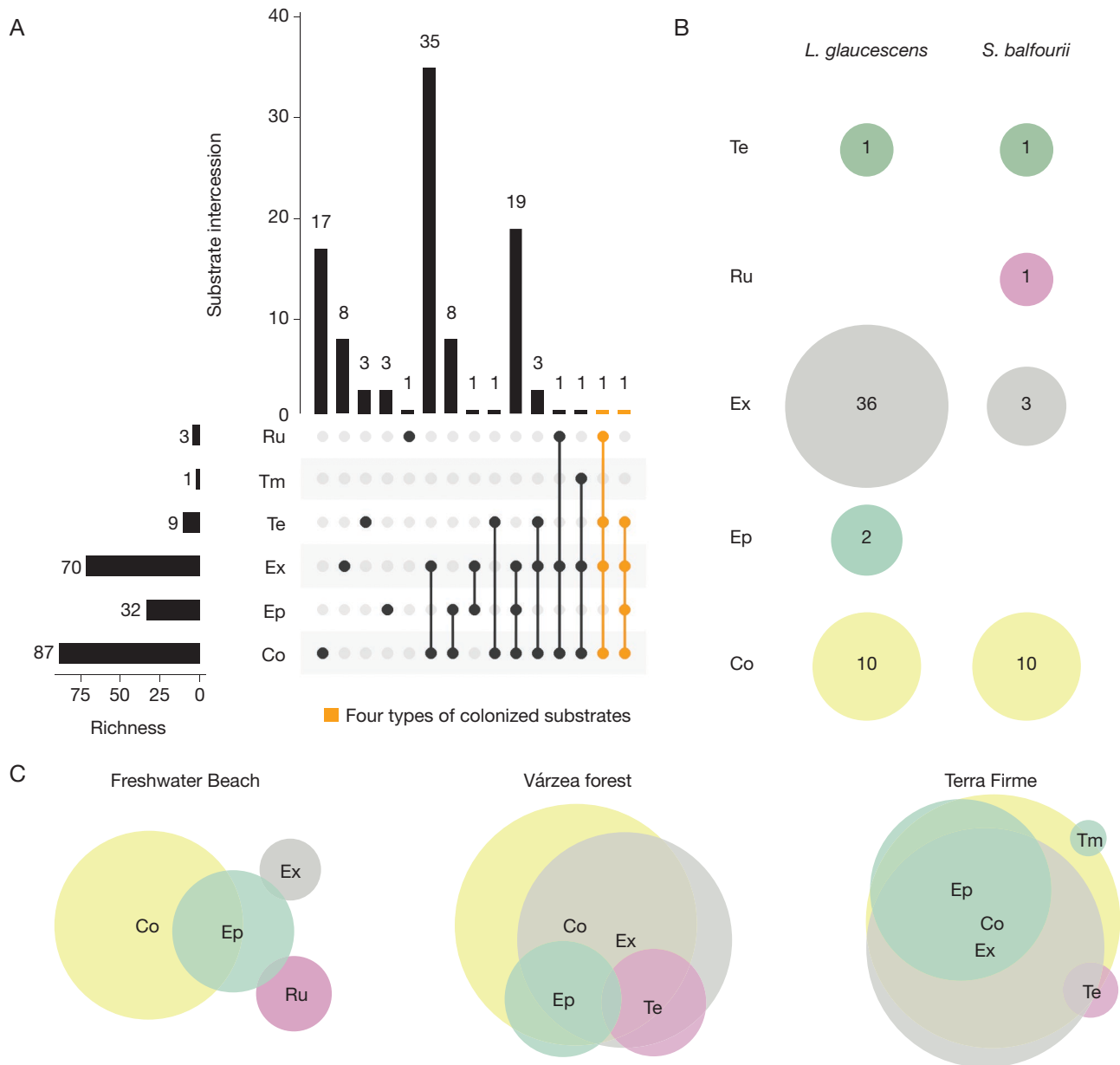


FIG. 6. — Classification of bryophyte species in different substrates in Abaetetuba, Lower Tocantins: **A**, substrate preference of bryophytes in Abaetetuba; **B**, occurrence of two species in four types of substrate; **C**, exclusive and shared species among substrates in environments. Abbreviations: **Co**, corticolous; **Ep**, epiphyllous; **Ex**, epixylic; **Ru**, rupicolous; **Te**, terricolous; **Tm**, termite mound.

distribution, having been found on roots and leaves in both VF and TF.

Cololejeunea setiloba is characterized by plants up to 0.8 mm wide, ovate leaves with entire margins, and obtuse to rounded apex. The lobules form a narrow basal fold with 2-3 cells in width and an uniserial tooth of 2-4 cells in length (Evans 1913; Breil 1970). *Cololejeunea setiloba* can be easily confused with *C. spruceana* Tixier since both have small lanceolate-shaped lobules with a very short keel. Despite their morphological similarity, *C. setiloba* has narrower lobules (2-3 cells in width), while *C. spruceana* has wider lobes (6-8 cells in width) (Pócs *et al.* 2014).

Leptolejeunea radicata (Fig. 5 E-J), a new occurrence for the state of Pará, had previously been recorded in the state

of Amazonas as an epiphyllous species in TF (Zartman & Ilkiu-Borges 2007), a pattern also observed in the TF of this inventory.

Leptolejeunea radicata is recognized by plants up to 0.5 mm wide, obovate leaves with entire margins and obtuse to rounded apex. This species also features one basal ocellus and two to six ocelli scattered throughout the leaf lobe (Zartman & Ilkiu-Borges 2007; Gradstein 2021). *Leptolejeunea radicata* resembles *L. elliptica* (Lehm. & Lindenb.) Besch. by entire margins and several ocelli on the leaf lobe. However, *L. radicata* has obovate leaves and scattered ocelli throughout the lobe, while in *L. elliptica*, leaves are elliptical, and ocelli are disposed in an interrupted row from the base toward the leaf apex (Gradstein 2021).

DISTRIBUTION OF SPECIES IN THE SUBSTRATES

The predominance of corticolous species was already expected because tree trunks are the most abundant and the preferred substrates of mosses and liverworts (Richards 1984; Glime 2017). This pattern of preference has been observed in other studies carried out in tropical forests (e.g. Acebey *et al.* 2003; Valente *et al.* 2009; Brito & Ilkiu-Borges 2013; Moura *et al.* 2013).

Although living tree trunks presented greater species richness than any other types of substrates, a higher proportion of exclusive species was observed on soil and rocks, which may indicate that these two substrates have characteristics that hinder indiscriminate colonization by bryophytes in the studied forests. The species recorded on soil and rocks were predominantly mosses (*Campylopus savannarum*, *Fissidens flaccidus* Mitt., and *F. zollingeri* Mont.) with morphological adaptations to control desiccation and facilitate water transport in the plant, such as the presence of costa, leaf margins with elongated cells, and hyaline tips (Bordin & Yano 2013; Glime 2017).

Living and decaying trunks are believed to have similar microenvironmental characteristics, leading to a greater number of shared species (Richards 1984). In the studied areas, it is also possible that the corticolous species on living trunks remained on the substrate after the tree fall and the conditions changed as the substrate started to decompose. The greater number of species shared between living and decaying trunks and these substrates with leaves agrees with previous studies in Amazonian lowland forests (e.g. Ilkiu-Borges *et al.* 2020; Takashima-Oliveira *et al.* 2020).

The occurrence of *Lejeunea glaucescens* and *Stictolejeunea balfourii* on four types of substrates can be explained by their wide ecological range, as they are reported as generalists in previous studies in Amazonia (Moura *et al.* 2013; Ilkiu-Borges *et al.* 2020). However, *L. glaucescens* is usually found on decaying trunks and *S. balfourii* on living trunks. Their frequency in these substrates is recurrently reported in the literature (Bastos & Gradstein 2020a; Gradstein 2021).

Regarding the forests, epixylic species were infrequent in FB. The greater exposure to desiccation resulting from greater sunlight incidence and constant air currents in FB explains the lower occurrence of this group in this forest. Epixylic species occur preferably in wetter and shaded places (Mägdefrau 1982). Similarly, the sandy soils of FB may also have limited the occurrence of terricolous species.

In VF, despite the flooding dynamics of the sites, the establishment of terricolous species was possible and the epixylic community showed a more successful colonization compared to FB. However, the terricolous species recorded in VF occurred in higher areas, free from frequent tidal interference. The flooding dynamics in VF may have been the limiting factor for the formation of termite mounds, often built on the ground. The colonization of this substrate by bryophytes is more frequently seen in lowland TF, as occurred in the present study (Fagundes *et al.* 2016; Takashima-Oliveira *et al.* 2020).

The vegetation structure of TF was characterized by the predominance of medium to large tree species. This may have favored the occurrence of larger and more similar corticolous, epixylic and epiphyllous communities than in the other forest types (Souza & Lisboa 2006). The lower frequency of terricolous species in TF compared with VF was expected since the thick litter layer that covers the forest floor in tropical regions acts as a barrier to soil colonization by bryophytes (Frahm *et al.* 2003).

CONCLUSION

The findings of this research indicate that Amazonian forests can be better understood by exploring new areas, even those encompassing seemingly similar forests. We observed that the bryophyte flora recorded in the forests studied in Abaetetuba increased accordingly with the complexity of the forests. It is made up of both species with a wide distribution and species with occurrence restricted to humid and xeric forests. Two new occurrences were recorded, one for South America and the other for the state of Pará, confirming the importance of carrying out inventories in little-studied areas to understand the Amazonian biodiversity. The richness and composition of species found in TF and FB are similar to those recorded in studies conducted in the Lower Amazon. However, the studied VF yielded discrepant results in contrast to other Várzea areas surveyed in the region. The different behavior of the bryophyte community in VF in Abaetetuba was noticed in the field, in the low frequency of tree species influenced by a highly managed species of particular interest (açai fruit production). The singular floristic composition of the studied VF (i.e., the dominance of the açai palm tree associated with mangrove trees) directly influenced the bryophyte community. Regarding the colonized substrates, the communities in each forest had a complex arrangement, especially in FB, in which extreme factors served as filters for the occurrence of the species.

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