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Ecologia de comunidades de briófitas em Savana Parque na Ilha de Marajó, Pará, Brasil

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Dissertação apresentada como requisitopara obtenção do título de mestre em Ciências Ambientais no Programa de Pós-Graduação em Ciências Ambientais da Universidade do Estado do Pará.
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“*Não há saber mais, nem saber menos, há saberes diferentes*”.

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RESUMO

As savanas amazônicas apresentam predomínio de gramíneas e densidade variável de árvores e arbustos, alta entrada de luz e baixa umidade. Nestes locais, as briófitas podem fornecer informações importantes sobre a qualidade ambiental, pois são sensíveis a flutuações ambientais pela ausência de vascularização,cutícula epidérmica e por sua natureza poiquiloídrica.Assim, objetivou-seanalisar a influência da sazonalidade e dos diferentes ambientes na estrutura das comunidades e nas estruturas reprodutivasdas briófitas em Savana Parque(SP) na Ilha de Marajó-PA.Foram realizadas 60 parcelas de 100m^2 distribuídas igualmente naestaçãoseca/2016 e chuvosa/2017 em cinco áreas de SP. Para estrutura de comunidades, testou-se a composição, densidade,riquezae diversidade das espécies entre as áreas e estações, além da colonização por substrato e as guildas de tolerância a luz. Paraas estratégias reprodutivas, analisou-se a influência da sazonalidade na composição de espécies com sistema sexual monoico e/ou dioico enas estruturas reprodutivas sexuadas e assexuadas em três áreas de SP. A área foio principal fator que influenciou na composição, densidade, riqueza e diversidade das briófitas.O predomínio das generalistas e corticícolas, indicou que a maioria das espécies são tolerantes as condições adversas das savanas e que o extrato arbóreo-arbustivoestá estritamente relacionado com a permanência das briófitas nas savanas, respectivamente. A área e a sazonalidade não influenciaram na composição de espécies monoicas e dioicas, contudo,a área influenciou significativamente na expressão de estruturas sexuadas e assexuadas e na produção dos gametângios (hepáticas) masculinos e femininos. Quanto aos esporófitos (musgos), a sazonalidade foi o fator determinante na fenofase maduro II (abertura dos esporófitos e dispersão dos esporos naestação seca). Portanto, acredita-se que o micro-habitat das diferentes áreas é o principal fator que influencia na estrutura das comunidades e nas estratégias reprodutivas das briófitas, com exceção da fenofase esporofítica, influenciada pela sazonalidade.

Palavras-chave: Musgos. Hepáticas. Expressão sexual.Salvaterra. Cachoeira do Arari.

ABSTRACT

Amazonian savannas have a predominance of grasses and variable density of trees and shrubs, high light intake and low humidity. In these places, bryophytes can provide important information on environmental quality, as they are sensitive to environmental fluctuations due to the absence of vascularization, epidermal cuticle and their poikilohydric nature. Thus, the objective of this study was to analyze the influence of seasonality and different environments on the structure of communities and on the reproductive structures of bryophytes in Park Savanna (PS) on Marajó Island. 60 plots of $100m^2$ were also distributed in the dry/2016 and rainy/2017 season in five areas of PS. For community structure, the composition, density, richness and diversity of species between areas and seasons were tested, in addition to substrate colonization and light tolerance guilds. For reproductive strategies, we analyzed the influence of seasonality on the composition of species with monoicous and/or dioicous sexual system and on sexual and asexual reproductive structures in three areas of PS. The area was the main factor that influenced the composition, density, richness and diversity of bryophytes. The predominance of generalists and corticolous indicated that most species are tolerant of the adverse conditions of savannas and that the tree-shrub extract is strictly related to the permanence of bryophytes in savannas, respectively. The area and seasonality did not influence the composition of monoicous and dioicous species, however, the area significantly influenced the expression of sexual and asexual structures and the production of male and female gametangia (liverwort). As for sporophytes (mosses), seasonality was the determining factor in mature phenophase II (opening of sporophytes and dispersal of spores in the dry season). Therefore, it is believed that the micro-habitat of the different areas is the main factor that influences the structure of communities and the reproductive strategies of bryophytes, with the exception of sporophytesphenophase, influenced by seasonality.

Keywords: Mosses. Liverworts. Sexual expression. Salvaterra. Cachoeira do Arari.

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INTRODUÇÃO GERAL

As principais formações de savana (Cerrado) no Brasil ocorrem no Planalto Central,formando o segundo maior domínio fitogeográfico brasileiro e neotropical (MIRANDA; ALMEIDA; DANTAS, 2006) com quatro principais fitofisionomias: campo limpo, campo sujo, cerrado *sensu stricto* e cerradão (IBGE, 2012). O clima no Planalto Central tem a sazonalidade bem definida com verões chuvosos e invernos secos (FRANCO, 2005), neste regime climático aumentam as chances da passagem do fogo, essencial para impedir a sucessão de espécies florestais que possam competir com as plantas nativas das savanas (HOFFMANN *et al*., 2012).

Assavanas também ocorrem no interior da Amazônia formadas por manchas disjuntas que somam cerca de 267 mil km^2 (CARVALHO; MUSTIN, 2017). As savanas amazônicas se distribuem nos estadosdo Amapá, Amazonas,Mato Grosso, Maranhão, Pará, Rondônia, Roraima e Tocantins (PRANCE, 1996; LEDRU, 2002; ROSSETTI*et al*., 2007), como predomínio de gramíneas e densidade variável de árvores e arbustos (EITEN, 1983; SILVA; OLIVEIRA, 2018). Contudo, a riqueza florística das savanas do Planalto Central é bem maior quando comparada as savanas amazônicas (SALGADO-LABOURIAU*et al*., 1997; RATTER; BRIDGEWATER; RIBEIRO, 2003).

Nas savanas amazônicas, registros de 136 estudos realizados em pouco mais de 80 anos, enfocaram as plantas, répteis, aves, mamíferos, invertebrados, anfíbios e peixes, ressaltando a carência de pesquisas nessas áreasem comparação aos demais estudos realizados em outros ecossistemas naturais (CARVALHO; MUSTIN, 2017). São necessários maisestudos para conservação da biodiversidade dassavanas, as quais compõe altas taxas de espécies endêmicas que são importantes para conservação desses ecossistemas (STRASSBURG *et al*., 2017). Muitas espécies das savanas encontram-se sob eminente risco de desaparecer antes mesmo de serem conhecidas, em razão do elevado desmatamento e queimadas para suprir as demandas da agricultura e pecuária, associados ao crescimento populacional (PLOTKIN; RIDING, 2011;CARVALHO; MUSTIN, 2017).

As savanasamazônicas encontradas no leste da Ilha de Marajó são classificadas na fitofisionomia Savana Parque (ROSSETTI *et al*., 2007; IBGE, 2012), que predominam as gramíneas representadas por Poaceae e Cyperaceae e estrato arbóreo formado por *Astrocaryumvulgare* Mart., *Attaleamaripa* (Aubl.) Mart., *Byrsonima chrysophylla*Kunth, *Curatella americana* L., *Hancornia speciosa*Gom., *Platoniainsignis* Mart. e *Salvertiaconvallariaeodora* A. St.-Hil. (BASTOS, 1984; ROSSETTI *et al*., 2010; LISBOA, 2012; LIMA, 2017).Dentre as investigações mais recentes realizadas em Savana Parque da Ilha de Marajó, destaca-se o estudo florístico de briófitas de Brito e Ilkiu-Borges (2013) com registro de 67 espécies (25 musgos e 42 hepáticas) distribuídas em diferentes ambientes, das quais, 12 espécies (sete musgos e cinco hepáticas) foram registradas em savana.

As briófitas compõem um grupo polifilético com 20.486 espécies agrupadas em três divisões: Anthocerotophyta (antóceros com 215 spp.), Marchantiophyta (hepáticas com 7271 spp.) e Bryophyta (musgos com 13.000 spp.) (SÖDERSTRÖM *et al*., 2016; GOFFINET; BUCK; SHAW, 2009). No Brasil, são encontradas 1524 espécies de briófitas (11 antóceros, 633 hepáticas e 880 musgos), com um terço registrado na floresta amazônica (570 spp.) (COSTA; PERALTA, 2015). Essas plantas ocorrem em todos os ecossistemas do mundo, exceto em ambientes marinhos (SLACK, 2011; GLIME, 2017a), habitando cascas de árvores vivas, folhas, troncos em decomposição, solo, carvão, rochas e cupinzeiros (FRAHM; GRADSTEIN, 1991).As briófitas podem ser encontradas em diferentes formas de vida, tais como coxim, dendróide, flabelado, folhosa, pendente, talosa, tapete, trama e tufo (COSTA, 2013), na perspectiva de minimizar a perda de água por transpiração e aumentar a captura de luz fotossintética (FRAHM, 2003).

As briófitasdestacam-se por sua importância ecológica nos ecossistemas, como a ciclagem da água e nutrientes, produção de biomassa, fixação de carbono, estabilidade dos solos e por servirem de hábitat e alimento para alguns invertebrados(HALLINGBÄCK; HODGETTS, 2000; VIRTANEN *et al*., 2000; TURETSKY, 2003; COSTA; LUIZI-PONZO, 2010). Em decorrência desses serviços ecossistêmicos, essas plantas são essenciais para a sustentabilidade das civilizações humanas e da sociedade (HALLINGBÄCK; TAN, 2010). Além disso, são utilizadas em estudo e monitoramento de metais tóxicos presentes na atmosfera de áreas rurais, urbanas e industriais, que são prejudiciais à saúde humana e aos ecossistemas (GONZÁLEZ *et al*., 2016).

A ausência de sistema vascular, cutícula epidérmica e o pouco controle na perda de água para o ambiente, tornam as briófitas mais sensíveis às flutuações ambientais, principalmente com as mudanças climáticas (ROBINSON; WATERMAN, 2014; TRENBERTH *et al*., 2014). As condições microclimáticas como luminosidade, temperatura, umidade e pHatuam como filtros ambientais que podem determinar a estrutura das comunidades de briófitas (WEIBULL; RYDIN, 2005; BELLO*et al*., 2010; SMITH; STARK, 2014; SANTOS*et al*., 2014). Em que as espécies mais bem adaptadas conseguem se estabelecer, tais como a tolerância a dessecação das briófitas que ocorrem nas savanas, que só é possível devido à sua natureza poiquiloídrica (VISNADI; VITAL, 1989; KÜRSCHNER, 2004; KÜRSCHNER; PAROLLY, 2005; PARDOW; LAKATOS, 2013).

As condições estabelecidas nassavanas, como a elevada entrada de luz e baixa umidade associada aos eventos de seca, dificultam o estabelecimento de espécies que não sejam adaptadas ecofisiologicamente a esses ambientes (FRANCO, 2005; HOFFMANN *et al*., 2012).Diante dessas condições, as briófitas podem ser severamente afetadas por não possuírem sistemas complexos para ajustar o uso da água (GLIME, 2017a), mas, algumas características como a plasticidade dos filídios e formas de vida em tufos, conferem as briófitas desses ambientes a capacidade de redução da perda de água (KÜRSCHNER, 2004). Os altos níveis de intensidade luminosa elevam as taxas de transpiração e perda de água favorecendo a diminuição da fotossíntese e conseguinte aumento da fotoproteção (PROCTOR; SMIRNOFF, 2011).

Dentre os pigmentos responsáveis pela fotoproteção das briófitas, estãoos flavonoides, compostos fenólicos simples e carotenoides, que se concentram na parede celular alterando a coloração das plantas e bloqueando os altos níveis de radiações ultravioleta (UV) (CASH; PAN; SIMON, 2007).Os carotenoides e flavonoides destacam-se ao reduzirem as moléculas de radicais livres gerada pela radiação UV (CLARKE; ROBINSON, 2008).Os pigmentos da fotoproteção são comuns em plantas com coloração castanha e parede celular espessa que bloqueiamo excesso de UVnos cloroplastos prevenindo a degradação da clorofila e mantendo a taxa fotossintética (GLIME, 2014; RICE; CORNELISSEN, 2014).Além disso, a presença de células leucocística em alguns táxons acumulam água para evitar a dessecação e protegem as células fotossintéticas do dano solar (FRAHM, 2003).As papilas são responsáveis por intensificar a condução da água por capilaridade e os filídios imbricados quando secos reduzem a perda de água por transpiração (KÜRSCHNER, 2003, 2004).

O ciclo de vida das briófitas émarcado pela alternância de gerações com uma fase dominante gametofítica (haploide) e outra passageira, caracterizada pela produção dos esporos (diploide) (GOFFINET; BUCK, 2012; GLIME, 2017b). Quanto ao sistema sexual, as briófitas são formadas por populações monoicas que apresentam os órgãos sexuais (masculino e feminino) no mesmo gametófito e por populações dioicas com somente um órgão sexual por gametófito. As populações monoicas e dioicas formam pequenas colônias que podem se propagar por reprodução sexuada, que é dependente da água para a locomoção dos anterozoides, ou de forma assexuada por meio de propagação vegetativa (GLIME, 2017b). O processosexuado possibilita a recombinação gênica, podendo tornar as briófitas mais adaptadas às mudanças ambientais, entretanto, a predominância das espécies monoicas, aumenta as chances da autofertilização e dispersão (FREY; KÜRSCHNER, 2011). Neste sentido, a monoicia visa preveniro gasto de energia na dispersão de diásporos a longas distâncias e consequentemente promover a manutenção da reprodução sexuada(BATISTA; PÔRTO; SANTOS, 2018; MACIEL-SILVA; FARIAS; PÔRTO, 2015), atuando como um sistema de segurança para a propagação e permanência das espécies nos ambientes.

Nas populações dioicas, a reprodução vegetativa caracteriza-se comoum meio de dispersão de alta eficiência favorável à rápida ocupação do hábitat em relação ao processo sexuado (ALVARENGA; PÔRTO; ZARTMAN, 2013). O alto custo energético no desenvolvimento e a falta de sincronia na maturação dos anterídios e arquegônios, além da distância entre populações masculinas e femininas, não garante a fecundação efetiva das espécies (BASTOS, 2008; MACIEL-SILVA; PÔRTO, 2014).A produção de anfigastrossemi-caducos, cládios, gemas, regenerantes, fragmentação de filídios e os filídios caducos são alguns dos meios de dispersão vegetativa mais comuns das briófitas (FREY; KÜRSCHNER, 2011; GLIME, 2017c).

Para investigar a influência da sazonalidade na estrutura das comunidadese na expressão sexual das briófitas em diferentes áreas de Savana Parque da Ilha de Marajó, esta dissertação foi estruturada em doisartigos (capítulo I e II) que se fundamentou nas seguintes questões norteadoras: a sazonalidade e as diferentes áreas de savana influenciam na distribuição espacial e temporal das comunidades de briófitas em Savana Parque da Ilha de Marajó? A sazonalidade e as diferentes áreas fitofisionômicas de savanas influenciam na proporção do sistema sexual de espécimes monoicas e dicoicas e na proporção de estruturas reprodutivas (sexuadas e assexuadas) de musgos e hepáticas?

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Capítulo I

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

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

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Bryophyte communities in savanna

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ABSTRACT

Aiming to enrich the knowledge about the floraof 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-m^2 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.

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 km^2 (Carvalho and 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 and 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 and Rydin 2005, Bello et al. 2010, Smith and Stark 2014, Santos et al. 2014). Desiccation tolerant bryophytes are common in savannas (Visnadi and Vital 1989), since only the best adapted species settle in these areas (Kürschner 2004, Kürschner and Parolly 2005, Pardow and 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 and Riding 2011, Carvalho and Mustin 2017).

In view of the heterogeneity and social value of their different phytophysiognomies of savannas (Plotkin and 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 briophyte communities (Dorrepaal 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.

MATERIAL AND METHODS

STUDY AREA

The study area corresponded to five savannas classified as belonging to the Park Savanna (SP) phytophysiognomy (Rossetti et al. 2007, IBGE 2012), located in the east side of the Marajó Island, state of Pará (Figure 1). Four Park Savanna areas are located in the municipality of Salvaterra; of these, SP-I (00º 47' 47.5" S and 48º 32' 39.7" W) and SP-IV (00º 52' 24.8" S and 48º 35' 07.7" W) can be easily seen from the Camará-Salvaterra 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).

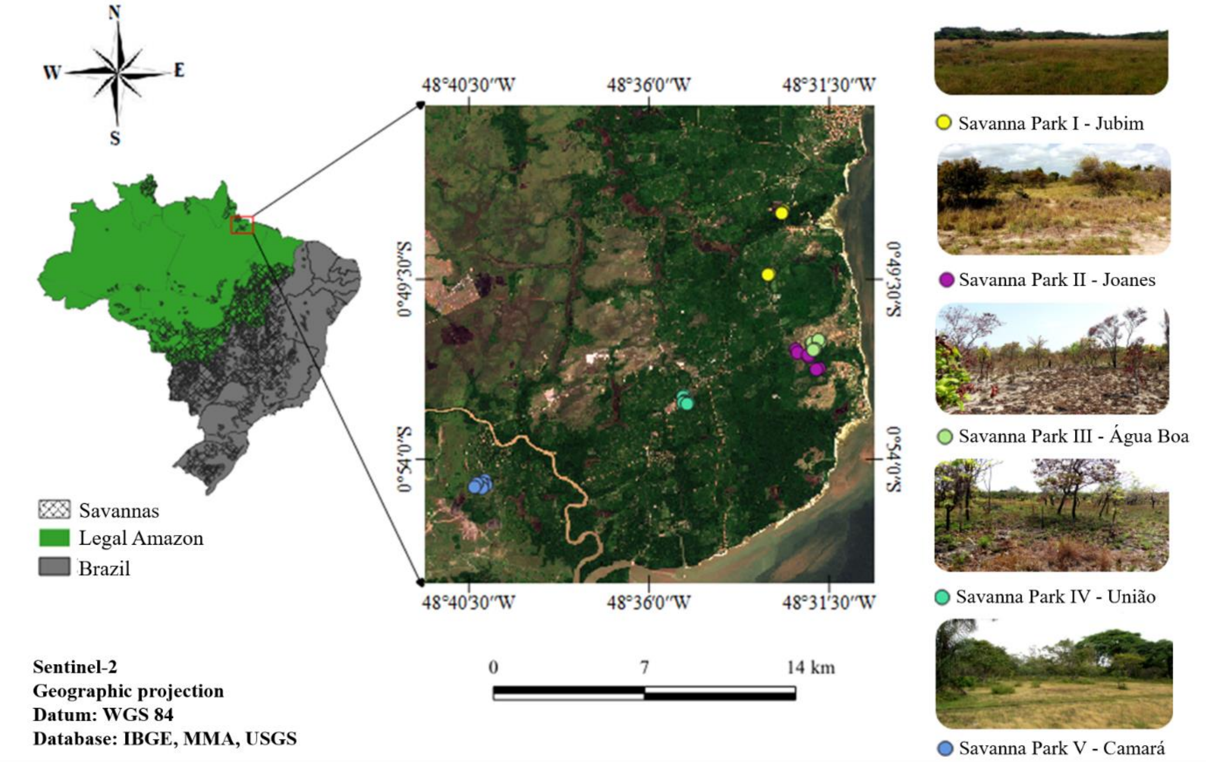

Figure 1 – Location of the studied areas of Park Savanna in Marajó Island, Pará, Brazil.

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 *Astrocaryum vulgare* Mart., *Attalea maripa*(Aubl.)Mart., *Byrsonima chrysophylla*Kunth, and *Curatella americana* 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 *Hancornia speciosa*Gom. and *C. americana*, in addition to *A. vulgare, B. chrysophylla, Platonia insignis* Mart., and *Salvertiaconvallariaeodora* 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 *H. speciosa* and *C. americana*, in addition to *A. vulgare, B. chrysophylla, P. insignis*, and *S. convallariaeodora.*
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 *C. americana* and *S. convallariaeodora*, in addition to *H. speciosa* and *B. chrysophylla*.
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 *C. americana* and *B. chrysophylla*, besides *P. insignis*, *S. convallariaeodora* and *A. vulgare*.

SAMPLING, COLLECTION AND TAXONOMIC IDENTIFICATION

Sixty 100 m^2 (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 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 and 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 doBrasil 2020 under construction (Costa 2013) 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 and 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 (Ayres 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 20185).

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 and 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 2a-d).

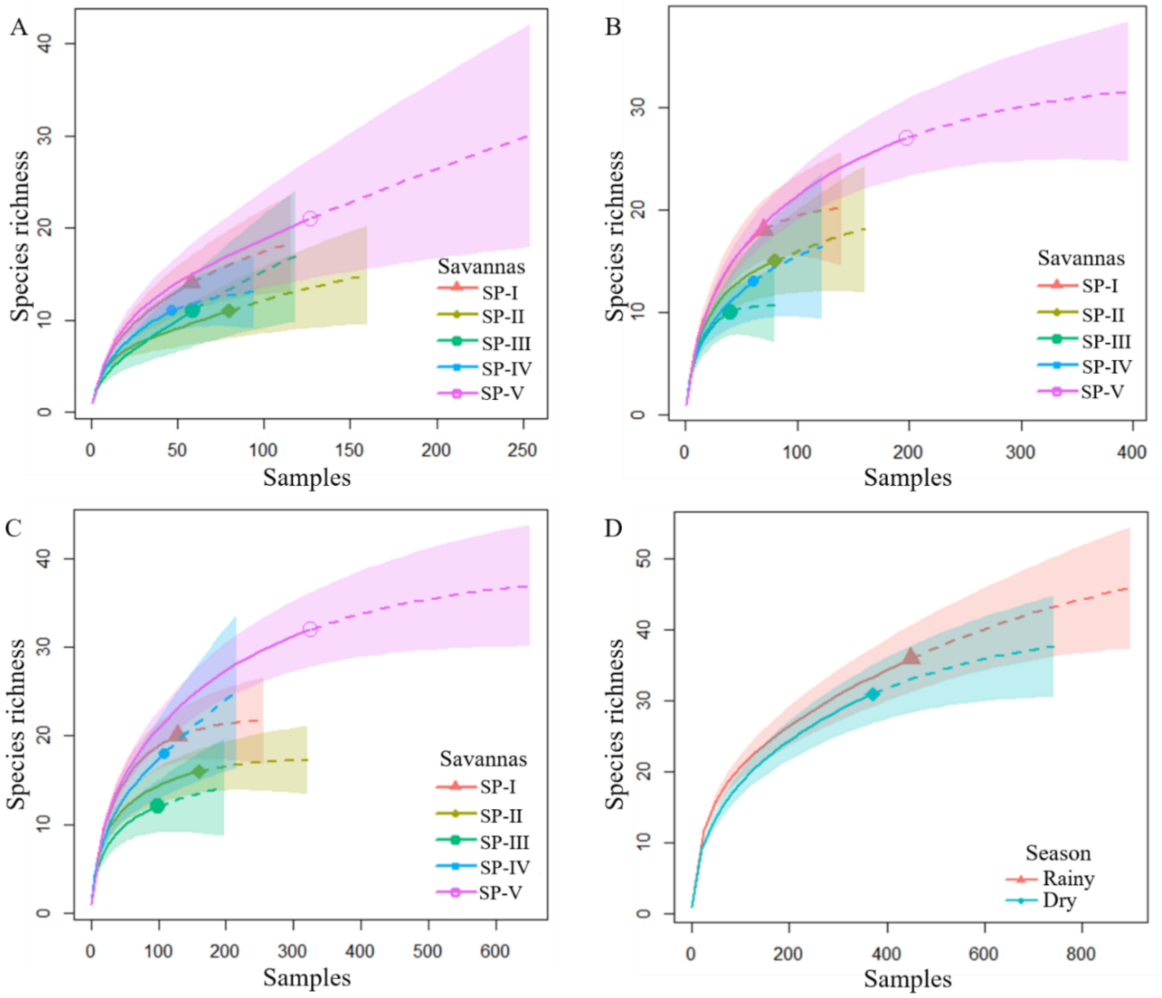

Figure 2 - Species accumulation curves in the sampled Park Savanna areas and seasons, Marajó Island, Pará. **(a)** all areas per dry season; **(b)** all areas per rainy season; **(c)** all areas; **(d)** all areas per rainy and dry season.

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 Bryaceae, Calymperaceae, Fissidentaceae, Leucobryaceae, and Orthotrichaceae.

TABLE II

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

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.

Bryophyte	**Park Savanna area**					**Season**		**EG**	**Substrates**				**Voucher**
	I	**II**	**III**	**IV**	**V**	**R**	**D**		**Co**	**E**	**T**	**TM**	
Bryophyta													
Bryaceae													
Bryumcoronatum Schwägr.			1	1	2	1	3	Gen	3		1		MFS007628
Calymperaceae													
Calymperes erosum Müll. Hal.	15	8	4	6	17	35	15	Gen	46	4			MFS007629
Calymperes palisotii Schwägr.	20	24	11	23	30	57	51	Gen	90	15	1	2	MFS007630
Octoblepharum albidum Hedw.	33	42	36	33	62	97	109	Gen	197	7	2		MFS007631
Syrrhopodon ligulatus Mont.		7		6	5	16	2	Gen	17	1			MFS007632
Syrrhopodonprolifer Schwägr.				1		1		Gen	1				MFS007633
Fissidentaceae													
*Fissidensangustifolius*Sull.					2		2	Gen	2				MFS008750
Fissidensguianensis Mont.					3	2	1	Gen	1		1	1	MFS008744
Fissidensprionodes Mont.	1			1	1	1	2	Gen			3		MFS007634
Leucobryaceae													
Campylopus surinamensis Müll. Hal.	12			4		7	9	Sun	8		8		MFS007635
Orthotrichaceae													
Groutiellatomentosa (Hornsch.) Wijk&Margad.					1	1		Gen	1				MFS008742
Sematophyllaceae													
Brittonodoxasubpinnata(Brid.) W.R.Buck					1	1		Gen	1				MFS008741

Bryophyte	Park Savanna area					Season		EG	Substrates				Voucher
	I	II	III	IV	V	R	D		Co	E	T	TM	
Microcalpe subsimplex (Hedw.) W.R. Buck	5	25	27	11	26	38	56	Gen	89	5			MFS007636
Sematophyllum adnatum (Michx.) Brid.					2	2		Gen	2				MFS008747
Trichosteleumpapillosum (Hornsch.) A.Jaeger					1	1		Gen		1			MFS008745
Marchantiophyta													
Frullaniaceae													
Frullaniaexilis Taylor					3	2	1	Sun	3				MFS008751
Frullaniagibbosa Nees					1	1		Sun	1				MFS008747
Lejeuneaceae													
Acrolejeuneaemergens (Mitt.) Steph.	2			2	16	11	9	Sun	17	3			MFS007637
Acrolejeunea torulosa (Lehm. &Lindenb.) Schiffn.	4		1	8	53	41	25	Sun	57	8		1	MFS007638
Archilejeuneafuscescens (Hampe ex Lehm.) Fulford.	2				1	1	2	Gen	3				MFS007639
Cheilolejeunea aneogyna (Spruce) A. Evans				1		1		Gen	1				MFS007640
Cheilolejeunea clausa (Nees & Mont.) R.M.Schust.		1				1		Sun	1				MFS007641
Cheilolejeunea comans (Spruce) R.M.Schust.	4	7	1	3	2	10	7	Gen	15	1		1	MFS007642
Cheilolejeunea discoidea (Lehm. &Lindenb.) Kachroo&R.M.Schust.		1					1	Gen	1				MFS007643
Cheilolejeunea holostipa (Spruce) Grolle & R.-L.Zhu					1	1		Gen	1				MFS008740
Cheilolejeunea oncophylla (Aongström) Grolle &E.Reiner	10	20	4	4	39	42	35	Gen	69	7		1	MFS007644
Cheilolejeunea rigidula (Mont.) R.M.Schust.	2	10	3	1	10	12	14	Gen	22	4			MFS007645
Cheilolejeunea trifaria (Reinw. et al.) Mizut.	3					1	2	Gen	2	1			MFS007646
*Drepanolejeuneafragilis*Bischl.					3		3	Gen	2	1			MFS008748
Frullanoidescorticalis (Lehm. &Lindenb.) Slageren	2					1	1	Sun	2				MFS007647
Lejeunea flava (Sw.) Nees				1	1	1	1	Gen	2				MFS007648
*Lejeunealaetevirens*Nees & Mont.	1	2	6		8	11	6	Gen	15	2			MFS007649

Bryophyte	Park Savanna area					Season		EG	Substrates				Voucher
	I	**II**	**III**	**IV**	**V**	**R**	**D**		**Co**	**E**	**T**	**TM**	
Lopholejeuneasubfusca (Nees) Schiffn.					2	2		Sun	2				MFS008739
Microlejeuneabullata(Taylor) Steph.					1		1	Gen		1			MFS008749
Microlejeunea epiphylla Bischl.	3	5	2		17	21	6	Gen	23	4			MFS007650
Microlejeunea globosa (Spruce) Steph.				1			1	Gen	1				MFS007651
Microlejeuneasubulistipa Steph.	3	2			3	7	1	Gen	7			1	MFS007652
Pycnolejeunea contigua (Nees) Grolle	1				4	4	1	Sun	3	2			MFS007653
Pycnolejeuneamacroloba (Nees & Mont.) Schiffn.	1	2		1		3	1	Sun	4				MFS007654
Pycnolejeuneapapillosa X.-L. He	4	3	3		2	10	2	Sun	10	2			MFS007655
Pycnolejeunea sp.		2			4	5	1	*	6				MFS008743
Total	128	161	99	108	324	449	371		728	69	16	7	

SPECIES COMPOSITION

The species composition of SP-V differed significantly from other areas (Pseudo-F = 4.111; p-value = 0.0001) (Figure 3a), and there were five indicator species: *Acrolejeuneaemergens* (Mitt.) Steph., *Acrolejeuneatorulosa* (Lehm&Lindenb.) Schiffn., *Microlejeunea epiphylla*Bischl., *Fissidensguianensis* Mont., and *Frullaniaexilis* Taylor. SP-I was significantly different only from SP-II and SP-III (p-value = 0.0234; p-value = 0.0069), with *Campylopussurinamensis* 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 3a).

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 3b). The first two dimensions of the PCA explained 59.8% of the variance in the data set; the first dimension accounted for 39.7%, and the second for 20.1%.

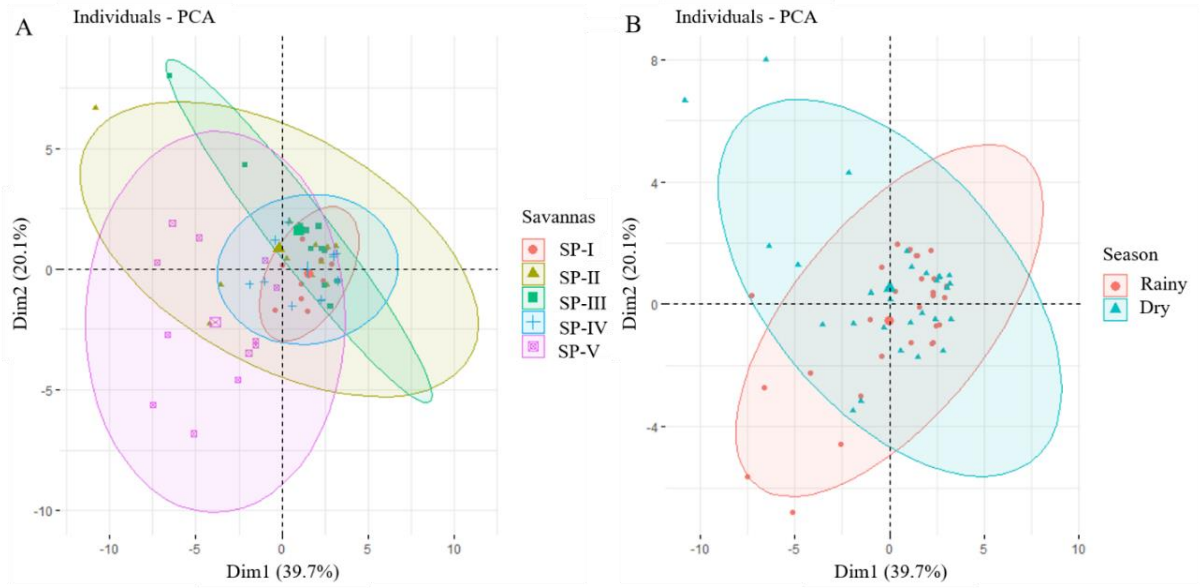

Figure 3 - Principal Component Analysis of bryophytes of the Marajó Island, Pará. **(a)** Sampled savanna áreas; **(b)** Seasons.

DENSITY, RICHNESS AND DIVERSITY

SP-V presented a significantly different density (Kruskal-Wallis = 23,176; p-value = 0.0001168) (Figure 4a) and richness (Kruskal-Wallis = 22,914; p-value = 0.0001317) in relation to the other sampled areas (Figure 4b).

Seasonality did not influence the density of bryophytes (W = 515; p-value = 0.3393) (Figure 4c), but richness was significantly lower in the dry season (t = 2.0939; p-value = 0.04065) (Figure 4d). 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.

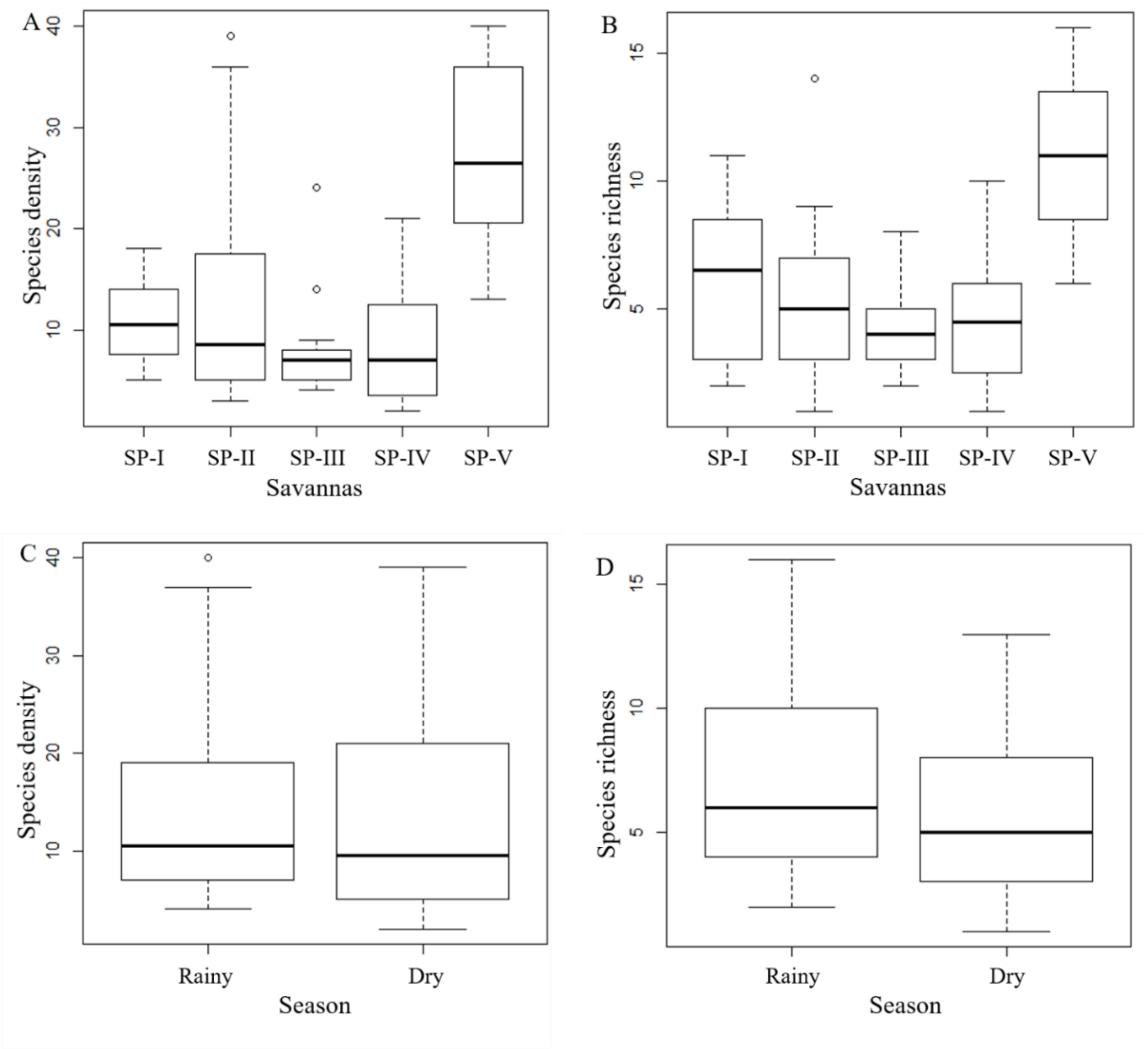

Figure 4 - Mean density and richness of species per plot in the studied areas and seasons in Marajó island, Pará. **(a)** Mean density in the five Park Savanna areas; **(b)** Mean richness in the five Park Savanna areas; **(c)** Mean density in the two seasons; **(d)** Mean richness in the two seasons.

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 5a) and richness (Figure 6a). The diagrams showed that the area was the main factor influencing the density (Figure 5b and c) and richness (Figure 6b and c) of bryophytes in the savannas sampled, with SP-V standing out among the others.

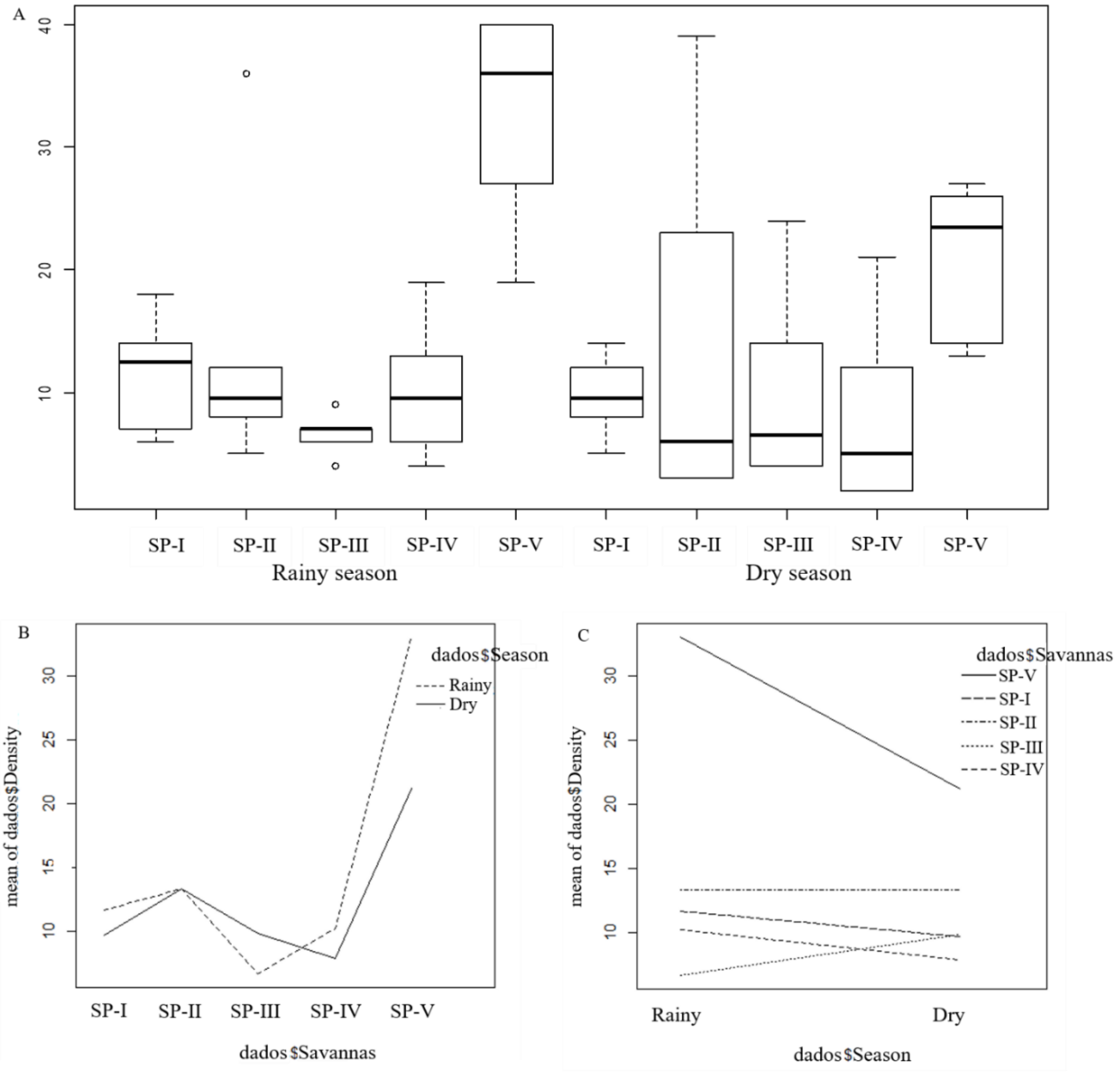

Figure 5 -(a) Mean density of bryophytes in the sampled savannas per season; **(b)** Interaction plot between sampled areas and seasons on mean density of bryophytes; **(c)** Interaction plot between seasons and sampled areas on mean density of bryophytes.

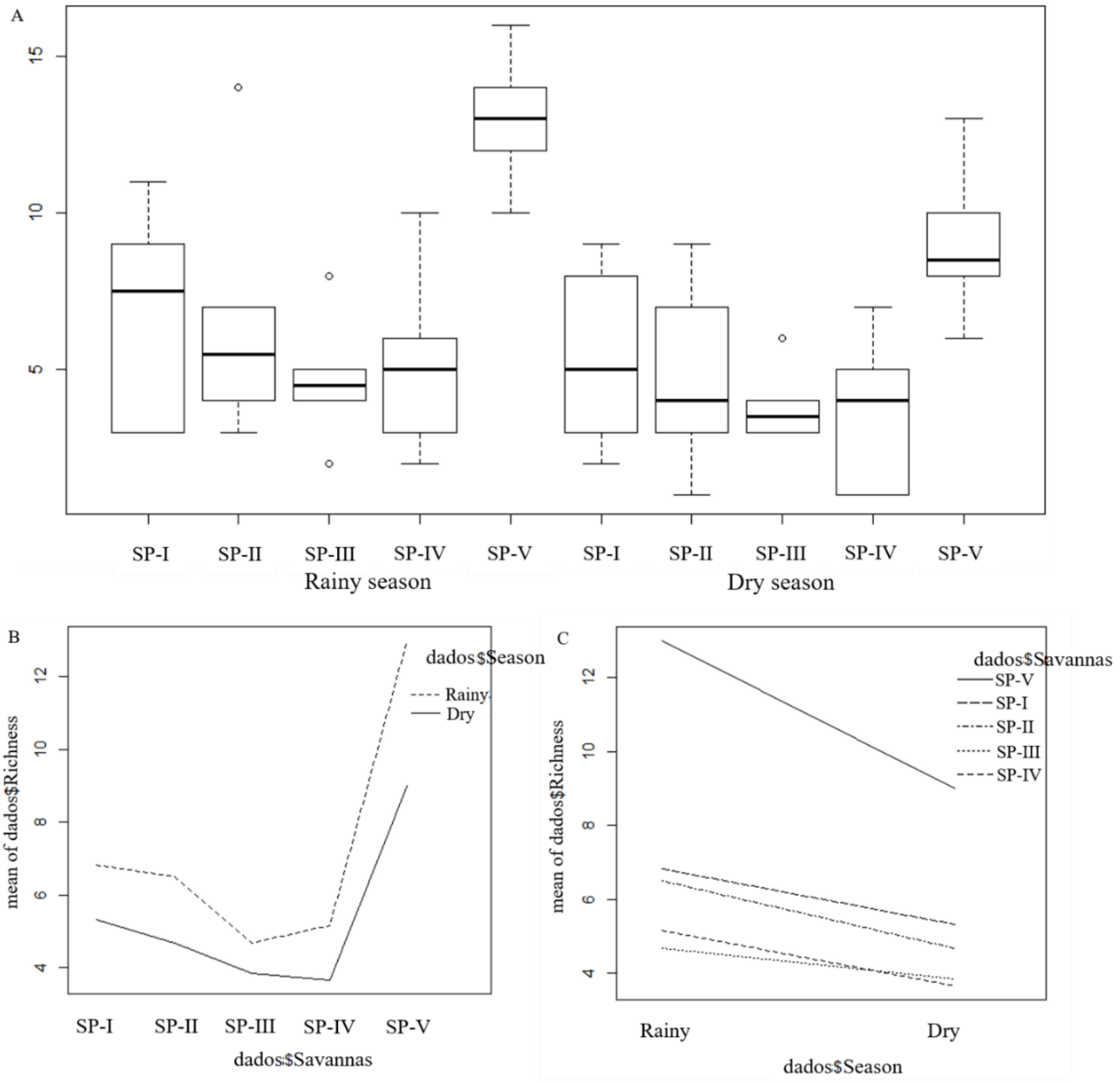

Figure 6 -(a) Mean richness of bryophytes in the sampled savannas per season; **(b)** Interaction plot between sampled areas and seasons on mean richness of bryophytes; **(c)** Interaction plot between seasons and sampled areas on mean richness of bryophytes.

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).

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

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 7a), 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 7b), 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).

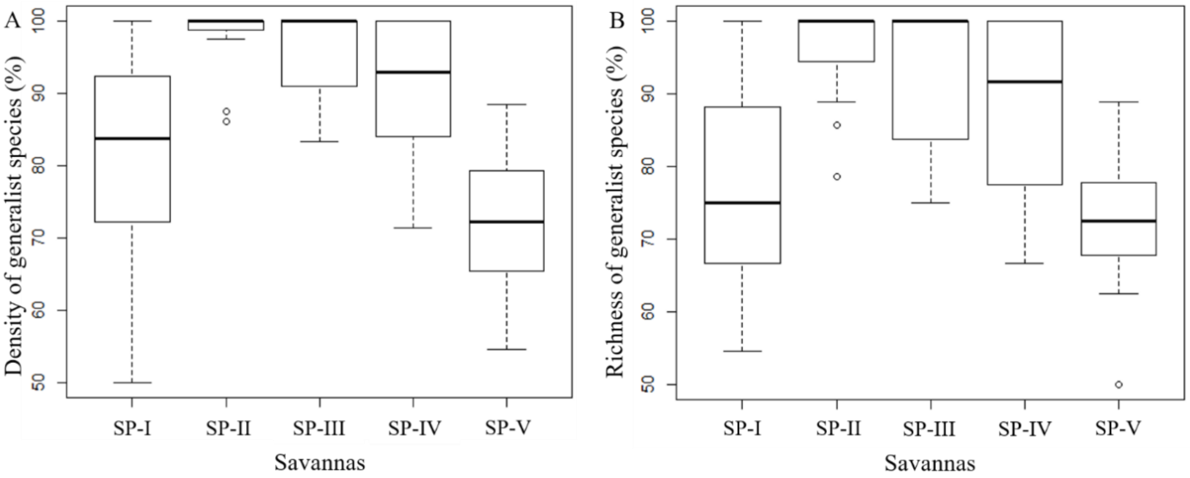

Figure 7 – Generalist species in the sampled areas. (**a**) Density; (**b**) Richness.

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 epyxilic 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 *Trichosteleumpapillosum* (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 and Lisboa 2009). Schilling and 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 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 and terSteege 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 and terSteege 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 and 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 and 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 and Bôas-Bastos 2008, Širka et al. 2019) because these taxa are more resistant to dehydration (Govindapyari 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 and 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 and Câmara 2015). The moss families recorded in this study were also found in savannas of the Central Plateau (Câmara and 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 and Yano 1993, Lisboa and Ilkiu-Borges 1995, Visnadi and 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 and 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 ºC (Lange 1955), some up to 85-110 ºC, while moist mosses are damaged or do not survive at temperatures of 42-51 ºC (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, *Calymperespalisotii* 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 *Acrolejeuneatorulosa* (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 and 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 *Archidiumglobiferum* 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 and 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 and 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 and 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 and 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 and 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 *Lejeunealaetevirens* 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 and 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 and 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 and 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 and Hodgetts 2000) are favorable conditions for the colonization of bryophytes with limited desiccation tolerance mechanisms (Proctor and Tuba 2002, Proctor 2008, Oliveira-da-Silva and 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 and 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 *Fissidensprionodes* 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 and 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 and 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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Capítulo II

The effect of seasonality and the different phytophysiognomic areas of Savanna Park on the sexual system and reproductive strategies of bryophytes in Marajó Island, Pará, Brazil

ARTIGO SUBMETIDO PARA PUBLICAÇÃO EM

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The effect of seasonality and the different phytophysiognomic areas of Savanna Park on the sexual system and reproductive strategies of bryophytes in Marajó Island, Pará, Brazil

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Sexual expression of bryophytes

BiologicalSciences

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ABSTRACT

The influence of seasonality and phytophysiognomic areas of Savanna Park on the proportion of sexual system and reproductive structures of bryophytes was analyzed. Six plots ($100m^2$) were distributed in each of three phytophysiognomic areas in the dry/2016 and rainy/2017 season. Using two-way ANOVA, the influence of seasonality and areas on the sexual system (monoicous/dioicous) and reproductive structures (sexual/asexual) of mosses and liverworts were tested, as well as interaction between two factors; these analyzes were tested for androecium /gynoecium (liverworts) expression and sporophyticphenophases (mosses). Area (F = 0.34, p> 0.05) and seasonality (F = 0.61, p> 0.05) did not influence the proportion of monoicous (48.7%) and dioicous (51.3%). Sexual expression (F = 4.3576, p <0.05) and asexual (F = 18.2404, p <0.001) were influenced by areas, with influence of both factors on sexual expression (F = 3.8354, p <0.05). The expression of androecium (F = 6.0770, p <0.005) and gynoecium (F = 5.7907, p <0.005) were influenced by areas, with seasonality determining for androecium (F = 6.0770, p <0.005). Seasonality influenced mature phenophase II (F = 7.7531, p <0.005) with spore opening and dispersion in dry season. Seasonality and areas act in different ways on sexual system and reproductive structures.

INTRODUCTION

Bryophytes form a diverse group of plants that have numerous adaptive strategies to colonize various environments (Peñaloza-Bojacá 2018), developing different sexual and asexual reproductive strategies according to their life stories and the habitat in which they live (Obesos 2002). The reproductive phase of bryophytes is subject to strong selective forces in the environment (Maciel-Silva et al. 2012) and studying plant reproduction allows us to understand the interaction of reproductive events over time in relation to climate and environmental changes in different habitats (Glime 2017b).

The sexual systems of bryophytes can generate different ecological patterns of distribution, since about 40% of species are monoicous and 60% dioicous (Maciel-Silva and Pôrto 2014), and the type of reproduction developed is directly associated with the sexual system. Among the liverworts, about 70% of the species are dioecious and in mosses it comprises about 55% to 60% of the species (Wyatt 1982, 1994, Vanderpoorten and Goffinet 2009). Thus, the chances of genetic recombination and adaptation to varying environments increase for liverworts and mosses, since sexual reproduction is more expected for dioicous populations, however self-fertilization guarantees sexual reproduction more frequently in monoicous populations (Stark and Brinda 2013). For this reason, it is common to find monoicous species with a higher proportion of sporophytes than dioecious ones, due to the proximity of male and female gametangium that favor the dispersion of antherozoid over short distances (Söderström and During 2005).

Dispersion by asexual reproduction is a notable and widespread characteristic found in bryophytes, with great importance in the maintenance of regional populations, in colonization and maintenance of habitat (Frey and Kürschner 2011). In this sense, in habitats subject to constant environmental stress (such as savannas), where selective pressures are more intense, asexual reproduction (or vegetative reproduction) can offer advantages over the sexual process. (Glime 2017c), since, the vegetative media reduce the energy expenditure that would be used for the production of gametangium and spore dispersion and guarantee the reproduction of species (Mogensen 1981).

The tolerance to bryophyte desiccation, guaranteed by its poikilohydric nature (Stark et al. 2007) and sexual and asexual reproductive strategies provided fitness for survival and development of these plants in adverse environments (Nath e Asthana 2004). In environments with adverse characteristics, such as the Caatinga, Nunes et al. (2015) observed that the greater production of gametangium of *Fabroniaciliaris* var. *polycarpa* (Hook.) W.R. Buck they occur in the rainy season and the dominance of sporophytes and the release of spores in the dry season, with phenology being influenced by seasonality. For African savannas, Egunyomi (1979), studying the phenology of *Octoblepharum albidum* Hedw., it was observed that the maturation of sporophytes is influenced by seasonality, with greater spore dispersion in the dry season. In an environment of Cangas (transition area between the Atlantic Forest and the Cerrado of Central Brazil), Peñaloza-Bojacá et al. (2017) observed the highest proportion of asexual reproduction in relation to the sexual process, with reproductive success being influenced by the sexual systems of the species, especially by the dioicous ones.

It is believed that seasonality acts in different ways on the bryophyte reproductive system, influencing the synchronization of gametangium production and the development of sporophytes with different levels of precipitation (Glime 2017a). In temperate environments, where seasonality is well defined, there is a marked influence of seasonality on the formation and development of gametangium, sexual reproduction and maturation of sporophytes (Longton 1990). In tropical rainforest, intense gametangium production occurs in the rainy season, due to the greater water availability that provides the release of male gametes and the respective fertilization of female (Nunes et al. 2015). In the savannas of Nigeria, Egunyomi(1979), reported the influence of the rainy season on the production of sporophytes and spore release in the dry season.

The savannas found in the Arari microregion, on Marajó Island, are formed by several disjoint patches of different sizes that experience two rainy seasons during the year, one rainier that extends mainly from January to April and the other less rainy with lower rainfall intensity from August through October. In general, in these savanna areas there is a predominance of herbaceous vegetation formed by grasses and variable density of trees and bushes, with emphasis on *Byrsonima chrysophylla*Kunth, *Curatella americana* L. and *Hancornia speciosa* Gomes. Although these savanna areas are classified in the same phytophysiognomy of Savanna Park, each area has its particularity, as they suffer constant anthropization and are also influenced by the surrounding vegetation, such as dense rain forests, open farm fields and igapó and forest forests floodplain which in the rainiest season influences the flooding of some savanna areas.

To formulate the question of the present study, we considered the effects of the high light intensity associated with drought events that are common in savannas and the influence of precipitation regimes in the Eastern Amazon, the latter is fundamental in the life cycle of bryophytes. In this context, do the different phytophysiognomic areas of Savanna Park and the variation of seasonality influence the reproductive expressions of bryophytes and the proportion of monoicous and/or dioicous species? Do monoicous and dioicous species differ in the type of reproduction developed? The objective was to answer the following questions: to analyze the influence of seasonality and phytophysiognomic areas of Savanna Park (considering the interaction factor between seasonality and phytophysiognomic areas) in the proportion of species with a monoicous sexual system and/or dioicous and proportion in the expression of reproductive structures.

MATERIAL AND METHODS

STUDY AREA

Three phytophysiognomic areas of Savanna Park (AI, AII and AIII) were selected (Figure 1), considering the differences in the density of phorophytes, in the surrounding vegetation and in the presence/absence of floods, levels of anthropization of the surrounding areas, located in the Arari microregion, in Marajó Island, Pará (Table I). The climate of the region is humid equatorial with an annual average temperature of 28 ° C with precipitation all year round, the months of greatest precipitation (rainy season -PI) during this study occurred between January and April (average of 504 mm) and lowest precipitation (dry season -PII) from August to October (average 19 mm), the relative humidity is around 82% in the rainy season and 66% in the dry season, this information was obtained from the database of the National Institute of Meteorology (http://www.inmet.gov.br/portal/index.php?r=home2/index).

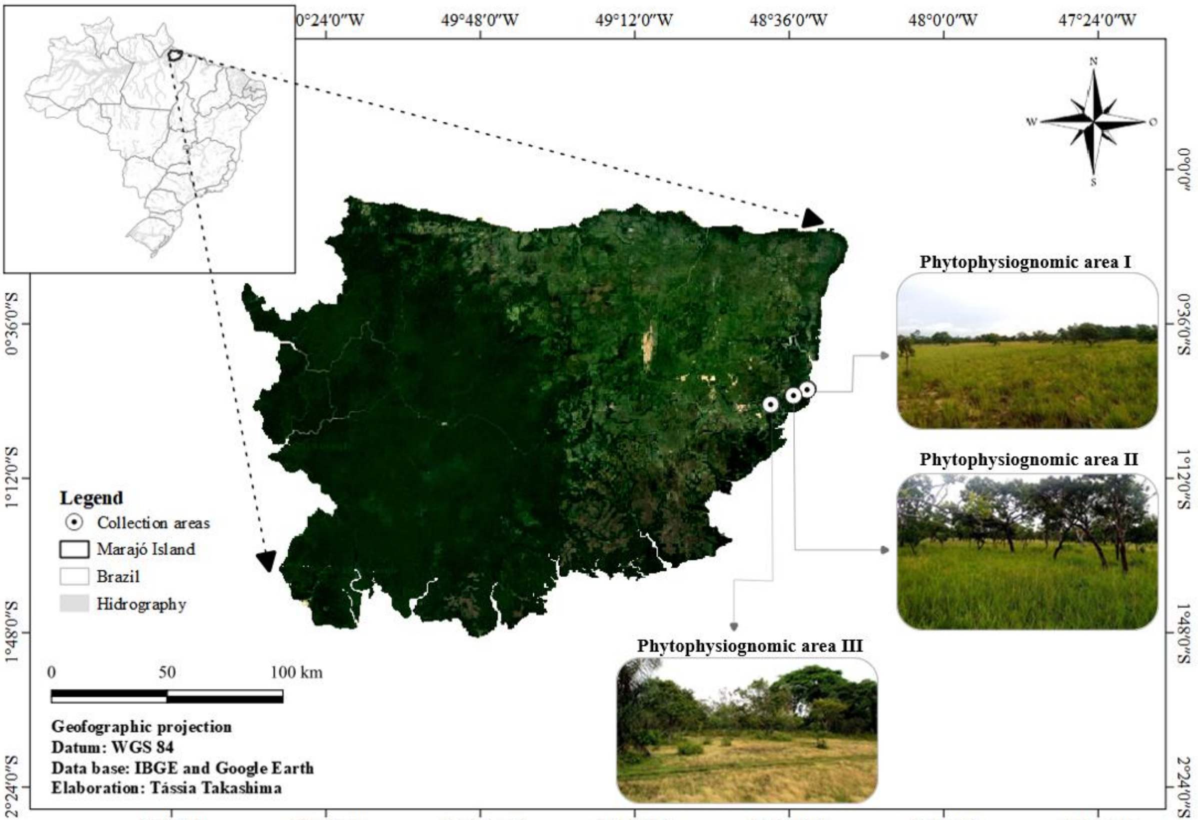

Figure 1 – Location of the studied areas of Savanna Park in Marajó Island, Pará, Brazil.

TABLE I

Description of the phytophysiognomic areas of Savanna Park in Marajó Island, Pará, Brazil.

Savanna Park	Geographic coordinates	Description of phytophysiognomicareas
Phytophysiognomicarea I	00°51'09,4"S 48°31'55,9"W	Sparse vegetation composed of arboreal-shrub stratum, with anthropogenic ombrophilous forest around. This phytophysiognomic area is constantly anthropized by the opening of roads and land subdivisions, the passage of fire is severe in the dry season, with no flooding in the rainy season.
Phytophysiognomicarea II	00º52'24,8"S 48º35'07,7"W	Vegetation with greater density of the tree-shrub layer in relation to phytophysionomic area I, the surrounding vegetation is formed by igapó forests and ombrophilous forest. This area is under pressure to open roads and anthropogenic and natural fires, which consume all the vegetation of grasses, which regenerate quickly in the rainy season, coinciding with the floods influenced by the floods of the igapós.
Phytophysiognomicarea III	00°54'32,3"S 48°40'06,9"W	Vegetation with greater density of the tree-shrub stratum in relation to phytophysiognomic areas I and II, has vegetation in the surroundings formed by dense anthropogenic ombrophilous forest. In addition, it suffers anthropic pressure due to the opening of roads, the passage of fire was not observed in the studied season, as well as there were no floods in the rainy season.

SAMPLING, COLLECTION AND TAXONOMIC IDENTIFICATION

The usual sampling methods for bryophytes were used, with plots of 10 x 10 m (100 m^2), according to Vanderpoorten et al. (2010). Thus, an extension of 600 m2 was established in each phytophysiognomic area of Savanna Park , subdivided into six permanent plots of 100 m^2, in which it was collected in the dry season (PII) of 2016 and rainy of 2017 (PI). The methods of field collection and preservation of botanical material followed the methodology of Glime (2017d), where the bryophytes were removed from the substrate with the aid of pocket knives and packed in wooden paper bags. In the plots, it was collected at the base of the trees and climbed up to the top of the phorophytes to collect the bryophytes, in decomposing trunks, soil and termite mounds. For the identification, specialized literatures were used (He 1999, Buck 2003, Florschütz-De Waard 1996, Gradstein and Ilkiu-Borges 2009) and the classification system of Crandall-Stotler et al. (2009) for liverworts and Goffinet et al. (2009) for mosses. To confirm the scientific names, the Flora do Brasil database was used 2020 (Costa 2013). The botanical material was incorporated in the Herbário Profª Drª Marlene Freitas da Silva (MFS) of the University of the State of Pará.

DATA ANALYSIS

Each paper bag in which the bryophytes were collected represented a sample, which in this study, corresponded to one occurrence of each identified species. The sexual systems of moss and liverworts, monoecious and/or dioecious (Figure 2a), were defined based on the identified material and data available in the aforementioned literature. For the sexual structures of the liverworts, the presence of gametangium (androecium- ♂ and gynoecium - ♀), that were considered as indicative of sexual expression (Longton and Greene 1969). For the sexual structures of mosses, the sporophyte phenophase was analyzed with three classifications according to Glime (2017b) and Nunes et al. (2015), with modifications: immature (closed capsule with green color), mature I (closed capsule with brown color) and mature II (open capsule) (Figure 2b). With regard to asexual reproduction, the occurrence of leaves with broken apex, gemma, caducous leaves and flagelliform branches was noted (Glime 2017c, Frey and Kürschner 2011).

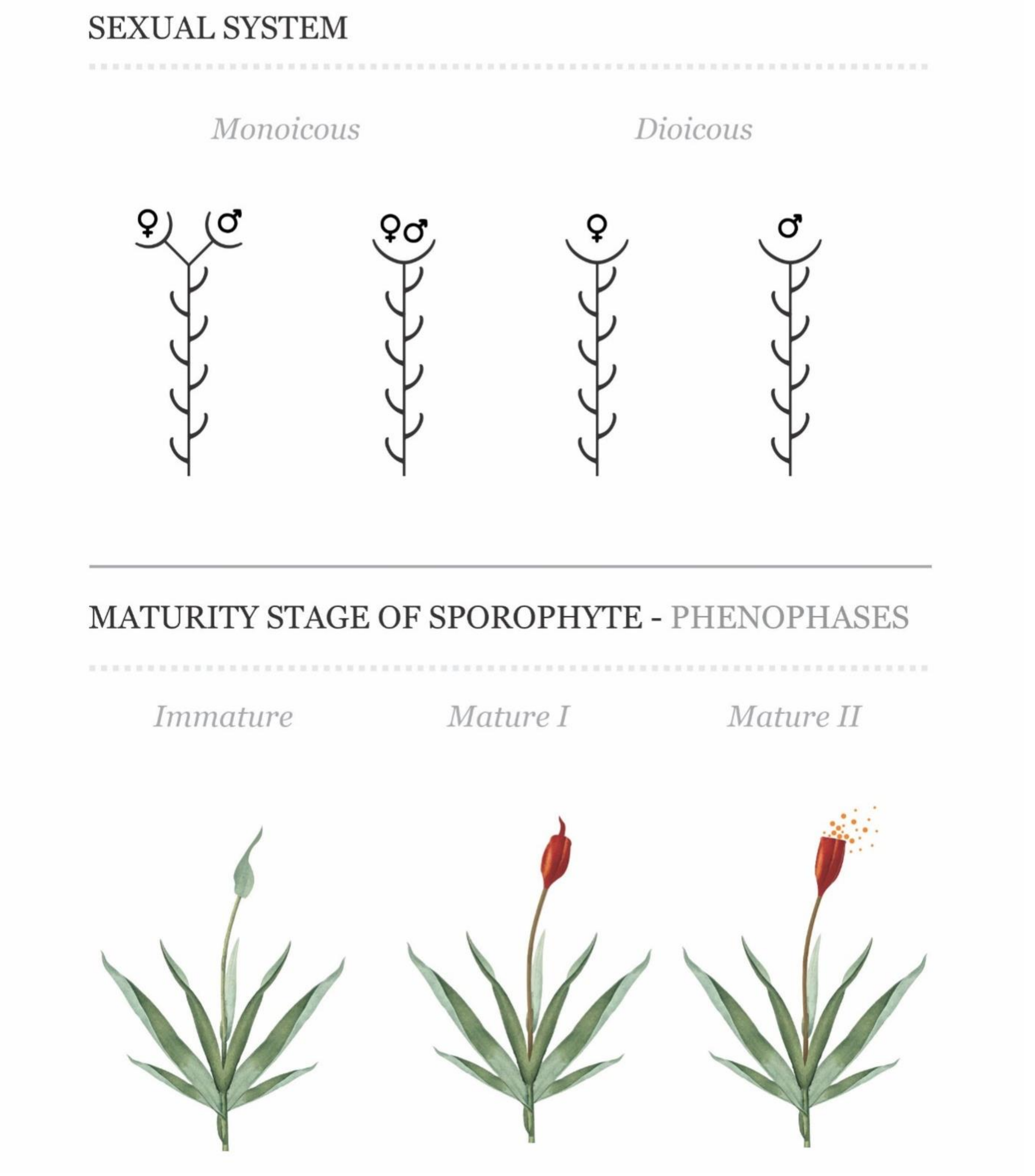

Figure 2 –Illustration of the different types of sexual system in bryophytes **(a)** and the phenophase of maturation stages of sporophytes in mosses **(b)**.

Through the Analysis of Variance (ANOVA) of two factors (Ayres et al. 2007), the influence of seasonality and different phytophysiognomic areas on the proportion in the sexual system (monoicous and dioicous specimens) and the proportion in the reproductive structures (sexual and asexual) was tested mosses and liverworts, as well as a possible interaction between the two factors (seasonality and phytophysiognomic area); the same analyzes were tested for the proportion of sexual expression of gametangium in the liverworts and in the sporophyticphenophases of mosses. To facilitate the interpretation of the boxplot graph generated in the two-factor ANOVA, the interaction diagram was used (*interaction plot*). All analyzes were performed using R v. 3.1.3 (R Development Core Team 2018).

RESULTS

COMPOSITION OF MONOICOUS AND DIOICOUS BRYOFLORA

After we analyze 180 samples, 547 specimens of bryophytes (327 mosses and 220 liverworts) classified into eight families eight families, 19 genera and 38 species distributed in the differentphytophysiognomic areas of Savanna Park (areas I, II and III), with 15 species of mosses (eight monoicous; seven dioicous) and 23 liverworts [10 monoicous; 12 dioicous and *Pycnolejeuneamacroloba* (Nees & Mont.) Schiffn, that presents the two sexual systems] (Table II).

In total, there is a balance in the proportion of species in relation to the sexual system, with about 48.7% monoicous and 51.3% dioicous. That is, seasonality was apparently not enough to select a set of species from only one sexual system with a higher proportion in the dry or rainy season (F = 0.61 p> 0.05), just as the phytophysiognomic area factor did not significantly influence the proportion of species monoicous and/or dioicous in any of the areas of Park Savanna (F = 0.34 p> 0.05). Likewise, the two variables analyzed together have no influence on the proportion of monoicous and dioicous species (F = 0.66, p> 0.05) (Figure 3b and d).

TABLE II

List of bryophytes and number of individuals registered in the sampling of communities in the phytophysiognomic areas of Savanna Park in Marajó Island, Pará. Si - Sexual System; AI - Phytophysiognomic Area I (Vila de Água Boa); AII - Phytophysiognomic Area II (Vila União); AIII - Phytophysiognomic Area III (Vila de Camará); PI - Rainy season; PII - Dry season; Sporophyte phenophases: IM - Immature; MI - Mature I; MII - Mature II; GA- Gametangium: AN - Androecium; GI - Gynoecium; EA - Asexual structures; AP - Apex broken; GE - Gemma; FC - Caducous leaves; FF - Flagelliform branches; (*) Structure not analyzed for the group.

Division/Family	**Si**	**Phytophysiognomic area**			**Season**		**Sporophyte**			**GA**		**EA**				**Voucher**
		AI	**AII**	**AIII**	**PI**	**PII**	**IM**	**MI**	**MII**	**AN**	**GI**	**AQ**	**GE**	**FC**	**FF**	
Bryophyta																
Bryaceae																
Bryumcoronatum Schwägr.	D	1	1	2	1	3	0	0	0	*	*	0	0	*	*	MFS007628
Calymperaceae																
Calymperes erosum Müll. Hal.	D	4	6	17	19	8	0	0	0	*	*	0	19	*	*	MFS007629
Calymperes palisotii Schwägr.	D	11	23	30	35	29	1	1	3	*	*	0	44	*	*	MFS007630
Octoblepharum albidum Hedw.	M	36	33	62	62	69	24	50	42	*	*	0	0	*	*	MFS007631
Syrrhopodon ligulatus Mont.	D	0	6	5	10	1	0	0	0	*	*	0	7	*	*	MFS007632
Syrrhopodonprolifer Schwägr.	D	0	1	0	1	0	0	0	0	*	*	0	0	*	*	MFS007633
Fissidentaceae																
*Fissidensangustifolius*Sull.	M	0	0	2	0	2	0	1	1	*	*	0	0	*	*	MFS008750
Fissidensguianensis Mont.	M	0	0	3	2	1	1	0	1	*	*	0	0	*	*	MFS008744
Fissidensprionodes Mont.	M	0	1	1	1	1	1	1	1	*	*	0	0	*	*	MFS007634
Leucobryaceae																
Campylopus surinamensis Müll. Hal.	D	0	4	0	0	4	0	0	0	*	*	0	0	*	*	MFS007635
Orthotrichaceae																
Groutiellatomentosa (Hornsch.) Wijk&Margad.	D	0	0	1	1	0	0	0	1	*	*	1	0	*	*	MFS008742
Sematophyllaceae																
Brittonodoxasubpinnata(Brid.) W.R.Buck	M	0	0	1	1	0	0	0	0	*	*	0	0	*	*	MFS008741
Microcalpe subsimplex (Hedw.) W.R. Buck	M	27	11	26	29	35	2	0	15	*	*	0	0	*	*	MFS007636
Sematophyllum adnatum (Michx.) Brid.	M	0	0	2	2	0	0	0	0	*	*	0	0	*	*	MFS008747
Trichosteleumpapillosum (Hornsch.) A.Jaeger	M	0	0	1	1	0	0	0	1	*	*	0	0	*	*	MFS008745

Division/Family	**Si**	**Phytophysiognomic area**			**Season**		**Sporophyte**			**GA**		**EA**				**Voucher**
		AI	**AII**	**AIII**	**PI**	**PII**	**IM**	**MI**	**MII**	**AN**	**GI**	**AQ**	**GE**	**FC**	**FF**	
Marchantiophyta																
Frullaniaceae																
Frullaniaexilis Taylor	D	0	0	3	2	1	*	*	*	1	2	*	*	0	0	MFS008751
Frullaniagibbosa Nees	M	0	0	1	1	0	*	*	*	0	0	*	*	0	0	MFS008747
Lejeuneaceae																
Acrolejeuneaemergens (Mitt.) Steph.	M	0	2	16	9	9	*	*	*	2	6	*	*	2	3	MFS007637
Acrolejeunea torulosa (Lehm. &Lindenb.) Schiffn.	M	1	8	53	39	23	*	*	*	4	21	*	*	24	27	MFS007638
Archilejeuneafuscescens (Hampe ex Lehm.) Fulford.	D	0	0	1	0	1	*	*	*	1	0	*	*	0	0	MFS007639
Cheilolejeunea aneogyna (Spruce) A. Evans	M	0	1	0	1	0	*	*	*	0	0	*	*	0	0	MFS007640
Cheilolejeunea comans (Spruce) R.M.Schust.	M	1	3	2	4	2	*	*	*	3	2	*	*	0	0	MFS007642
Cheilolejeunea holostipa (Spruce) Grolle & R.-L.Zhu	D	0	0	1	1	0	*	*	*	0	0	*	*	0	0	MFS008740
Cheilolejeunea oncophylla (Aongström) Grolle &E.Reiner	M	9	5	39	31	22	*	*	*	14	21	*	*	0	0	MFS007644
Cheilolejeunea rigidula (Mont.) R.M.Schust.	D	2	1	10	7	6	*	*	*	6	2	*	*	0	0	MFS007645
*Drepanolejeuneafragilis*Bischl.	D	0	0	3	0	3	*	*	*	0	0	*	*	0	0	MFS008748
Lejeunea flava (Sw.) Nees	D	0	1	1	1	1	*	*	*	0	1	*	*	0	0	MFS007648
*Lejeunealaetevirens*Nees & Mont.	D	6	0	8	9	5	*	*	*	4	2	*	*	0	0	MFS007649
Lopholejeuneasubfusca (Nees) Schiffn.	M	0	0	2	2	0	*	*	*	0	0	*	*	0	0	MFS008739
Microlejeuneabullata(Taylor) Steph.	D	0	0	1	0	1	*	*	*	0	0	*	*	0	0	MFS008749
Microlejeunea epiphylla Bischl.	D	4	0	17	15	6	*	*	*	3	8	*	*	0	0	MFS007650
Microlejeunea globosa (Spruce) Steph.	D	0	1	0	0	1	*	*	*	1	0	*	*	0	0	MFS007651
Microlejeuneasubulistipa Steph.	D	0	0	3	3	0	*	*	*	1	2	*	*	0	0	MFS007652
Pycnolejeunea contigua (Nees) Grolle	D	0	0	4	3	1	*	*	*	3	4	*	*	0	0	MFS007653
Pycnolejeuneamacroloba (Nees & Mont.) Schiffn.	M/D	0	1	0	0	1	*	*	*	0	0	*	*	0	0	MFS007654
Pycnolejeuneapapillosa X.-L. He	M	3	0	2	3	2	*	*	*	2	2	*	*	0	0	MFS007655
Pycnolejeunea sp.	M	0	0	4	4	0	*	*	*	0	0	*	*	0	0	MFS008743
Total		105	109	324	300	238	29	53	65	45	73	1	70	26	30	

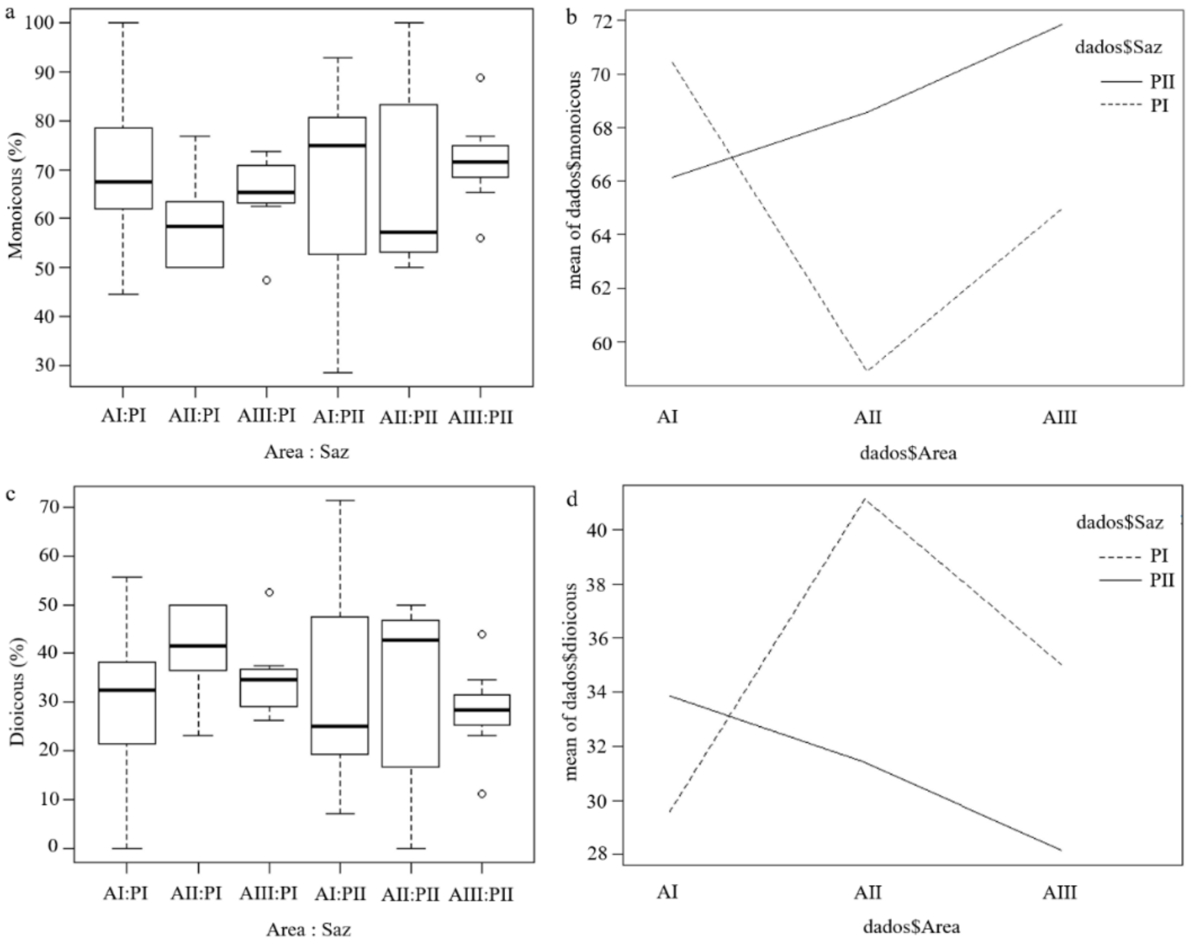

Figure 3 -Proportion of monoicous individuals **(a)** and dioicous **(c)** in the Savanna Park phytophysiognomic areas (AI, AII and AIII) with the influence of the rainy season (PI) and dry season (PII). Diagram of interaction between phytophysiognomic areas and seasonal season s of the proportion of monoicous **(b)** and dioicous individuals **(d).**

SEXUAL AND ASEXUAL REPRODUCTION STRUCTURES

There were 256 (46.86%) specimens without reproductive structures, 194 (35.46%) were reproducing sexually, 85 (15.53%) were reproducing asexually and 12 (2.15%) specimens expressed sexual and asexual reproductive structures.

Considering the occurrence of reproductive structures, it was observed that the environmental conditions of the phytophysiognomic areas significantly influenced the proportion of sexual (F = 4.3576, $p < 0.05$) (Figure 4a) and asexual (F = 18.2404, $p < 0.001$) structures (Figure 4c). The phytophysiognomic area III showed to be more influential in the proportion of sexual and asexual structures, with significant variations ($p < 0.005$) between AIII and AI and between AIII and AII. The levels of the seasonality factor were not sufficient to significantly influence the proportion of reproductive structures, however, it was observed that there is an interaction between seasonality and the type of environment (savanna area) that influenced in different ways the proportion of sexual structures (F = 3.8354, p <0.05) (Figure 4b).

Four patterns of asexual reproduction were observed: liverworts, flagelliform and caducous leaves branches were registered both in *Acrolejeuneaemergens* (Mitt.) Steph. (1.3% of specimens with flagelliformis branches and 0.9% with caducous leaves) and in *Acrolejeuneatorulosa*(Lehm. &Lindenb.) Schiffn. (12.2% and 10.4%); on mosses, the yolk was recorded in *Calymperes erosum* Müll. Hal. (5.8% of specimens with gemma), *Syrrhopodonligulatus* Mont. (2.4%) and *Calymperes palisotii* Schwägr. (13.4%) and leaves with broken apices in *Groutiellatomentosa* (Hornsch.) Wijk&Margad. (0.3%).

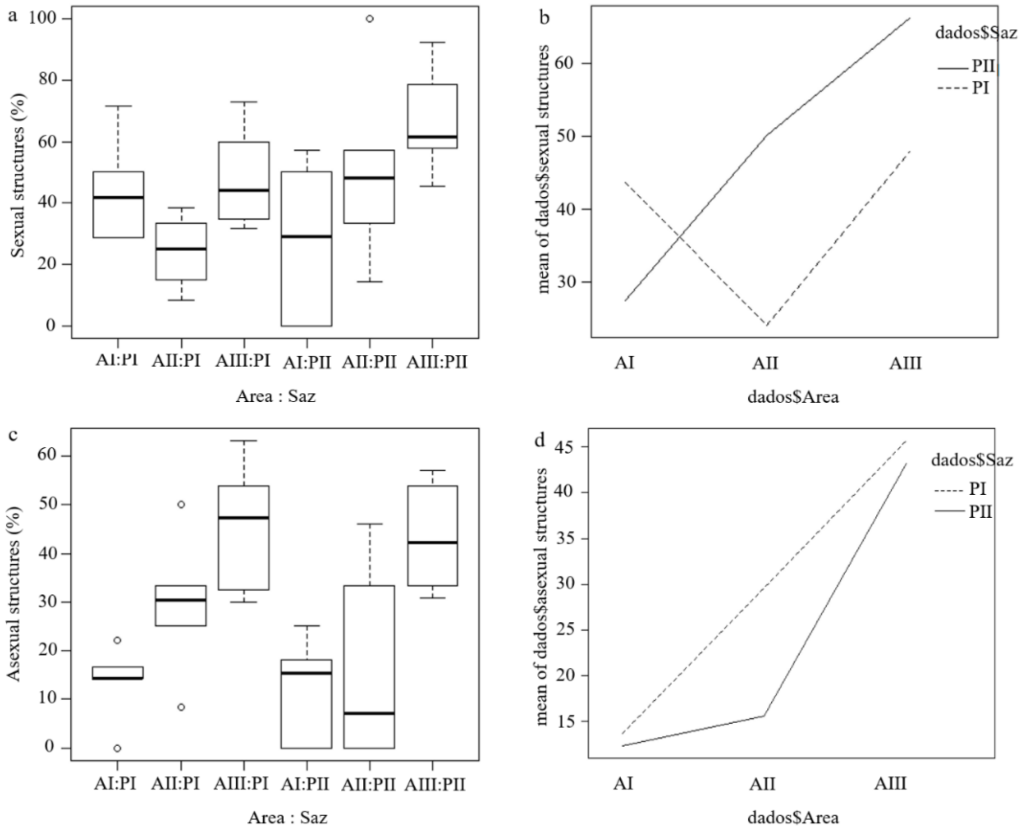

Figure 4 - Proportion of sexual expression **(a)** and asexual **(c)** in the phytophysiognomic areas of Savanna Park (AI, AII and AIII) with the influence of the rainy season (PI) and dry season (PII). Diagram of interaction between phytophysiognomic areas and seasonal season s of the proportion of sexual expression **(b)** and asexual **(d).**

EXPRESSION OF LIVERWORTS GAMETANGIUM

In the monoicous and dioicous liverworts, 118 gametangium structures were observed, among which the expression of gynoecium with a higher proportion (62%) occurring in 12 spp.; followed by androecium (38%) at 13 spp. The expression of androecium and gynoecium was higher in the rainy season with 24 and 44 occurrences, respectively, in relation to the dry season (21 and 29). Seasonality emerged as a determining factor only for the proportion of androecium in the dry season (F = 6.0770, p <0.005) (Figure 5b). Although seasonality does not significantly influence the proportion of gynoecium, it was observed in phytophysiognomic area I a difference in the proportion of gynoecium from the rainy season to the dry season (Figure 5d). The expression of androecium (F = 6.0770, p <0.005) (Figure 5a) and gynoecium (F = 5.7907, p <0.005) (Figure 5c) are variables dependent on the environmental conditions of the Savanna Park phytophysiognomic areas, where the expression of androecium it differed significantly (p <0.005) between the phytophysiognomic areas III and II and the expression of gynoecium between the phytophysiognomic areas AIII and AI and between AIII and AII. The tested interaction between seasonality and phytophysiognomic areas did not influence the expression of androecium (F = 0.92, p> 0.05) and gynoecium (F = 0.40, p> 0.05).

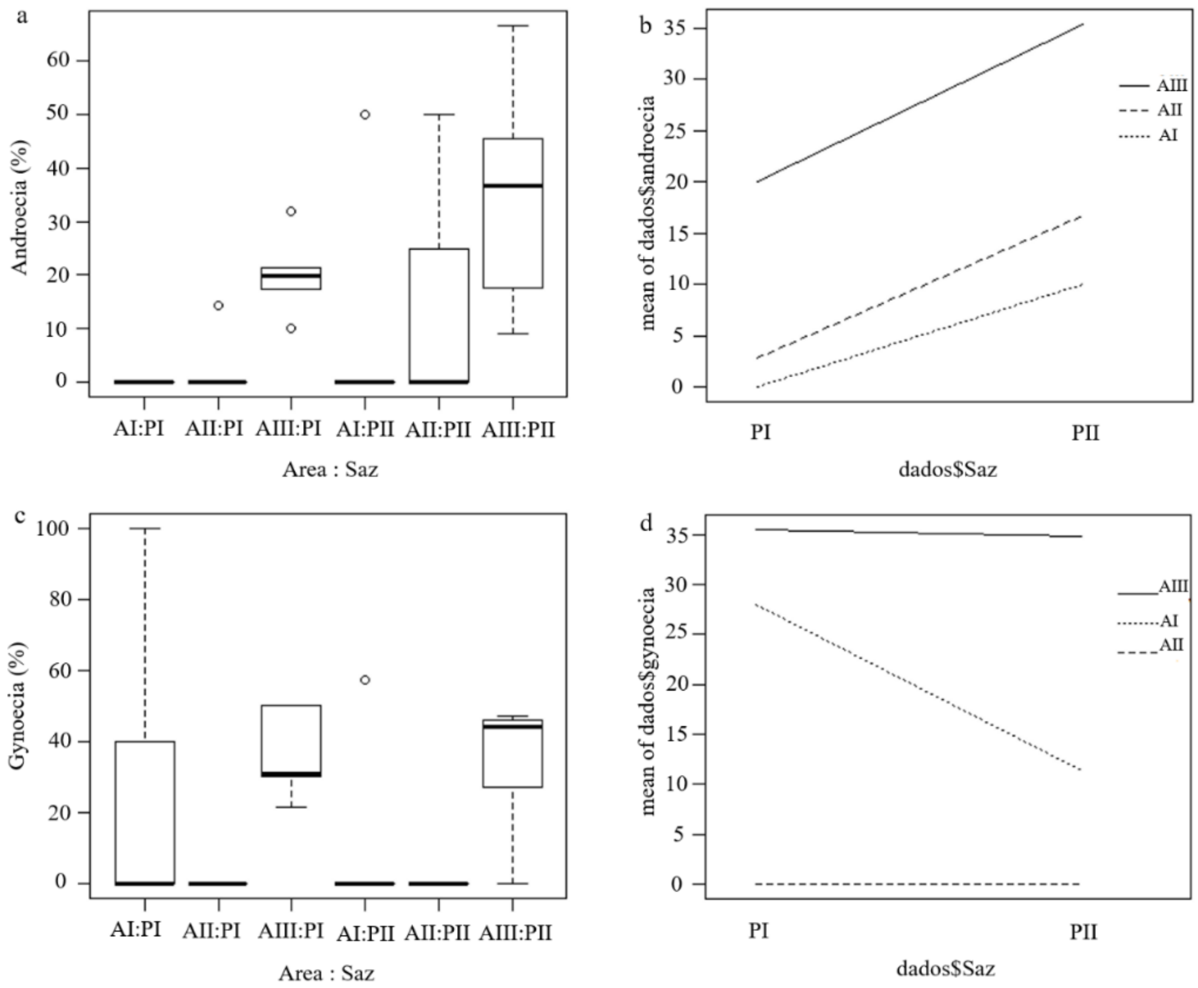

Figure 5 - Proportion of the expression androecium **(a)** and gynoecium **(c)** in the phytophysiognomic areas of Savanna Park (AI, AII and AIII) with the influence of the rainy season (PI) and dry season (PII). Diagram of interaction between phytophysiognomic areas and seasonal season s of the proportion of androecium **(b)** and gynoecium **(d).**

SPOROPHYTIC PHENOPHASES IN MOSSES

The presence of sporophytes was observed in nine species, among which, four are acrocarp monoecious - *Fissidensangustifolius*Sull. (two specimens with sporophytes), *Fissidensprionodes* Mont. (three), *Fissidensguianensis* Mont. (two) and *Octoblepharum albidum* Hedw. (116); three are acrocarpdioicouss - *Calymperes erosum* Müll. Hal. (a specimens with sporophyte), *Calymperes palisotii* Schwägr. (five) and *Groutiellatomentosa* (Hornsch.) Wijk&Margad. (one) and two are monoecious pleurocarp - *Microcalpe subsimplex* (Hedw.) W.R. Buck (17) and *Trichosteleumpapillosum* (Hornsch.) A.Jaeger (um).

Seasonality is the determining factor in mature phenophase II (F = 7.7531, p <0.005), in which the opening of the sporophytes and consequently the release and dispersion of the spores coincided with the dry season. The presence of sporophytes in the immature (F = 2.6406, p> 0.05) or mature I (F = 0.8317, p> 0.05) phenophase are not related to the seasonal variable. However, although there are no significant differences, in *Octoblepharum albidum* Hedw the constant production of sporophytes in the two seasonal seasons, in the dry season the mature I (45.16%) and mature II (48.38%) stages predominated, while in the rainy season , immature phenophase occurred in a greater proportion (37 , 03%) and mature I (40.7%). The phytophysiognomic areas do not appear as an important variable for the different stages of development of the sporophytes (Immature: F = 1.9878, p> 0.05; Mature I: F = 0.1035, p> 0.05; Mature II: F = 2.0227, p> 0.05;), as well as the interaction between seasonality and phytophysiognomic areas (Immature: F = 1.9878, p> 0.05; Mature I: F = 3.1261, p> 0.05; Mature II: F = 0.2251, p> 0.05) (Figure 6) .

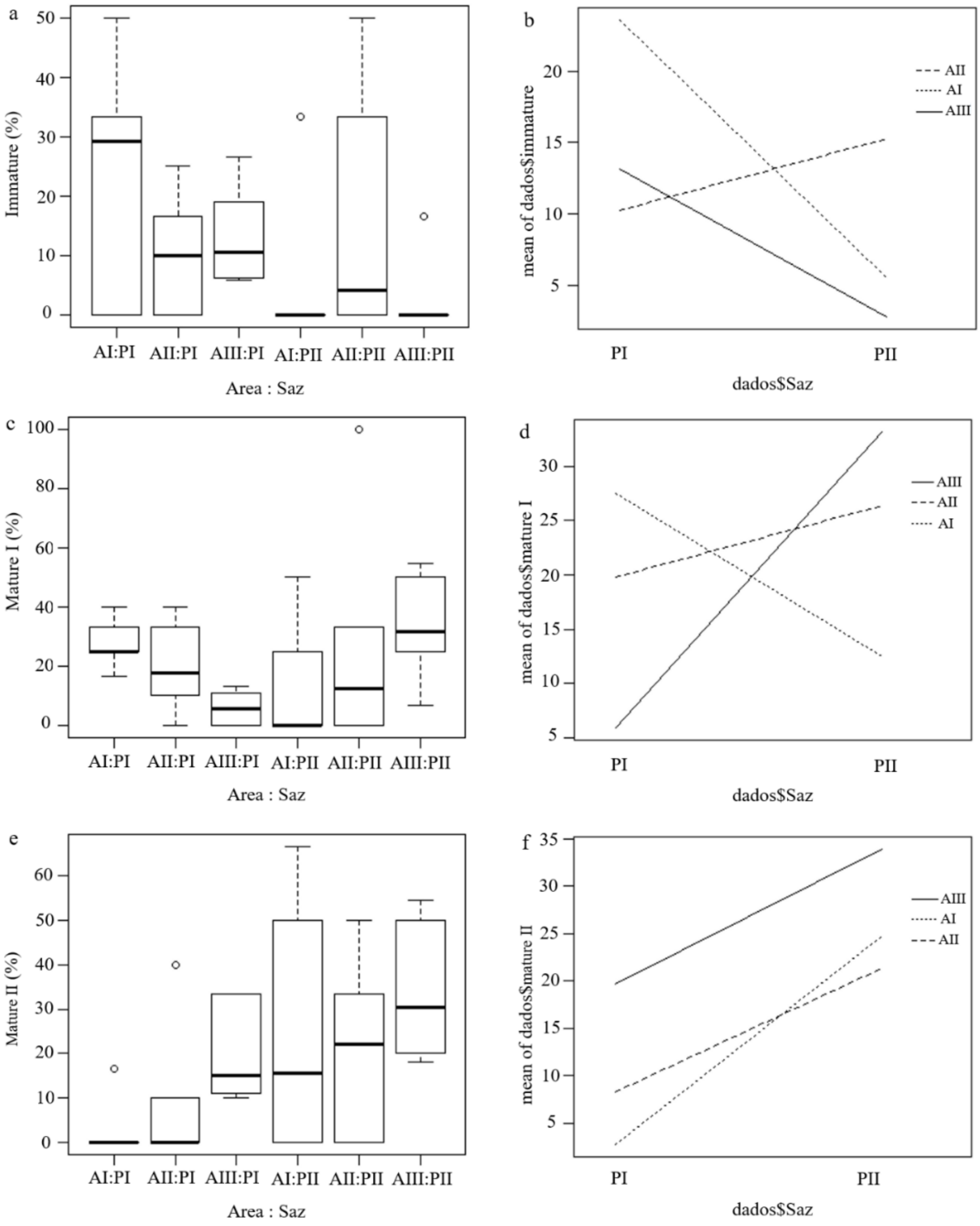

Figure 6 - Sporophyte proportion in immature **(a)**, mature I **(c)** and mature II **(e)**phenophases in the Savanna Park phytophysiognomic areas (AI, AII and AIII) with the influence of the rainy season (PI) and dry season (PII). Diagram of interaction between phytophysiognomic areas and seasonal season s of the proportion of sporophytes in immature **(b)**, mature I **(d)** and mature II **(f)**phenophase.

DISCUSSION

COMPOSITION OF MONOICOUS AND DIOICOUS BRYOFLORA

The environmental variation found in the phytophysiognomic areas and the influence of seasonality did not have enough effects to select the sexual systems of the bryophytes, nor the interaction between the two factors. Possibly the balance in the proportion of monoicous and dioicous species, is a reflection of the total proportion of sexual systems, with about 40% monoicous and 60% dioicous (Maciel-Silva and Pôrto 2014), although not always the same pattern for other ecosystems of tropical forest. For example, the predominance of monoicous species in rocky outcrops in the Caatinga (Silva et al. 2014) and in the rainforest in Chapada do Araripe (Batista et al. 2018). On the other hand, some studies have reported the highest proportion of dioecious species in areas of the Atlantic Forest and in rocky outcrops in the Cerrado (Silva 2013, Santos et al. 2017, Peñaloza-Bojacá et al. 2017).

If the levels of anthropization remain constant in the phytophysiognomic areas II and III, these areas tend to be similar to the phytophysiognomic area I, which is characterized by the greater spacing of the tree-shrub layer and greater state of anthropization with the opening of roads, subdivision of land and fires. Moreover, other Amazonian ecosystems may become similar to phytophysionomic area I, considering the effects of climate change increasingly evident, announcing a possible savanization of the Amazon forest (Lawrence; Vandecar, 2015). For the group of bryophytes, this means that, the anthropic factors and the drought resulted in the decrease of the diversity of these plants, mainly of the dioecious populations (see interaction diagram in Figure 2d). In other words, the majority of bryophyte populations in the Amazonian savannas can be monoic, which facilitates sexual reproduction by self-fertilization (but does not guarantee genetic variability), since the greater distance between the forophytes in the savannas does not guarantee that the gamete male will fertilize the female gamete in dioecious populations.

SEXUAL AND ASEXUAL REPRODUCTION STRUCTURES

The higher proportion of specimens with no reproductive structures recorded in this study may be related to the adverse conditions found in the different phytophysiognomic areas of Savanna Park, such as high light input and low humidity in the substrates. Similar results were reported by Peñaloza-Bojacá et al. (2017) in rocky outcrop sites of Cangas in Minas Gerais, where the conditions of humidity and light are similar to areas of the Amazonian savannas, however, it was observed that the occurrence of asexual reproduction (345) was greater than the sexual process (294), probably as an alternative to low water availability. Studying the reproductive phenology of bryophytes in tropical forests in Brazil, Maciel-Silva and Valio (2011), observed that the pattern of constant sexual expression over time is characterized as opportunistic, in which relatively high temperatures and humidity are factors favorable to continuous production of sexual organs.

It is possible to raise the hypothesis that in the phytophysiognomic area II, the reduction of rainfall in the dry season can be an important variable for the decrease in the production of asexual structures, since, in environments such as dense forests, the wide occurrence of vegetative reproduction is related to humidity and light conditions that are more stable in the forest understory (Bastos 2008). In this sense, even though asexual reproduction does not contribute to genetic recombination, it functions as a security system guaranteeing reproduction, being essential in maintaining populations of bryophytes (Laaka-Lindberg 2000; Frey and Kürschner 2011). Probably the highest proportion of asexual reproduction in the phytophysiognomic area III is related to the environmental conditions of the studied area, which presented a greater density of phorophytes and absence of fires in the studied season , which may have influenced the dispersion and colonization of bryophytes due to the greater proximity between the phorophytes and humidity in the substrates. Since, the dispersion capacity can be affected by the environment through which the propagule must disperse (Wiens 1997).

The greater representativeness of *Acrolejeunea torulosa* (Lehm. &Lindenb.) Schiffn. among the liverworts diseases registered in this study, it may be related to the combination of the monoicous condition with the occurrence of asexual reproduction, increasing the chances of dispersion. Among the three dioecious species of Calymperaceae (*Calymperes erosum* Müll. Hal., *Calymperes palisotii* Schwägr. and *Syrrhopodon ligulatus* Mont.)found with gemma in this study, sexual reproduction and the formation of sporophytes are rare conditions (Sharp et al. 1994), so that the predominance of asexual structures is to guarantee the production of new gametophytes. In addition, acrocarpous dioecious mosses are less likely to fertilize, due to a single branch with only one sexual organ produced at the apex of the gametophyte per growth season (La Farge 1996). However, it was noted that the dioicousity of *Calymperes palisotii* Schwägr. did not prevent the species from investing in sexual reproduction, observing sporophytes and gemma in the same gametophyte, which probably guaranteed the wide distribution and second largest occurrence shared with the monoicous species *Microcalpe subsimplex* (Hedw.) W.R. Buck. considering all identified species.

Among dioecious mosses, the high energy cost in development and the lack of synchrony in the maturation of antheridia and archegonia, in addition to the distance between male and female populations, are factors that do not guarantee the effective fertilization of species (Longton and Schuster 1983, Bowker et al. 2000, Maciel-Silva and Pôrto 2014). Thus, vegetative reproduction has become a means of dispersion of high efficiency favorable to the rapid occupation of the habitat in relation to the sexual process (Bastos 2008, Alvarenga et al. 2013). As in *Groutiellatomentosa* (Hornsch.) Wijk&Margad., in which the leaves with broken apexes became a characteristic of vegetative propagation frequently observed in this species (Crum and Anderson 1981).

EXPRESSION OF LIVERWORTS GAMETANGIUM

The balance in the proportion of gametangium in monoicous and dioicous populations was also found by Cerqueira et al. (2016) studying the influence of seasonality in epiphyte bryophyte communities in the Caxiuanã National Forest, noting that such result may be promoting the maintenance of bryophyte communities. That may also be happening in the phytophysiognomic areas of Savanna Park. Although seasonality does not significantly influence the expression of gametangium in this study, it seems to be a greater investment in the production of male and female gametângios in the rainy season, due to the record of higher proportions in the production of these sexual structures this season. Results similar to these were reported by Haupt (1929) in the state of California (United States) in his first observations of the development of gametangium in the liverworts *Fossombronialongiseta* Austin, which had better conditions for fertilization in the wettest season of winter. Almost a century later, in a tropical forest ecosystem, Maciel-Silva and Valio (2011) point out that fertilization time is dependent on the rainy season and spore dispersion occurs in the dry months. That is, bryophytes adjust gametangium production mechanisms according to the water availability of each ecosystem. Nunes et al. (2015), studying the sexual reproduction of *Fabroniaciliaris* var. *polycarpa* (Hook.) W.R. Buck in the caatinga, he observed the intense production of gametangium in the rainy season, as the greater water availability provides better conditions for the male gamete to reach the female gamete.

Considering environmental conditions such as high light input and low humidity in savannas (Franco 2005), bryophytes can be severely affected because they do not have complex systems to adjust water use (Glime 2017e). Thus, the lower energy expenditure for the production and development of gynoecium in relation to androecium (Glime 2017b), may explain the higher proportion of female gametangium recorded in this study.

SPOROPHYTIC PHENOPHASES IN MOSSES

The higher proportion of sporophytes in monoicous species found in this study is justified by the fact that these plants reproduce by spores more frequently than dioecious and therefore have higher rates of sporophytes, since the distance between the sexes facilitates the self-fertilization and ensures that sexual reproduction occurs (Longton and Schuster 1983, De

La Cerda 1989), although this is not always the case. As a result of this study, monoicous is associated with the production of sporophytes in the vast majority of mosses, which occurs with greater intensity in the months of the rainy season, where the chances of fertilization increase with the presence of male and female gametangium in the same gametophyte (Oliveira and Pôrto 1998). On the other hand, the lack of synchrony in the maturation of male and female gametangium and the distance between populations are factors that hinder sexual reproduction in dioicous species (Maciel-Silva and Pôrto 2014).The greater occurrence of fertilization and the development of sporophytes in the rainy season and the release and dispersion of spores in the dry season was also confirmed from the phenological study in four mosses from the savannah of southwestern Nigeria, being *Racopilumafricanum* Mitt., *Fissidensglauculus* C. Mfill., *Thuidiumgratum*Jaeg., and *Stereophyllurn* sp. (Makinde and Odu 1994). In acrocarpous mosses in the state of Pernambuco, a pattern of greater representation of sporophytes was observed in the immature stage in months of the rainy season, while mature sporophytes were observed more frequently in the dry season, which coincides with spore dispersion (Oliveira and Pôrto 1998).

Data recorded in this study for *Octoblepharum albidum* Hedw. Were also similar in remnants of Atlantic Forest in Pernambuco (Pôrto and Oliveira 2002), in which the majority of sporophytes were dispersing spores in the dry season (August to December), where the conditions of low humidity favor the transport of spores by the wind. In addition, it was found that there is a similarity in the reproductive behavior of *O. albidum* recorded in the Amazonian savannas with those found by Egunyomi (1979) in the savannah of Nigeria, with a synchronization in the greatest spore dispersion coinciding with the dry season.

CONCLUSION

Seasonality and differences in the phytophysiognomic areas of Savanna Park, analyzed solely and together, do not influence the proportion of species with specific sexual systems in the bryophyte communities of the Marajó savannas. Therefore, the life history of these species seems to better explain their presence in this ecosystem. On the other hand, the development of sexual and asexual reproductive structures depends on the micro-habitat in which the species are inserted. Thus, future studies to understand the relationship between bryophyte reproductive strategies and micro-habitat conditions should consider the factors of humidity, temperature, luminosity and the pH of the substrate.

In the liverworts, the different phytophysiognomic areas directly influence the production of gametangium and among mosses, monoicous was prone to the greater production of sporophytes influenced by the effect of seasonality. Thus, this study proves and reinforces the data in the literature that seasonality has a direct effect on sporophyticphenophases, as shown by the development stages of sporophytes in different rainfall season. These structures, and the abundance of species, can elucidate studies that explain how bryophytes grow, disperse and colonize new micro-habitats in savannas on a local and regional scale.

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CONCLUSÃO GERAL

Com este estudo, foi possível conhecer a influênciada sazonalidade na estrutura e nos aspectos reprodutivos das comunidades de briófitas presente nas formações de Savana Parque da região leste da Ilha de Marajó, além de contribuir com os dados da brioflora para a Amazônia.As briófitas das Savanas Parque da Ilha de Marajó mostraram-se bem estabelecidasas variações de precipitação e aos eventos do fogo que ocorrem nas savanas, com maior proporção de espécies associadas na literatura à ambientes abertos, áridos e perturbados, tais como os musgos acrocárpicos e as hepáticas folhosas com atributos de tolerância a dessecação.

Observou-se que embora as áreas apresentem a mesma fitofisionomia, as ações antrópicas e a vegetação ao entorno implicam na paisagem gerando diferentes padrões de savanas, o que influenciou na composição, riqueza, densidade e diversidade das briófitas. Além disso, a alta frequência das espécies raras reforça a necessidade de conservação das savanas amazônicas, visto que, este ecossistema vem sofrendo com o constante uso da terra para a agricultura, pecuária e abertura de estradas e rodovias, ameaçando o elevado índice de endemismo e biodiversidade presente nesses ambientes.

Notou-se que, mesmo o sistema sexual não sendo influenciado pela diferença de precipitação e as áreas de savanas, o mesmo foi responsável por gerar diferentes padrões de reprodução sexuada e assexuada, as quais foraminfluenciadas tanto pela sazonalidade quanto pelas condições ambientais do micro-habitat das savanas. Dessa forma, tais informações são importantes para entender a biologia reprodutiva das briófitas presente nessas áreas e elucidar questões que explique como as briófitas crescem, se dispersam e colonizam novos micro-habitat nas savanas em escala local e regional.

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