Anais da Academia Brasileira de Ciências (2017) 89(3 Suppl.): 2371-2382
(Annals of the Brazilian Academy of Sciences)
Printed version ISSN 0001-3765 / Online version ISSN 1678-2690
http://dx.doi.org/10.1590/0001-3765201720160860
www.scielo.br/aabc | www.fb.com/aabcjournal

Species richness and composition of epiphytic bryophytes in flooded forests of Caxiuanã National Forest, Eastern Amazon, Brazil

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Manuscript received on December 12, 2016; accepted for publication on June 29, 2017

ABSTRACT

This study aimed to compare the richness and composition of the epiphytic bryoflora between *várzea* and *igapó* forests in Caxiuanã National Forest, Brazilian Amazon. Bryophytes were collected on 502 phorophytes of *Virola surinamensis*. Average richness per phorophyte and composition between forests and between dry and rainy periods was tested by two-way analysis and by cluster analysis, respectively. In total, 54 species of 13 families were identified. Richness was greater in *igapó* forest (44 species) compared to *várzea* forest (38 species). There was no significant difference in the number of species between the studied periods. Cluster analysis showed the bryoflora composition was different between *várzea* and *igapó*, but not between dry and rainy periods. Results did not corroborate the hypothesis that *várzea* forests harbor higher species richness than *igapó* forests.

Key words: Floristics, liverworts, mosses, seasonality.

INTRODUCTION

Tropical rainforests are rich in epiphyte bryophytes due to high humidity levels (Richards 1954, 1984, Uniyal 1999, Germano and Pôrto 1998, Valente and Pôrto 2006, Santos and Costa 2008). One of the intrinsic characteristics of the Amazonian climate is the wide variation in its rainfall regime (Souza et al. 2009). In Amazonia, the richness of plant species, including epiphytes, is strongly correlated with absolute annual rainfall (Gentry 1988). The precipitation is one of the factors defining the floods in forests by white, black or light water rivers, called *várzeas* and *igapós*, both being representative in the Amazon biome (Prance 1979, Junk and Piedade 2005, Wittmann et al. 2006, Melack and Hess 2010, Junk et al. 2011).

Várzea forests are located on river margins and have Andean and pre-Andean origin, being associated with white water rivers, rich in nutrients with high concentration of sediments and dissolved minerals, as well as pH close to neutral. *Igapó* forests are also found on river banks, but have their origin from erosive resistant shields of Guiana and Central Brazil, being associated with black or light water rivers, poor in nutrients, with high amount of dilute organic matter, especially humic and fulvic acids, and an acid pH (Junk and Furch 1980).

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Floristic and ecological studies in Amazonian floodable forests have mainly focused on trees (including palms) and lianas (Jardim and Vieira 2001, Wittmann et al. 2002, 2006, Carim et al. 2008, Ferreira et al. 2010, 2013, Lau and Jardim 2013, Montero et al. 2014), and vascular epiphytes (Quaresma and Jardim 2013, Medeiros et al. 2014, Travassos et al. 2014). Although floristic studies on non-vascular epiphytes of floodable forests in the Brazilian Amazon have already been performed by means of inventories (Lisboa et al. 1999, Ilkiu-Borges and Lisboa 2002, Moura et al. 2013) or comparative studies between vegetation formations (Ilkiu-Borges and Lisboa 2002, Santos and Lisboa 2003, Moraes 2006, Alvarenga and Lisboa 2009), studies comparing bryophyte richness and species composition among *várzea* and *igapó* forests are nonexistent.

Species richness from *várzea* and *igapó* forests varies depending on the organisms and/or region. Studies on arboreous groups and ferns in the two types of forests showed greater species richness in *várzea* forests, either in Central or Eastern Amazonia (Haugaasen and Peres 2006, Montero et al. 2014, Travassos et al. 2014). Opposite results, however, were found in Caxiuanã National Forest, where *Virola surinamensis* (Rol. ex Rottb.) Warb. (Myristicaceae), among other species, was reported as a common and frequent tree in both forest types (Ferreira et al. 2005, 2013).

Differences between plant groups in these two types of floodable forests are expected, since they are highly dynamic environments, with different geological ages and submitted to different nutrient regimes, as well as differences in luminosity and humidity (Junk et al. 2011, Ferreira et al. 2013). Variations in precipitation directly influence the moisture levels, which, in turn, support the development and reproduction of bryophytes, as they are plants with reproductive cycles dependent on the presence of water (Gentry 1988, Lisboa 1993).

The aim of this study was to compare the richness and species composition of epiphytic bryophytes on phorophytes of *Virola surinamensis* in floodable forests of Caxiuanã National Forest in two periods of precipitation (dry and rainy periods). Floristic and ecological knowledge of the bryophytes in these forests are essential in order to include it in the conservation strategies and management of the Amazonian biodiversity.

MATERIALS AND METHODS

Study area – Caxiuanã National Forest is located in the interfluve Xingu and Tocantins rivers, state of Pará, in the municipalities of Portel and Melgaço (01°42’30”S and 51°31’45”W; 62 m above sea-level). The annual average air temperature is 25.7 ± 0.8°C, the annual average relative air humidity is 82.3%. According to the Köppen climate classification, the climate is “Am” tropical wet climate and climate subtype with a short dry season (Oliveira et al. 2008). Precipitation from July 2013 to June 2014 in the Caxiuanã National Forest ranged from 65.3 to 324.11 mm, respectively (source: Projeto Estudo da Seca na Floresta - ESECAFLOR).

The Caxiuanã National Forest is predominantly composed by dense ombrophilous lowland forests or upland forests (85%), alluvial dense ombrophilous lowland forests or *igapó* and *várzea* forests (10%), enclaves of grassland, scrub vegetation, and patches of secondary vegetation resulting from human actions (Almeida et al. 2003).

Várzea forests in the Caxiuanã National Forest are seasonally flooded by annual and daily tidal fluctuations of main and small rivers and especially by the Caxiuanã Bay. Forest canopy is open and the understory is characterized by the presence, in natural regeneration, of individuals of arboreous species (Ferreira et al. 2013). The forests located near the Caxiuanã Bay are flooded by rivers with higher load of sediments and the soils are classified as Plinthosols, mineral soils formed under conditions of restriction of water percolation, submitted to the temporary effect of excess moisture. They are poorly drained and with greater proportion of nutrients (Piccini and Ruivo 2012).

Igapó forests are seasonally flooded by annual fluctuation of rivers and igarapés of black water and also by daily tidal flooding. This vegetation is characterized by having more closed canopy and dense vegetation in understory, with abundance of the herbaceous species *Diplasia karatifolia* Rich. and *Calyptrocarya glomerulata* (Brongn.) Urb., belonging to the family Cyperaceae, as well as representatives of Rapateaceae and Araceae (Ferreira et al. 2013, C.C. Souza et al., unpublished data). Soils are classified as Gleysols, presenting silty texture, with conditions of poor drainage and excessive regime of permanent or periodic moisture. They are poor in nutrients and with high fragility (Piccini and Ruivo 2012).

Data collection and identification - Collections were made on bark of *Virola surinamensis* (Rol.) Warb. located within the PELD plots (Pesquisas Ecológicas de Longa Duração - two plots in each forest) and surrounding areas in *igapó* (247 trees) and *várzea* (255 trees). *Virola surinamensis* was chosen due to its high density in both types of forest (Ferreira et al. 2005, 2013, C.C. Souza et al., unpublished data).

Sampling took place in two different periods, covering periods with lower and higher precipitation rates. Excursions occurred in July, September and November 2013 (precipitation of 65.3 mm, 35.1 mm and 119 mm, respectively) and in February, April and June 2014 (440 mm, 344 mm and 324 mm, respectively) (Table I).

Bryophyte samples were taken from phorophyte trunks in a standardized manner, using dimensions of 20 x 20 cm, as suggested by Frahm (2003), measured with a polystyrene frame.

Only phorophytes with diameter at breast height (DBH) above 20 cm were selected for sampling, which was always accomplished at a height of 1.30 m from the ground and face east. Sampling was performed independently, so new phorophytes were used in every collection, excluding the possibility of repetition of bryophyte collections on the same phorophyte.

Botanical material was identified with aid of keys in specialized literature, such as Gradstein and Costa (2003) and Gradstein and Ilkiu-Borges (2009). Adopted taxonomic classifications are in accordance with Goffinet et al. (2009) for Bryophyta and Crandall-Stotler et al. (2009) for Marchantiophyta. Botanical reference material was incorporated in the João Murça Pires Herbarium (MG) of the Museu Paraense Emílio Goeldi, and part of the material was donated to the Herbarium Rondoniensis of the Universidade Federal de Rondônia (UFRO).

Data Analysis - Based on the species occurrence number (Silva and Pôrto 2007, Pantoja et al. 2015) the absolute and relative frequencies of bryophytes were calculated for the two forest types. Comparison of the number of bryophyte species per phorophyte (dependent variable) in relation to forest type and the periods of lowest and highest

TABLE I
Number of collections per forest type and dry and rainy periods.

2013/2014	July	September	November	February	April	June	Sample
Várzea forest	44	50	44	45	36	36	255
Igapó forest	42	49	40	43	38	35	247
Period	**Lower precipitation (drought)**			**Higher precipitation (rain)**			**502**

precipitation (factors) was tested using a two-factor analysis of variance model, and the normality of the dependent variable was determined by the Shapiro-Wilk test (Zar 2010).

To verify the differences in the species composition between forest types and periods of lower and higher precipitation, a multivariate analysis of ordering (NMDS) was used, using the Sorensen similarity index and as a connecting measure the nearest neighbor (PC-ORD 4) (McCune and Mefford 1999).

RESULTS

In total 502 samples of bryophytes were analyzed, which correspond to 54 species of 13 families. The most representative family in both forest types was Lejeuneaceae, with 30 species, followed by Calymperaceae (5 spp.), Pylaisiadelphaceae (3 spp.), Plagiochilaceae (3 spp.), Fissidentaceae (2 spp.), Pilotrichaceae (2 spp.), Pterobryaceae (2 spp.), Sematophyllaceae (2 spp.), Hypnaceae, Leucobryaceae, Leucomiaceae, Neckeraceae, Radulaceae and Thuidiaceae (with one species each) (Table II).

Species with the highest number of occurrences in *várzea* forest were *Ceratolejeunea cubensis*, *Plagiochila montagnei*, *Radula javanica* and *Neckeropsis undulata*, while the most frequent in *igapó* forest were *Calymperes lonchophyllum*, *Ceratolejeunea cubensis*, *Prionolejeunea muricatoserrulata*, *Lejeunea cerina* and *Radula javanica*.

Species richness was higher in *igapó* (44 spp.) than in *várzea* forest (38 spp.) ($F_{[1,502]} = 6.77$; $p = 0.01$). However, there was no significant difference in species number in relation to periods with lower (dry period) and higher precipitation (rainy period), ranging from 33 to 31 species in *várzea* forests and from 36 to 35 in *igapó* forests, respectively ($F_{[1,502]} = 0.47$; $p = 0.493$).

The ordering analysis showed the formation of two groups, and the first arrangement axis completely separates the species composition of epiphytic bryophyte community between the two types of forests, but there was no variation in species composition between dry and rainy periods (Fig. 1).

DISCUSSION

The epiphytic bryoflora found in floodable forests in Caxiuanã National Forest in this study did not differ in species composition from other studies conducted in different forest types the Amazon region (Alvarenga and Lisboa 2009, Garcia et al. 2014, Tavares-Martins et al. 2014, Pantoja et al. 2015).

Regarding the distribution of species per families, the bryoflora of the studied floodable forests was consistent with what is known in tropical lowland forests, concerning the predominance of liverworts, especially because of the richness of Lejeuneaceae (Gradstein et al. 2001, Oliveira and Mota-de-Oliveira 2016). This has been a frequent result in studies with bryophytes performed in

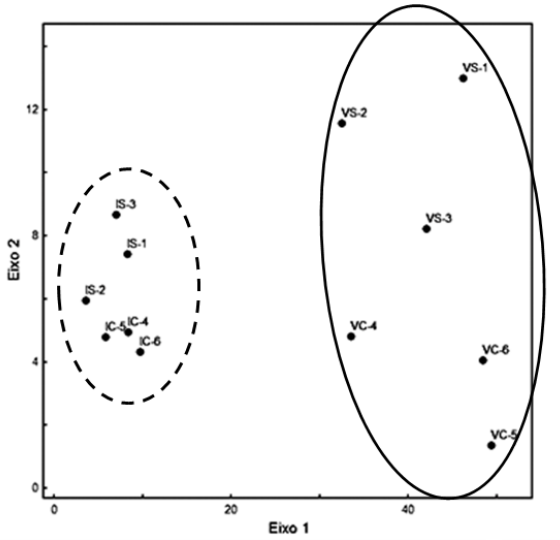

Figure 1 - Distribution of species composition between *igapó* (i) and *várzea* (v) forests, and between dry (s) and rainy (c) periods.

TABLE II
Frequency of the bryophyte species in *várzea* and *igapó* forests during dry and rainy periods. R = rainy period; D = dry period; AF= absolute frequency; RF = relative frequency.

	VÁRZEA				IGAPÓ				
Family/Species	**AF**	**RF**	**AF**	**RF**	**AF**	**RF**	**AF**	**RF**	**Voucher**
	R		**D**		**R**		**D**		
Calymperaceae									
Calymperes erosum Müll. Hal.	29	25.4	27	23.7	17	14.9	11	9.6	C04
C. lonchophyllum Schwägr.	25	21.9	29	25.4	90	78.9	87	75.7	C06
C. palisotii Schwägr.	8	7	9	7.9	2	1.8	6	5.2	C352
Octoblepharum albidum Hedw.	-	-	-	-	3	2.6	3	2.6	C369
O. cocuiense Mitt.	-	-	-	-	4	3.5	-	-	C373
Fissidentaceae									
Fissidens guianensis Mont.	-	-	-	-	-	-	4	3.5	C368
F. prionodes Brid.	1	0.9	1	0.9	30	26.3	44	38.3	C247
Lejeuneaceae									
Archilejeunea parviflora (Nees) Schiffn.	7	6.1	3	2.6	-	-	6	5.2	C216
Ceratolejeunea cubensis (Mont.) Schiffn.	79	69.3	96	84.2	78	68.4	90	78.3	C43
C. guianensis (Nees & Mont.) Steph.	18	15.8	2	1.8	16	14	-	-	C467
Cheilolejeunea comans (Spruce) R.M.Schust.	28	24.6	32	28.1	1	0.9	-	-	C08
C. oncophylla (Ångstr.) Grolle & M.E.Reiner	33	28.9	20	17.5	11	9.6	10	8.7	C12
C. rigidula (Nees & Mont.) R.M.Schust.	1	0.9	36	31.6	-	-	2	1.7	C18
Cololejeunea contractiloba (A.Evans) R.M.Schust.	16	14	4	3.5	1	0.9	-	-	C306
Cyclolejeunea convexistipa (Lehm. & Lindenb.) A.Evans	-	-	-	-	4	3.5	-	-	C472
Harpalejeunea oxyphylla (Nees & Mont.) Steph.	5	4.4	-	-	-	-	-	-	C518
H. stricta (Lindenb. & Gottsche) Steph.	-	-	1	0.9	-	-	-	-	C294
Lejeunea adpressa Nees	37	32.5	2	1.8	-	-	1	0.9	C350
L. asperrima Spruce	-	-	1	0.9	1	0.9	16	13.9	C222
L.boryana Mont.	-	-	-	-	30	26.3	11	9.6	C61
L. cerina (Lehm. & Lindenb.) Gottsche	5	4.4	12	10.5	33	28.9	54	47	C213
L. controversa Gottsche	8	7	-	-	15	13.2	16	13.9	C223
L. laetevirens Nees & Mont.	4	3.5	5	4.4	-	-	1	0.9	C17
L. phyllobola Nees & Mont.	4	3.5	-	-	-	-	-	-	C513
L. tapajosensis Spruce	8	7	4	3.5	-	-	-	-	C178
Lepidolejeunea involuta (Gottsche) Grolle	-	-	9	7.9	2	1.8	4	3.5	C154
Lopholejeunea subfusca (Nees) Schiffn.	5	4.4	5	4.4	-	-	-	-	C11
Mastigolejeunea auriculata (Wilson) Schiffn.	11	9.6	6	5.3	-	-	-	-	C25
Microlejeunea acutifolia Steph.	-	-	10	8.8	4	3.5	5	4.3	C227
Neurolejeunea seminervis (Spruce) Schiffn.	-	-	-	-	1	0.9	-	-	C485
Prionolejeunea denticulata (F.Weber) Schiffn.	-	-	1	0.9	16	14	36	31.3	C46

TABLE II (continuation)

Family/Species	VÁRZEA				IGAPÓ				Voucher
	AF	RF	AF	RF	AF	RF	AF	RF	
	R		D		R		D		
P. muricatoserrulata (Spruce) Steph.	-	-	-	-	79	69.3	79	68.7	C78
P. scaberula (Spruce) Zwickel	-	-	-	-	2	1.8	3	2.6	C204
Rectolejeunea versifolia (Schiffn.) L.Söderstr. & A.Hagborg	47	41.2	22	19.3	3	2.6	1	0.9	C24
Stictolejeunea squamata (Willd. ex F.Weber) Schiffn.	6	5.3	3	2.6	11	9.6	5	4.3	C07
Symbiezidium barbiflorum (Lindenb. & Gottsche) A.Evans	19	16.7	22	19.3	33	28.9	24	20.9	C48
Symbiezidium sp.	20	17.5	11	9.6	32	28.1	34	29.6	C472
Leucobryaceae									
Leucobryum martianum (Hornsch.) Hampe ex Müll. Hal.	-	-	-	-	7	6.1	-	-	C479
Leucomiaceae									
Leucomium strumosum (Hornsch.) Mitt.	-	-	-	-	7	6.1	-	-	C570
Neckeraceae									
Neckeropsis undulata (Hedw.) Reich.	47	41.2	30	26.3	-	-	2	1.7	C81
Plagiochilaceae									
Plagiochila montagnei Nees	82	71.9	85	74.6	7	6.1	6	5.2	C90
P. simplex (Sw.) Lindenb.	-	-	-	-	2	1.8	3	2.6	C238
P. subplana Lindenb.	3	2.6	-	-	26	22.8	26	22.6	C57
Pilotrichaceae									
Callicostella rufescens (Mitt.) A.Jaeger	-	-	-	-	-	-	2	1.7	C233
Pilotrichum bipinnatum (Schwägr.) Brid.	-	-	-	-	7	6.1	8	7	C54
Pterobryaceae									
Jaegerina scariosa (Lorentz) Arzeni	12	10.5	5	4.4	-	-	-	-	C302
Pireella pohlii (Schwägr.) Cardot	9	7.9	-	-	4	3.5	-	-	C516
Pylaisiadelphaceae									
Isopterygium tenerum (Schwägr.) Mitt.	-	-	3	2.6	-	-	-	-	C23
Taxithelium planum (Brid.) Mitt.	1	0.9	-	-	-	-	-	-	C521
T. pluripunctatum (Renauld & Cardot) W.R. Buck	-	-	-	-	-	-	1	0.9	C309
Radulaceae									
Radula javanica Gottsche	51	44.7	65	57	40	35.1	36	31.3	C01
Sematophyllaceae									
Sematophyllum subsimplex (Hedw.) Mitt.	-	-	-	-	3	2.6	1	0.9	C305
Trichosteleum papillosum (Hornsch.) A. Jaeger	-	-	-	-	-	-	1	0.9	C375
Thuidiaceae									
Pelekium scabrosulum (Mitt.) Touw	-	-	1	0.9	-	-	-	-	C313
Total	**629**		**562**		**622**		**639**		

tropical forests in South America (Cornelissen and Gradstein 1990, Acebey et al. 2003, Gradstein and Costa 2003, Campelo and Pôrto 2007, Mota-de-Oliveira et al. 2009, Brito and Ilkiu-Borges 2014, Garcia et al. 2014, Tavares-Martins et al. 2014, Pantoja et al. 2015, Oliveira and Mota-de-Oliveira 2016). This family experienced recent periods of rapid diversification coinciding with the rise of the angiosperms in the Cretaceous (Feldberg et al. 2014, Bechteler et al. 2016), providing a wide morphological variation that allows them to develop in different environments, especially in tropical forests representing up to 70% of the bryoflora (Gradstein 1979, 1994, 1997, Gradstein et al. 2001).

Calymperaceae and Sematophyllaceae appear as most predominant among moss families in tropical rainforests, which coincide with the statement of Gradstein et al. (2001), and corroborate with further results from studies performed in the Amazon region (Lisboa et al. 1998, 1999, Santos and Lisboa 2003, Mota-de-Oliveira et al. 2009, Mota-de-Oliveira and ter Steege 2013, Brito and Ilkiu-Borges 2014, Garcia et al. 2014, Tavares-Martins et al. 2014, Pantoja et al. 2015).

Considering species frequencies, some bryophytes were found to be restricted to a single forest with a low number of occurrences. *Harpalejeunea stricta*, *Pelekium scabrosulum* and *Isopterygium tenerum* occurred exclusively in *várzea* forest. The first species is known from the understory to the higher zones of forest canopy (Tavares-Martins et al. 2014, Oliveira and Mota-de-Oliveira 2016), while *Pelekium scabrosulum* and *Isopterygium tenerum* occur in various types of vegetation, especially in humid and well-lit habitats (Moraes and Lisboa 2009, Florschütz-de-Waard 1986). *Callicostella rufescens* was, though, found only once in *igapó* forest. It has been commonly reported on trunks of living trees, decaying trunks and stones in tropical rainforests (Florschütz-de-Waard 1986).

Lopholejeunea subfusca and *Mastigolejeunea auriculata* are epiphytes preferring sunny environments, but were registered in the understory up to the canopy of different types of tropical forests (Gradstein 1994, Ilkiu-Borges and Lisboa 2002, Gradstein and Costa 2003, Mota-de-Oliveira and ter Steege 2013). In the present study, they were commonly found in the understory of *várzea* forest. It shows a displacement probably as the result of factors such as canopy openness (Acebey et al. 2003), characteristic of this type of forest, providing greater light-input.

Taxithelium planum, *Taxithelium pluripuntactum*, *Trichosteleum papillosum*, *Octoblepharum cocuiense*, *Sematophyllum subsimplex*, *Fissidens prionodes* and *Fissidens guianensis* are common species in upland forests, but a drastic reduction in their frequencies was noticed in floodable forests in this study, in which they had a maximum of five records. This reduction corroborates the data found by Moraes (2006) in *várzea* and *igapó* forests of Caxiuanã, and by Santos and Lisboa (2008) in northeastern Pará, when comparing bryophytes in different vegetation types.

Low frequency of these species has also been reported in a study conducted only in *várzea* forest (Moura et al. 2013), in which samples of various substrates were analyzed and the frequency of these species was consistent to that previously reported in flooded forests. In *várzea* and *igapó* forests of Caxiuanã, all these species had low frequency and this reduction was also observed in *Octoblepharum albidum*, *Leucobryum martianum* and *Leucomium strumosum*.

A wide variation in the species frequency among *várzea* and *igapó* forests was observed (Table II), such as *Calymperes lonchophyllum* colonizing a 177 phorophytes in *igapó* forest, but only 54 phorophytes in *várzea* forest. It is a species preferably found in living trunks and shady places (Reese 1993), which found better conditions to develop in the closed canopy of *igapó* forests. A similar correlation to *várzea* forest was observed on *Plagiochila montagnei*, which was present on 167 phorophytes in *várzea* and 13 in *igapó*. It had been reported occurring in canopy or understory of tropical forests, as well as in open vegetation, at low altitudes on living or decaying trunks and on rocks (Gradstein and Costa 2003, Gradstein and Ilkiu-Borges 2009).

These differences evidence how species behavior is apparently responding to conditions imposed by the environment, since even the most frequent species are presenting their reduced occurrences between environments, as well as the turnover of species from understory to canopy is best explained by microhabitat conditions in a forest instead of dispersion limitation (Mota-de-Oliveira et al. 2009).

Another factor contributing to these differences is the reproductive capacity of the species, since the bryophytes are plants with diverse reproductive strategies, which depend on the presence of water enabling the reproduction (Silva and Silva 2013). Low frequency of some species may be linked to their sexual system, for example, the dioecious species which have their fertilization rates affected by the spatial segregation between male and female colonies (Longton and Schuster 1983, Bowker et al. 2000, Oliveira and Pôrto 2002, Stark et al. 2005, 2010), as well as dioecious acrocarpous mosses, in which the sporophyte production rates in some families are very low (La Farge 1996).

As the low frequency, high frequency can also be associated with reproductive strategies of bryophytes, which reproduce not only sexually, but asexually as well (Löbel and Rydin 2009, Frey and Kürschner 2011, Maciel-Silva and Válio 2011, Maciel-Silva et al. 2013, Cerqueira et al. 2016). Various means of asexual reproduction represent a successful strategy allowing species to maintain the equilibrium between populations, given the difficulties imposed by the environment preventing sexual reproduction (Laaka-Lindberg 2000). Among epiphytic bryophytes, this strategy is widely adopted, especially by liverworts, as the colonization through new gemmae facilitates the establishment on vertical substrates (Glime 2007, Bastos 2008, Cerqueira et al. 2016). The lack of dispersion limitation among epiphytic bryophyte communities from Amazonian lowland forests indicated a predominance of niche-assembly rules over dispersal-assembly rules according to Mota-de-Oliveira et al. (2009).

The largest species richness of the epiphytic bryophyte community observed in *igapó* forests in comparison to *várzea* forests, is similar to the results of Ferreira et al. (2013) concerning the species richness of trees, lianas and stipes in these two forest types. However, these data contrast the results of Travassos et al. (2014), who showed species richness in *várzea* was twice that found in *igapó* forest.

In this study, it is believed that the difference in richness between the forests, being richer the *igapó*, is due to abundant presence of an herbaceous community (C.C. Souza et al., unpublished data), the presence of other types of substrates available for colonization (dead trunks, leaves), and the greater proximity between individuals of *Virola surinamensis*. Despite these phorophytes present a quite uniform distribution in both forest types, its occurrence is aggregated in *igapó* and dispersed in *várzea* (Ferreira et al. 2013). An aggregate distribution of phorophytes plus the fact that many bryophytes disperse their diaspores at short distances (Tan and Pócs 2000), may favor the eventual colonization by diaspores of bryophytes present on other phorophytes. Dispersion can also occur from diaspores of epiphyllous species present on herbaceous plants, and epixylic species, since the presence of dead trunks works as dispersion center to the colonization of living trunks (Wen-Zhang et al. 2009).

By choosing only one tree species widespread in *várzea* and *igapó* forests in Caxiuanã, characteristics relating to roughness of bark were not analyzed in this work, which seems to play a role in the establishment of bryophyte species (Gradstein and Culmsee 2010). However, a study by L.V. Ferreira et al. (unpublished data) about thickness of phorophytes, showed there is difference in the proportion of DBH of *Virola surinamensis* between *igapó* and *várzea* forests of Caxiuanã, where the *igapó* forest is characterized by having higher proportion of individuals presenting DBH from 10 to 20 cm, while the *várzea* forests have a greater proportion of individuals with larger DBH. Gradstein and Culmsee (2010) were the first to correlate trunk diameter with bryophyte diversity in species-rich tropical forest, which was previously shown only in temperate forests (McGee and Kimmerer 2002). According to Gradstein and Culmsee (2010), diameter of host trees correlated with distribution of few individual species, but not with community composition or species richness.

Trees with larger diameter and smoother barks seem to favor the development of bryophytes which grow more adherent to substrates, such as the members of Lejeuneaceae, as also observed by Bastos and Yano (2006) and those highlighted in these forests, including the four species recorded exclusively in *várzea*. However, in *igapó* forest, trees are thinner due to the low availability of nutrients (Schngart et al. 2005), but barks present more crevices and cracks. Such characteristics provide more microhabitats favoring water retention. They contribute to the development of species with growth forms producing mats on the substrate (Wen-Zhang et al. 2009), such as mosses, especially for members of Calymperaceae (Bastos 1999), which were more frequent in *igapó*, including eight species reported in this type of forest only.

Thus, it was found environmental action on the structure and distribution of phorophytes influences the epiphytic bryophyte community of understory and acts secondarily on its arrangement. More inclusion of phorophytes with detailed analysis of their cortex, researching along the vertical gradient, and monitoring for longer time of the lowest and highest precipitation periods, are strategies that can provide further details on the epiphytic bryoflora of floodable forests.

ACKNOWLEDGMENTS

The authors are grateful to Dr. Roberta Macedo Cerqueira and to the AABC reviewers for constructive comments on the manuscript; to Dr. Daniela Zappi for grammatically reviewing the manuscript; to the Programa de Pós-Graduação em Ciências Biológicas – Botânica Tropical of the Universidade Federal Rural da Amazônia (UFRA) and Museu Paraense Emílio Goeldi (MPEG) for the infrastructure and additional support; to the Ferreira Penna Research Station for the infrastructure and availability of field guide during the collections; to the Programa de Pesquisas Ecológicas de Longa Duração (PELD-Caxiuanã) for financing the field work; to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for granting scholarship to the first author; and to the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for granting productivity fellowship for the second and third authors.

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