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Spatial Distribution and Substrate Preferences of Bryophyte Species in Mangrove Ecosystems of the East Coast of Marajó Island, Brazil

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ABSTRACT

We evaluated bryophytes composition between the fringe and inland zones and spatial distribution in mangrove ecosystems, and determined bryophytes composition in Brazilian mangroves. To calculate the composition between zones, we used species richness, density, Shannon-Wiener index, Pielou's evenness, analysis of similarities and indicator species. We calculated sex expression, light-tolerance guilds and type of substrate colonized between zones using two-way ANOVA. We compiled floristic articles with lists of bryophyte species occurring in other mangroves and we calculated the similarity between the areas with the Jaccard index and the UPGMA. We recorded 12 species distributed in 136 occurrences, including 11 species (64 occurrences) that occur in the fringe zone and seven (72 occurrences) in the inland. Our analyses showed that species richness, density, Shannon index and Pielou's evenness did not present statistical significance between zones. We observed that 25% of the monoicous species do not exhibit sex expression, compared with 57.14% of dioicous species. Seven species are generalists and four are sun specialists, with the richness and density varying significantly among the light tolerance guilds. The living tree bark was the most colonized substrate, but the average species richness among the different types of substrates does not vary significantly, while the average density of species per colonized substrate showed a significant difference of epixyloous and termite mounds. The dissimilarity in species composition between the mangroves of Marajó Island and the state of São Paulo shows the role of environmental filters in the selection of species assemblage in the ecosystem.

KEY WORDS

Brazil,
bryoflora,
biological conservation,
coastal ecosystem,
floristic composition.

RÉSUMÉ

Répartition spatiale et préférences de substrat des espèces de bryophytes dans les écosystèmes de mangroves de la côte est de l'île de Marajó, Brésil.

Nous avons évalué la composition des bryophytes entre les zones marginales et intérieures, et leur répartition spatiale dans l'écosystème des mangroves. Nous avons également déterminé la composition des bryophytes dans les mangroves brésiliennes. Pour calculer la composition entre zones, nous avons utilisé la richesse spécifique, la densité, l'indice de Shannon-Wiener, la régularité de Pielou, l'analyse des similarités et les espèces indicatrices. Nous avons calculé l'expression sexuelle, les guildes de tolérance à la lumière et le type de substrat colonisé entre les zones en utilisant une ANOVA bidirectionnelle. Nous avons compilé des articles floristiques avec des listes d'espèces de bryophytes présentes dans d'autres mangroves et nous avons calculé la similarité entre les zones avec l'indice Jaccard et l'UPGMA. Nous avons recensé 12 espèces réparties dans 136 occurrences, incluant 11 espèces (64 occurrences) présentes dans la zone marginale et sept (72 occurrences) à l'intérieur des terres. Nos analyses ont montré que la richesse spécifique, la densité, l'indice de Shannon et la régularité de Pielou ne présentaient pas de signification statistique entre les zones. Nous avons observé que 25 % des espèces monoïques ne présentent pas d'expression sexuelle, contre 57,14 % des espèces dioïques. Sept espèces sont généralistes et quatre sont des spécialistes du soleil, la richesse et la densité variant considérablement selon les guildes de tolérance à la lumière. L'écorce des arbres vivants était le substrat le plus colonisé, mais la richesse moyenne en espèces entre les différents types de substrats ne varie pas de manière significative, tandis que la densité moyenne des espèces par substrat colonisé montre une différence significative entre les épixyles et les termitières. La différence dans la composition des espèces entre les mangroves de l'île de Marajó et de l'État de São Paulo souligne le rôle des filtres environnementaux dans la sélection de l'assemblage d'espèces dans l'écosystème.

MOTS CLÉS

Brésil,
bryoflore,
conservation biologique,
écosystème côtier,
composition floristique.

INTRODUCTION

In mangrove ecosystems, bryophytes can be found growing on mangrove trees, which play an important role in the establishment of epiphytic plants (Schaeffer-Novelli *et al.* 2004, 2015). Mangroves are composed of woody species (Schaeffer-Novelli 2018) and, in Brazil, they occur from the coast of the extreme North in the state of Amapá to the southern limit in Santa Catarina (Soares *et al.* 2012).

Mangroves are coastal ecosystems with vegetation adapted to soils with low oxygen and high salt concentrations due to seawater flooding during high tides (Schaeffer-Novelli *et al.* 2004, 2015; Alongi 2008). The vegetation presents low floristic diversity when compared to terrestrial tropical forests (Schaeffer-Novelli *et al.* 2004), since few species are adapted to the abiotic conditions of tidal flooding regimes and unconsolidated soils with high salinity and low oxygen levels (Mehlig *et al.* 2010; Oliveira & Tognella 2014).

Mangroves can be structured as a *continuum* of physiognomies according to the specific characteristics existing in each of the zones, which are classified as “lavado”, mangrove forest and “apicum” (Schaeffer-Novelli *et al.* 2015). The “lavado” is the physiognomy exposed to the highest frequency of floods and does not present any vascularized vegetation cover. The zone “mangrove forest”, in turn, is composed of trees typical of mangroves such as *Rhizophora mangle* L., *Laguncularia racemosa* (L.) C.F.Gaertn., and *Avicennia germinans* (L.) Stearn. Finally, the “apicum” is the innermost portion of the ecosystem, where an apparently lifeless sandy-muddy surface, affected by estuarine waters or syzygy tides, is observed.

The fragmentation of mangroves results in canopy opening and gap formation, directly affecting the microclimatic conditions because the canopy cover controls the temporal and spatial distribution of solar radiation, and determines air humidity, temperature and soil humidity (Galvani & Lima 2010; Medellu & Berhimpon 2012; Lima *et al.* 2013). Studies show that such microclimatic conditions can trigger different reproductive traits within and among bryophyte species (Chopra & Bhatla 1983; Kumra & Chopra 1983; Longton 1990). In addition, reproductive performance in bryophytes depends on factors such as habitat, temperature, moisture, light and pH; and characteristics such as the sexual systems (monoicy and dioicy) and form of growth (acrocarpous and pleurocarpous) (Maciel-Silva *et al.* 2012).

When microclimatic conditions are altered, bryophyte assemblages exhibit changes in their composition and vertical distribution along host trees (Acebey *et al.* 2003; Frego 2007; Sporn *et al.* 2010). This is because the microclimate acts as an environmental filter that determines and shapes the bryophyte community in the environment (Weibull & Rydin 2005; De Bello *et al.* 2010; Santos *et al.* 2014; Smith & Stark 2014). The environmental conditions in tropical forests change along the vertical gradient, from the understory to the canopy: temperatures are higher, and humidity is lower in the canopy than in the understory, limiting the survival of drought intolerant species (Kumagai *et al.* 2001). Löbs *et al.* (2020) observed that epiphytic bryophytes that grew in the understory of an area of Amazon Forest were limited by light availability and responded mainly to rainfall patterns, while those that grew in the canopy were affected by greater variations in microclimatic



FIG. 1. — Location map of collection points in Marajó Island, Pará, Brazilian Amazon: **A**, localization of Marajó Island in Pará, Brazil, South America (red rectangle); **B**, localization of Salvaterra in Marajó Island; **C**, localization of sampling points on the east coast of the Salvaterra, with 1 km between the fringe zone and the inland zone in each area (map prepared by P.W.P. Gomes).

conditions, such as relative humidity and condensation. In addition, the light intensities experienced by the bryophytes varied depending on the location within the canopy.

Bryophytes have developed various morphological and physiological mechanisms that allow them to survive under different conditions within the limits of their environmental

tolerances (Širka *et al.* 2019). These limits are reflected on the composition of species. For example, clearly distinct niches are generally occupied by species in epiphytic bryophyte communities of tropical forests (Mota de Oliveira *et al.* 2009), as confirmed by the repeatedly recorded relationship between species composition and height zones along host trees (Acebey *et al.* 2003; Holz & Gradstein 2005; Sporn *et al.* 2010).

This study has two main objectives: 1) to calculate species composition between the fringe zone and an inland zone and spatial distribution on the mangroves; and 2) to determine species composition in Brazilian mangroves.

We specifically investigate the following hypotheses:

1) Considering that the canopy cover controls the temporal and spatial distribution of solar radiation and the fragmentation of mangroves results in canopy opening and gap formation (Galvani & Lima 2010; Medellu & Berhimon 2012; Lima *et al.* 2013), our hypothesis is that microclimatic conditions in anthropized mangroves provide a fundamental niche for bryophytes tolerant to greater solar radiation, while species sensitive to greater exposure to sunlight present a competitive disadvantage to colonize the microhabitat.

2) Considering that the monoicous species can self-fertilize and therefore tend to produce sporophytes more frequently than dioicous ones (Gemmell 1950; Longton 1992; Maciel-Silva *et al.* 2012), our hypothesis is that the monoicous species had a higher frequency in the production of gametangia and sporophyte production than dioicous species, or that such frequencies are mainly affected by habitat (fringe and inland zones).

MATERIAL AND METHODS

STUDY AREA

This study was carried out in mangroves on the east coast of the Marajó Island, in the municipality of Salvaterra, Pará (Fig. 1). In this study, four locations (Table 1) were selected to access eight mangrove forests with tree coverage described by De Oliveira Faro *et al.* (2023). The mangrove complex of the Marajó Island can be observed between streams and on the banks of the Tocantins and Amazon rivers that drain the island and that flow into the bays and the Atlantic Ocean (Schaeffer-Novelli 2018). This complex is called the Marajoara Gulf (Ab'Saber & Holmquist 2001). In the municipality of Salvaterra, the mangroves have a well-known structure, with an arboreal stratum formed by *Avicennia germinans*, *Laguncularia racemosa*, *Pachira aquatica* Aubl., *Pterocarpus officinalis* Jacq., *Rhizophora racemosa* G.Mey and *Virola surinamensis* (Rol. ex Rottb.) Warb. (Lisboa *et al.* 1993; De Oliveira Faro *et al.* 2023).

According to the Köppen system, the municipality of Salvaterra is positioned at seven meters of altitude and has been classified as Am climate (Tropical monsoon climate), with an average annual temperature of 27°C and average annual precipitation of 253 mm (Köppen 1936; Alvares *et al.* 2013). This municipality is subject to two rainfall regimes: a rainier regime mainly marked between February and May, with average monthly rainfall exceeding 400 mm, while the less

rainy regime extends mainly from September to November, with average monthly rainfall of less than 100 mm (Alvares *et al.* 2013).

SAMPLING AND DATA COLLECTION METHODS

The orientation of the plots followed the protocol of Schaeffer-Novelli *et al.* (2015), considering two areas of the mangrove forest: the fringe, which is the anterior part of the mangrove forest that is close to the watercourse; and the inland, corresponding to mangrove forests developed within the continent and in transition zones with adjacent ecosystems.

Four 400 m² plots were placed in the fringe zone (Fig. 2A, B) of the mangrove forests along the coast of the municipality of Salvaterra and four 400 m² plots in the inland zone (Fig. 2C, D), at a distance of 1 km from the fringe plots. Bryophytes were surveyed in each plot by searching different available substrates (living and decaying tree trunks, leaves, termite mounds, and artificial substrates) up to a maximum height of 10 m, removing the bryophytes from the substrate with the aid of a pocket knife and packing them in wooden paper bags (Glime 2017a).

TAXONOMIC IDENTIFICATION

The identifications of the botanical material were based on Florschütz-De Waard *et al.* (1996), Buck (2003), Gradstein & Costa (2003), Gradstein & Ilkiu-Borges (2009) and Yano *et al.* (2019) among other more specialized texts, and by consulting experts on the taxa. Regarding the classification system, we adopted Crandall-Stotler *et al.* (2008) for liverworts and Goffinet *et al.* (2009) for mosses. The botanical material was incorporated into the Prof. Dr. Marlene Freitas da Silva Herbarium (MFS) of the State University of Pará.

DATA ANALYSIS

In this section, for all statistical analyzes and graph production, we used packages and functions implemented in the statistical software R version 4.2.3 (R Core Team 2023).

Sampling efficiency

To determine the optimal sample size between fringe and inland zones, we generated species accumulation curves based on rarefaction and extrapolation of Hill numbers using an abundance data matrix with 95% confidence intervals (Chao *et al.* 2014; Hsieh *et al.* 2022) using the iNEXT package (Hsieh *et al.* 2016). Hill numbers are parameterized by a diversity order q : estimation of species richness ($q = 0$) and estimation of Shannon diversity ($q = 1$).

Richness, species composition and indicator species analysis

To assess the α -diversity in the fringe and inland zones, we used ecological indices such as Shannon-Wiener diversity index (H) and Pielou's evenness index (J). Species richness, species density, Shannon-Wiener diversity index, and Pielou's evenness were compared between the two zones using the Student's t-test (Dunn 1964). The beta-diversity between fringe and inland zones was analyzed using Analysis of Similarities (ANOSIM) implemented in Vegan package (Oksanen *et al.*



FIG. 2. — Mangroves on the east coast of the municipality of Salvaterra, Marajó Island, Pará: **A, B**, mangrove in inland zone; **C, D**, fringe zone.

2022), and to investigate aspects of community composition we used the Indicator Species Analysis using *indicpecies* package (Cáceres & Legendre 2009). Indicator species are species that are used as ecological indicators of community.

Sexual system frequency analysis

The sexual systems (monoicous and dioicous) of the moss and liverwort species were defined based on the identified material and data available in the literature previously mentioned (see Taxonomic identification). Each specimen was examined for determination of the presence of sex expression and the type of reproduction: sexual (with sporophytes) or asexual (with asexual diaspores). We evaluated the richness and density of monoicous and dioicous species between the fringe and inland zones using the two-way Analysis of Variance (ANOVA). Two-way ANOVA was also used to test whether the expression of sexual and asexual reproduction was influenced by the sexual system between the fringe and inland zones.

Light tolerance guilds

The light tolerance guilds were classified based on a literature review, considering “generalist species” as those that do not

show specific restrictions to humidity and light tolerance; “shade specialists” as species that prefer certain types of microenvironments requiring constant shade and humidity; while “sun specialists” tolerate high levels of light incidence (Richards 1954, 1984; Gradstein 1992; Da Costa 1999; Gradstein *et al.* 2001; Pantoja *et al.* 2015; Fagundes *et al.* 2016). The two-way Analysis of Variance (ANOVA) was used to compare the richness and density of bryophytes between different light tolerance guilds in the fringe zone and inland zone. We observed a possible interaction between the variables using interaction plot. For this, we used the *ggpubr* package to visualize and facilitate the interpretation of the boxplot generated in the two-way ANOVA.

Substrate specificity

The species were classified based on the colonized substrates according to Robbins (1952) with adaptations: growing on living tree trunks and branches (corticolous); growing on fallen and decaying branches and trunks (epixylous); and growing on termite mounds. We compared the richness and density of bryophytes between different substrates in the fringe zone and interior zone using two-way Analysis of Variance (ANOVA).

TABLE 1. — Mangrove sampling site in the municipality of Salvaterra with its geographic coordinates in the Universal Transversa de Mercator (De Oliveira Faro *et al.* 2023).

Area	Mangrove site	Zone	Longitude	Latitude
1	Near the Paracauari river in Caldeirão village	Fringe	48.550159	0.710705
	Andrade farm in Caldeirão village	Inland	48.549489	0.723062
2	Near the Guajará warehouse	Fringe	48.524603	0.745309
	Close to the state highway 154 km in the village of São Veríssimo	Inland	48.534006	0.746846
3	São João beach in Mata do Bacurizal Ecological Reserve	Fringe	48.519083	0.779847
	Near the Pousada dos Guarás in Mata do Bacurizal Ecological Reserve	Inland	48.515332	0.773295
4	Jubim village beach	Fringe	48.534425	0.798339
	Near Jubim village bridge	Inland	48.544093	0.797913

The interaction plot was used to facilitate the interpretation of the boxplot generated in the two-way ANOVA.

Comparison of similarity among Brazilian mangroves

The bryophyte flora of the mangroves of Salvaterra published in previous works (Lisboa *et al.* 1993; Garcia *et al.* 2014) with additional records of the present study was compared with surveys of mosses and liverworts available in the literature conducted in mangroves from other Brazilian municipalities, namely, Cacheira do Arari and Soure in Marajó Island (Brito & Ilkiu-Borges 2013) and seven municipalities on the coast of São Paulo: Ubatuba (Vital & Pursell 1992; Peralta & Yano 2006; Visnadi 2008), São Vicente (Visnadi *et al.* 1994; Yano 2002; Visnadi 2008), Praia Grande (Visnadi 2008), Itanhaém (Yano & Carvalho 1994; Yano & Mello 1999; Yano 2002; Visnadi 2008), Peruíbe (Mello & Yano 1991; Yano & Mello 1999; Vital & Visnadi 2000; Yano 2002; Visnadi 2008), Iguape (Yano & Mello 1999; Yano 2002), and Cananéia (Visnadi 2008). A presence/absence matrix was built for 126 species. We calculated the similarity between the areas by the Jaccard index, and the unweighted pair grouping method with arithmetic means (UPGMA) (Sokal & Michener 1958) was adopted for calculations and construction of the dendrogram, using the Vegan package (Oksanen *et al.* 2022). In addition, we analyzed the variation in terms of richness among mangroves. To test whether the floristic groups defined by region were significantly different, we used the analysis of similarities (ANOSIM), and to investigate aspects of community composition, we used the Indicator Species Analysis (Cáceres & Legendre 2009), both implemented in Vegan package in R software (Oksanen *et al.* 2022).

Geographical distribution of epiphytic species in relation to biomes in Brazil

To determine the geographical distribution of the species, we investigated their occurrence in different phytogeographic domains and states in Brazil, classifying them into: widely distributed (when found in more than five Brazilian states) or rare (when found in four or less states), according to Batista *et al.* (2018) with adaptations. Species distribution data in the phytogeographic domains of Brazil were obtained from the Flora e Funga do Brasil database (Rio de Janeiro Botanical Garden, data collected in December 2020, <http://floradobrasil.jbrj.gov.br/>).

RESULTS

SAMPLING EFFORT ANALYSIS

A total of 12 species of epiphytic bryophytes (three mosses and nine liverworts) distributed in eight genera and four families were found in the studied mangroves (Table 2). These species are widely distributed in the mangroves studied, which contributed to the stabilizing trend observed in the estimated curves of accumulated richness (Fig. 3A) and Shannon diversity (Fig. 3B). Among the mosses, only *Calymperes palisotii* Schwägr. was found both in the fringe and inland zones. Among liverworts, Lejeuneaceae had a key role in maintaining biodiversity, since 58.3% (seven species) of the bryophytes belonged to this family, and *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn. and *Lejeunea laetevirens* Nees & Mont stood out, being present in all plots.

RICHNESS, SPECIES COMPOSITION AND INDICATOR SPECIES ANALYSIS

We found 12 species (three mosses and nine liverworts) distributed in 136 occurrences (21 mosses and 115 liverworts). In the fringe zone, the observed species richness (11 species) represented 73.6% of the estimated richness, while in the inland zone, the richness (seven species) represented 93.4% of the estimated richness. No significant difference was observed between the fringe and inland zones in terms of richness ($t = 1.768$; $p\text{-value} = 0.127$) (Fig. 4A) and density ($t = -0.307$; $p\text{-value} = 0.768$) patterns (Fig. 4B).

The Shannon-Wiener diversity index (H) was 1.87 in the fringe zone and 1.58 in the inland zone (Fig. 4C), while the estimated Shannon diversity was 1.99 and 1.63, respectively. Our analyses showed that the Shannon diversity between the zones were not statistically different ($t = 1.877$; $p\text{-value} = 0.109$). The index (J) values indicated that 88 to 96% of the maximum theoretical diversity was obtained in our sample, as they ranged from 0.88 to 0.96 in the fringe zone and from 0.89 to 0.94 in the inland zone (Fig. 4D). However, we found no significant variation in the Pielou's evenness index (J) between zones ($t = 0.022$; $p\text{-value} = 0.982$).

Our similarity analysis (ANOSIM) showed that the bryoflora between the fringe and interior zones were relatively homogeneous ($R: -0.270$; $p\text{-value} = 0.971$), without distinguishing groups by zones. Therefore, no species was associated as an ecological indicator in the fringe and interior community ($p\text{-value} > 0.05$).

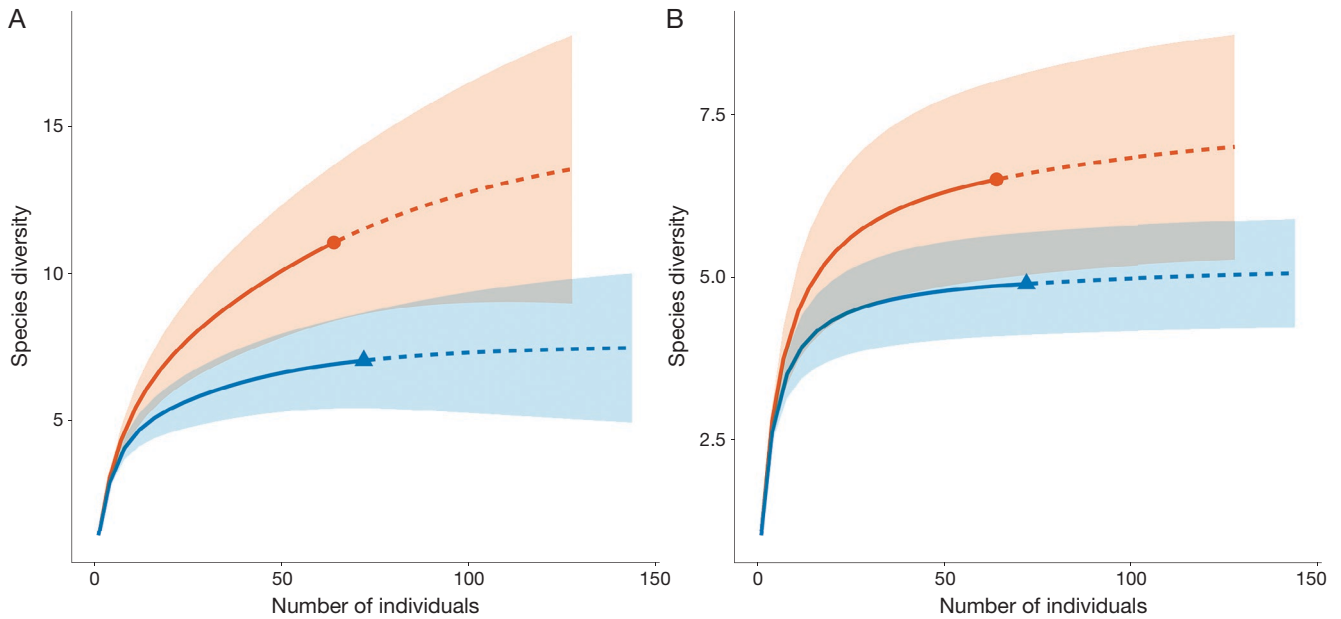


Fig. 3. — Accumulation curves based on the abundance of individuals in the fringe and inland zones of the mangroves of Salvaterra, Pará, Brazil: **A**, species richness ($q=0$); **B**, Shannon diversity ($q=1$). The fringe zone is shown in red color and the inland zone in blue color. Continuous line represents interpolation and dotted line represents extrapolation.

SEXUAL SYSTEMS AND SEX EXPRESSION

We found seven dioicous and four monoicous species and one taxon, identified to the genus level, with an undetermined sexual system. In the fringe, six dioicous species were recorded, among which, *Calymperes erosum* Müll.Hal., *Cheilolejeunea clausa* (Nees & Mont.) R.M.Schust. and *Microlejeunea epiphylla* Bischl. were exclusive to this zone. Among the four monoicous species recorded in the fringe, *Acrolejeunea emergens* (Mitt.) Steph. and *Trichosteleum subdemissum* (Besch.) A.Jaeger were found only in this area. In the inland zone, the dioicous species represent the majority with four records, but a single species exclusive to this zone, such as *Frullania caulisequa* (Nees) Nees. *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn. and *Cheilolejeunea oncophylla* (Aongström) Grolle & E.Reiner were the only species recorded in the interior zone. Our analyses revealed that the sexual system of the species differs significantly in both richness ($F = 11.538$; $p\text{-value} = 0.005$) and density ($F = 5.247$; $p\text{-value} = 0.04$). However, the interaction of the sexual system between the fringe and inland zones does not vary for species richness and density.

Here, we note that only 25% of the monoicous species do not exhibit sex expression, compared with 57.14% of dioicous species. Regarding the presence of gametangia (sexual organs), 50% of the monoicous species presented male and female gametangia in fringe and inland zones, while 42.85% of the dioicous species were observed with male or female gametangia in both zones. All records of the sporophytes (sexual reproduction) were observed occurring simultaneously in fringe and inland zones, about 50% of the monoicous species as *A. torulosa* and *C. oncophylla*, while it was observed in 28.57% of the dioicous species as *Cheilolejeunea rigidula* (Mont.) R.M. Schust. and *L. laetevirens*. We observed sporophytes in a taxon identified at the genus level, *Cheilolejeunea* sp. Flagelliform

branches (asexual reproduction) were observed in 50% of the monoicous species, including *A. emergens* in fringe zone only and *A. torulosa* in both zones, the latter presented sexual and asexual reproduction simultaneously.

Our results showed that the expression of sexual reproduction did not vary significantly between sexual systems or in the interaction between sexual system and fringe and inland zones ($F = 0.752$; $p\text{-value} = 0.403$). On the other hand, the analyses revealed that asexual reproduction was strongly associated with the monoicous sexual system ($F = 3.245^{e+32}$; $p\text{-value} = 2^{e-16}$).

LIGHT TOLERANCE GUILDS

Seven generalist species were found in the studied mangroves, including three mosses and four liverworts. Among the generalists, four species were shared between the two zones, while three species were exclusive to the fringe zone, being *Calymperes erosum* Müll.Hal., *Microlejeunea epiphylla* Bischl. and *Trichosteleum subdemissum* (Besch.) A.Jaeger. The sun specialists were represented by four liverwort species, being *Acrolejeunea emergens* (Mitt.) Steph. and *Cheilolejeunea clausa* (Nees & Mont.) R.M.Schust. (exclusive occurrence in fringe zones), *Frullania caulisequa* (Nees) Mont. (exclusive occurrence in inland zones), and *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn. (occurring in both zones).

The richness of bryophyte species varied significantly among the light tolerance guilds ($F = 13.235$; $p\text{-value} = .003$) (Fig. 5A), as well as species density by light tolerance guilds ($F = 7.178$; $p\text{-value} = 0.020$) (Fig. 5B). Although the interaction graphs indicated variations in both richness (Fig. 5C) and density (Fig. 5D) of species between the zones, we observed that the fringe and inland zones were not sufficient factors to significantly influence the mean richness ($F = 1.471$; $p\text{-value} = 0.248$) and mean density ($F = 0.009$; $p\text{-value} = 0.927$) of species by light tolerance guilds.

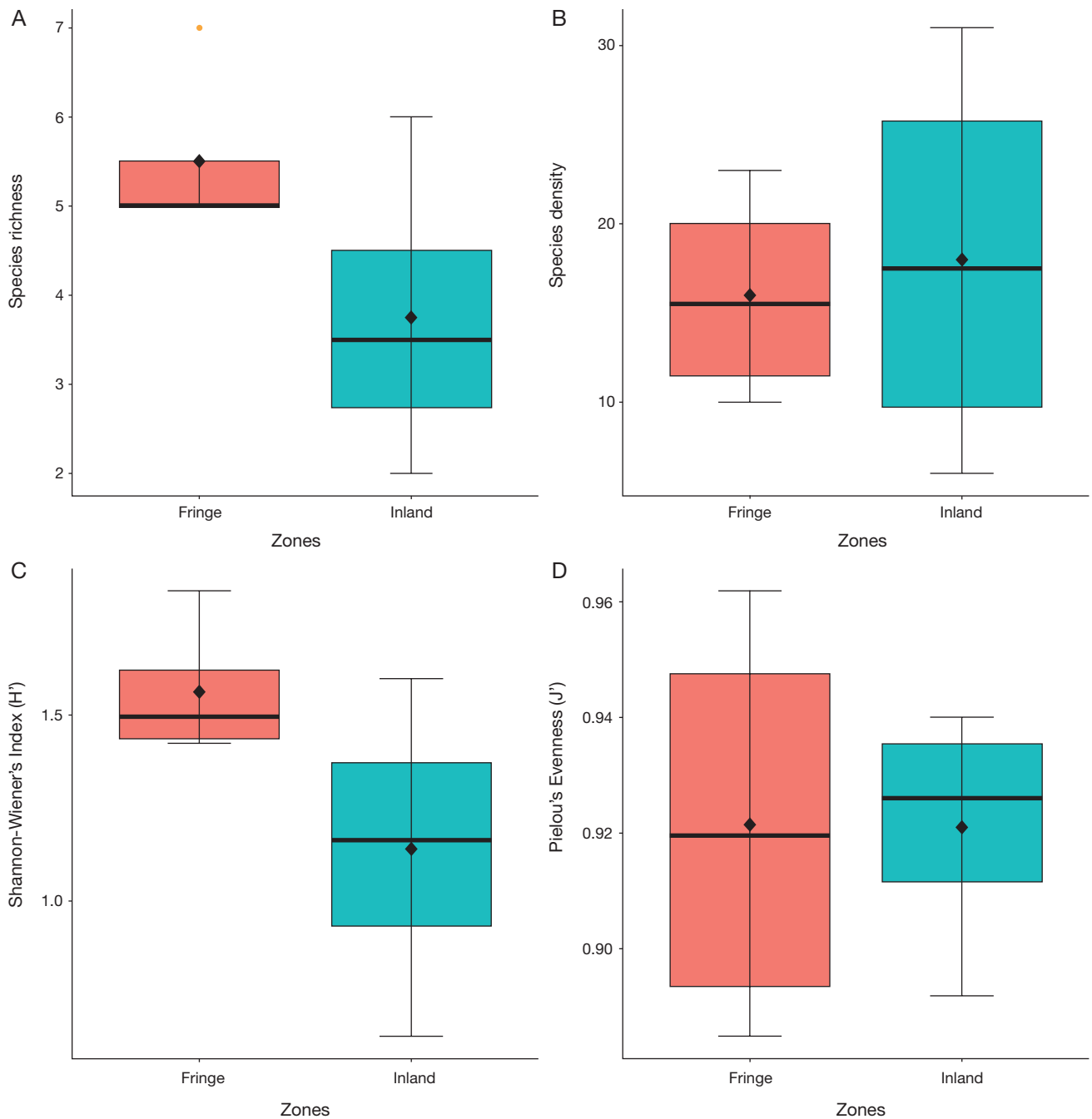


FIG. 4. — Violin plot with included boxplot: **A**, species richness; **B**, species density. Alpha-diversity indices: **C**, Shannon Index (H'); **D**, Pielou's Evenness (J').

SUBSTRATE SPECIFICITY

Living tree bark was the most colonized substrate by 91.66% of the species (eleven species), at an average height of three meters from the soil. Five species were exclusively corticolous, among them *Acrolejeunea emergens* (Mitt.) Steph., *Calymperes erosum* Müll.Hal., *Cheilolejeunea clausa* (Nees & Mont.) R.M.Schust., and *Trichosteleum subdemissum* (Besch.) A.Jaeger. were recorded only in the fringe zone, while *Frullania caulisequa* (Nees) Nees occurred only in the inland zone.

Decaying trunk was the second most colonized substrate with 58.33% of the species (seven species), with *Microlejeunea epiphylla*

Biscl. being the only exclusively epixyloous species. In fringe zone, six species were registered on decaying trunks, with *Cheilolejeunea rigidula* (Mont.) R.M.Schust. and *M. epiphylla* occurring only in this zone. On the other hand, five species were found in the inland zone, but only *Cheilolejeunea* sp. was unique to this zone.

Termite mound was the third most colonized substrate with 50% of the species (six species), but no species grew exclusively on this substrate. We recorded six species that shared the same substrate and only these species occurred in both the fringe and inland zones. Among the species under termite mounds, *Cheilolejeunea oncophylla* (Aongström) Grolle & E.Reiner was

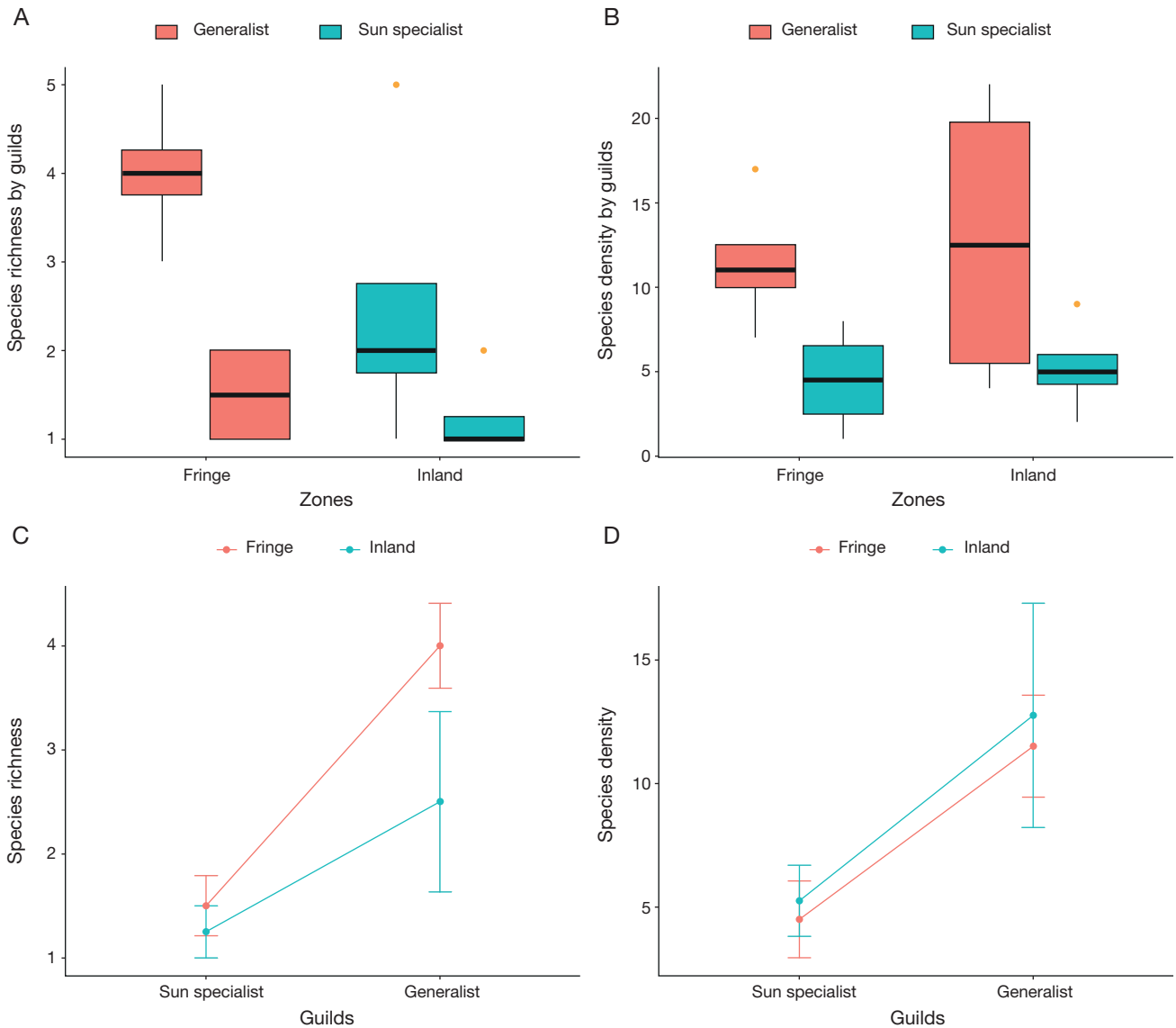


Fig. 5. — **A**, mean richness; **B**, density of bryophytes in the sampled mangroves per light tolerance guilds; **C**, interaction plot between sampled zones and light tolerance guilds on mean richness of bryophytes; **D**, interaction plot between sampled zones and light tolerance guilds on mean density of bryophytes.

the only species that occurred in the fringe, while *Cheilolejeunea* sp. was the only species in the inland.

We observed that the average species richness among the different types of substrates does not vary significantly ($F = 0.589$; $p\text{-value} = 0.570$) (Fig. 6A). The average density of species per colonized substrate showed a significant difference ($F = 5.298$; $p\text{-value} = 0.022$) (Fig. 6B), with variations between corticolous and epixyloous ($p\text{-value} = 0.035$), and corticolous and termite mounds ($p\text{-value} = 0.018$). We observed that the fringe and interior zones were not sufficient factors to significantly influence the mean richness ($F = 0.138$; $p\text{-value} = 0.873$) (Fig. 6C) and mean density ($F = 0.281$; $p\text{-value} = 0.759$) (Fig. 6D) of bryophytes according to the type of substrate colonized.

COMPARISON OF SIMILARITY AMONG BRAZILIAN MANGROVES

We observed the formation of two groups with greater floristic similarity in the dendrogram: the first large group positioned

to the left with the epiphytic bryophyte flora from the mangroves of seven municipalities on the coast of the state of São Paulo (Fig. 7). In this first group, there were three subgroups with increasing order of dissimilarity, namely São Vicente and Praia Grande, Itanhaém and Igape, and Peruíbe and Cananéia. Although the epiphytic bryophyte flora of mangroves of Ubatuba presented greater similarity with the mangroves of São Paulo than with those of Marajó Island, this area was isolated and was not part of any subgroup due to its discrepant richness (83 species). The second large group, positioned to the right of the dendrogram, shows the high similarity among the epiphytic bryophytes of mangroves in three municipalities on the east coast of Marajó Island. In this group, the bryophyte floras of Soure and Cachoeira do Arari were closer to each other than to that of Salvaterra.

ANOSIM showed significant ($R = 0.912$; $p\text{-value} = 0.010$) values for distinctness of the environment groups formed

TABLE 2. — List and characteristics of bryophyte species from mangroves in Salvaterra, Marajó Island, Pará. Phylogeographic domain (PD): AM, Amazon Forest; AF, Atlantic Forest; CA, Caatinga; CE, Cerrado; PM, Pampa; PL, Pantanal. Light tolerance guilds (Gui): Gen, generalist; Sun, sun specialist. Substrate (Subs): DT, decaying trunk; T, living tree; TM, termite mound. Sexual system (S): D, dioicous; M, monoicous. Sexual structures (SS): FG, female gametangia; MG, male gametangia; Sp, sporophytes; Asex, asexual propagule.

Species	Zone	Geographic Distribution		Ecological Strategies		Reproduction Strategies	
		PD	Brazil	Gui	Subs	S	SS
Calymperaceae							
<i>Calymperes erosum</i> Müll.Hal.	Fringe	AM/AF/CE	Wide	Gen	T	D	–
<i>Calymperes palisotii</i> Schwägr.	Fringe/Inland	AM/AF/CA/CE	Wide	Gen	T/DT/TM	D	–
Frullaniaceae							
<i>Frullania caulisequa</i> (Nees) Nees	Inland	AM/AF/CA/CE/PM	Wide	Sun	T	D	FG
Lejeuneaceae							
<i>Acrolejeunea emergens</i> (Mitt.) Steph.	Fringe	AM/CE/AF/PM/PL	Wide	Sun	T	M	Asex
<i>Acrolejeunea torulosa</i> (Lehm. & Lindenb.) Schiffn.	Fringe/Inland	AM/CE/AF/PL	Wide	Sun	T/DT/TM	M	FG/MG/Sp/Asex
<i>Cheilolejeunea clausa</i> (Nees & Mont.) R.M.Schust.	Fringe	AM/CE/AF/PL	Wide	Sun	T	D	–
<i>Cheilolejeunea oncophylla</i> (Aongström) Grolle & E.Reiner	Fringe/Inland	AM/AF	Wide	Gen	T/DT/TM	M	FG/MG/Sp
<i>Cheilolejeunea rigidula</i> (Mont.) R.M.Schust.	Fringe/Inland	AM/AF/CA/CE/PL	Wide	Gen	T/DT/TM	D	FG/Sp
<i>Cheilolejeunea</i> sp.	Fringe/Inland	–	–	–	T/DT/TM	–	FG/MG/Sp
<i>Lejeunea laetevirens</i> Nees & Mont.	Fringe/Inland	AM/AF/CA/CE/PL	Wide	Gen	T/DT/TM	D	FG/MG/Sp
<i>Microlejeunea epiphylla</i> Bischl.	Fringe	AM/AF/CA/CE/PL	Wide	Gen	DT	D	–
Sematophyllaceae							
<i>Trichosteleum subdemissum</i> (Besch.) A.Jaeger	Fringe	AM/AF/CE	Wide	Gen	T	M	–

(Marajó Island and on the coast of the state of São Paulo mangroves). Our analysis of indicator species showed three species significantly associated with a group to all municipalities on the coast of the state of São Paulo, except municipality of Cananéia. The indicator species were: *Frullania brasiliensis* Raddi (p-value = 0.035), *Frullania ericoides* (Nees) Mont. (p-value = 0.008), and *Frullania kunzei* (Lehm. & Lindenb.) Lehm. & Lindenb. (p-value = 0.008).

GEOGRAPHICAL DISTRIBUTION OF EPIPHYTIC SPECIES IN RELATION TO BIOMES IN BRAZIL

All species have a wide geographic distribution. We found that 72% of the recorded species occur in more than three phyto-geographic domains, mainly in the Atlantic Forest, Amazon and Cerrado; only *Cheilolejeunea oncophylla* (Aongström) Grolle & E.Reiner is restricted to the Amazon and Atlantic Forest (Table 2).

DISCUSSION

SAMPLING COMPLETENESS

In the mangroves studied, the absence of rare species contributed to the stabilizing trend in the curves. However, in areas with greater microhabitat variability, such as non-flooded

(*Terra Firme*) forest ecosystems (Mota de Oliveira 2018), species accumulation curves for bryophytes are not observed to stabilize, as it was found in *Terra Firme* forest fragments in the Lago de Tucuruí Environmental Protection Area of Lake – PA (Garcia *et al.* 2014), in Volta Grande do Xingu – PA (Pantoja *et al.* 2015), and in the Gunma Ecological Park (Fagundes *et al.* 2016).

RICHNESS, SPECIES COMPOSITION AND INDICATOR SPECIES ANALYSIS

Our analysis indicated that more than 70% of the estimated richness of bryophytes was sampled. The greater representativeness of Lejeuneaceae species in the studied mangroves is related to the predominance of this family in the Neotropics, which comprises about 70% of the Amazonian bryophyte flora (Gradstein *et al.* 2001; Gradstein & Costa 2003; Gradstein & Ilkiu-Borges 2009). Such success is due to the wide morphological plasticity of these plants that allows them to colonize different environments and height zones along host trees (Gradstein *et al.* 2001; Oliveira & Ter Steege 2013; Mota de Oliveira 2018). This family was the only one represented among the liverworts from mangroves on the east coast of Marajó Island and it is also often the best represented in floristic studies in general (Brito & Ilkiu-Borges 2013; Garcia *et al.* 2014). Frullaniaceae, another family recorded in our

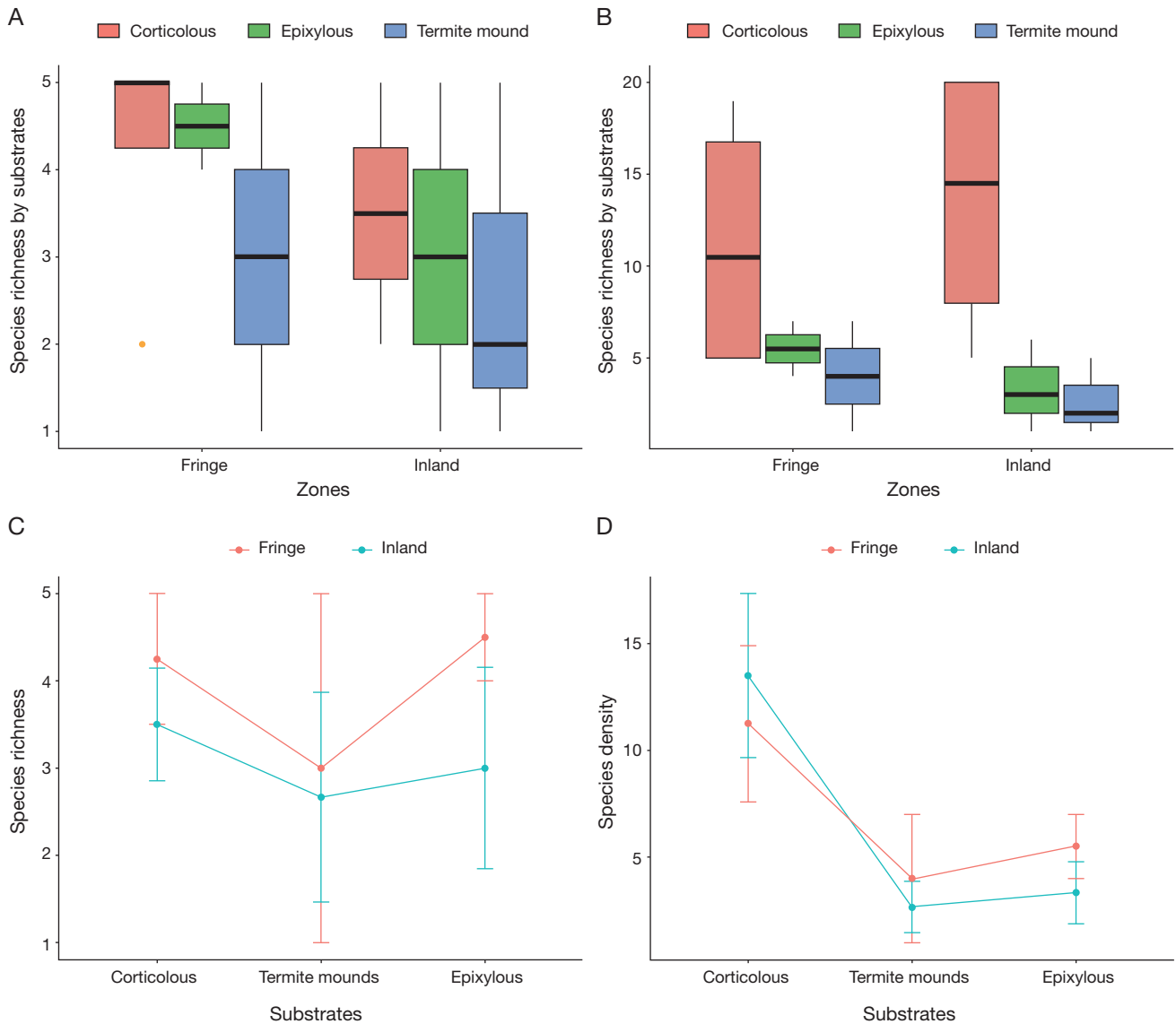


FIG. 6. — **A**, mean richness; **B**, density of bryophytes in the sampled mangroves per substrate; **C**, interaction plot between sampled zones and substrate on mean richness of bryophytes; **D**, interaction plot between sampled zones and substrate on mean density of bryophytes.

study, although with a discrete representation, represents a new record of liverworts for the mangroves of Marajó Island.

Frullaniaceae and Lejeuneaceae are taxa that normally occur in environments with more adverse conditions (such as mangroves), as they are families that have a wide range of environmental tolerance. Among the liverworts that occurred in this study, some species such as *A. torulosa*, *C. oncophylla*, *C. rigidula* and *M. epiphylla* are cited for the Amazon with morphological traits that are influenced by the microclimatic conditions of the different height zones in host trees (Mota de Oliveira 2018), such as convolute leaves and cell wall thickening, which are observed more frequently in the canopy, where light intensity is higher.

Similarly, to our finding of low richness of mosses, other studies carried out in Pará demonstrated the presence of few moss species in mangrove vegetation (Santos & Lisboa 2008; Brito & Ilkiu-Borges 2013). This may be associated with the

low availability of hosts, which is limited to a small number of species, and the absence of other types of substrates for colonization. Calymperaceae and Sematophyllaceae are the two most well represented moss families in the Amazon (Gradstein *et al.* 2001). These families are often found in disturbed areas under anthropic influence (Visnadi & Monteiro 1990; Bastos & Yano 1993; Lisboa & Ilkiu-Borges 1995; Garcia *et al.* 2014). Among the registered families, Calymperaceae had been previously cited for the mangroves of Marajó Island (Lisboa *et al.* 1993; Brito & Ilkiu-Borges 2013; Garcia *et al.* 2014), but Sematophyllaceae was found only in the present study.

It is likely that the predominance of acrocarpous mosses – represented by *C. erosum* and *C. palisotii* – is associated to the fact that this life form type is common in anthropic environments (Bastos & Bôas-Bastos 2008; Širka *et al.* 2019) and exhibits peculiar physiological characteristics that provide the species with specialized mechanisms of desiccation

tolerance (Govindaparyari *et al.* 2012; Wagner *et al.* 2014). For example, in the life form tuft, hyaline cells accumulate water to prevent desiccation and protect photosynthetic cells from high luminous intensity (Vitt 1979; Frahm *et al.* 2003; Kürschner 2004), and the costae have the function of promoting the rapid absorption and transport of water, in addition to providing structural support to the leaves during desiccation (Frahm 1985).

SEXUAL SYSTEMS AND SEX EXPRESSION

Identifying the sexual system of bryophytes is a fundamental step to understand the main mechanisms of reproduction developed by these plants, as the monoicous sexual system can facilitate sexual reproduction by the proximity between antheridia and archegonia (Wyatt & Anderson 1984; Stark *et al.* 2005). Although the richness of dioicous species was higher than that of monoicous species, we observed the highest proportion of sex expression in monoicous species. This is because monoicous species tend to prevail over dioicous species in such environments due to their lesser specialization in water requirements (Maciel-Silva *et al.* 2015; Batista *et al.* 2018).

In our study, 50% of the species found with sporophytes and gametangia were monoicous, demonstrating the efficiency of this sexual system in performing sexual reproduction (Söderström & During 2005; Stark & Brinda 2013). The reproductive performance of 11 species of a Brazilian Atlantic rainforest showed that monoicous species had the highest reproductive performance, particularly for sexual branches, fertilized gametangia and sporophyte production (Maciel-Silva *et al.* 2012). The production of asexual structures by dioicous species recorded in this study was also observed in the study by Batista *et al.* (2018) carried out in a wet forest enclave in Chapada do Araripe, Ceará.

Asexual reproduction was observed in two monoicous species in the fringe and inland zones. Dispersal through asexual propagules is a notable and widespread feature found in bryophytes and has a key role in maintaining regional and local populations (Frey & Kürschner 2011). In this context, asexual structures can offer advantages and ensure the maintenance of populations, especially in habitats subject to constant environmental stress and unfavorable conditions for sexual reproduction (Longton 1998; Glime 2017b).

LIGHT TOLERANCE GUILDS

The predominance of generalist species found in this study shows that most species have attributes that allow their distribution and tolerance over a wide range of environments. Generalist species are also associated with disturbed areas (Pantoja *et al.* 2015; Fagundes *et al.* 2016). Mangroves, for example, are threatened by the anthropogenic suppression or degradation of habitat that has caused the elimination of large areas of these ecosystems, resulting in both environmental and socioeconomic impacts (Schaeffer-Novelli 2002). In mangroves on the east coast of Marajó Island, five generalist species were distributed in the municipalities of Cachoeira do Arari and Soure (Brito & Ilkiu-Borges 2013) and Salvaterra (Lisboa *et al.* 1993; Garcia *et al.* 2014), and three of these

species were also present in the mangroves surveyed in our study: *C. palisotii*, *C. oncophylla* and *C. rigidula*.

The entry of light into the mangrove forests allowed the sun specialist species to be found along the vertical gradient of the trees, except at the base of the trees, which are exposed to floods. Light incidence and the intensity of solar radiation are factors that influence the distribution of bryophytes (Király *et al.* 2013). For example, Mota de Oliveira (2018) showed that microenvironmental conditions are determinant in the distribution of bryophyte species along the vertical gradient in the Amazon. Mota de Oliveira (2018) showed that the flora of the canopy was composed of species with dark pigmentation and convolute leaves, which are traits capable of protecting plants from light-induced damage and allowing longer periods of photosynthesis. On the other hand, the author points out that these traits showed significantly lower occurrence in the darker zone of the understory.

SUBSTRATE SPECIFICITY

The predominance of corticolous species recorded in this study (73%) was also observed in mangrove ecosystems in the Amazon (Lisboa *et al.* 1993; Brito & Ilkiu-Borges 2013; Garcia *et al.* 2014) and in the Atlantic Forest (Visnadi 2008). In tropical forests, the marked abundance of corticolous species is associated to the great availability of the substrate as well as its high-water retention capacity, important factors for colonization by bryophytes (Richards 1984; Gradstein 1992; Hallingbäck & Hodgetts 2000). However, unlike upland tropical forests, mangroves have a low floristic diversity of hosts (Schaeffer-Novelli *et al.* 2004) and this can directly influence the richness of bryophytes, since the latter is known to be strongly correlated with the richness of vascular plants in the environment (Ingerpuu *et al.* 2001).

In the studied mangroves, 50% of the species did not show preference for a single substrate, what was probably explained by the low variety of substrates available for colonization. Furthermore, the abiotic conditions present in mangroves (Tomlinson 1983; Mehlig *et al.* 2010) act as a limiting factor for the distribution of bryophytes along the vertical gradient in hosts. Most bryophytes in this study were found at an average height of three meters from the ground, always above the last branch of the stems specialized in supporting the mangrove tree. This probably indicates a strategy used by bryophytes to thrive in these mangroves, since the high salinity when the forest is flooded by tides would imply the elimination of these species from the base of the trees. Indeed, few bryophytes are adapted to survive salt stress (Buck & Schofield 1986), although some mosses of the genus *Fontinalis* can tolerate brackish waters.

SIMILARITY BETWEEN THE BRYOPHYTE FLORA OF DIFFERENT BRAZILIAN MANGROVES

The greatest similarity between the bryophyte floras of the municipalities of Ilha do Marajó (Soure, Salvaterra and Cachoeira do Arari) can be attributed to the configuration of the studied areas, which have a similar floristic composition (Lisboa *et al.* 1993; Carvalho & Jardim 2017; De Oliveira Faro *et al.* 2023) and are also influenced by tributaries of Baía do

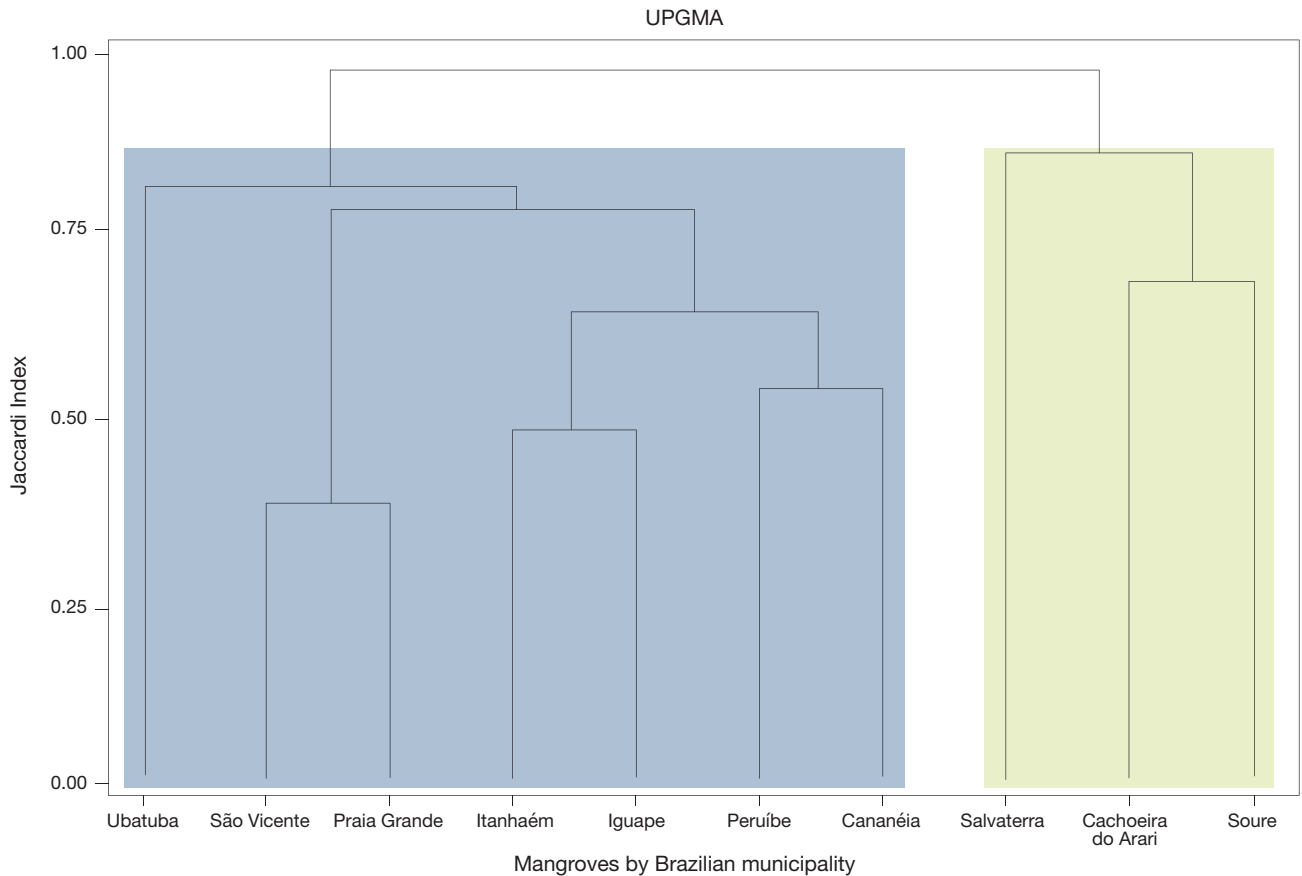


Fig. 7. — Dendrogram of floristic similarity of the bryophyte flora of mangroves on the Northern and Southeastern coast of Brazil.

Marajó (Gregório & Mendes 2009). These mangroves have a low richness of bryophytes when compared to the mangroves on the coast of São Paulo, which can be attributed mainly to the pressures of degradation and deforestation in this ecosystem. Bryophyte communities are known for the fact that their composition and species richness are strongly influenced by external factors, mainly water, light and temperature (Mägdefrau 1982). Thus, the openness of the tree canopy allows a high incidence of light along the vertical gradient within the mangrove, resulting in environmental conditions that lead to a pool of generalist and sun specialist species that are commonly found among the studied areas.

The bryophyte flora of the mangroves of the coast of the state of São Paulo showed greater similarity to each other and presented a high number of species compared to the bryophyte flora of the mangroves of Marajó Island. Adverse environmental conditions, as well as the type and use of vegetation surrounding the mangrove forests, may be implied in the lower richness in Marajó Island. The diversity of plant species in mangroves depends, in part, on the proximity to other vegetation formations (Visnadi 2008). Mangrove forests in Marajó Island are highly fragmented and their surroundings consist of savannas, secondary forests, black-water (igapó) and white-water (várzea) floodplain forests.

To better explain the patterns observed in the mangroves of São Paulo, we consider important the fact that these ecosys-

tems are located in areas with altitude and steep topography, unlike the mangroves of Marajó Island that are established at low altitude. This is relevant mainly because bryophytes are highly sensitive to altitudinal variations and the richness of species increases at higher altitudes (Van Reenen & Gradstein 1984; Frahm 1990; Frahm & Gradstein 1991; Kessler 2000; Ah-Peng *et al.* 2007). Furthermore, some species may be migrating from the forests surrounding the mangroves, since several areas of mangroves along the southeastern coast are bordered by Atlantic Forest (Vannucci 2003) and the bryophyte species listed for the mangroves of São Paulo are not restricted to this ecosystem, but rather occur in other types of environments (Visnadi 2008).

In this study, we showed that the assemblages of epiphytic bryophytes developing in the same type of landscape (mangroves) but in different locations (Marajó Island versus state of São Paulo) have relatively low similarity. In fact, Lönnell *et al.* (2012) showed that the presence and frequency of epiphytic bryophytes is correlated with the connectivity to colonized trees that are in the same landscape and separated by a few kilometers.

GEOGRAPHICAL DISTRIBUTION OF EPIPHYTIC SPECIES IN RELATION TO BIOMES IN BRAZIL

The occurrence of the recorded species in up to five phyto-geographic domains in Brazil can be explained by the fact

that the geographic distribution of bryophytes is generally not limited by dispersal (Campos *et al.* 2019). Bryophytes frequently have wide geographical distributions and are found in more than one continent (Heinrichs *et al.* 2009). Compared to other groups of organisms, bryophytes have relatively low endemism rates and larger distribution ranges (Patiño & Vanderpoorten 2018). In general, bryophytes tend to present broader distributions than vascular plants (Vanderpoorten & Goffinet 2009). Some mechanisms that play a key role in dispersal contribute to this feature of bryophytes. For example, the small, lightweight spores of bryophytes are easily transported by the wind, allowing them to travel several kilometers (Miller & McDaniel 2004; Sundberg *et al.* 2006).

The action of rain splashes on spores and vegetative buds is a short-distance dispersal mechanism observed in bryophytes in the understory. Wind transportation, in contrast, is a long-distance dispersal mechanism acting in the outer canopy (Campos *et al.* 2019). In addition, the fact that the Amazon and the Atlantic Forest are phytogeographic domains that had a biogeographic connection in the past, when they formed a single extensive forest (Sobral-Souza *et al.* 2015), probably explains the greater representativeness of species shared between these domains until present day.

CONCLUSION

The bryophytes from the mangroves of Salvaterra have a wide geographical distribution, as they are mostly generalist species that colonize various types of environments, confirming our first hypothesis that the opening of the tree canopy directly influences the composition of the species. To confirm our second hypothesis, our results showed a higher frequency of sex expression in monoicous species than in dioicous species, with the expression of asexual structures strongly associated with monoicous species. These results highlight the ability of monoicous species to prevail over dioicous species in such environments, due to their lower specialization in water needs. In addition, the prevalence of sexual reproduction represents a strategy of these species to survive in mangroves, since spores are more desiccation tolerant than asexual propagules and may persist in the spore bank.

We highlight the important role of environmental filters in the selection of the assemblage of species in the ecosystems, illustrated by the low similarity between the composition of mangroves from the Marajó Island and those from the state of São Paulo. However, it is still necessary to address in future studies some issues that have not been raised here, such as the processes that rule the assembly of these communities and the environmental filters that affect the distribution of epiphytic bryophyte species specifically in mangroves.

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Conflict of interests

The authors declare no conflict of interests.

Author' contributions

The research idea was developed by PWPG and ACCTM; PWPG, MCS and ACCTM collected bryophytes; PWPG and ACCTM validated the taxonomic identity of all records; PWPG performed the statistical analyses; PWPG was responsible for preparing and writing the manuscript; PWPG and ACCTM revised the manuscript; all authors approved the final version of the text.

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