



ECOSYSTEMS

Composition and structure of the bryophyte community of Park Savanna in Marajó Island, Pará, Brazil

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Abstract: Aiming to enrich the knowledge about the flora of savannas, this paper studied the composition and structure of the bryophyte community of Park Savanna areas in Marajó Island - PA. Biological material was collected within 60 100-m² plots equally distributed in the dry season of 2016 and the rainy season of 2017 in five Park Savanna areas (SP-I to SP-V). The composition, density, richness and diversity of species and presence of indicator species were compared between the sampled areas and seasons. The species were classified according to the substrates colonized and ecological groups of light tolerance. Significant differences in SP-V indicated that the area was the main factor influencing the composition of bryophytes ($p = 0.0001$), with five indicator species. There were also significant differences in density ($p = 0.0001168$) and richness ($p = 0.0001317$) of bryophytes between seasons (p -value = 0.3393; p -value = 0.04065; $p = 0.1081$). There was a predominance of generalist (25 spp.) and corticolous (728 individuals) species, which were widely distributed in the sampled areas. Therefore, the structure of the bryophyte communities was not influenced by seasonality, and this indicates that these plants are adapted to the environmental conditions.

Key words: amazonian savannas, bryoflora, ecology, seasonal precipitation.

INTRODUCTION

Brazilian savannas (Cerrado) are predominantly distributed in the Central Plateau region, forming the second largest neotropical biome and considered one of the biodiversity hotspots for conservation priorities (Myers et al. 2000, Rios et al. 2016). Savannas also occur within the Amazon biome (Amazonian savannas) formed by disjoint patches that altogether cover an area of about 267 km² (Carvalho & Mustin 2017). They reach the east portion of the Marajó island and other spots distributed in the states of Amapá, Amazonas, Pará and Roraima (Prance 1996, Rossetti et al. 2007), and are characterized by the

predominance of grasses and a variable density of trees and shrubs (Silva & Oliveira 2018).

Savannas are ecosystems influenced by high light intensity and drought events, which increase the chances of spread of fires (Hoffmann et al. 2012). Microclimatic conditions such as luminosity, temperature, humidity, and pH act as environmental filters that can determine the structure of bryophyte communities (Weibull & Rydin 2005, Bello et al. 2010, Smith & Stark 2014, Santos et al. 2014). Desiccation tolerant bryophytes are common in savannas (Visnadi & Vital 1989), since only the best adapted species settle in these areas (Kürschner 2004, Kürschner & Parolly 2005, Pardow & Lakatos 2013).

The composition of bryophytes in tropical forest is influenced by microhabitat variability along the different height zones of host trees (Holz et al. 2002, Gosselin et al. 2017). The relationship of bryophytes with the microhabitat can be explained by structural and chemical characteristics of the substrate and exposure to light, wind and precipitation (Hespanhol et al. 2011, Gosselin et al. 2017).

The distribution pattern of plant communities in Amazonian savannas is still little known (Cavalcante et al. 2014) and more studies are needed to promote the conservation of their biodiversity, which has a high rate of endemic species (Strassburg et al. 2017). Many of these species in Amazonian savannas are threatened with extinction due to constant clearance of forest areas to meet agriculture and livestock demands associated with population growth (Plotkin & Riding 2011, Carvalho & Mustin 2017).

In view of the heterogeneity and social value of their different phytogeographies of savannas (Plotkin & Riding 2011, Fearnside 2015), their conservation requires investments in research for the implementation of new Environmental Protection Areas (Mustin et al. 2017). Knowledge of the ecology of bryophytes can be useful because these plants can serve as models for management and conservation strategies of these savannas. Since, some studies simulating environmental changes and micro fossil analyses have suggested that climate change will strongly affect both the abundance and composition of the bryophyte communities (Dorrepal et al. 2004, Walker et al. 2006, Lang et al. 2009, Elmendorf et al. 2012), which in turn affects the structure and functioning of the ecosystem where bryophytes and vascular plants cooccur (He et al. 2016).

The objective of the present study was to evaluate the composition and structure of

bryophyte communities in Park Savanna areas in Marajó Island, state of Pará.

MATERIALS AND METHODS

Study area

The study area corresponded to five savannas classified as belonging to the Park Savanna (SP) phytogeography (Rossetti et al. 2007, IBGE 2012), located in the east side of the Marajó Island, state of Pará. Four Park Savanna areas are located in the municipality of Salvaterra; of these, SP-I (00° 47' 47.5" S and 48° 32' 39.7" W) and SP-IV (00° 52' 24.8" S and 48° 35' 07.7" W) can be easily seen from the Camará-Salaterra road margins, and SP-II (00° 51' 44.4" S and 48° 31' 45.0" W) and SP-III (00° 51' 09.4" S and 48° 31' 55.9" W) from the Salvaterra-Joanes road. The SP-V (00° 54' 32.3" S and 48° 40' 06.9" W) is located at the margins of the PA-154 road, in the municipality of Cachoeira do Arari. The peculiar characteristics of the current physiognomic aspect of these savannas are described in Table I. The climate is humid equatorial with average annual temperature of 28°C and precipitation all the year round. The months with less precipitation in the period studied were August through October (average of 19 mm) and the ones with more precipitation were January through April (average of 504 mm). This information was obtained from the database of the National Institute of Meteorology (<http://www.inmet.gov.br/portal/index.php?r=home2/index>).

Sampling, collection and taxonomic identification

Sixty 100 m² (10 m x 10 m) plots were established and usual sampling techniques for bryophytes were adopted (Vanderpoorten et al. 2010). Thirty plots were equally distributed in the five savannas during the dry season of 2016, and 30 during the rainy season in 2017. Field

Table I. Phytophysiognomy characterization of the five Park Savanna areas in Marajó Island, Pará, Brazil.

Park Savanna	Description of the area
SP-I	Prevalence of Poaceae and Cyperaceae grasses, forming large open fields affected by heavy flooding during the rainy season due to proximity to mangrove water courses; less dense tree stratum formed by <i>Astrocaryum vulgare</i> Mart., <i>Attalea maripa</i> (Aubl.) Mart., <i>Byrsonima chrysophylla</i> Kunth, and <i>Curatella americana</i> L.
SP-II	Vegetation similar to the cerrado of the Central Plateau, with well drained soils and absence of floods; prevalence of Poaceae and Cyperaceae grasses, and tree stratum with sparse and less dense vegetation mainly composed of <i>Hancornia speciosa</i> Gom. and <i>C. americana</i> , in addition to <i>A. vulgare</i> , <i>B. chrysophylla</i> , <i>Platonia insignis</i> Mart., and <i>Salvertia convallariaeodora</i> A. St.-Hil.
SP-III	Vegetation similar to the cerrado of the Central Plateau, with well drained soils and absence of floods; prevalence of Poaceae and Cyperaceae grasses, and tree stratum with sparse and less dense vegetation mainly composed of <i>H. speciosa</i> and <i>C. americana</i> , in addition to <i>A. vulgare</i> , <i>B. chrysophylla</i> , <i>P. insignis</i> , and <i>S. convallariaeodora</i> .
SP-IV	Vegetation similar to the cerrado of the Central Plateau, presence of floods due to overflow of creeks in the rainy period; predominance of Poaceae and Cyperaceae grasses, and vegetation mainly composed of <i>C. americana</i> and <i>S. convallariaeodora</i> , in addition to <i>H. speciosa</i> and <i>B. chrysophylla</i> .
SP-V	Denser vegetation in relation to the previous ones and similar to the cerrado of the Central Plateau, with well drained soils and absence of floods; predominance of Poaceae and Cyperaceae grasses; vegetation mainly composed of <i>C. americana</i> and <i>B. chrysophylla</i> , besides <i>P. insignis</i> , <i>S. convallariaeodora</i> and <i>A. vulgare</i> .

collection and preservation of botanical material followed the methodology of Glime (2017). The bryophytes were collected in wooden paper bags and a single bag corresponded to a sample, which in this study was adopted the theme occurrence to represent the species found in each sample. Within each plot, it had at least five living trees, where the bryophytes were collected from the base to the crown of host trees (accessed through climbing techniques), but without dividing crown into zones. In some plots, bryophytes were also collected in decomposing trunks, soil, and termite mounds. Specialized literature (Buck 2003, Florschütz-De Waard 1996, Gradstein & Ilkiu-Borges 2009) was used for identification and the classification

system adopted was the one of Crandall-Stotler et al. (2009) for liverworts and Goffinet et al. (2009) for mosses. The database of the Flora do Brasil 2020 under construction (Costa & Peralta 2015) was used to confirm scientific names. The botanical material was incorporated in the Prof. Dr. Marlene Freitas da Silva (MFS) Herbarium of the State University of Pará.

Data analysis

Species accumulation curves were generated in the iNEXT software (Hsieh et al. 2013), using an individual based data matrix of the bryophyte communities to evaluate sampling sufficiency.

The composition of the community was compared between the two seasons and

between areas through PERMANOVAs based on a Bray-Curtis distance matrix (Zar 2010) and summarized through a Principal Component Analysis (PCA). Indicator species analysis (IndVal), carried out in the R software (Dufrêne & Legendre 1997), was used to identify whether some of the species could indicate differences in composition. Mean values of density, richness and diversity per plot were adopted to analyze the structure of the community. The Student's t-test (or the non-parametric equivalent test) was used to compare the density and richness between seasons, and the Kruskal-Wallis rank-sum test (Dunn 1964) was used for pairwise multiple comparisons between areas. Two-way Analysis of Variance (ANOVA) was used to compare the density and richness of bryophytes between different areas in the two seasons (Aires et al. 2007). The interaction plot (interaction plot) was used to facilitate the interpretation of the boxplot generated in the two-way ANOVA. The Fisher's alpha diversity index (Magurran 1988) was used to analyze the variations of species richness and abundance between seasons and areas sampled, using the "vegan" package (Oksanen et al. 2007) in the R software v. 3.1.3 (R Development Core Team 2018).

For the study of species distribution, the species were classified according to the ecological groups of light tolerance, namely, sun specialists, shade specialists, and generalists. This classification was based on the works of Richards (1984), Gradstein et al. (2001), Pantoja et al. (2015), and Fagundes et al. (2016). To verify whether there were specific communities in the different areas or if there was a single community of generalist species throughout the savannas, the density and richness of generalist species was analyzed by multiple comparisons with the Kruskal-Wallis rank-sum test (Dunn 1964). The species were classified as to substrate colonized, based on Robbins (1952)

with adaptations, and the absolute frequency of the rare species was classified according to the number of occurrences ($> 1 < 5$), based on Silva & Pôrto (2007).

RESULTS

Species accumulation curves

Less than 25% of the species were shared between the five areas, which include four taxa of mosses - *Calymperes erosum* Müll. Hal., *Calymperes palisotii* Schwägr., *Microcalpe subsimplex* (Hedw.) W.R. Buck, and *Octoblepharum albidum* Hedw. - and three of liverworts - *Cheilolejeunea comans* (Spruce) R.M.Schust., *Cheilolejeunea oncophylla* (Aongström) Grolle & E.Reiner, and *Cheilolejeunea rigidula* (Mont.) R.M.Schust.

Rare species represented about 63% (26) of the sample; 11 species were represented by one occurrence each and five species by two occurrences each. The presence of these levels of rarity contributed to the non-stabilization of accumulation curves, as demonstrated by the fact that there was no saturation of species in the five sampled areas and seasons (Figure 1a-d).

Floristic composition

Three hundred and sixteen samples of bryophytes were analyzed, resulting in 41 species with 820 occurrences. Liverworts had a higher richness, with Lejeuneaceae (24 spp., 306 occurrences) followed by Frullaniaceae (two spp., four occurrences). Mosses (15 spp.) were more abundant, with 510 occurrences, of which 383 belonged to Calymperaceae (five spp.), especially *Calymperes palisotii* Schwägr. (108) and *Octoblepharum albidum* Hedw. (206), which were widely distributed in the studied areas (Table II). There was a predominance of acrocarpous over pleurocarpous mosses, with 78% (11) of the species distributed in the families

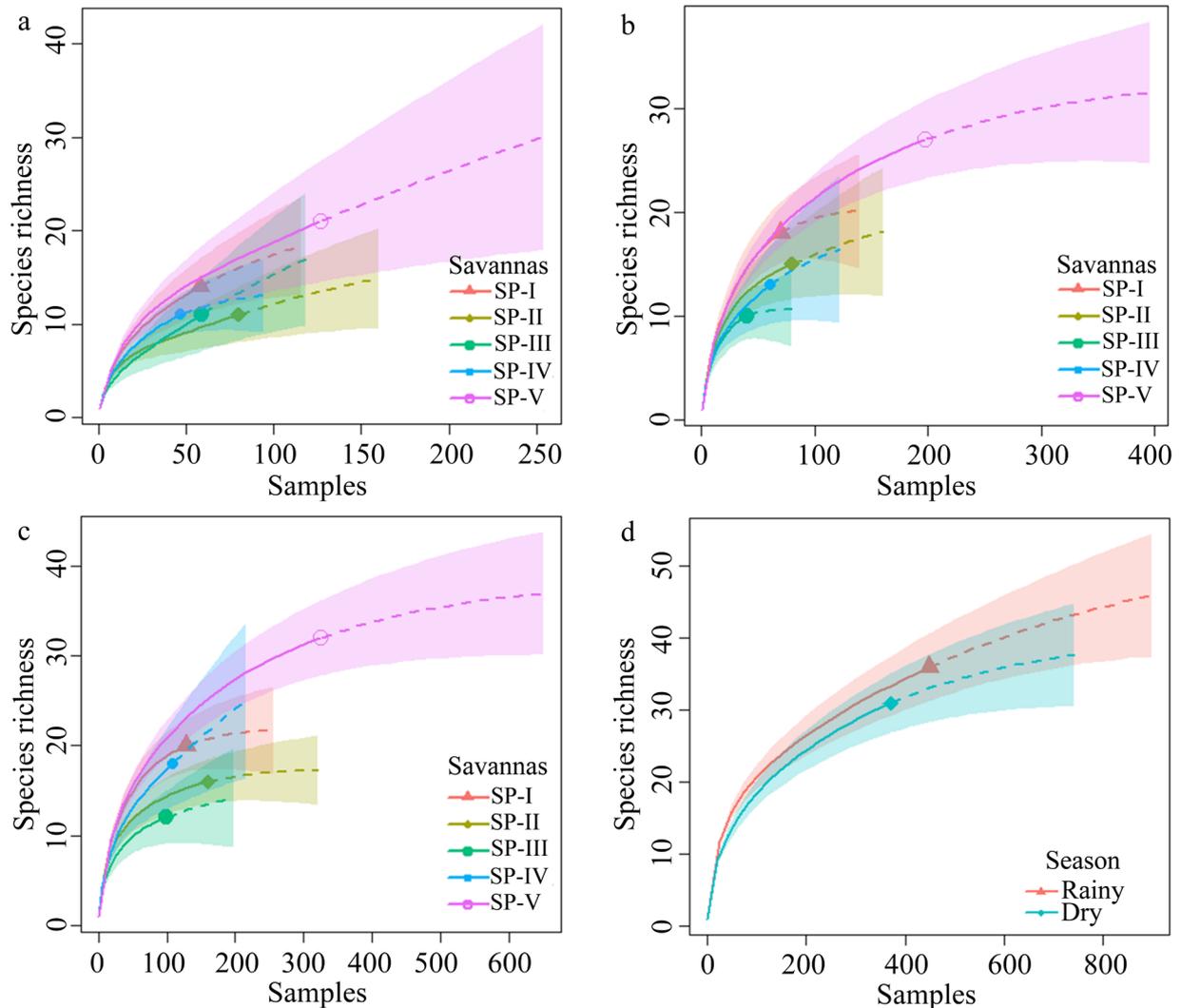


Figure 1. Species accumulation curves in the sampled Park Savanna areas and seasons, Marajó Island, Pará. (a) all areas per dry season; (b) all areas per rainy season; (c) all areas; (d) all areas per rainy and dry season.

Bryaceae, Calymperaceae, Fissidentaceae, Leucobryaceae, and Orthotrichaceae.

Species composition

The species composition of SP-V differed significantly from other areas (Pseudo-F = 4.111; p-value = 0.0001) (Figure 2a), and there were five indicator species: *Acrolejeunea emergens* (Mitt.) Steph., *Acrolejeunea torulosa* (Lehm & Lindenb.) Schiffn., *Microlejeunea epiphylla* Bischl., *Fissidens guianensis* Mont., and *Frullania exilis* Taylor. SP-I was significantly different only from SP-II and SP-III (p-value = 0.0234; p-value

= 0.0069), with *Campylopus surinamensis* Müll. Hal. and *Cheilolejeunea trifaria* (Reinw. et al.) Mizut. as indicator species. The sets of SP-I and SP-IV presented similar bryoflora in both seasons, as observed in the large overlap of these groups (Figure 2a).

No significant variation was observed in species composition between wet and dry season (Pseudo-F = 1.7059; p-value = 0.1081) due to the large overlap of groups (Figure 2b). The first two dimensions of the PCA explained 59.8% of the variance in the data set; the first

Table II. List of bryophytes of the five Park Savanna areas in Marajó Island, Pará.

Bryophyte	Park Savanna area					Season		EG	Substrates				Voucher
	I	II	III	IV	V	R	D		Co	E	T	TM	
Bryophyta													
Bryaceae													
<i>Bryum coronatum</i> Schwägr.			1	1	2	1	3	Gen	3		1		MFS007628
Calymperaceae													
<i>Calymperes erosum</i> Müll. Hal.	15	8	4	6	17	35	15	Gen	46	4			MFS007629
<i>Calymperes palisotii</i> Schwägr.	20	24	11	23	30	57	51	Gen	90	15	1	2	MFS007630
<i>Octoblepharum albidum</i> Hedw.	33	42	36	33	62	97	109	Gen	197	7	2		MFS007631
<i>Syrrhopodon ligulatus</i> Mont.		7		6	5	16	2	Gen	17	1			MFS007632
<i>Syrrhopodon prolifer</i> Schwägr.				1		1		Gen	1				MFS007633
Fissidentaceae													
<i>Fissidens angustifolius</i> Sull.					2		2	Gen	2				MFS008750
<i>Fissidens guianensis</i> Mont.					3	2	1	Gen	1		1	1	MFS008744
<i>Fissidens prionodes</i> Mont.	1			1	1	1	2	Gen			3		MFS007634
Leucobryaceae													
<i>Campylopus surinamensis</i> Müll. Hal.	12			4		7	9	Sun	8		8		MFS007635
Orthotrichaceae													
<i>Groutiella tomentosa</i> (Hornsch.) Wijk & Margad.					1	1		Gen	1				MFS008742
Sematophyllaceae													
<i>Brittonodoxa subpinnata</i> (Brid.) W.R.Buck					1	1		Gen	1				MFS008741
<i>Microcalpe subsimplex</i> (Hedw.) W.R. Buck	5	25	27	11	26	38	56	Gen	89	5			MFS007636
<i>Sematophyllum adnatum</i> (Michx.) Brid.					2	2		Gen	2				MFS008747
<i>Trichosteleum papillosum</i> (Hornsch.) A.Jaeger					1	1		Gen		1			MFS008745
Marchantiophyta													
Frullaniaceae													
<i>Frullania exilis</i> Taylor					3	2	1	Sun	3				MFS008751
<i>Frullania gibbosa</i> Nees					1	1		Sun	1				MFS008747
Lejeuneaceae													
<i>Acrolejeunea emergens</i> (Mitt.) Steph.	2			2	16	11	9	Sun	17	3			MFS007637

Table II. Continuation

Bryophyte	Park Savanna area					Season		EG	Substrates				Voucher
	I	II	III	IV	V	R	D		Co	E	T	TM	
<i>Acrolejeunea torulosa</i> (Lehm. & Lindenb.) Schiffn.	4		1	8	53	41	25	Sun	57	8		1	MFS007638
<i>Archilejeunea fuscescens</i> (Hampe ex Lehm.) Fulford.	2				1	1	2	Gen	3				MFS007639
<i>Cheilolejeunea aneogyna</i> (Spruce) A. Evans				1		1		Gen	1				MFS007640
<i>Cheilolejeunea clausa</i> (Nees & Mont.) R.M.Schust.		1				1		Sun	1				MFS007641
<i>Cheilolejeunea comans</i> (Spruce) R.M.Schust.	4	7	1	3	2	10	7	Gen	15	1		1	MFS007642
<i>Cheilolejeunea discoidea</i> (Lehm. & Lindenb.) Kachroo & R.M.Schust.		1					1	Gen	1				MFS007643
<i>Cheilolejeunea holostipa</i> (Spruce) Grolle & R.-L.Zhu					1	1		Gen	1				MFS008740
<i>Cheilolejeunea oncophylla</i> (Aongström) Grolle & E.Reiner	10	20	4	4	39	42	35	Gen	69	7		1	MFS007644
<i>Cheilolejeunea rigidula</i> (Mont.) R.M.Schust.	2	10	3	1	10	12	14	Gen	22	4			MFS007645
<i>Cheilolejeunea trifaria</i> (Reinw. et al.) Mizut.	3					1	2	Gen	2	1			MFS007646
<i>Drepanolejeunea fragilis</i> Bischl.					3		3	Gen	2	1			MFS008748
<i>Frullanooides corticalis</i> (Lehm. & Lindenb.) Slageren	2					1	1	Sun	2				MFS007647
<i>Lejeunea flava</i> (Sw.) Nees				1	1	1	1	Gen	2				MFS007648
<i>Lejeunea laetevirens</i> Nees & Mont.	1	2	6		8	11	6	Gen	15	2			MFS007649
<i>Lopholejeunea subfusca</i> (Nees) Schiffn.					2	2		Sun	2				MFS008739
<i>Microlejeunea bullata</i> (Taylor) Steph.					1		1	Gen		1			MFS008749
<i>Microlejeunea epiphylla</i> Bischl.	3	5	2		17	21	6	Gen	23	4			MFS007650
<i>Microlejeunea globosa</i> (Spruce) Steph.				1			1	Gen	1				MFS007651

Table II. Continuation

Bryophyte	Park Savanna area					Season		EG	Substrates				Voucher
	I	II	III	IV	V	R	D		Co	E	T	TM	
<i>Microlejeunea subulistipa</i> Steph.	3	2			3	7	1	Gen	7			1	MFS007652
<i>Pycnolejeunea contigua</i> (Nees) Grolle	1				4	4	1	Sun	3	2			MFS007653
<i>Pycnolejeunea macroloba</i> (Nees & Mont.) Schiffn.	1	2		1		3	1	Sun	4				MFS007654
<i>Pycnolejeunea papillosa</i> X.-L. He	4	3	3		2	10	2	Sun	10	2			MFS007655
<i>Pycnolejeunea</i> sp.		2			4	5	1	*	6				MFS008743
Total	128	161	99	108	324	449	371		728	69	16	7	

I - Vila de Jubim (SP-I); II - Vila de Joanes (SP-II); III - Vila de Água Boa (SP-III); Vila União (SP-IV); Vila de Camará (SP-V); R - Rainy season; D - Dry season; EG - Ecological group; Gen - Generalist; Sun - Sun specialist; *Not determined; Co - Corticolous; E - Epyxilic; T - Terricolous; TM - Termite Mound.

dimension accounted for 39.7%, and the second for 20.1%.

Density, richness and diversity

SP-V presented a significantly different density (Kruskal-Wallis = 23,176; p-value = 0.0001168) (Figure 3a) and richness (Kruskal-Wallis = 22,914; p-value = 0.0001317) in relation to the other sampled areas (Figure 3b).

Seasonality did not influence the density of bryophytes ($W = 515$; p-value = 0.3393) (Figure 3c), but richness was significantly lower in the dry season ($t = 2.0939$; p-value = 0.04065) (Figure 3d). The number of species in the dry season was about 86% of the species recorded during the rainy season (31 against 36). Most species (26 spp.) occurred in both seasons and less than one quarter was exclusive of the dry (five spp.) or rainy (10 spp.) season.

The interaction plots indicated that there were variations in the number of occurrences and species among the savannas in the rainy and dry season, but seasonality did not significantly affect the mean density (Figure 4a) and richness (Figure 5b). The diagrams showed that the area was the main factor influencing the density

(Figure 4b and c) and richness (Figure 5b and c) of bryophytes in the savannas sampled, with SP-V standing out among the others.

Fisher's alpha indices were consistent with changes in species richness and abundance between sampled areas and seasons, with a pattern of increasing diversity, richness and abundance indices, as well as with species accumulation curves, with higher values for SP-V (8.80) in both seasons (Table III).

Ecological groups

More than half of the species were generalist (30 spp.), found throughout the height of host trees. They were followed by the sun specialists (11 spp.). There was a significant variation in the density of generalist species between the sampled areas (Kruskal-Wallis = 30.54; p-value = 0.0005) (Figure 6a), with significant difference between areas I and II (p-value = 0.001) and III (p-value = 0.006), between areas II and V (p-value = 0.005), between areas III and V (p-value = 0.005), and between areas IV and V (p-value = 0.0008). The richness of the generalist species also varied between the sampled areas (Kruskal-Wallis = 25.019; p-value = 0.0005) (Figure

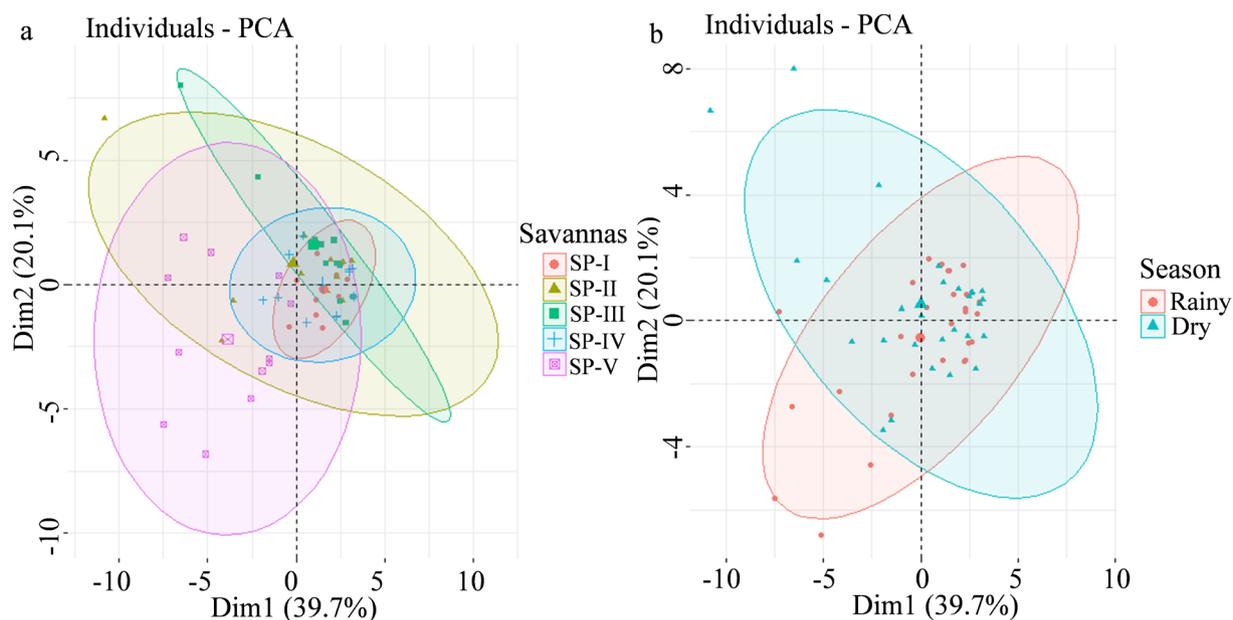


Figure 2. Principal Component Analysis of bryophytes of the Marajó Island, Pará. (a) Sampled savanna áreas; (b) Seasons.

6b), with significant differences between area I and II (p -value = 0.001) and III (p -value = 0.009), between areas II and V (p -value < 0.005), and between areas IV and V (p -value = 0.005).

Distribution of bryophytes by substrate

The corticolous species were predominant with 88.7% (728) of occurrences, observed along the host trees. Dead trunks were the second most colonized substrates, with 8.4% (69) of occurrences of the epixylic species, followed by termite mounds (1.9%, 16) and soil (0.8%, seven).

Rare species (26 spp.) were mostly established in live substrates, of which 84% (22) were in live substrate samples, and of these, 17 species occurred on SP-V and with low values in SP-I and SP-IV (six spp.), SP-II (three spp.) and SP-III (one sp.). Of the 32 species recorded in SP-V, 29 (270 occurrences) were found on live trunks and 16 on dead branches; only the taxa *Microlejeunea bullata* (Taylor) Steph. and *Trichosteleum papillosum* (Hornsch.) A. Jaeger occurred exclusively on dead branches, while

the others occurred synchronously in the two substrates.

DISCUSSION

Accumulation curves

The non-stabilization of accumulation curves in floristic studies in tropical forests is common due to the overrepresentation of rare species. In the case of bryophytes in the Amazon, the predominance of rare species has been cited for the Caxiuanã National Forest in Pará, in non-flooded areas and floodplains, “campinas”, “campinaranas”, and savanna vegetation (Alvarenga & Lisboa 2009). Schilling & Batista (2008) pointed out that the widespread distribution of rare species is common in tropical forests and contributes to an marked growing trend in species accumulation curves.

Highly represented rare species in certain sites, such as in the savannas studied, are considered by Myers et al. (2000) to represent a

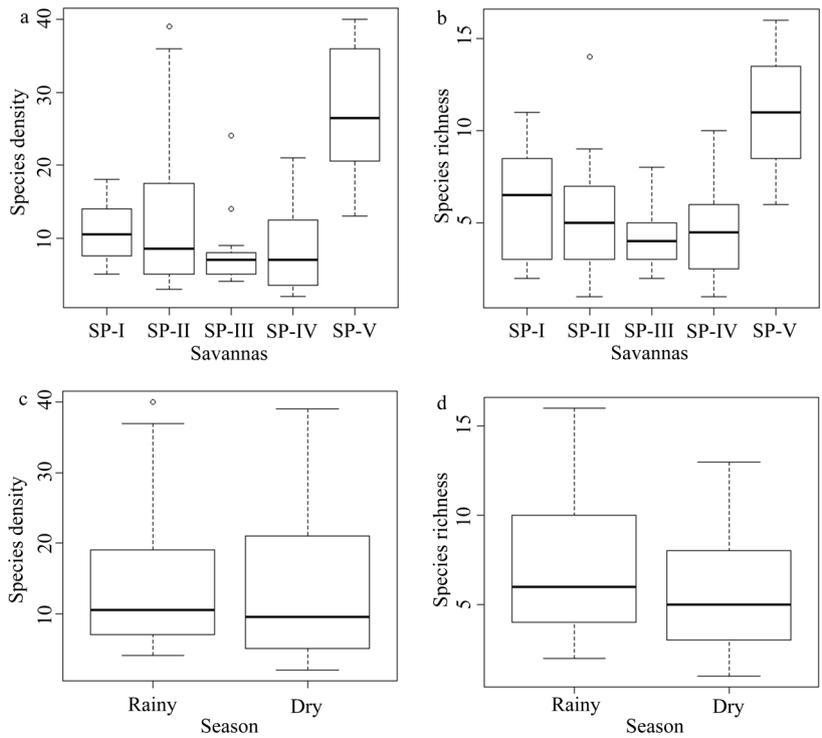


Figure 3. Mean density and richness of species per plot in the studied areas and seasons in Marajó island, Pará. (a) Mean density in the five Park Savanna areas; (b) Mean richness in the five Park Savanna areas; (c) Mean density in the two seasons; (d) Mean richness in the two seasons.

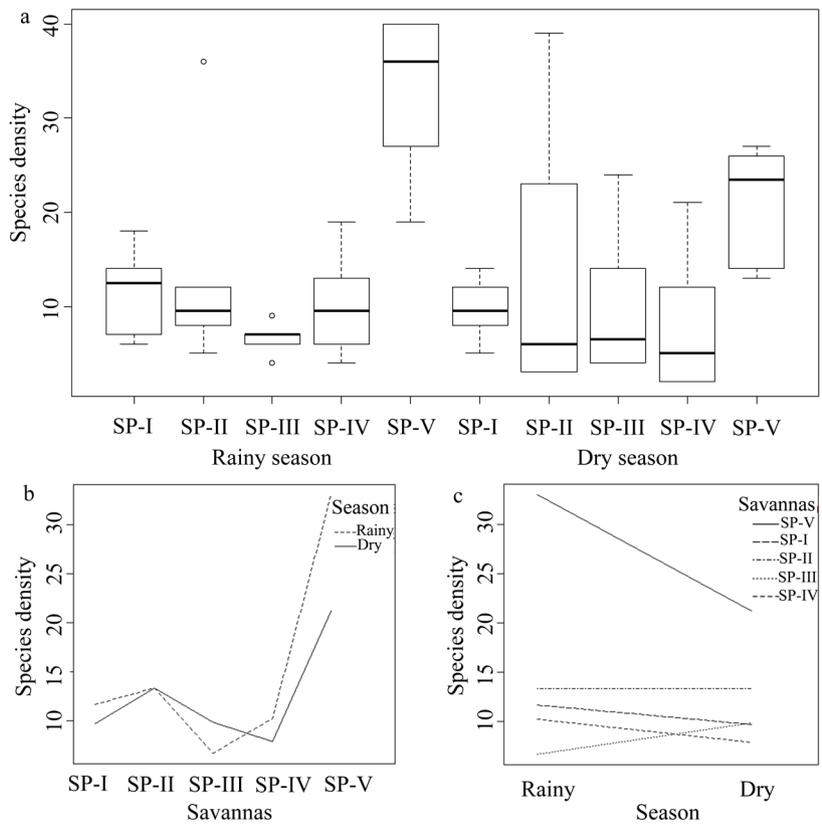


Figure 4. (a) Mean density of bryophytes in the sampled savannas per season; (b) Interaction plot between sampled areas and seasons on mean density of bryophytes; (c) Interaction plot between seasons and sampled areas on mean density of bryophytes.

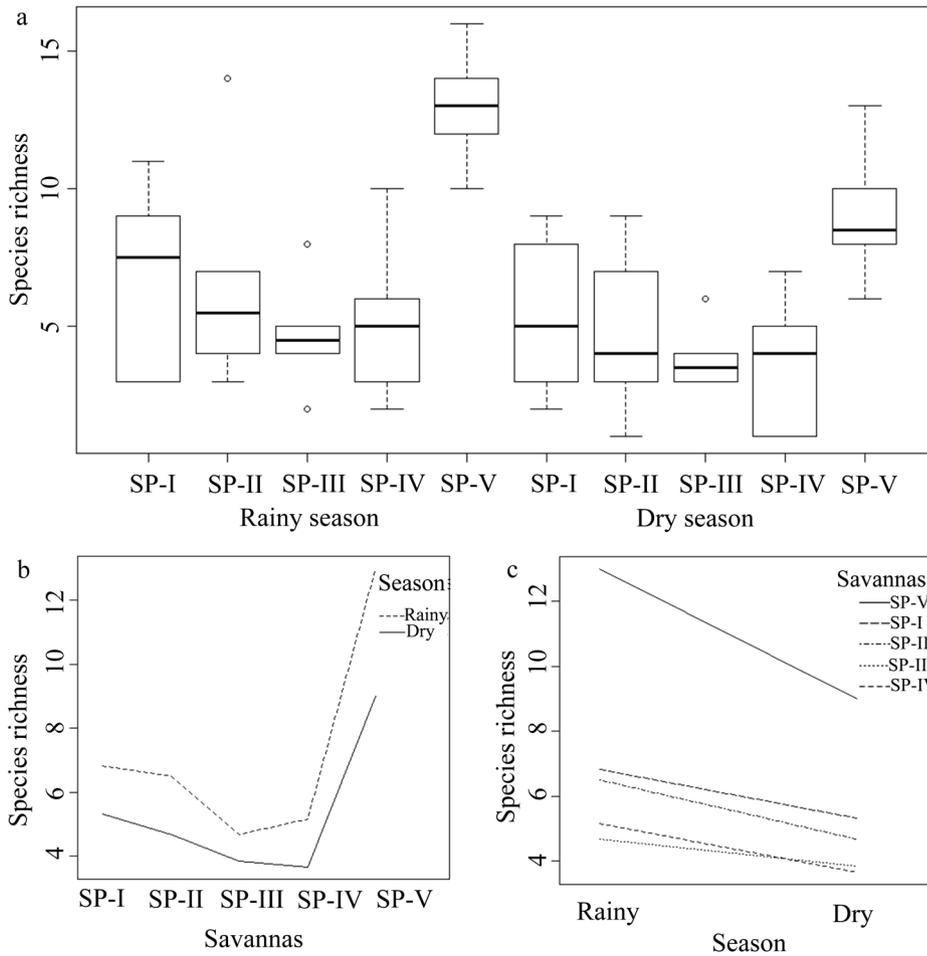


Figure 5. (a) Mean richness of bryophytes in the sampled savannas per season; (b) Interaction plot between sampled areas and seasons on mean richness of bryophytes; (c) Interaction plot between seasons and sampled areas on mean richness of bryophytes.

group with great importance to the conservation of biological diversity.

Species composition

The results indicated that the composition was influenced by local conditions of the habitat rather than by seasonality. Since, although all areas were classified as Park Savanna, differences were observed in terms of density of host trees and soil drainage influenced by riverine forests. Rainfall occurs throughout the year in the Amazon, but two rain periods can be distinguished: one rainiest season influenced by the Intertropical Convergence Zone (ITCZ), and another dry season, with undefined dry season (Fisch et al. 1998). In this sense, the results were expected that the composition would not be

influenced by seasonality, considering that most bryophytes are perennial with life cycles with more than one year (necessary for a reproductive cycle and ripening of the spores) and therefore live both wet and dry seasons several times (Geissler 1982). On the other hand, a minority of bryophytes are ephemeral with very short life cycles that probably vary with seasonality, such as the moss model *Physcomitrium* (Cove et al. 2006).

SP-V presented 11 exclusive species, nine of which occurred in live trunks and two in dead trunks. These results indicate that the amount of host trees, light incidence, and the structural and chemical conditions of the substrates are vital for the creation of different microhabitats (Hylander 2009, Sundberg 2013, Lonnell et al.

2014). These conditions act as environmental filters that influence the composition of the bryoflora (Raabe et al. 2010) and shape plant communities (Mota-de-Oliveira & ter Steege 2015).

The predominance of Lejeuneaceae in the sampled savannas is explained by the fact that this family comprises about 70% of Amazonian bryophyte richness, due to its wide morphological plasticity that allows the colonization of different environments and height zones in host trees (Gradstein et al. 2001, Oliveira & ter Steege 2013, Mota-de-Oliveira 2018). However, in spite of the greater richness of Lejeuneaceae, the number of occurrences recorded in the sampled savannas

was not as high as that of Calymperaceae and Sematophyllaceae. Similar results were found by Bôas-Bastos & Bastos (1998) in a savanna in Bahia, where Frullaniaceae and Lejeuneaceae were the only liverwort families present. Such families have great ecological amplitude and are common in xerophytic vegetation, although they are usually represented by few occurrences. These families were also the most represented among liverworts recorded in savannas of the Federal District (Câmara & Leite 2005), Goiás (Pinheiro et al. 2012, Aquino et al. 2015, Rios et al. 2016) and Maranhão (Oliveira et al. 2018, Costa et al. 2018).

The predominance of acrocarpous moss families is common in open, sunny, dry, xeric or anthropic habitats (Bastos & Bôas-Bastos 2008, Širka et al. 2019) because these taxa are more resistant to dehydration (Govindaparyi et al. 2012). For example, turf life form, leaves imbricate and slightly folded, smaller leaves, lengthy costa, leaves with papilla, leaves with hairpoint and hyalocysts/hyaline cells, confers desiccation resistance the acrocarpous mosses and are the result of xerophytic adaptations (Watson 1914, Frahm 2003, Kürschner 2004, Kürschner & Parolly 2005, Henriques et al. 2017). Similar results were recorded in savanna of Minas Gerais, where acrocarpous mosses accounted for roughly 53% of moss species (Sousa & Câmara 2015). The moss families recorded in this study were also found in savannas of the Central Plateau (Câmara & Leite 2005, Câmara et al. 2005, Peralta et al. 2008, Sousa et al. 2010, Porfírio-Júnior et al. 2016).

Calymperaceae and Sematophyllaceae particularly prominent families as colonizers of disturbed or dry environments in the Amazon, represented mainly by *Calymperes palisotii* Schwägr., *Microcalpe subsimplex* (Hedw.) W.R. Buck and *Octoblepharum albidum* Hedw. (Bastos & Yano 1993, Lisboa & Ilkiu-Borges 1995, Visnadi

Table III. Fisher's alpha values calculated for the bryophyte community.

	Taxa	Individuals	α
Savanna			
SP-I	20	128	6.64
SP-II	16	160	4.42
SP-III	12	99	3.57
SP-IV	18	108	6.18
SP-V	32	325	8.80
Rainy season			
SP-I	18	70	7.84
SP-II	15	80	5.45
SP-III	10	40	4.28
SP-IV	13	61	5.06
SP-V	27	198	8.44
Dry season			
SP-I	14	58	5.86
SP-II	11	80	3.45
SP-III	11	59	3.98
SP-IV	11	47	4.52
SP-V	21	127	7.16
Total			
Dry season	31	371	8.047
Rainy season	36	449	9.216

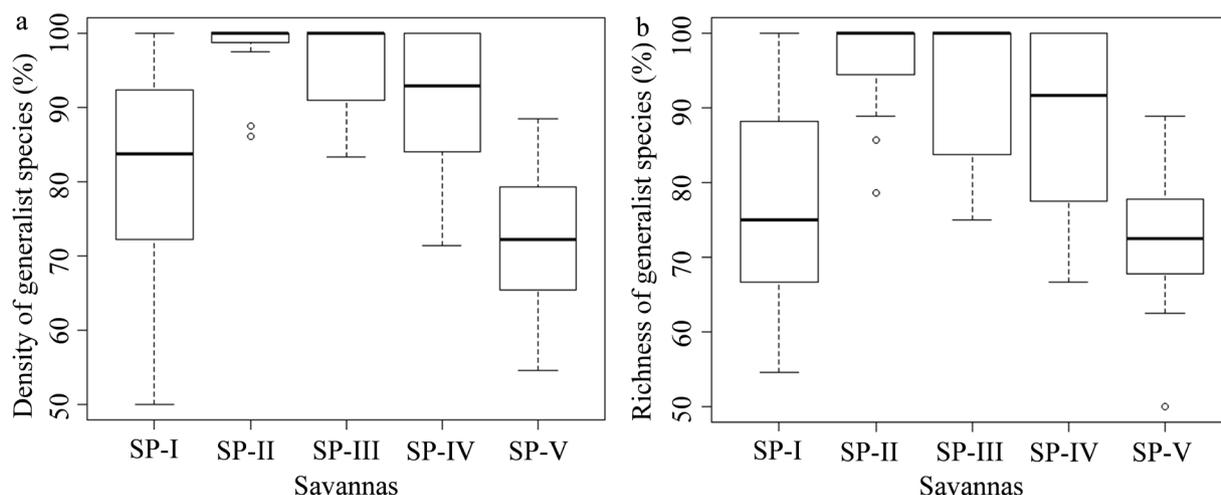


Figure 6. Generalist species in the sampled areas. (a) Density; (b) Richness.

& Monteiro 1990). The peculiar physiological characteristics of these groups confers them specialized desiccation tolerance mechanisms (Wagner et al. 2014).

The greater abundance of mosses than liverworts in dry sites may be related to more members of this lineage having specialized morphological, anatomical, and physiological traits of desiccation tolerance (Proctor & Tuba 2002, Proctor et al. 2007, Goffinet et al. 2009), which can survive successfully in deserts or extreme environments, especially at high temperatures (Mertens et al. 2008). As for example, dry mosses can survive at exposed temperatures of habitats above 70-110 °C (Lange 1955), some up to 85-110 °C, while moist mosses are damaged or do not survive at temperatures of 42-51 °C (Nörr 1974). Among the morphological traits associated with desiccation tolerance in mosses, stand out the coast of leaves that aid in rapid absorption and transport of water, in addition to structural support to leaves during desiccation (Frahm 1985); hyaline cells at the base of the leaves that store water to prevent desiccation (Frahm 2003) and turf life forms and acrocarpous habit, which decreases water loss by evaporation and reduces radiation damage to photosynthetic

cells, optimizes water absorption rain or air humidity (Vitt 1979, Kürschner 2004).

Among the most frequent taxa that were shared among the savannas and seasons, *Calymperes palisotii* Schwägr., *Microcalpe subsimplex* (Hedw.) W.R. Buck and *Octoblepharum albidum* Hedw. stood out; they have hyaline cells that accumulate water to prevent desiccation and protect photosynthetic cells from sun damage (Kürschner 2004). The greater occurrence of *Calymperes erosum* Müll. Hal. in the rainy season (35 against 15) is in line with the ecological descriptions made by Lisboa (1993), who portrayed this species as widely distributed in humid places such as riverine forests or also in more open areas such as savannas. Thus, *C. erosum* has become an important model to understand the dynamics of Amazonian savannas, since its greater occurrence has been associated to the recovery of degraded areas (Lopes et al. 2016).

Among liverworts, the species *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn., *Cheilolejeunea oncophylla* (Aongström) Grolle & E.Reiner, *Cheilolejeunea rigidula* (Nees ex Mont.) R.M. Schust. and *Microlejeunea epiphylla* Bischl. are cited for the Amazon as

having morphological traits influenced by the microclimatic conditions of the different height zones of host trees (Mota-de-Oliveira 2018), with asexual propagules, convoluted leaves and cell wall thickening observed more frequently in the canopy, where irradiance is more intense.

Density, richness and diversity

The low values of density and richness of the savannas sampled in comparison to other tropical ecosystems may be related to their microclimatic conditions such as intense light incidence and low water availability. These conditions act as environmental filters determining the number and mutual species that can coexist, implying the sharing of resources (Slack 1990) and prevent the coexistence of species in long-term equilibrium (Werner 1979). Thus, only the most tolerant species are able to establish in the climatic conditions of this environment (Bello et al. 2010, Smith & Stark 2014). The variations in density and richness patterns observed in the communities of SP-V in relation to the other areas may be associated with a greater amount of resources present in the environment (Corrales et al. 2010) and high variability of microhabitats with favorable conditions for colonization, respectively (Holz et al. 2002).

Most mosses and liverworts species are perennial, some exceptions such as *Archidium globiferum* and *Riccia* are annual, respectively (Frahm 1996). In this sense, the greatest exclusive occurrence of species recorded during the rainy season of this study can be explained by the passage of fire in the dry season that often affects vegetation, where extreme ecological conditions reduce the species number of bryophyte (Frahm 1996), in addition, fire is a factor that reduces the chances of developing a diversified bryoflora (Inácio-Silva et al. 2017).

In this study, the richness of bryophyte communities followed the same pattern of other Amazonian lowland ecosystems, in which the specific richness of liverworts is always greater than that of mosses (Richard 1984, Brito & Ilkiu-Borges 2013, Garcia et al. 2014, Pantoja et al. 2015, Fagundes et al. 2016). On the other hand, the pattern of number of occurrences found was similar to that recorded in dry forests, as is the case of savannas of the Central Plateau, where mosses are better represented in terms of richness and occurrences than liverworts (Bôas-Bastos & Bastos 1998, Visnadi 2004, Câmara et al. 2005, Aquino et al. 2015, Rios et al. 2016, Costa et al. 2018, Oliveira et al. 2018).

The low diversity of bryophytes recorded in the studied savannas may be related to the microclimatic conditions, which result from the interaction between substrate quality, pH, temperature, light and humidity (Weibull & Rydi 2005). Among the intrinsic conditions of this vegetation, the prevalent prolonged droughts and lack of nutrients hinder the succession of new species that are not adapted to this ecosystem (Franco 2005). As observed by Bastos & Bôas-Bastos (2008), the diversity of bryophytes is affected by the regime of fires, as well as by the low availability of water in savannas, for they affect the reproduction and development of these plants. On the other hand, Holz et al. (2002) pointed out that the high diversity of bryophytes found in dense forests occurs due to the great diversification of microhabitats that are distributed from the base to the canopy of trees, as well as in rotting trunks and soil.

Ecological groups

The greater abundance of the generalist species is associated with areas under environmental disturbance (Pantoja et al. 2015, Fagundes et al. 2016) or areas that are typically open (like savannas). Generalist species possess great

ecological amplitude and greater desiccation tolerance (Lopes et al. 2016). The widespread occurrence of generalist species in the sampled areas demonstrates their tolerance to xerophytic environments, colonizing several substrate types and occurring near forest edges and in more open areas with high light levels (Cerqueira et al. 2015). Brito & Ilkiu-Borges (2013) reported seven generalist species for the savannas of the municipality of Soure, namely, *Calymperes palisotii* Schwägr., *Cheilolejeunea oncophylla* (Aongström) Grolle & E.Reiner, *Cheilolejeunea rigidula* (Nees ex Mont.) R.M. Schust. and *Lejeunea laetevirens* Nees & Mont. These generalist species are also found in the present study. Other species, including *Microcalpe subsimplex* (Hedw.) W.R. Buck and *Octoblepharum albidum* Hedw., are cited by Brito & Ilkiu-Borges (2014) as the best adapted taxa for growth and establishment in a variety of environmental conditions.

The absence of canopy in the savannas and increased availability of light (Ribeiro & Walter 2008) allowed the sun specialists to be found along different gradients, from the base to the top of the trees and shrubs, because light levels and desiccation tolerance are linked and crucial factors that influence the distribution of bryophytes (Király et al. 2013). Shade specialists were also rarely found near the treetops, because they are more common in moist and shaded forests (Gradstein et al. 2001). According to Wagner et al. (2014), species with lower desiccation tolerance do not resist the high light incidence and water stress, and they are therefore mostly excluded from the environment.

Distribution of bryophytes in the substrates

The highest incidence of corticolous species in this study (88%) is also predominant in non-flooded forests in the Amazon (Saldanha et al.

2018, Oliveira-da-Silva & Ilkiu-Borges 2018) and savannas of the Central Plateau (Aquino et al. 2015). Decomposing trunks are the following most colonized substrate (Richards 1984). The greater availability of live trunks and increased pH and water retention capacity of barks (Studlar 1982, Richards 1984, Hallingbäck & Hodgetts 2000) are favorable conditions for the colonization of bryophytes with limited desiccation tolerance mechanisms (Proctor & Tuba 2002, Proctor 2008, Oliveira-da-Silva & Ilkiu-Borges 2018). It is believed that host trees available in savannas are the refuge of bryophytes which seek greater availability of water, where bryophytes are often observed in humid microhabitats such as cracks in tree trunks. Thus, to ensure the maintenance of the communities of bryophytes it is essential that there be the conservation of the plant community, since the richness of species of bryophytes and vascular plants is positively correlated (Ingerpuu et al. 2001).

The abundance of corticolous species observed in this study is distinct from the pattern found in dense tropical forests with high levels of precipitation. In these forests, substrate preference is neutralized by high humidity; most species have weak or no preference for substrate types, and are able to colonize a variety of available environments (Frahm 2003). Germano & Pôrto (2006) pointed out that 87% of the bryophytes of a remnant area of the Atlantic Forest with high annual precipitation (2,450 mm) did not show strong preferences for specific substrates.

The exclusive occurrence of *Fissidens prionodes* Mont. in soil and the low representation of terrestrial species (1.95%) may be related to the variety of morphological traits of this genus, such as presence of limbidium and papillae that act in desiccation tolerance (Pursell 2007, Bordin & Yano 2013). The chemical composition of the soil of savannas, particularly

the acidity, high saturation of aluminum, poor drainage, and low fertility, may be a hindering factor for the colonization of species other, less specialized (Cavalcante et al. 2014). These conditions reinforce the general idea that soil acidification may be responsible for the decline of bryophyte richness (Delgado & Ederra 2013). Müller et al. (2019) observed that the richness of terrestrial bryophytes decreased with decreasing soil pH in managed forests of Central Europe. Moreover, the abundant grass layer mainly represented by Poaceae and Cyperaceae in the sampled savannas (Bastos 1984) may be a limiting factor for terrestrial bryophytes, as observed by Jagodziński et al. (2015), who reported that grasses competed with bryophytes in the soil.

CONCLUSION

This study reveals that bryophytes in savannas of the Marajó Island are well adapted to the environmental conditions of this ecosystem, indicated by the high representation of the generalists and sun specialists among the species, with specialized desiccation tolerance strategies. It was observed that despite the greater availability of water in the rainy season, there is no sufficient succession of new species to prove the influence of this abiotic variable on the structure of the bryophyte communities. In this context, these results were expected, since most bryophytes are perennials, whose life cycle is longer than one year and would be found in both wet and dry seasons. In turn, differences between the sampled areas were the main factor explaining the changes in the composition, richness, density, and diversity of bryophytes.

The sampled savannas presented a richness of bryophytes similar to the other Amazonian

ecosystems and the number of occurrences had the same pattern of representation of savannas from the Central Plateau, where mosses are more abundant despite lower levels of species richness than liverworts. Finally, the high frequency of rare species endorses the need for conservation of this ecosystem.

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Author contributions

Paulo Weslem Portal Gomes: this paper is the result of his master's dissertation. He participated in the planning of the experimental design of the research and carried out the data collection in the field, as well as in the identification and herbarization of the botanical material. He collaborated in the analysis and interpretation of data and writing of the article. Priscila Sanjuan de Medeiros-Sarmento: she was co-supervisor of the first author's master's degree. She participated in the planning of the experimental design of the research and in the treatment of the statistical analysis of the data, as well as the readings and corrections in the article. Rita de Cássia Pereira dos Santos: Participated in the planning of the experimental design of the research and guidance of data collection in the field. She taught the first author to identify bryophytes, specifically mosses, at the species level. Ana Cláudia Caldeira Tavares-Martins: she was the master's advisor of the first author. She participated in the planning of the experimental design of the research and guidance of data collection in the field. She did several readings and corrections to this paper. She taught the first author to identify bryophytes, specifically hepatic ones, at the species level.

