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ECOSYSTEMS

Bryophytes in Amazon savannas: richness and composition in disjunct areas in the Eastern Amazon

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Abstract: The Brazilian Amazon forests are interspersed by savanna ecosystems distributed in the states of Amapá, Amazonas, Pará, Rondônia and Roraima, presenting different distribution patterns. The objective of this work was to evaluate the richness, composition and floristic similarity of the bryophyte flora from five disjunct savanna areas in the eastern Amazon and compare the richness with those of other savannas in Brazil. The collections were carried out from 2017 to 2018 in five localities of the eastern Amazon. Twenty-two species of mosses and 22 species of liverworts were registered. The composition was expected for savanna ecosystems with 27 species of generalists and 16 sun specialists. There was a striking floristic difference between the areas, and the clusters showed that the eastern Amazon savannas are formed by different compositions related to their area. This study made it possible to discover one new record for the state of Pará, five new records for the state of Amapá and one new record for the North region.

Key words: Amazonia, Liverworts, Mosses, savannas.

INTRODUCTION

The Brazilian Amazon covers approximately 4,196,943 km² (60% of the Amazon region) and is generally known for its extensive forests, high biodiversity and large biomass (Pires & Prance 1985, IBGE 2004, Tejada et al. 2019). Interspersed in these forest areas are open ecosystems, ranking as the second largest vegetation physiognomy (Sanaiotti et al. 2002, Adeney et al. 2016) and occurring as patches that together correspond to approximately 200,000 km² and about 5% of the coverage in the region (Barbosa & Campos 2011, Cavalcante et al. 2014).

Savanna is a type of xeromorphic fire-tolerant open vegetation with predominance of an herbaceous layer, trees and shrubs with different densities, rainy and dry seasons, poor and acidic soils, and areas subject to periodic waterlogging (Eiten 1972, Ribeiro & Walter 1998, IBGE 2012). This open vegetation was also called as Guianan savanna and Southern Amazonian campo/cerrado by Adeney et al. (2016) while defining the Brazilian regional terms campina and campinarana as white-sand ecosystem in the Amazon. The term savanna is broad and related to distribution, types of physiognomies, climate, geography, seasonality, and presence or absence of grassy field and forest formations (Sarmiento 1983, Goedert et al. 2008, Ribeiro & Walter 2008, Borghetti et al. 2020).

In the Amazon, these ecosystems have physiognomies similar to those of neotropical savannas and are distributed in a matrix of tropical rainforest that covers the states of Amapá, Amazonas, Pará, Rondônia and Roraima (Gottsberger & Morawetz 1986, Prance 1996, Miranda & Absy 2000, Barbosa et al. 2005, Miranda et al. 2006, Vasconcelos et al. 2011). These savannas present different distribution patterns, occurring as small or large patches and physiognomies that vary according to the region in which they are inserted (Sarmiento 1983, Ribeiro & Walter 1998, Barbosa et al. 2007).

Floristic studies in Amazonian savannas have mainly evaluated the composition and structure of tree communities (Miranda 1993, Miranda et al. 2002, 2006, Magnusson et al. 2008), the richness, composition and diversity of the tree-shrub layer (Barbosa et al. 2005), the floristic composition of the herbaceous and tree-shrub layer and phytosociology of the herbaceous-shrub layer (Costa-Neto et al. 2017, Rocha & Costa-Neto 2019), specific floristic aspects of certain taxa (Flores & Rodrigues 2010, Costa et al. 2012, Menezes & Flores 2013, Rocha & Miranda 2014, Rocha et al. 2014, Silva et al. 2015), and wood biomass and density (Barbosa & Fearnside 2004, 2005, Barbosa et al. 2012, Jati et al. 2014, Jati & Maulaz 2019). These studies made it possible to assess and understand how plant communities are formed and structured in savanna enclaves in the Amazon.

Research including bryophytes (Bryophyta, Marchatiophyta and Antocerotophyta) in Amazonian savannas has been carried out mainly in the eastern Amazon. In the state of Amapá, two taxonomic studies with collections in these environments reported eight species of mosses (Yano & Lisboa 1988, Churchill 1998). In the Marajó archipelago, a study about Lejeuneaceae included surveys in savanna areas in the Caxiuanã National Forest and 10 species were recorded, of which three occurred exclusively in this type of vegetation (Ilkiu-Borges & Lisboa 2002).

In the survey of the bryophyte flora of different ecosystems in Marajó Island, 12 species distributed among seven mosses and five liverworts belonging to nine genera and five families occurred in savanna areas. Differences in richness and predominance of mosses and liverworts between the studied areas were linked to microclimatic and abiotic variations of the various ecosystems studied (Brito & Ilkiu-Borges 2013).

Another study on bryophytes from savannas in Marajó Island registered 41 species, among 15 mosses and 26 liverworts distributed in 21 genera and in eight families (Gomes et al. 2021). According to the authors, the evaluated communities are formed by typical species of this type of ecosystem, tolerant to environmental stress, which are not influenced by seasonality and remain in the environment.

In the western Amazon, Gottsberger & Morawetz (1993) compared the abundance and distribution of epiphytes, including non-vascular species, on phorophytes in savannas located in Humaitá, Amazonas. They observed that bryophytes tended to dominate older trees in relation to lichens as an apparent succession in the trunks and branches of the analyzed phorophytes. In this study, bryophytes were pooled and registered as the avascular plant group.

Studies on bryophytes from savannas in other regions of Brazil were carried out mainly in the Northeast, Southeast and Midwest of the country, presenting the richness, composition and floristic similarity in different phytophysiognomies that cover transition areas between the Atlantic Forest and savannas of the Central Brazilian (Cerrado) and the Chapada Diamantina ecoregion with elevations above 900 m (Yano 1994, Bastos et al. 1998, Bôas-Bastos & Bastos 1998, Visnadi & Vital 2001, Visnadi 2004, Câmara et al. 2005, Oliveira et al. 2006, Yano & Peralta 2009, 2011, Santos & Conceição 2010, Valente et al. 2013, Carmo & Peralta 2016, Rios et al. 2016, Carmo et al. 2018). This compilation of data produced knowledge about the species that grow in this type of environment and allowed the assessment and inference of factors that influence the richness and composition of bryophytes in neotropical savannas.

Despite the records of bryophytes in Brazilian savannas, little is known about variations in the richness and composition of the bryophyte flora of different savanna patches in the Amazon, likewise the structure and composition of vascular plants in different savanna physiognomies in the neotropical region. Furthermore, due to deforestation resulting from anthropic activities and human occupation associated with natural fires (Medina & Silva 1990, Barbosa & Campos 2011), Amazonian savannas comprise highly threatened and under-protected areas (Carvalho & Mustin 2017), with landscapes which have been changed over time (Silva & Oliveira 2018).

Although few studies explored the bryophytes of Amazonian savannas, they provided information about the richness and ecological aspects of these plants, pointing out species that are indicators of these ecosystems such as *Acrolejeunea emergens* (Mitt.) Steph., *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn., *Calymperes palisotii* Schwägr., *Cheilolejeunea lobulata* (Lindenb.) C.J.Bastos & Gradst. (previously known as *Cheilolejeunea oncophylla* (Ångstr.) Grolle & M.E. Reiner), *C. rigidula* (Mont.) R.M. Schust., *Lejeunea laetevirens* Nees & Mont. and *Pycnolejeunea contigua* (Nees) Grolle (Ilkiu-Borges & Lisboa 2002, Brito & Ilkiu-Borges 2013, Gomes et al. 2021).

The objective of this study was to evaluate the richness, composition and floristic similarity of the bryophyte flora from five disjunct savanna areas in the eastern Amazon and to compare the richness with those of other savannas in Brazil.

MATERIALS AND METHODS

Study area and data collection

The study areas were distributed in five disjunct savanna areas in the eastern Amazon, close to the mouth of the Amazon River (Figure 1). Information on geographic location, collection periods, types of savanna and dominant plant species in each area are shown in Table I. Savanna formations were characterized as savanna *sensu stricto* and classified as physiognomies of the typical and sparse savanna subtype (Ribeiro & Walter 1998, Costa-Coutinho 2020). Adeney et al. (2016) reclassified this open vegetation as Guianan savannas and Southern Amazonian campo/cerrado, which were not included in his discussion of white-sand ecosystem.

Five sub-areas were established in each savanna for sampling, with 25 collection points in each area, totaling 125 plots. Plot size was 10 m x 10 m, and plots had a minimum distance of 200 m between each other (Moura et al. 2013). The collection was carried out in the whole extension of the plots and in all available substrates including soil, bushes, treelets, trees, decaying wood and termite mounds.

The collection methodology was according to Yano (1989), with a record of the substrate which the specimens were found. The collected material was sun dried or dried in an air-conditioned room. All samples were registered under the collection number of the first author. After identification, the samples were deposited at the João Murça Pires Herbarium (MG) of the Museu Paraense Emílio Goeldi.

Identification, classification and data analysis

Botanical identification was carried out in the Bryophytes laboratory of the Botanical Coordination of the Museu Paraense Emílio

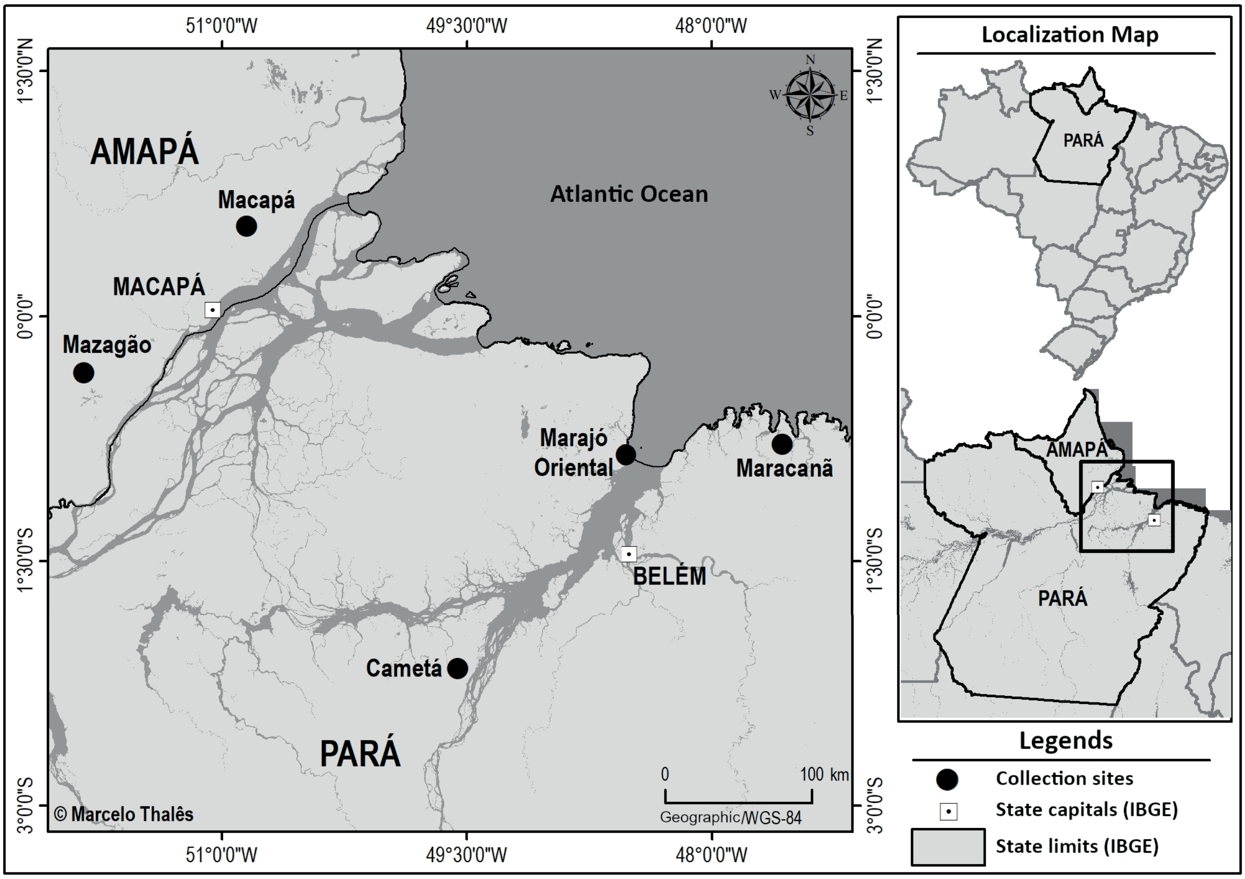

Figure 1. Map indicating the five studied savanna areas in eastern Amazon.

Goeldi, based on the following specialized literature: Frahm (1991), Sharp et al. (1994), Florschütz-De Waard (1986, 1996), Reese (1993), Gradstein (1994), Buck (2003), Gradstein et al. (2001), Gradstein & Costa (2003), Pursell (2007), Gradstein & Ilkiu-Borges (2009). Was performed the taxonomic actualizations followed by Bastos & Gradstein (2020) and Gradstein (2021). The classification adopted for Bryophyta and Marchantiophyta is in agreement with Goffinet et al. (2009) and Crandall-Stotler et al. (2008), respectively.

The classification of the absolute frequency of each species was based on Silva & Pôrto (2007). It was determined by the number of occurrences in the study areas (comprising our complete dataset), defined in five classes: 1 to 5 = rare; 6 to 10 = infrequent; 11 to 20 = assiduous; 21 to 30 = frequent; and > 30 = very frequent. Species were classified according to tolerance guilds into sun specialists, shade specialists and generalists, based on the work of Richards (1984), Gradstein et al. (2001), Gradstein & Costa (2003), Gradstein & Ilkiu-Borges (2009), Tavares-Martins (2009), Visnadi (2013) and Fagundes et al. (2016), and also based on the experience of the authors and discussions about this group of plants, and observations made by Oliveira-da-Silva & Ilkiu-Borges (2018) about unexpected species for dry environments, such as members of Fissidentaceae.

The Brazilian and world geographic distribution of the species was based on the work of Pursell (2007), Costa et al. (2011), Flora do Brasil (2020), Gradstein & Costa (2003), Yano

Table I. Local, geographic coordinates, data colection, physiognomic classification and dominant plant species.

Locality	Geographic coordinates	Data collection	Savanna type	Dominant plant species (in order of importance)
Cametá, Pará state	02°09’46.6”S, 049°33’15.2”W; 02°09’46.0”S, 049°33’55.8”W; 02°09’44.7”S, 049°34’02.9”W; 02°09’36.8”S, 049°33’58.8”W; 02°09’33.6”S, 049°33’50.8”W; 02°09’37.7”S, 049°33’14.0”W; 02°09’28.2”S, 049°32’53.6”W; 02°09’00.7”S, 049°33’08.3”W; 02°08’50.2”S, 049°33’05.3”W; 02°08’52.2”S, 049°33’ 32.1”W.	June 4-7, 2018	Typical	*Byrsonima crassifolia* (L.) Kunth, *Byrsonima coccolobifolia* Kunth, *Curatella americana* L. and *Couepia bracteosa* Benth.
Macapá, Amapá state	00°33’00.0”S, 050°50’57.2”W; 00°33’01.1”S, 050°50’28.5”W; 00°33’08.0”S, 050°50’30.0”W; 00°33’07.5”S, 050°50’58.6”W; 00°32’57.9”S, 050°50’21.5”W; 00°32’47.2”S, 050°50’15.7”W; 00°30’50.8”S, 050°50’54.2”W; 00°30’46.8”S, 050°51’06.1”W; 00°06’44.7”S, 051°07’15.0”W; 00°06’30.4”S, 051°07’12.8”W.	April 28-30, 2018	Typical	*Hancornia speciosa* Gomes and presence of *Myrcia cuprea* (O.Berg) Kiaersk.
Maracanã, Pará state	00°47’05.3”S, 047°33’52.1”W; 00°46’58.4”S, 047°33’39.3”W; 00°47’06.6”S, 047°33’36.4”W; 00°47’04.0”S, 047°33’59.8”W; 00°46’08.2”S, 047°33’06.4”W; 00°46’32.2”S, 047°32’54.4”W; 00°46’21.2”S, 047°33’15.0”W; 00°46’12.7”S, 047°33’37.0”W; 00°45’43.0”S, 047°33’01.4”W; 00°45’55.5”S, 047°32’58.5”W.	March 21-23, 2018	Sparce	*Byrsonima crassifolia*, *Hancornia speciosa* and *Himatanthus articulatus* (Vahl) Woodson
Marajó, Pará state	00°50’59.0”S, 048°31’21.0”W; 00°51’03.6”S, 048°31’15.8”W; 00°54’20.3”S, 048°40’29.6”W; 00°54’19.4”S, 048°40’49.0”W; 00°51’06.0”S, 048°31’45.0”W; 00°51’17.5”S, 048°32’20.2”W; 00°54’58.1”S, 048°39’48.1”W; 00°55’17.7”S, 048°39’51.8”W; 00°54’32.3”S, 048°40’06.9”W; 00°54’46.1”S, 048°40’04.5”W.	September 19-21, 2017 and December 11-13, 2017	Typical	*Curatella americana*, *Byrsonima crassifolia*, *Hancornia speciosa*, presence of *Himatanthus articulatus*, *Byrsonima chrysophylla* Kunth and palms
Mazagão, Amapá state	00°20’43.8”S, 051°50’47.7”W; 00°20’39.3”S, 051°50’32.9”W; 00°20’31.4”S, 051°52’00”W; 00°20’31.6”S, 051°52’ 21.7”W; 00°20’35.1”S, 051°53’17.7”W; 00°20’21.5”S, 051°53’34.9”W; 00°19’58.4”S, 051°54’ 17.8”W; 00°20’09.1”S, 051°54’18.6”W; 00°19’51.9”S, 051°55’52.7”W; 00°20’07.1”S, 051°56’10.4”W.	October 22-24, 2017	Typical	*Byrsonima coccolobifolia*, *B. crassifolia*, *Curatella americana* and *Himatanthus articulatus*

(2011) and Oliveira-da-Silva & Ilkiu-Borges (2020).

One-way Analysis of Variance (ANOVA) was performed to compare the richness of bryophytes and a quantidade de mosses and liverworts between the areas (Armstrong & Hilton 2010). A presence–absence matrix was created for the species recorded in the 25 sub-areas and similarity was calculated to evaluate floristic differences using the Jaccard coefficient, followed by a cluster analysis using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA). The ANOVA analysis was performed using the car package (Fox & Weisberg 2019) and the ordination analysis was performed using the vegan package (Oksanen et al. 2019). All statistical analyses were performed in the R Software (R Development Core Team 2019).

For comparisons with other savannas in Brazil in terms of species richness, a bibliographic survey of research studies that included mosses and liverworts in these ecosystems was carried out (Table II).

RESULTS AND DISCUSSION

The sampling generated 613 records in this study, in which 44 species were identified being 22 mosses (12 genera, 7 families) and 22 liverworts (14 genera, 3 families) (Table III). Lejeuneaceae (18 spp./511 specimens), Calymperaceae (7 spp./383 specimens), Sematophyllaceae (5

Table II. Comparison of the richness of savannas in the eastern Amazon with savannas in Brazil.

Brazilian region of the studied area in the publication	Publication	Studied ecosystems	No. of species	No. of species shared with this study
Northeast	Yano 1994	Savanna physiognomies	29	2
	Bastos et al. 1998	Savanna physiognomies	31	3
	Bôas-Bastos & Bastos 1998	Savanna *sensu lato*	27	9
	Santos & Conceição 2010	Savanna *sensu lato*	23	6
	Valente et al. 2013	Savanna physiognomies	400	20
Central western	Câmara et al. 2005	Savanna *sensu lato*	176	13
	Oliveira et al. 2006	Savanna *sensu lato*	65	10
	Rios et al. 2016	Savanna physiognomies	37	5
Southeast	Visnadi & Vital 2001	Savanna *sensu lato*	94	15
	Visnadi 2004	Savanna physiognomies	92	13
	Yano & Peralta 2009	Savanna physiognomies	38	5
	Yano & Peralta 2011	Savanna physiognomies	114	9
	Carmo & Peralta 2016	Savanna physiognomies	289	21
	Carmo et al. 2018	Savanna physiognomies	439	23
North	Gomes et al. 2021	Savanna park	41	21

spp./30 specimens) and Fissidentaceae (5 spp./16 specimens) represented 79.54% of the richness. These families are on the list of the 15 that hold 90% of the richness generally found in tropical regions (Gradstein & Pócs 1989, Gradstein et al. 2001). Lejeuneaceae and Fissidentaceae are among the most diverse families and are responsible for 15% of the number of species reported in Brazil and 54% in savannas of the Central Brazilian (Costa & Luizi-Ponzo 2010).

Lejeuneaceae presented 12 genera, with *Cheilolejeunea* being the most represented. This family had the greater number of species, confirming its importance and abundance in the neotropical region (Gradstein et al. 2001). Lejeuneaceae is the most important family in terms of diversity and endemism among liverworts and plays a relevant taxonomic and ecological role in the areas where it occurs (Gradstein 1994, Gradstein et al. 2001, Zartman & Ilkiu-Borges 2007), standing out as a major determinant of richness and composition, and as predominant among liverworts in inventories in the tropics, both in forest and open vegetation (Mota de Oliveira & ter Steege 2013, Silva & Pôrto 2013, Pantoja et al. 2015, Cerqueira et al. 2017, Oliveira-da-Silva & Ilkiu-Borges 2018, Sierra et al. 2018).

Twenty-six species were considered locally rare, three infrequent, four assiduous, three frequent, and eight very frequent (Table III). Rare species totaled 48 specimens, while frequent and very frequent species totaled 960 occurrences. Despite the fact that diverse phytophysiognomies are present within the limits of tropical forests, the bryophytes occurring in them were observed with similar frequency patterns, where many species (26 in this study) are represented by few individuals and few species (11 in this study) by many individuals. Similar proportions were observed in research with bryophytes from flooded (*Várzea*) and non-flooded (*Terra Firme*) forests (Moura et al. 2013, Macedo & Ilkiu-Borges 2014, Fagundes et al. 2016) or with tree communities, as shown by Carim et al. (2007) who reported that 10 of the 154 species accounted for 44% of the individuals, and Silva et al. (2011) who reported that 10 of 264 species corresponded to 36.5% of the total of individuals.

The most colonized substrates were living tree trunks (87.18%), followed by soil (5.50%), termite mounds (4.22%), decomposing trunks (2.65%), and rocks (0.45%). Due to greater availability and capacity of retaining moisture, living tree trunks are the substrates most used by bryophytes (Pócs 1982, Richards 1984). *Byrsonima crassifolia, Curatella americana*, *Himatanthus articulatus, Byrsonima coccolobifolia* and *Hancornia speciosa* held 49.54% of the collected specimens (Figure 2), indicating the importance of these plant species for the bryophyte flora of Amazonian savannas.

Richness and composition of bryophytes in disjunct savannas in the eastern Amazon

Higher richness (24 spp.) was registered in the savanna of Marajó, followed by Macapá (19 spp.), Cametá (18 spp.), Maracanã (16 spp.) and Mazagão (14 spp.). As expected, the richness and composition of bryophytes in these enclaves were lower than those of forest areas in the Amazon (Gradstein 2006, Moura et al. 2013, Macedo & Ilkiu-Borges 2014, Tavares-Martins et al. 2014, Mota de Oliveira & ter Steege 2015, Fagundes et al. 2016, Campos et al. 2019). Due to their biology, bryophytes are finely tuned with environmental conditions, mainly due to their need for water supply (Bates 1998, Proctor & Tuba 2002, Glime 2017a, b). Regarding this relationship with the environment, tropical forests exhibit a greater variety of microhabitats favorable to the establishment of a rich bryophyte flora (Pócs 1982). In turn, savannas have physiognomies of

Table III. Richness and composition of bryophytes from savannas in the eastern Amazon.

Family/Species	Total	CMT				MCP				MRCN			MRJ			MZG				D	Guilds	Voucher
		LT	T	S	DT	LT	T	S	DT	LT	T	S	LT	T	DT	LT	T	R	S			
Bryaceae																						
Bryum coronatum Schwägr.**	21					2		5		3	1	4	1	1		1	2		1	W	gen	LPC Macedo 1534, 1677
Calymperaceae																						
Calymperes erosum Müll. Hal.	5					2			1				1			1				P	gen	LPC Macedo 1500, 1654
Calymperes palisotii Schwägr.	150	3				20			2	82	1		41			1				W	gen	LPC Macedo 1537, 1650
Calymperes rubiginosum (Mitt.) Reese	5												3		2					A	gen	LPC Macedo 1782, 1783
Octoblepharum albidum Hedw.	211	28	1		1	31		2	1	21			98	1	1	21	4		1	N	gen	LPC Macedo 1497, 1507
Syrrhopodon africanus subsp. *graminicola* (R.S. Williams) W.D. Reese	1	1																		N	sun	LPC Macedo 2110
Syrrhopodon ligulatus Mont.	10	2											4			4				N	gen	LPC Macedo 1571, 1819
Syrrhopodon parasiticus (Brid.) Besch.	1	1																		P	sun	LPC Macedo 2113
Dicranaceae																						
Dicranella hilariana (Mont.) Mitt.	2							1						1						N	sun	LPC Macedo 1736, 1815
Fissidentaceae																						
Fissidens bryoides Hedw.*	2		1		1															W	gen	LPC Macedo 2141, 2157
Fissidens guianensis Mont.	1													1						N	gen	LPC Macedo 1934
Fissidens hornschuchii Mont.	1		1																	N	gen	LPC Macedo 2103
Fissidens submarginatus Bruch	11		2			1	2	2					1	3						N	gen	LPC Macedo 1732, 2125
Fissidens zollingerii Mont.	1											1								P	gen	LPC Macedo 1996
Leucobryaceae																						
Campylopus savannarum (Müll. Hal.) Mitt.	1		1																	P	sun	LPC Macedo 2174
Campylopus surinamensis Müll. Hal.**	75	2	3	8				6		1		1				3	20	5	26	N	sun	LPC Macedo 1639, 1497
Leucomiaceae																						
Leucomium strumosum (Hornsch.) Mitt.	1											1								P	sun	LPC Macedo 2006
Sematophyllaceae																						
Brittonodoxa subpinnata (Brid.) W.R.Buck et al.	1															1				P	gen	LPC Macedo 1602

Table III. Continuation.

Microcalpe subsimplex (Hedw.) W.R.Buck	26									3			21		1	1				N	gen	LPC Macedo 1494
Trichosteleum papillosum (Hornsch.) A.Jaeger	1				1															N	gen	LPC Macedo 2141
Trichosteleum subdemissum (Besch.) A.Jaeger	1					1														P	gen	LPC Macedo 1623
Vitalia cuspidifera (Mitt.) P.E.A.S.Câmara et al.	1												1							N	gen	LPC Macedo 1807
Frullaniaceae																						
Frullania gibbosa Nees	1					1														N	sun	LPC Macedo 1717
Frullania subtilissima (Mont.) Lindenb.	32					10				18			1			3				N	sun	LPC Macedo 1640, 1989
Frullania vitalii Yuzawa & S. Hatt.***	18	2				15			1											N	sun	LPC Macedo 1672, 1686
Lejeuneaceae																						
Acrolejeunea emergens (Mitt.) Steph.**	2					1				1										P	sun	LPC Macedo 1723, 2087
Acrolejeunea torulosa (Lehm. & Lindenb.) Schiffn.**	190	30				42			4	4			70		5	35				N	sun	LPC Macedo 2098, 1491
Archilejeunea fucescens (Lehm.) Fulford	4	3											1							N	gen	LPC Macedo 1938, 2154
Cheilolejeunea acutangula (Nees) Grolle	1												1							W	gen	LPC Macedo 1869
Cheilolejeunea lobulata (Lindenb.) C.J.Bastos & Gradst.	106	3				17			1	48			25		4	8				N	gen	LPC Macedo 2100, 1504
Cheilolejeunea rigidula (Mont.) R.M. Schust.	10	2				2			1				5							AA	gen	LPC Macedo 1642, 2154
Cheilolejeunea savannae L.P.C.Macedo et al. ****	41									24						17				-	gen	LPC Macedo 1600, 2028
Cololejeunea cardiocarpa (Mont.) A.Evans	1												1							P	gen	LPC Macedo 1818
Cololejeunea surinamensis Tixier	1												1							SA	gen	LPC Macedo 1890
Drepanolejeunea fragilis L. Söderstr.	3									2			1							N	sun	LPC Macedo 2030, 2083
Lejeunea controversa Gottsche	1												1							N	gen	LPC Macedo 1899
Lejeunea laetevirens Nees & Mont.	3												3							N	gen	LPC Macedo 1898, 1899
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	1									1										N	gen	LPC Macedo 2091
Metalejeunea cucullata (Reinw. et al.) Grolle	9	9																		P	gen	LPC Macedo 2124, 2127
Microlejeunea epiphylla Bischl.	81					8				69			4							N	sun	LPC Macedo 1959, 1965

Table III. Continuation.

Myriocoleopsis minutissima R.L.Zhu, Y.Yu & Pócs subsp. *minutissima* **	27					25			1							1				P	sun	LPC Macedo 1525, 1611
Pycnolejeunea contigua (Nees) Grolle	12	2								1			7			2				P	sun	LPC Macedo 2109, 2159
Thysananthus innovans (Spruce) Sukkharak & Gradst.	18					17			1											N	sun	LPC Macedo 1640, 1646
Lepidoziaceae																						
Protocephalozia sp.	1							1													-	LPC Macedo 1639
Total	1092	88	9	8	3	195	2	17	13	278	2	7	292	7	13	99	26	5	28			

CMT - Cametá; MCP - Macapá; MRCN - Maracanã; MRJ - Marajó; MZG - Mazagão; LT - live trunk; T - termites; S - soil; DT - dead trunk; R - Rock; * new records to Pará state; ** news records to Amapá state; * new reference to northern region; **** new species; W - Wide; P - Pantropical; N - Neotropical; A - America; AA - African- American; SA - South American.**

open vegetation, more exposed to radiation and with little availability of microhabitats, which contribute to lower richness of species.

As expected, there were no significant differences in the richness between the studied areas (p-value = 0.519, F-value = 0.834) but it is striking the lack of significant differences between the number of mosses (p-value = 0.449, F-value = 0.964) and liverworts (p-value = 0.358, F-value = 1.16) as well. At local and regional scales, species richness and diversity are determined by dispersion associated with biotic factors, such as species attributes, and abiotic factors, such as climate and environmental conditions (Hillebrand & Blenckner 2002, Ricklefs & Fangliang 2016). Therefore, the high dispersion capacity (Heinrichs et al. 2009) coupled with environmental conditions and characteristics of the species (Pócs 1982, Bates 1998, Glime 2017a) may be the regulating factors of bryophyte richness in Amazonian savannas. Also, areas that exhibit more similar environmental parameters may have similar proportions of richness.

Although there were no differences in the richness and in the number of mosses and liverworts among the areas (confirmed by the ANOVA), differences in the composition were noticed (Tables III and IV). Macapá presented the largest number of families (nine) and Mazagão the smallest (six), while Marajó had the largest number of genera (Table IV). The savannas of Cametá and Marajó presented a greater number of mosses, but regarding the proportion between mosses and liverworts in the areas, mosses prevailed only in Cametá and Mazagão (Table IV). On the other hand, liverworts occurred in greater numbers in the savannas of Marajó, Macapá and Maracanã, where they also predominated over mosses considering each area separately.

As mentioned, bryophytes are strongly responsive to environmental conditions, especially due to water requirements (Bates 1998, Proctor & Tuba 2002, Glime 2017a, b). Although mosses are generally better represented in xeromorphic ecosystems (Bastos et al. 2000, Visnadi 2004, Oliveira-da-Silva & Ilkiu-Borges 2018), in the present study, savannas with areas hosting slightly denser vegetation such as Marajó, Macapá and Maracanã provided microclimatic conditions (higher humidity and lower light incidence) that favored the predominance of liverworts.

In areas where liverworts occur in greater number, the influence of the surrounding forest matrix, where they are predominant, should also be taken into account (Gradstein et al. 2001). This was confirmed by the fact that liverworts that

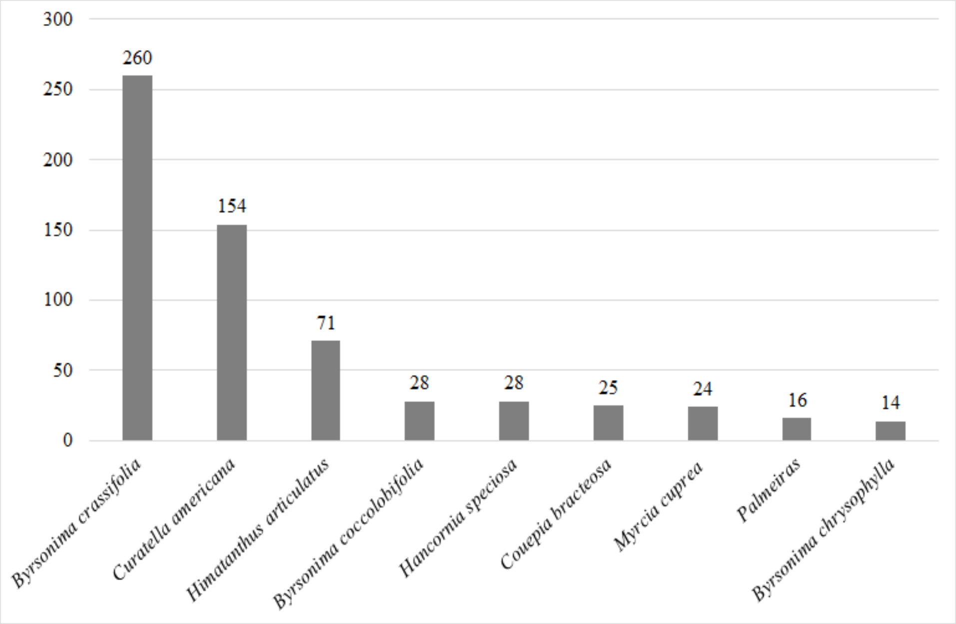

Figure 2. **Graphic illustrating the number of specimens on main phorophytes in the studied savannas in eastern Amazon.**

occurred exclusively in savannas in Marajó and Macapá were seen to occur in forest areas in the Amazon (Moura et al. 2013, Tavares-Martins et al. 2014, Flora do Brasil 2020), and in ecosystems adjacent to or close to these areas (Ilkiu-Borges & Lisboa 2002, Oliveira-da-Silva & Ilkiu-Borges 2020). Thus, in addition to environmental factors and characteristics of the bryophyte species, the forest matrix can be identified as an important agent influencing the richness and composition of the bryophyte flora of Amazonian savannas.

Vascular plants reported in savannas in Brazil have also been found in forests adjacent to these ecosystems (Gottsberger & Morawetz 1986, Balduino et al. 2005, Pinheiro & Monteiro 2006, Pinheiro & Durigan 2012). Méio et al. (2003) corroborated the contribution of the Atlantic and Amazonian floras to the vegetation of the Cerrado biome, and Pinheiro & Monteiro (2006) observed that gallery forests could act as access paths for generalist species of forest origin registered in a small area composed of savannas and other types of forests.

Although Cametá had fewer species in relation to Macapá, Maracanã and Marajó, it shared an approximate number of exclusive species with Marajó, and presented a greater number of exclusive species in relation to Macapá and Maracanã (Tables III and IV). However, the species reported as exclusive to savannas of the eastern Amazon can be found in ecosystems such as Caatinga, Canga, coastal areas, savannas and forests in Brazil (Sharp et al. 1994, Bastos et al. 1998, Gradstein & Costa 2003, Visnadi 2004, Costa et al. 2006, Lisboa et al. 2006, Yano & Peralta 2006, 2009, Oliveira-da-Silva & Ilkiu-Borges 2018, 2020, Moura et al. 2013, Macedo & Ilkiu-Borges 2014, Tavares-Martins et al. 2014, Fagundes et al. 2016).

Acrolejeunea torulosa, *Cheilolejeunea lobulata*, *Calymperes palisotii* and *Octoblepharum albidum* occurred in all areas. These species are commonly found in xeromorphic vegetation (Castro et al. 2002, Visnadi 2004, Lisboa et al. 2006, Ilkiu-Borges et al. 2009, Valente et al. 2013, Carmo et al. 2018, Oliveira-da-Silva & Ilkiu-Borges 2018). As these species are generalists, they are therefore often found in forests and wetlands in the Amazonian region (Santos & Lisboa 2003, Brito & Ilkiu-Borges 2013, Mota de Oliveita & ter Steege 2013, Moura et al. 2013, Macedo & Ilkiu-Borges 2014,

Table IV. Richness and differences in floristic composition between areas.

	CMT	MCP	MRCN	MRJ	MZG
Number of species	18	19	16	24	14
Number of families	7	9	8	7	6
Number of genera	13	14	14	17	12
Number of mosses	11	8	7	11	8
Number of liverworts	7	11	9	13	6
Number of exclusive species	7	4	3	8	1

CMT - Cametá; MCP - Macapá; MRCN - Maracanã; MRJ - Marajó; MZG – Mazagão.

Tavares-Martins et al. 2014, Fagundes et al. 2016, Sierra et al. 2018).

Despite the lack of significant differences in richness and in the number of mosses and liverworts between areas (Tables III and IV), the composition and the number of exclusive species distributed between areas (23 spp., 52.27% of the richness, Tables III and IV) indicated that the savannas of the eastern Amazon are home to different bryophyte communities, formed by taxa that present a wide distribution and can be found either in forests or in savanna environments in Brazil.

Similarity between disjunct savannas of the eastern Amazon

There were clear floristic differences, with formation of clusters for each area, although two clusters included different areas (Figure 3). The similarity of the sub-area MRJ_3 (Marajó) with Maracanã areas may be due to the sharing of five species between MRJ_3 and MRCN_3. In turn, the Marajó cluster may have been explained by the large number of locally rare species among the sub-areas and few species shared with the other savannas. Moreover, savannas which were closer to each other in terms of geographical location and had more similar environmental conditions, which was the case of Marajó and Macapá, were related in the cluster (Figure 3).

Varied clustering patterns have been observed in different savanna physiognomies in Brazil, influenced by the presence or absence of mosses and liverworts in the studied areas (Visnadi 2004, Rios et al. 2016). However, Valente et al. (2013) found that the groups formed in different physiognomies reflected the environmental conditions of each area. As for the savannas of the eastern Amazon with similar physiognomies, probably the different communities formed are the result of environmental characteristics and colonizing species, as well as of the influence of forests close to each area.

While assessing the floristic similarity of vascular plants in Brazilian savannas, Ratter et al. (2003) observed eight phytogeographic patterns in the distribution of these ecosystems, including the disjunct areas of the Amazon, which formed a very distinct and separate group from the other formed in the country. Considering the mosaic of Amazonian phytophysiognomies, it can be inferred that the savannas of the Amazon exhibit different communities of bryophytes related to their area of distribution.

Although Amazonian savannas had different bryophyte floras, the similarities between areas were low, even between geographically closer plots, except for MZG_4 and MZG_5, and MRCN_1 and MRCN_2. Valente et al. (2017) also reported low similarity between clusters formed by

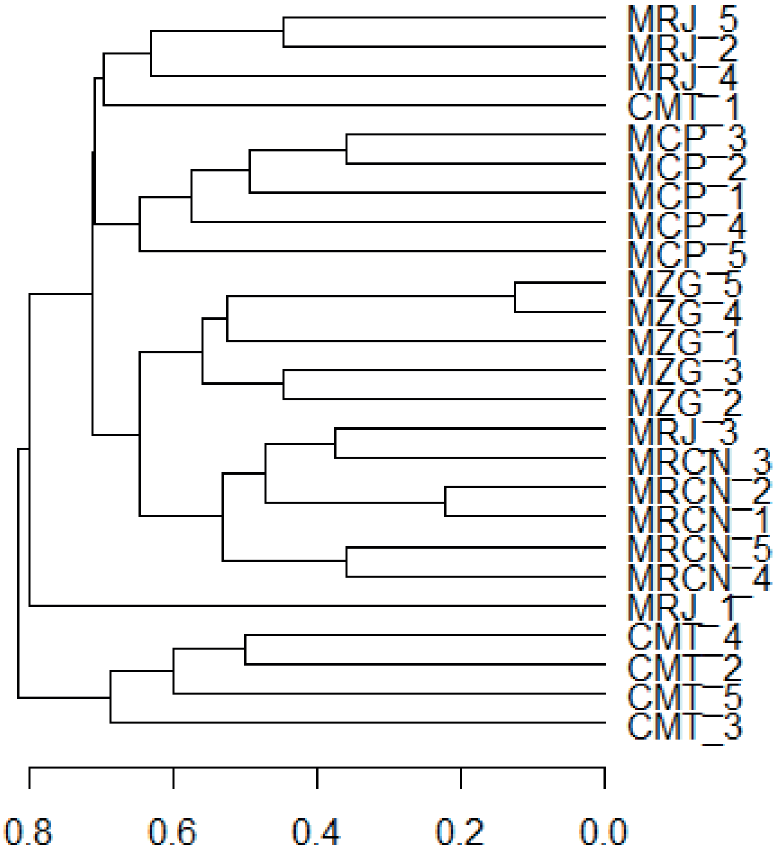

Figure 3. **Floristic similarity between the collection points in the studied savanna areas in eastern Amazon. Cophenetic correlation coefficient: 0.78.**

exposed areas in rupestrian fields, even between those that included geographically close areas. According to the latter authors, the low degree of similarity observed probably reflected differences in habitat, relief, quantity and size of rock blocks, presence and size of cracks, proportion of exposed rock, and exposure to wind. In the case of the savannas in this study, the low similarity was the result of the different composition of the areas and local influences, and also of matrices of adjacent forests or other types of vegetation.

Difference in richness between savannas of Brazil

The savannas of the eastern Amazon showed low to high richness when compared to those in other studies on mosses and liverworts from savanna ecosystems in Brazil (Table II). This difference may be due to the coverage of different types of physiognomies and savanna formations, the heterogeneity of environments, and the phytogeographic distribution of taxa and it is extremely sensitive to sampling effort, meaning that in some cases the apparent difference in richness is not real, but the consequence of collection methodology or lack of collection. Only *Cololejeunea surinamensis* Tixier and *Myriocoleopsis minutissima R.L.Zhu, Y.Yu & Pócs subsp. minutissima* were not common to other areas, but have already been collected in these ecosystems (Flora do Brasil 2020).

The richness and composition of vascular plants in disjunct savannas in the Amazon region are also low in contrast to other savannas in Brazil (Ratter et al. 2003, Barbosa et al. 2005, 2007). However, in addition to adapting to fire, other factors, such as edaphic conditions, altitude, climate, and seasonality contribute to the formation and structuring of these plants in these types of environments (Eiten 1972, Ratter et al. 2003, Oliveira et al. 2005, Silva & Batalha 2010, Melo Júnior et al. 2012, Pausas 2015, Massi & Franco 2016, Souchie et al. 2017).

The richness and composition of bryophyte communities in Amazonian savannas are possibly the result of geographical location, micro-environmental conditions and local and regional influences such as the bordering position in relation to other types of vegetation, which are abiotic and biotic factors that may be tested in the future. Additionally, fire-related events reduce and modify the landscape of this vegetation (Frost et al. 1986, Medina & Silva 1990, Barbosa & Campos 2011, Silva & Oliveira 2018), and may consequently decrease the richness and composition of bryophytes in these enclaves of savannas in the Amazon.

Environmental conditions related to fires, functional groups and new records

During field work, traces of fires, a common characteristic of this ecosystem, were observed in the studied areas. This was done because (natural or anthropogenic) fire is an important determining agent in savanna formations (Medina & Silva 1990, Lehmann et al. 2014). There is no information about the periods in which fires occur in the studied areas, but *Octoblepharum albidum* was collected on carbonized bark in Maracanã and Cametá. Bryophytes produce resilient, long-lived spores, highly resistant to intense light incidence, which can germinate after long dormant periods (Glime 2017c). These characteristics may justify the development of *Octoblepharum albidum* after a period of fire. Furthermore, the development of sporophytes of *Octoblepharum albidum* occurs both during the rainy and the dry season, when the spores were dispersed (Pôrto & Oliveira 2002), indicating that it is not affected by the intensity of rainfall.

Bryophytes can survive after low-intensity fires (Johnson 2007) and species may have different dynamics of colonization of forests affected by fires (De Las Heras et al. 1994). Oliveira-da-Silva & Ilkiu-Borges 2018) recorded *Campylopus savannarum* sprouting from the remains of carbonized tufts on iron rock exposed in a Canga area that suffered a fire in Serra do Carajás.

Twenty-seven species registered in this study were generalists and 16 were sun specialists (Table III). Based on the literature used on geographic distribution, and because they were recorded in savannas, seven taxa previously classified as shade specialists were determined as generalists in this study: *Calymperes rubiginosum, Fissidens bryoides, Fissidens guianensis, Syrrhopodon ligulatus, Trichosteleum subdemissum, Cololejeunea surinamensis* and *Lejeunea controversa* (Gradstein & Ilkiu-Borges 2009, Tavares-Martins 2009, Alvarenga et al. 2010, Fagundes et al. 2016).

Bryophytes are generally related to the phytophysiognomy and the region in which they are occurring, but some species may show preferences for a given habitat or environmental gradient (Cornelissen & ter Steege 1989, Gradstein & Costa 2003, Gradstein 2006, Gradstein & Ilkiu-Borges 2009, Mota de Oliveira & ter Steege 2015, Glime 2019). However, species such as *Fissidens guianensis* and *Lejeunea controversa* were observed growing in broader conditions, varying from humid tropical forest (Buck 2003, Gradstein & Ilkiu-Borges 2009) to an open and dry Canga vegetation (Oliveira-da-Silva & Ilkiu-Borges 2018). The latter vegetation type shares similar xeric condition with Amazonian savanna.

Bryophytes present adaptive structures related to the acquisition and retention of water, tolerance to light and resistance against desiccation (Bates 1998, Glime 2017d), which allow them to colonize different environmental conditions and support wide ranges of microclimate variations, showing their evolutionary success. Additionally, generalist species can be found in a wide variety of environments, while sun specialists form an ecological group generally restricted to tree canopies or occurring in open forests (Cornelissen & ter Steege 1989, Gradstein & Costa 2003). In the studied areas, the guild of sun specialists results from the type of ecosystem or from the dispersion from the forest matrix canopy to the understory of the savanna areas. The presence of *Frullania subtilissima,* reported in forest canopies (Cornelissen & Steege 1989, Silva & Pôrto 2013), is an example of this process of dispersion and colonization.

The species *Fissidens bryoides* is a new record for the state of Pará, *Bryum coronatum,* and *Campylopus surinamensis, Acrolejeunea emergens, A. torulosa* and *Myriocoleopsis minutissima* ssp. *minutissima* are new records for the state of Amapá. *Frullania vitalii* is reported for the first time for the North region and *Cheilolejeunea savannae* collected in the Mazagão and Maracanã savannas was recently described (Macedo et al. 2020).

The registered bryophyte flora is composed of widely distributed and typical species of xeric ecosystems, such as the studied savannas. Both the composition and the richness found in the study were expected considering that open vegetation areas present a small variety of microhabitats, which contribute to greater richness and diversity of these plants (Gradstein & Pócs 1989, Gradstein 1995). The formed communities present a floristic composition possibly related to local factors and influences of the phytophysiognomic sets present in the Amazonian environment in which each savanna is inserted.

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