

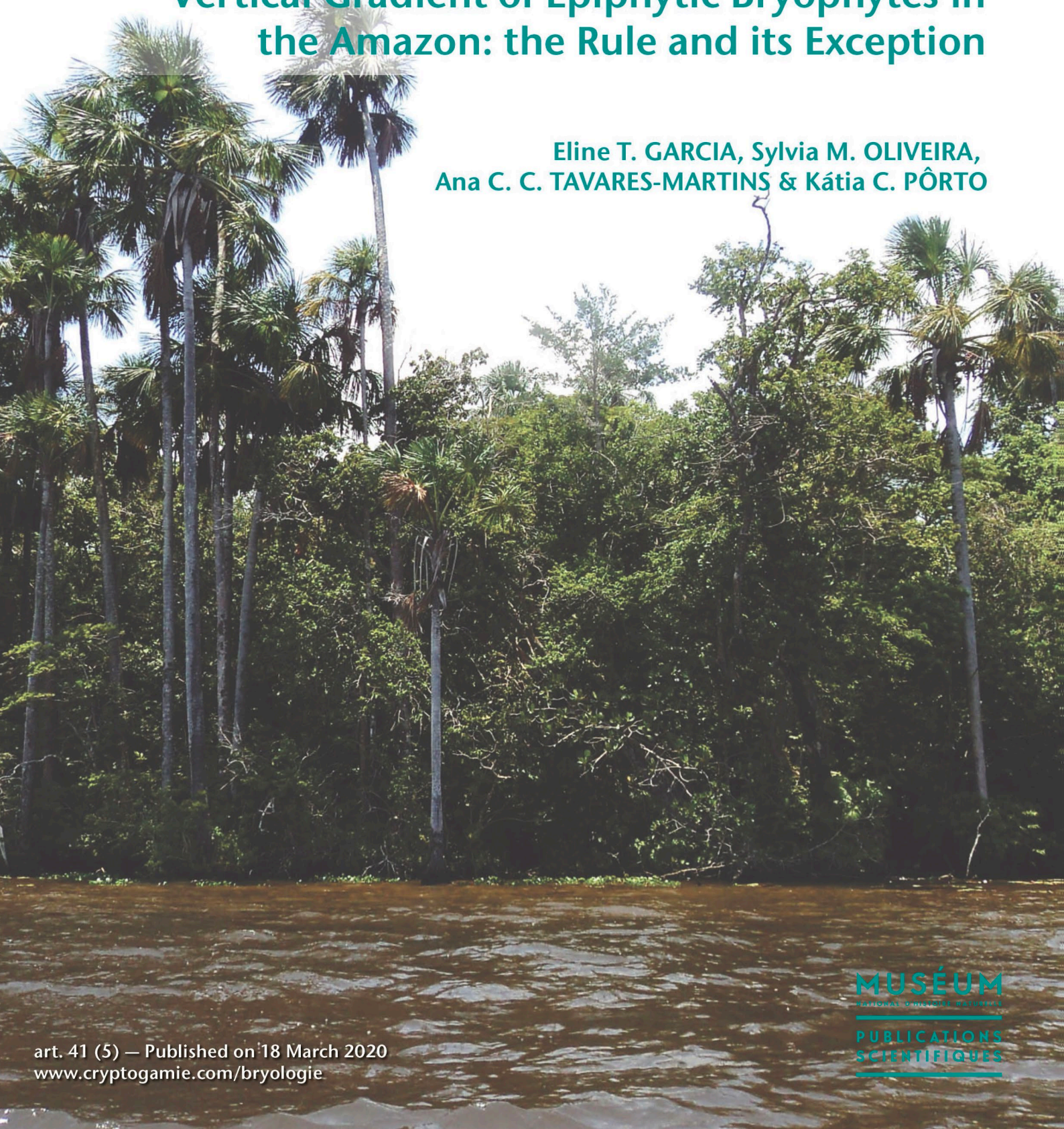
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Vertical Gradient of Epiphytic Bryophytes in the Amazon: the Rule and its Exception

Eline T. GARCIA, Sylvia M. OLIVEIRA,
Ana C. C. TAVARES-MARTINS & Kátia C. PÔRTO



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Vertical Gradient of Epiphytic Bryophytes in the Amazon: the Rule and its Exception

Eline T. GARCIA

Federal University of Pernambuco. Biology of Bryophytes Laboratory, Botany Department,
Bioscience Center, Federal University of Pernambuco, 50740-570, Recife, PE (Brazil)
elinetgarcia@gmail.com (corresponding author)

Sylvia M. OLIVEIRA

Naturalis Biodiversity Center. Biodiversity Discovery Group,
Naturalis Biodiversity Center, Leiden (Netherlands)
sylvia.motadeoliveira@naturalis.nle

Ana C. C. TAVARES-MARTINS

State University of Pará. Natural Sciences Department,
State University of Pará, 156 Una st., 66113-200, Belém, PA (Brazil)
tavaresmartins7@gmail.com

Kátia C. PÔRTO

Federal University of Pernambuco. Biology of Bryophytes Laboratory, Botany Department,
Bioscience Center, Federal University of Pernambuco, 50740-570, Recife, PE (Brazil)
kcntiporto@gmail.com

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ABSTRACT

In Amazonian Terra Firme vegetation, epiphytic bryophytes present a deterministic distribution along height zones in host trees, at both local and regional scale. Recent findings about the influence of vegetation structure variation on epiphytic bryophyte assemblages suggest that the vertical gradient may also change among adjacent vegetation types. In order to analyze this influence, bryophytes were sampled in five zones from the base to the top of 24 host trees in Várzea and Igapó (flooded) and Terra Firme (non-flooded) vegetation. The species richness and diversity, distribution of guilds of tolerance to light incidence, floristic similarity, and turnover of species composition were evaluated within and between vegetation types. The vertical gradient was observed only in Igapó and Terra Firme. Species richness and diversity were higher at the base in flooded forests, and at the outer canopy in non-flooded forests. These zones also showed higher floristic similarities among vegetation types. The distribution of guilds explained the main patterns observed in assemblages. The spatial distribution of epiphytes in the studied forests is regulated by the interaction between the height zone and vegetation type, and light tolerance is one of the most important attributes explaining the distribution patterns of epiphytes in the Amazon.

KEY WORDS

Amazonia,
canopy,
community assembly,
Igapó vegetation,
beta diversity,
environmental heterogeneity,
conservation units.

RÉSUMÉ

Gradient vertical des bryophytes épiphytes en Amazonie : la règle et son exception

La végétation des bryophytes épiphytes de la Terra Firme d'Amazonie présente une distribution déterministe le long de huit zones d'arbres hôtes, à la fois à l'échelle locale et à l'échelle régionale. De récentes découvertes à propos de l'influence de la variation structurelle de la végétation sur les assemblages de bryophytes épiphytes suggèrent que le gradient vertical peut aussi changer au sein des types de végétation adjacents. Le gradient vertical a été observé uniquement à Igapo et Terra Firme. La richesse et la diversité spécifique était plus haut à la base des forêts inondées, qu'à l'extérieur de la canopée dans les forêts non inondées. Ces zones montrent de grandes ressemblances floristiques au sein des types de végétation. La répartition des guildes expliquent les principaux modèles observés dans les assemblages. La répartition spatiale des épiphytes dans les forêts étudiées est régulées par l'interaction entre la zone en hauteur et le type de végétation, et la tolérance à la lumière est l'un des attributs les plus importants expliquant les modèles de distribution des épiphytes en Amazonie.

MOTS CLÉS

Amazonie, canopée, communauté d'assemblage, végétation d'Igapo, beta diversité, hétérogénéité environnementale, unités de conservation.

INTRODUCTION

Plant communities in the Amazon respond to different environmental gradients, both locally and regionally (Tuomisto & Poulsen 2000; Tuomisto *et al.* 2002; Wittmann *et al.* 2006; Oliveira & ter Steege 2015; Quaresma *et al.* 2017). In this context, the assembly of epiphytic bryophytes is strongly influenced by local environmental filters, involving vertical zoning, successional stages and variation in vegetation types (Acebey *et al.* 2003; Oliveira *et al.* 2009; Tavares-Martins *et al.* 2014; Oliveira & ter Steege 2015; Cerqueira *et al.* 2017).

The vertical distribution of epiphytes in tropical forests is mainly determined by variations in environmental conditions that occur from the understory to the canopy (Allee 1926; Cornelissen & ter Steege 1989). This gradient is one of the most consistently observed in bryophytes and reflects the environmental filtering associated to changes in the availability of light, water and temperature (Pócs 1982; Richards 1984; Acebey *et al.* 2003), however, without taking into account the interactions between species (Kraft *et al.* 2015).

The vertical distribution of bryophytes in tropical forests has been mainly addressed in the context of effects of habitat loss and fragmentation in the natural environments of these plants (Alvarenga *et al.* 2010; Sporn *et al.* 2010; Silva & Pôrto 2010, 2013). Particularly in the Amazon, studies on the vertical gradient of epiphytic bryophytes have been concentrated in Terra Firme vegetation (Oliveira *et al.* 2009; Tavares-Martins *et al.* 2014; Oliveira & ter Steege 2015), while information about floodplains such as Várzea and Igapó is still missing. Among other characteristics, these forest types differ from each other by their arboreal vegetation structure and floristic composition as well as the periodic and seasonal flood flows ruled by regimes of adjacent rivers (Junk *et al.* 2011). In the eastern Amazon, the richness and composition of epiphytic bryophytes has been observed to vary among these vegetation types on a local scale (Cerqueira *et al.* 2017), where Igapó forests are richer and more diverse than those of Várzea, in

agreement with the patterns found for vascular plants in the region (Ferreira *et al.* 2013).

In Terra Firme vegetation of the Amazon basin, the vertical gradient of bryophytes has been observed both at local and regional scale: height zone is a significant element in these assemblages (Oliveira & ter Steege 2015) while species composition per zone is relatively homogeneous across large distances (Oliveira & ter Steege 2013). The pattern was attributed to the combination of strong niche assembly with high dispersal potential of bryophytes. In view of these patterns and the responses of bryophyte assemblages to changes in host tree structure and composition recently reported in the understory of flooded forested areas (Cerqueira *et al.* 2017), it is possible that the vertical distribution of bryophytes also changes on a local scale even between preserved habitats.

Thus, we hypothesized that: 1) the vertical gradient is present in the non-flooded (Terra Firme) and flooded (Igapó and Várzea) vegetation types, but weaker in the latter due to differences in landscape structure and the existence of flood dynamics in the understory; 2) the proportion of generalist taxa is greater in the flooded forests in response to their more intense dynamics, which filter species with wider niches; and 3) the species richness and diversity, as well as the similarity between communities are higher at the base and outer canopy of host trees within and between vegetation types because these zones represent the two extremes of the microenvironmental gradient.

METHOD

The study was conducted in the Caxiuanã National Forest (Caxiuanã FLONA), located in the eastern portion of the Amazon (01°42'30"S and 51°31'45"W, 62 m altitude) (Montag *et al.* 2008). The climate of the region is tropical according to Köppen's classification (Köppen & Geiger 1928; Alvares *et al.* 2014). The average annual precipitation varies between 2000 and 2500 mm, with a pronounced dry season

from June to November (Costa *et al.* 2010), the annual average temperature is 25.9°C and the relative humidity of the air varies around 82% (Castro *et al.* 2013).

SAMPLING AND TAXONOMIC IDENTIFICATION

Samples were collected in Terra Firme (TF, non-flooded), Igapó (IG, flooded) and Várzea (VZ, flooded) vegetation. Fieldwork was carried out between September 2015 and July 2016. Eight 20-25 meter-tall host trees, with diameter at breast height (DBH) ≥ 20 cm, and bark presenting intermediate roughness were selected in each vegetation type, totaling 24 trees. The minimum distance between sampled trees was 20 m, and their canopies were not in contact with each other. To facilitate climbing, we selected trees with branches that could resist the weight of an adult person and upper branches that were visible from the ground (Gradstein *et al.* 1996).

Bryophytes were collected in five height zones, namely: zone 1 = from the base up to 1 m; zones 2 and 3 = lower and upper trunk, respectively; zone 4 = base of crown; and zone 5 = outer sun-lit twigs/leaves (outer canopy). A set of four 10 cm² plots were collected in each height zone and pooled into a single sample (40 cm²) (Oliveira *et al.* 2009; Oliveira & ter Steege 2013), thus totaling five samples per host tree (Fig. 1). DBH and shaft height of each host tree were measured with a metric tape and canopy height was visually estimated. Each host tree served as the central point of a 10 m² plot, and hemispheric photographs were taken with a digital camera (Nikon Coolpix 5400) and 8 mm fisheye lens (Nikon FC-E9) at the corners of each plot. The canopy openness of the areas surrounding each host tree corresponded to the average of the four photographs. The mean values and standard deviations (SD) of the samples in each vegetation type are listed in Table 1.

Bryophytes were identified with the aid of specialized bibliography and specimens of difficult determination were sent to taxonomists for confirmation and taxonomic identification. The most used works were Florschütz (1964), Reese (1993), Reiner-Drehwald (2000), Reiner-Drehwald & Goda (2000), Dauphin (2003), Gradstein & Costa (2003), Gradstein & Ilkiu-Borges (2009), Moraes & Lisboa (2009), Reiner-Drehwald & Grolle (2012), Bordin & Yano (2013) and Ilkiu-Borges (2016). The classifications of Goffinet *et al.* (2009) for Bryophyta and Crandall-Stotler *et al.* (2009) for Marchantiophyta were adopted in this study. Taxonomic updates of some species were made based on recently published literature for the genera *Microcalpe* Mitt., *Archilejeunea* (Spruce) Steph., *Cheilolejeunea* (Spruce) Steph. and *Myriocoleopsis* Schiffn. (Yu *et al.* 2014; Shi *et al.* 2015; Bastos *et al.* 2017; Carvalho-Silva *et al.* 2017), the “World checklist of hornworts and liverworts” (Söderström *et al.* 2016), and Flora do Brasil 2020 database (Flora do Brasil 2020). Vouchers were deposited in the collections of the Geraldo Mariz (UFP) and João Murça Pires (MG) herbaria. In this study we use the following definition of guild “group of species that exploit the same class of environmental resources in a similar way” (Root 1967; Blondel 2003). Also, the term guild was used as a synonymous of the synusia defined by Richards (1984). The considered resources for bryophytes were light and moisture.

TABLE 1. — Mean and standard deviation (SD) of host tree variables and canopy openness per vegetation type. Abbreviations: IG, Igapó; TF, Terra Firme; VZ, Várzea.

Variables	Vegetation Type		
	IG	TF	VZ
DBH	29.16 ± 5.8	36.21 ± 4.3	44.80 ± 10.8
Height of the shaft	10.16 ± 2.5	13.96 ± 2.8	10.75 ± 1.8
Height of the canopy	10.56 ± 3.3	9.62 ± 1.5	10.87 ± 2.1
Total height	20.72 ± 2.2	23.58 ± 2.9	21.62 ± 2.4
Canopy openness	12.50 ± 2.7	12.15 ± 1.8	12.89 ± 1.6

In this study guild was used being synonymous of the synusia defined for Richards (1984).

DATA ANALYSIS

Bryophyte assemblages were analyzed to evaluate the variation of richness, diversity, proportion of guilds of tolerance to light incidence, and species composition along height zones within and between vegetation types, as well as to check the existence of a vertical gradient in the assemblages of each vegetation type. All analyses were performed using R (R Core Team 2019).

Richness corresponded to the number of species recorded in each height zone or forest type. Species richness was compared between height zones in each vegetation type, and between each height zone in different vegetation types. These comparisons were tested by one-way analysis of variance (ANOVA) at 5% level of significance, whenever assumptions were met. Species richness data were checked for normality using the Shapiro-Wilk test, and the homogeneity of the variances was tested with the Levene's test of the Car package (Fox & Weisberg 2011). The Tukey Honestly Difference Test (HSD) was applied *a posteriori* to verify the existence of significant differences between groups.

The Fisher's alpha (α) was calculated to determine the species diversity per height zone in each vegetation type, as this index ($S = a * \ln(1 + n/a)$) where S is number of taxa, n is number of individuals and a is the Fisher's alpha) is considered a robust measure, not so sensitive to sample size (Fisher *et al.* 1943; Magurran 2004; Beck & Schwanghart 2010). For this calculation, we considered the abundance and richness of species recorded per height zone in each vegetation type. Because of the impossibility of dissociating bryophyte individuals present in the samples, the incidence of each species in the plot was used to define its abundance, which could vary along the different zones of the same host tree (1-5) and between host trees of the same vegetation type (1-8).

The floristic composition of height zones within and between forest types was compared using the Sørensen's similarity index, which attributes double weight to double presences (Legendre & Legendre 1998), and the Bray-Curtis dissimilarity index (Bray & Curtis 1957). Two matrices with presence-absence and abundance data per height zone of each vegetation type were created. The Sørensen and Bray-Curtis indexes were calculated by the betadiver function of the vegan package (Oksanen *et al.* 2018).

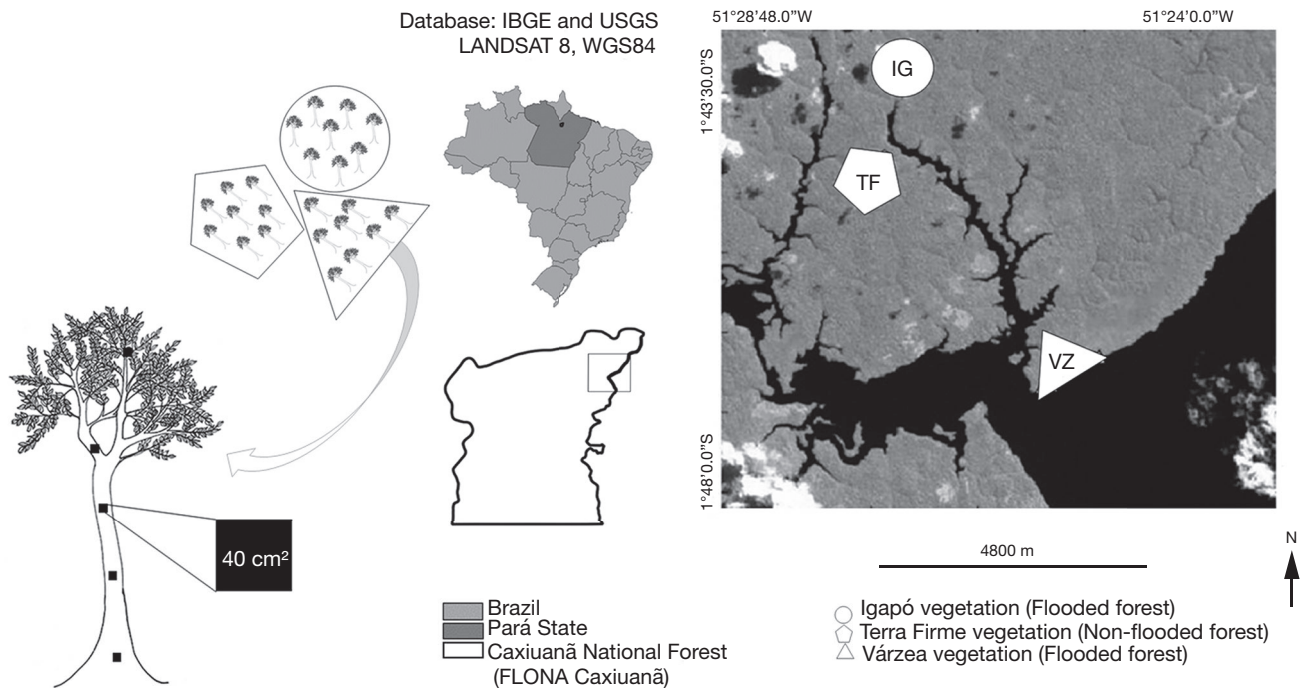


FIG. 1. — Sampling methods and study area.

TABLE 2. — Similarity (Sorensen) and dissimilarity (Bray-Curtis) indices between height zones and vegetation types. Species richness and diversity per height zone are highlighted in **gray**.

	VZ1	VZ2	VZ3	VZ4	VZ5	IG1	IG2	IG3	IG4	IG5	TF1	TF2	TF3	TF4	TF5	
Sorensen	VZ1	39/28.2	0.36	0.41	0.46	0.64	0.81	0.85	0.86	0.8	0.82	0.79	0.65	0.6	0.6	0.65
	VZ2	0.71	26/13.9	0.24	0.33	0.47	0.82	0.82	0.84	0.76	0.75	0.82	0.7	0.64	0.57	0.66
	VZ3	0.66	0.78	25/14.0	0.24	0.39	0.86	0.87	0.85	0.69	0.76	0.84	0.71	0.74	0.64	0.66
	VZ4	0.56	0.67	0.8	25/14.4	0.36	0.87	0.87	0.84	0.7	0.77	0.91	0.78	0.75	0.67	0.67
	VZ5	0.45	0.6	0.72	0.72	14/9.1	0.92	0.9	0.87	0.73	0.84	0.94	0.84	0.87	0.76	0.74
Bray-Curtis	IG1	0.36	0.34	0.28	0.28	0.19	39/24.2	0.42	0.54	0.67	0.82	0.63	0.65	0.76	0.83	0.88
	IG2	0.28	0.31	0.2	0.24	0.2	0.65	26/14.6	0.32	0.46	0.71	0.81	0.73	0.76	0.77	0.83
	IG3	0.29	0.32	0.33	0.37	0.32	0.51	0.64	24/14.5	0.38	0.69	0.83	0.77	0.77	0.78	0.82
	IG4	0.31	0.36	0.41	0.36	0.36	0.45	0.49	0.56	19/10.2	0.63	0.87	0.78	0.78	0.72	0.76
	IG5	0.25	0.33	0.31	0.27	0.21	0.25	0.33	0.34	0.42	34/18.9	0.9	0.81	0.73	0.7	0.62
	TF1	0.31	0.27	0.27	0.2	0.15	0.52	0.35	0.28	0.27	0.17	26/15.8	0.32	0.58	0.76	0.88
	TF2	0.43	0.36	0.36	0.29	0.23	0.46	0.36	0.3	0.29	0.22	0.79	30/19.8	0.36	0.53	0.71
	TF3	0.41	0.36	0.33	0.24	0.16	0.35	0.28	0.29	0.28	0.28	0.6	0.74	24/14.3	0.32	0.67
	TF4	0.42	0.44	0.45	0.34	0.33	0.3	0.26	0.31	0.38	0.35	0.37	0.55	0.65	28/18.6	0.5
	TF5	0.49	0.38	0.42	0.39	0.36	0.22	0.24	0.27	0.3	0.47	0.18	0.33	0.39	0.6	42/33.4

The non-metric multidimensional scaling (NMDS) method was used to evaluate the variation of species composition between vegetation types and between height zones. For this purpose, a presence/absence matrix was created using samples from each height zone of the 24 host trees. One of the samples had to be excluded due to low number of species. The metaMDS function of the vegan package was used to perform the NMDS (Oksanen *et al.* 2018). This ordination (resizing) tries to represent objects by reducing them to a few dimensions and at the same time preserving the respective distance between them (Legendre & Legendre 1998).

A multivariate analysis by permutation – PERMANOVA (“Adonis” function) was used to test the existence of statistically significant differences in species composition between

the three vegetation types in relation to the five height zones, whose groups were defined *a priori*. Changes in the composition of species with respect to the guilds of tolerance to light incidence (*sensu* Richards 1984) were evaluated in the three vegetation types, correlating them with the height zones of occurrence. To this end, the species were classified according to the works of Richards (1984), Cornelissen & ter Steege (1989), Gradstein (1992a), Gradstein *et al.* (2001), Oliveira *et al.* (2009), and Tavares-Martins *et al.* (2014). The following literature-based classification was used: shade specialist epiphytes – Sha, present in the understory microhabitat; sun specialist epiphytes – Sun, present in the canopy; and generalist epiphytes – Gen, occurring in both microhabitats (Richards 1984).

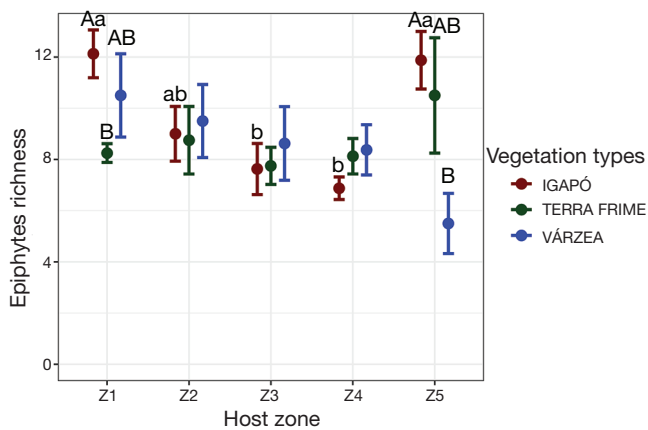


FIG. 2. — Mean and standard error of the richness of epiphytic bryophytes in the height zones per vegetation type. Lowercase letters are used to indicate differences between height zones and uppercase letters to indicate differences between height zones compared in the different vegetation types in Igapó.

TABLE 3. — PERMANOVA results for the different groups (height zones and vegetation types) of epiphytic bryophytes in the Caxiuanã FLONA.

	Df	Sums Sqs	Mean Sqs	F. Model	R2	Pr (> F)
Vegetation type	2	11.622	5.8109	23.471	0.28987	0.001
Residuals	115	28.471	0.2476	0.71013	—	—
Total	117	40.093	1	—	—	—
Height zone	4	4.063	1.01563	3.1852	0.10133	0.001
Residuals	113	36.031	0.31885	0.89867	—	—
Total	117	40.093	1	—	—	—

The correlation between the occurrence of guilds in the height zones was checked with the chi-square test, analyzing the degree of association between categorical variables (height zone x guild). In this analysis, we used matrices of guild abundance per height zone in each forest type. The chi-square (X^2) test assumes the null hypothesis that the observed frequencies are not different from those generated by chance, and there is therefore no difference between them due to the absence of association between the variables (Gotelli & Ellison 2011).

RESULTS

A total of 112 species of epiphytic bryophytes, among 21 mosses and 91 liverworts, were recorded in Igapó (73 spp.), Terra Firme (66 spp.) and Várzea (48 spp.) (Appendix 1). The mean species richness per height zone increased in the outer canopy in Igapó and in Terra Firme, while the opposite occurred in Várzea (Fig. 2). The mean richness varied between zones in all forest types, but this variation was statistically significant only in Igapó ($F_{[4, 35]} = 6.48$, $p = 0.0005$) where the richest zones (base and outer canopy) differed from the upper trunk and the inner canopy (Fig. 2, lowercase letters).

The base of the trunks was the richest zone in the flooded forests (Z1), while the outer canopy had the highest number of species in Terra Firme (Z5) (Fig. 3A-C). The mean species

richness of height zones compared across the different vegetation types showed significant differences only in the case of the extreme zones, i.e., base and outer canopy ($F_{[2, 24]} = 3.113$, $p = 0.065$); this differences were slight between the base of Igapó and Terra Firme and consistent between the outer canopy of Igapó and Várzea (Fig. 2, uppercase letters).

The base and the outer canopy were the zones with the greater number of exclusive species in the forests. In Igapó and Terra Firme, species that occurred exclusively in the outer canopy stood out (Fig. 3A, B), while in Várzea, 25% of the species were restricted to the trunks and more than 50% of them occurred in all zones (Fig. 3C).

The diversity of species followed the patterns observed for richness in the vegetation types. In Várzea, the recorded diversity was greatest at the base of the trunks and decreased towards the canopy; in Terra Firme, there was an increase towards the outer canopy, where the greatest diversity of all zones and vegetation types was observed ($\alpha 33.4$); and in Igapó, although the base had the greatest diversity as in Várzea, both extremities concentrated a high diversity. The base was one of the least rich and diverse height zones in Terra Firme (Table 2).

The composition of epiphytes between the intermediate height zones within each vegetation type was highly similar, always sharing more than 30% of the species (Table 2, Sørensen index). The extremities (base and outer canopy) of the host trees were more similar to the corresponding zones in Igapó and Terra Firme (base/Z1, 0.52; outer canopy/Z5 0.47, Sørensen index). The composition of bryophytes in the outer canopy (Z5) of Terra Firme also closely resembled that of the base (Z1) of Várzea (0.49). The floristic composition was less similar between the flooded forests (Fig. 4, Table 2), which was distant from that of Terra Firme, mainly in relation to the outer canopy and the understory (Igapó/Z5 - Terra Firme/Z1, 0.90, Várzea/Z5 - Terra Firme/Z1, 0.94, Terra Firme/Z5 - Igapó/Z1, 0.88, Bray-Curtis index).

In addition, the structure of the floristic composition in the ordination evidenced the influence of two factors shaping the assemblages (Fig. 4). The first one is related to the vegetation type (1st axis, colors) and the second to the height zone in the host tree (2nd axis, symbols). These factors (vegetation type and height zone) were tested and found to be consistent (Table 3). A turnover in the composition of species along height zones was observed in Terra Firme and Igapó, which characterized the vertical gradient of bryophytes. This pattern was not observed in Várzea, where species composition was very similar between zones (Fig. 4).

The distribution of specialist species varied between zones (Fig. 3D) and there was a reduction in the proportion of shade specialists and a concomitant increase of sun specialists and generalists towards the canopy. Specialist taxa were correlated with the height zones in the Igapó and Terra Firme vegetation (Igapó, $X^2 = 64.4$, $df = 8$, $p < 0.001$; Terra Firme, $X^2 = 68.5$, $df = 8$, $p < 0.001$) (Fig. 3E-F). The exception of this pattern was seen in Várzea, where generalist and sun specialist taxa predominated in all height zones, and there was no association between the distribution of guilds and height zones ($X^2 = 15.1$, $df = 8$, $p = 0.057$) (Fig. 3G).

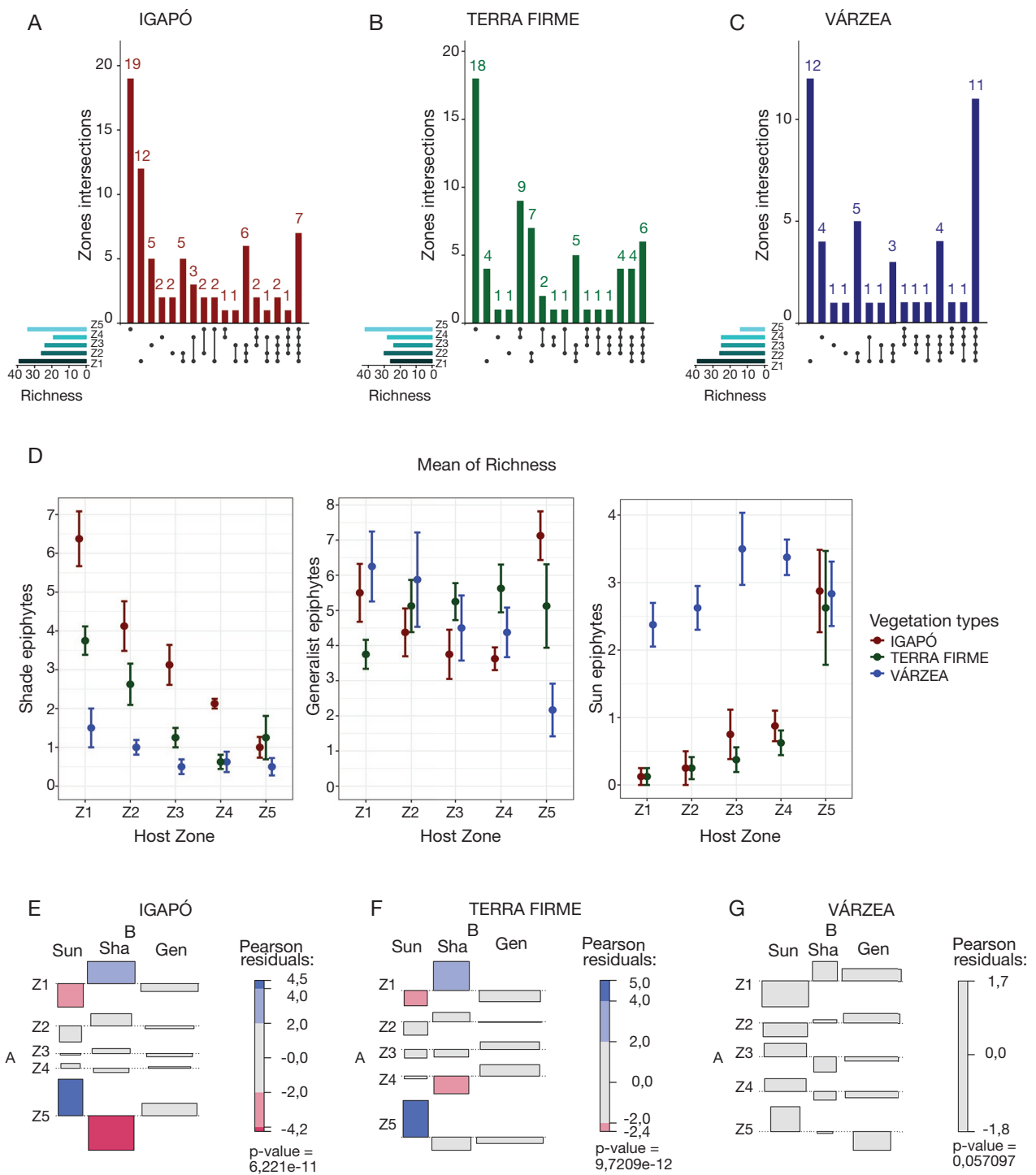


FIG. 3. — **A-C**, Overview of the number of species and shared species per vegetation type. Horizontal bars represent the total richness per zone; vertical bars represent the number of species found per each zone (points) and the number of species shared between zones (points connected by lines); **D**, mean and standard error of species richness per guild in the zones; **E-G**, association between zones and guilds based on the absolute frequency of taxa. Abbreviations: **Sun**, Sun specialist epiphytes; **Sha**, Shade specialist epiphytes, **Gen**, Generalist epiphytes; **Z**, Zone.

DISCUSSION

VERTICAL GRADIENT AND TURNOVER OF EPIPHYTIC BRYOPHYTES IN DIFFERENT AMAZONIAN VEGETATION TYPES
 The expectation that the composition of species would present

a vertical gradient in the host trees was supported in Igapó and Terra Firme vegetation. On the other hand, the composition was more homogeneous along the height zones in Várzea. These data show that the turnover of species (vertical gradient) is consistent at local scale in Terra Firme, as previously

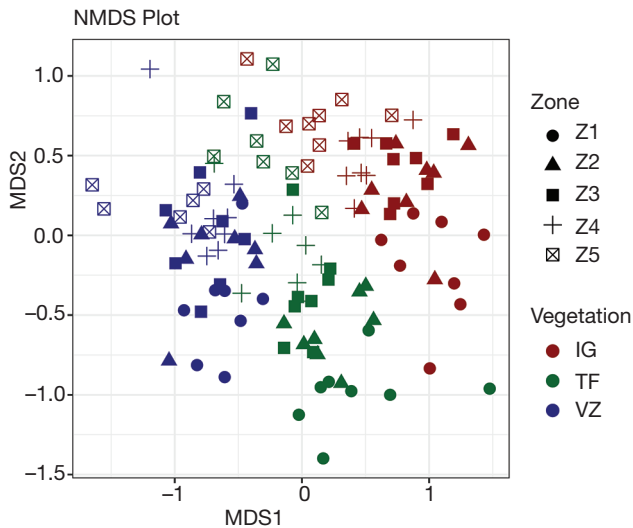


FIG. 4. — Non-metric multidimensional scaling (NMDS) plot of samples per zone in the vegetation types (stress = 0.1942709) using Sørensen distance. (Z1, base to 1 m; Z2, lower trunk; Z3, upper trunk; Z4, inner canopy; Z5, outer sun-lit twigs/leaves [outer canopy]).

reported (Oliveira *et al.* 2009), as well as in Igapó, and it is also regulated by the type of vegetation, since this pattern was observed in these vegetation types but not in Várzea. In Igapó and Terra Firme, the similarity in the composition of bryophytes found in the extreme height zones (base and outer canopy) of trees across vegetation types was higher than that among zones of host trees within the same vegetation type. This ratifies the relation between the height of occurrence and distribution of species, as previously observed in Terra Firme in the Amazon (Oliveira & ter Steege 2015). Thus, the sharing of exclusive taxa of the understory (e.g. *Prionolejeunea denticulata* (F.Weber) Schiffl. and *P. muricatosserrulata* (Spruce) Steph.) and the canopy (e.g. *Diplasiolejeunea brunnea* Steph. and *D. rudolphiana* Steph.) supports the fact that, regardless of the vegetation type, these species have typical niches adapted to these microhabitats. These results are in line with the literature, since bryophytes have been reported to have their occurrence strongly regulated by niche (Slack 1990; Oliveira *et al.* 2009), responding efficiently to fluctuations in light incidence, humidity and temperature (Schofield 1985; Gradstein *et al.* 1996; Hallingbäck & Hodgetts 2000; Gradstein *et al.* 2001). These abiotic factors vary greatly from the base to the canopy in humid tropical forests (Allee 1926; Cornelissen & ter Steege 1989), establishing the well documented vertical gradient of bryophyte species (Pócs 1982; Oliveira *et al.* 2009; Sporn *et al.* 2010; Oliveira & ter Steege, 2015), although not observed in the Várzea forest in the present study. The floristic similarity between Terra Firme and Igapó has already been highlighted in previous studies (Lopes *et al.* 2016). In the present work, we further found that such similarity is associated with the extreme zones (base and outer canopy) of the host trees, thus not reflecting only the geographic proximity but also, and mainly, the niche of the species. Despite of correlation between the floristic composition of the samples and the

spatial distance observed when considered the samples of all vegetation types, this effect disappears if analyzed specifically each vegetation types (Mantel tests performed additionally, supports independence of host trees). Thus, both spatial distance and species niche appear to determine the occurrence of species. At the local scale, similarity between height zones is well supported in the literature, although the available data almost always consist of comparisons between zones of the same vegetation type (Cornelissen & ter Steege 1989; Oliveira *et al.* 2009; Oliveira & ter Steege 2015).

The weaker turnover across the height zones in Várzea can be a response to the more extreme conditions to which the species are subjected in this environment, which may be associated with greater canopy openness in this vegetation (Matos *et al.* 2018). According Richards (1984) differences in forest structure may cause changes in the internal microclimate, which in turn regulate the distribution of epiphytes (Cornelissen & ter Steege 1989; Oliveira *et al.* 2009). The reduction of canopy cover has shown to negatively affect the composition and diversity of epiphytic bryophytes (Benítez *et al.* 2015). In our results, if greater canopy openness is taken as an indication of a less dense canopy, the absence of vertical gradient in Várzea may be related to the loss and/or shift of species with low tolerance to high levels of light incidence. Similarly, a homogenous floristic composition in the vertical distribution and predominance of sun specialists and generalists have been reported in the literature, almost always attributed to the state of conservation and the history of fragmentation of the area (Alvarenga *et al.* 2010; Silva & Pôrto 2013; Oliveira & Oliveira 2016).

The difference in the species composition of flooded vegetation types has been previously reported in other studies (Cerqueira *et al.* 2017), and our data indicates that it can be partly explained by the vertical distribution of species. According to Slack (1990), bryophytes do not disappear from the habitats due to competitive exclusion, but migrate to more favorable environments, thus being considered fugitive species. This would explain the greater similarity between species found in Várzea and those of the extreme zones of the canopy (outer canopy) in Igapó and Terra Firme, where more desiccation tolerant (Pardow *et al.* 2012) and light demanding taxa occur. In this case, the different vegetation types would act as reservoirs of species with distinct characteristics that occur in habitats better suited to their niche requirements.

Our results suggest that variations in abiotic factors occur in the studied environment in relation to both height in the host tree and type of vegetation, causing a differentiation in the assemblages. The moisture content of the air, temperature and daily variation of UV radiation, as well as the structure of the substrates are ecological factors that determine local patterns in the composition of bryophytes in tropical forests (Richards 1984; Wolf 1993; Bader *et al.* 2013; Wagner *et al.* 2014). In this way, both can represent surrogates of abiotic filters that determine high beta diversity even on a small local scale.

SPECIES COMPOSITION: REPRESENTATION OF GUILDS IN THE VEGETATION TYPES

The distribution of guilds in the different vegetation types confirmed the vertical gradient in terms of taxonomic composition of species in Terra Firme and Igapó, and explained the non-existence of such gradient in Várzea. Guilds are established according to their responses to microclimatic variations over the vertical gradient in the host trees (Pócs 1982; Richards 1984). The patterns observed in our data followed the expectation for tropical forests, with a clear variation in the proportion of specialists (reduction of Shade specialist and increase of Sun specialist) from the base to the canopy of hosts in the forests (Cornelissen & ter Steege 1989).

In Várzea vegetation, generalist and sun specialist species prevailed in all zones, becoming gradually less represented towards the canopy. Taxa with these characteristics are common in open habitats such as rocky outcrops, fragmented areas, and secondary forests (Silva & Germano 2013; Tavares-Martins *et al.* 2014; Pantoja *et al.* 2015). On the other hand, the displacement of sun specialists towards the understory, as well as the loss of shade specialists in this stratum is observed in areas with poor canopy coverage (Richards 1984; Gradstein *et al.* 2001; Benítez *et al.* 2015). Because habitat quality affects practically all species and is relevant to the survival and reproduction of species (Kawecki 2008) the change in the abundance of species among vegetation types is maybe a response to the strong restrictions imposed by habitats on the taxa. This was evident, for instance, in the occurrence of *Pycnolejeunea papilosa* Xiao L.He (Sunesp) (23 spp. in Várzea, 5 in Terra Firme, and 1 in Igapó), which was present and frequent in all zones in Várzea, but little frequent in the other vegetation types. Another example is *Syrrhopodon ligulatus* Mont. and *S. incompletus* Schwägr. (Shaesp), rare in Várzea but very common in Igapó and Terra Firme. On the other hand, of the 30 shade tolerant epiphytes recorded in this study, 10 occurred exclusively in Igapó vegetation, where taxa such as *Prionolejeunea scaberula* (Spruce) Steph. and *P. trachyoides* (Spruce) Steph. were very frequent and restricted to the understory. In spite of the lower richness found in Várzea, the number of occurrences of bryophytes was not much different between the vegetation types, being common or rare species frequently abundant in other vegetation types. These data indicate that rarity of bryophytes in the studied environments may be partially a result of the ecological restrictions imposed by availability of light and humidity. Therefore, guilds can be taken as an informative and robust measure of the ecological range of taxa that explain, at least in part, the abundance distribution of the species.

SPECIES RICHNESS ALONG THE VERTICAL GRADIENT IN HOST TREES IN THE EASTERN AMAZON

In the flooded forests, the base of the trees (Z1) was richer and more diverse than the outer canopy. The outer canopy, in turn, stood out in Terra Firme. The diversity of species in this zone was also greater in relation to the zones of the other vegetation types. The canopy is commonly reported as the richest microhabitat for epiphytes in tropical forests (Gradstein

1992b), which is likely associated with the filtering of species at the extremes where establishment is more limited (Oliveira & ter Steege 2015). It is important to highlight that the outer canopy (Z5) included canopy leaf and branch samples, but only in Terra Firme the leaves were colonized by bryophytes. Epiphyll species were mainly sun specialists and were also eventually found in other height zones of other vegetation types (e.g. *Caudalejeunea lehmanniana* (Gottsche) A.Evans, *Cololejeunea cardiocarpa* (Mont.) A.Evans, *C. subcardiocarpa* Tixier, *C. surinamensis* Tixier, *Pycnolejeunea gradsteinii* Illk.-Borg. and *Vitalianthus* sp.). Coverage of epiphylls in tropical forests can be considered a proxy for relative humidity because pronounced fluctuations have the potential to constrain the growth and occurrence of these species (Sonnleitner *et al.* 2009). The greater connectivity between the crown of the trees in Terra Firme may have contributed to minimize the effects of the increase of air temperature and decrease of humidity that takes place from the base towards the canopy, promoting better conditions for the establishment of epiphylls. Moreover, richness can be increased by means of colonization by foreign species to the community as well as by speciation (Warren *et al.* 2014) and may be more evident on a local scale (Oliveira & ter Steege 2015). High canopy richness has been reported in previous studies carried out in the Amazon (Oliveira *et al.* 2009; Tavares-Martins *et al.* 2014) and in the Brazilian Atlantic Forest (Costa 1999).

Although our expectations were confirmed, the greater diversity in the extreme zones in the forests reveals still other aspects yet to be analyzed, such as the fact that the base of the host trees was the zone with lower richness in Terra Firme, while it presented a major importance in the other vegetation types. Bryophytes are poikilohydric and therefore unable to regulate the loss or storage of water (Vanderpoorten & Goffinet 2009). For this reason, they are more susceptible to adjacent environmental fluctuations (Schofield 1985; Gradstein *et al.* 1996; Hallingbäck & Hodggets 2000; Gradstein *et al.* 2001). Unlike in Terra Firme vegetation, the availability of substrates in Várzea and Igapó may be lower due to periodic flooding, making the base of the trees more suitable for the establishment of species.

The high richness and diversity of bryophytes (Oliveira & ter Steege 2015) and vascular epiphytes (Pos & Slegers 2010) in the vertical gradient had already been reported for Terra Firme vegetation in the study area of the present work. Here, we also highlight the representativeness of these attributes in Igapó vegetation were, the variations in abiotic conditions along the hosts explain the observed diversity at the extremes of the gradient. Thus, the spatial distribution of epiphytic bryophytes in the zones meets the assembly of species according to the distribution of guilds, because the differentiation of composition over the height zones (beta diversity) was shaped by the niche of the species.

The vertical gradient in the composition of the epiphytic bryophytes along trees is consistent, but varies depending on the type of vegetation, and the local spatial distribution of the species is a combination of niche (height zone) and characteristics of the vegetation type. Species guilds are important

attributes that indicate the processes that shape the epiphytic assemblages and regulate the vertical gradient, which may not exist even in forests with good conservation status. Due to changes in community and species attributes from one vegetation type to the other, we highlight the importance of investigations of the diversity patterns of epiphytes in the Amazon to include different habitats. In view of the responses of guilds to the environmental gradients, we emphasize the need for studies focused on traits of the species related to their environmental tolerance and also reproductive aspects, since the latter also regulate the distribution of the taxa.

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APPENDIX 1. — Bryophytes epiphytes and distribution in the zones per vegetations in the Caxiuanã National Forest, Pará state, Brazil. Floristic Group: **M**, Moss; **L**, Liverworts; Guild: **Sun**, Sun specialist epiphytes; **Sha**, Shade specialist epiphytes; **Gen**, Generalist epiphytes; Zones: 1-5.

Species Name/Guild	Group	Igapó					Terra Firme					Várzea				
		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Shade specialist epiphytes																
<i>Archilejeunea crispistipula</i> (Spruce) Steph.	L	-	-	-	-	-	x	-	-	x	x	x	x	x	x	x
<i>Calymperes platyloma</i> Mitt.	M	x	x	x	x	x	-	-	-	-	-	-	-	-	-	-
<i>Cololejeunea camillii</i> (Lehm.) A. Evans	L	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-
<i>Cololejeunea contractiloba</i> A. Evans	L	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-
<i>Cololejeunea surinamensis</i> Tixier	L	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
<i>Cyclolejeunea convexistipa</i> (Lehm. & Lindenb.) A.Evans	L	-	-	-	x	-	-	-	-	x	-	-	-	-	-	-
<i>Fissidens guianensis</i> Mont.	M	x	-	-	x	-	x	x	x	-	-	-	-	-	-	-
<i>Fissidens pellucidus</i> Hornsch.	M	x	x	-	-	-	x	x	-	-	-	x	-	-	-	-
<i>Haplolejeunea amazonica</i> Ilkiu-Borges & Gradst.	L	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-
<i>Harpalejeunea tridens</i> (Besch. & Spruce) Steph.	L	x	x	x	x	-	-	-	-	-	-	-	-	-	-	-
<i>Lejeunea asperrima</i> Spruce	L	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lejeunea controversa</i> Gottsche	L	x	x	-	-	-	x	x	-	-	-	-	-	-	-	-
<i>Leucobryum martianum</i> (Hornsch.) Hampe ex Müll. Hal.	M	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Leucomium strumosum</i> (Hornsch.) Mitt.	M	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-
<i>Metalejeunea cucullata</i> (Reinw., Blume et Nees) Grolle	L	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
<i>Pictolejeunea picta</i> (Steph.) Grolle	L	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-
<i>Plagiochila aerea</i> Taylor	L	x	-	-	-	-	x	x	-	-	-	-	-	-	-	-
<i>Plagiochila montagnei</i> Nees	L	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-
<i>Plagiochila raddiana</i> Lindenb.	L	-	-	-	-	-	-	-	-	-	-	x	x	x	-	-
<i>Plagiochila subplana</i> Lindenb.	L	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-
<i>Prionolejeunea aemula</i> (Gottsche) A.Evans	L	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Prionolejeunea denticulata</i> (F.Weber) Schiffn.	L	x	x	x	-	-	x	x	x	-	-	-	-	-	-	-
<i>Prionolejeunea muricatoserrulata</i> (Spruce) Steph.	L	x	-	x	-	-	x	x	-	-	-	-	-	-	-	-
<i>Prionolejeunea scaberula</i> (Spruce) Steph.	L	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-
<i>Prionolejeunea trachyodes</i> (Spruce) Steph.	L	x	x	x	x	x	-	-	-	-	-	-	-	-	-	-
<i>Radula stenocalyx</i> Mont.	L	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Syrrhopodon incompletus</i> Schwägr.	M	x	x	x	-	-	x	x	x	-	-	-	-	-	-	x
<i>Syrrhopodon ligulatus</i> Mont.	M	-	-	-	-	-	-	x	x	x	x	x	-	-	-	-
<i>Trichosteleum subdemissum</i> (Besch.) A.Jaeger	M	x	-	-	-	-	-	-	-	-	-	x	-	-	-	-
<i>Xylolejeunea crenata</i> (Nees et Mont.) Xiao L.He et Grolle	L	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-
Generalist epiphytes																
<i>Archilejeunea fuscescens</i> (Hampe ex Lehm.) Fulford	L	-	-	-	-	-	-	x	x	x	x	-	-	-	-	-
<i>Calymperes erosum</i> Müll. Hal.	M	-	-	x	-	-	x	x	x	x	-	x	x	-	-	-
<i>Calymperes lonchophyllum</i> Schwägr.	M	x	x	-	-	-	x	x	x	x	x	-	-	-	-	-
<i>Calymperes palisotii</i> Schwägr.	M	x	x	-	x	-	-	-	-	-	-	x	x	x	x	x
<i>Ceratolejeunea coarina</i> (Gottsche) Schiffn.	L	x	-	-	-	-	-	-	-	x	x	x	x	x	x	x
<i>Ceratolejeunea confusa</i> R.M.Schust.	L	-	-	-	-	-	-	-	-	-	x	x	-	-	x	-
<i>Ceratolejeunea cornuta</i> (Lindenb.) Steph.	L	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Ceratolejeunea cubensis</i> (Mont.) Schiffn.	L	x	-	-	-	x	x	x	x	-	-	x	x	x	x	x
<i>Ceratolejeunea guianensis</i> (Nees et Mont.) Steph.	L	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x
<i>Ceratolejeunea minuta</i> G.Dauphin	L	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-
<i>Cheilolejeunea adnata</i> (Kunze ex Lehm.) Grolle	L	x	-	-	-	-	x	x	x	x	x	x	x	x	x	-
<i>Cheilolejeunea aneogyna</i> (Spruce) A.Evans	L	x	-	-	x	-	x	-	-	-	-	x	x	x	x	x
<i>Cheilolejeunea clausa</i> (Nees et Mont.) R.M.Schust.	L	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
<i>Cheilolejeunea comans</i> (Spruce) R.M.Schust	L	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-
<i>Cheilolejeunea holostipa</i> (Spruce) Grolle & R.-L.Zhu	L	-	-	-	-	x	-	-	-	x	-	-	x	x	x	x
<i>Cheilolejeunea oncophylla</i> (Ångstr.) Grolle & M.E. Reiner	L	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Cheilolejeunea rigidula</i> (Nees ex Mont.) R.M.Schust.	L	-	x	-	-	x	-	x	x	x	x	x	-	-	-	-
<i>Cololejeunea cardiocarpa</i> (Mont.) A.Evans	L	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
<i>Dibrachiella parviflora</i> (Nees) X.Q.Shi, R.L.Zhu & Gradst.	L	-	-	-	-	-	x	x	x	x	x	x	-	-	x	-
<i>Drepanolejeunea fragilis</i> Bischl.ex L.Söderstr.,A.Hagborg et von Konrat	L	-	-	-	x	-	-	-	-	x	-	-	-	-	-	-
<i>Harpalejeunea stricta</i> (Lindenb. et Gottsche) Steph.	L	-	x	-	-	x	-	-	-	-	-	-	x	-	-	-
<i>Isopterygium tenerum</i> (Sw.) Mitt.	M	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-
<i>Lejeunea adpressa</i> Nees	L	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-
<i>Lejeunea boryana</i> Mont.	L	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lejeunea cerina</i> (Lehm. et Lindenb.) Lehm. et Lindenb.	L	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lejeunea flava</i> (Sw.) Nees	L	-	-	-	-	-	-	-	x	-	x	-	-	-	-	-
<i>Lejeunea grossitexta</i> (Steph.) E.Reiner et Goda	L	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-
<i>Lejeunea immersa</i> Spruce	L	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lejeunea laetevirens</i> Nees et Mont.	L	x	x	-	-	-	-	-	-	-	-	x	x	-	-	-
<i>Leptolejeunea elliptica</i> (Lehm. et Lindenb.) Besch.	L	-	-	-	-	x	-	-	-	-	x	-	-	-	-	-
<i>Microcalpe subsimplex</i> (Hedw.) W.R. Buck	M	-	-	-	-	-	x	x	x	-	-	x	-	-	-	-
<i>Microlejeunea bullata</i> (Taylor) Steph.	L	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
<i>Microlejeunea epiphylla</i> Bischl.	L	-	-	x	x	-	-	x	x	x	x	x	x	x	x	x
<i>Mniomalia viridis</i> (Mitt.) Müll. Hal.	M	x	x	x	x	-	-	-	-	-	-	-	-	-	x	-
<i>Neurolejeunea seminervis</i> (Spruce) Schiffn.	L	x	x	x	x	x	-	-	-	-	x	-	-	-	-	-

APPENDIX 1. — Continuation

Species Name/Guild	Group	Igapó					Terra Firme					Várzea				
		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
<i>Octoblepharum albidum</i> Hedw.	M	x	-	-	x	-	x	x	x	x	-	x	x	x	-	-
<i>Octoblepharum pulvinatum</i> (Dozy & Molk.) Mitt.	M	-	-	-	-	-	x	x	x	-	-	-	-	-	-	-
<i>Pilosium chlorophyllum</i> (Hornsch.) Müll. Hal.	M	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
<i>Rectolejeunea berteriana</i> (Gottsche ex Steph.) A.Evans.	L	-	-	-	x	-	-	-	-	x	x	-	-	-	-	-
<i>Rectolejeunea flagelliformis</i> A.Evans	L	-	-	-	x	x	-	-	-	x	x	x	x	x	x	-
<i>Symbiezidium barbiflorum</i> (Lindenb. & Gottsche) A. Evans	L	x	x	x	x	x	-	-	-	x	x	-	-	-	-	-
<i>Syrrhopodon gaudichaudii</i> Mont.	M	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-
<i>Syrrhopodon simmondsii</i> Steere	M	-	-	-	-	x	x	x	x	-	-	-	-	-	-	-
<i>Trichosteleum papillosum</i> (Hornsch.) Jaeg.	M	x	-	-	-	-	-	-	-	-	-	x	-	-	-	-
<i>Zoopsisidella integrifolia</i> (Spruce) R.M.Schuster	L	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sun specialist epiphytes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Acrolejeunea emergens</i> (Mitt.) Steph.	L	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-
<i>Acrolejeunea torulosa</i> (Lehm. et Lindenb.) Schiffn.	L	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x
<i>Archilejeunea badia</i> (Spruce) Steph.	L	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
<i>Caudalejeunea lehmanniana</i> (Gottsche) A.Evans	L	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
<i>Cheilolejeunea cyrtolejeuneoides</i> C.J. Bastos & Schäf.-Verw.	L	-	-	x	x	x	-	-	-	-	-	-	-	-	-	-
<i>Cheilolejeunea neblinensis</i> Ilk-Borg. et Gradst.	L	-	-	-	-	x	x	x	-	-	-	-	-	-	-	-
<i>Cololejeunea subcardiocalpa</i> Tixier	L	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-
<i>Dibrachiella auberiana</i> (Mont.) X.Q.Shi, R.L.Zhu & Gradst.	L	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
<i>Diplasiolejeunea brunnea</i> Steph.	L	-	-	-	x	-	-	-	-	x	-	-	-	-	-	-
<i>Diplasiolejeunea cobrensis</i> Steph.	L	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
<i>Diplasiolejeunea rudolphiana</i> Steph.	L	-	-	-	x	-	-	-	-	x	-	-	-	-	-	-
<i>Frullania caulisequa</i> (Nees) Mont.	L	-	-	-	x	-	-	x	-	x	-	-	-	-	-	-
<i>Frullania gibbosa</i> Nees, Ann	L	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-
<i>Lejeunea tapajosensis</i> Spruce	L	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
<i>Lopholejeunea subfusca</i> (Nees) Schiffn.	L	-	x	x	x	x	-	x	-	x	x	x	-	x	x	x
<i>Mastigolejeunea auriculata</i> (Wilson et Hook.) Steph.	L	-	-	x	-	-	-	-	-	-	-	x	x	x	x	-
<i>Mastigolejeunea innovans</i> (Spruce) Steph.	L	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
<i>Mastigolejeunea plicatiflora</i> (Spruce) Steph.	L	-	-	x	-	-	-	-	-	-	x	x	x	x	x	x
<i>Myriocoleopsis minutissima</i> (Sm.) R.L.Zhu, Y.Yu et Pócs	L	-	-	-	-	-	-	-	-	-	-	x	-	x	x	-
<i>Pycnolejeunea contigua</i> (Nees) Grolle	L	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x
<i>Pycnolejeunea gradsteinii</i> Ilk.-Borg.	L	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
<i>Pycnolejeunea papillosa</i> Xiao L.He	L	-	-	x	-	-	-	-	-	x	x	x	x	x	x	x
<i>Radula javanica</i> Gottsche	L	x	x	-	-	-	-	-	-	-	-	x	x	-	-	-
<i>Symbiezidium transversale</i> (Sw.) Trevis.	L	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-
<i>Thysananthus amazonicus</i> (Spruce) Schiffn.	L	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-
Unclassified	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cololejeunea</i> sp.	L	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
<i>Cololejeunea</i> sp. 3	L	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
<i>Frullania exilis</i> Taylor	L	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
<i>Frullania</i> sp.	L	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
<i>Lejeunea</i> sp. 1	L	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
<i>Lejeunea</i> sp. 2	L	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
<i>Lejeunea</i> sp. 3	L	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
<i>Lejeunea</i> sp. 4	L	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pycnolejeunea</i> sp.	L	-	-	-	-	x	-	-	-	-	-	-	-	x	x	x
<i>Syrrhopodon cymbifolius</i> Müll. Hal.	M	x	-	-	-	x	x	x	x	x	x	-	-	-	-	-
<i>Vitalianthus</i> sp. 1	L	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-
<i>Vitalianthus</i> sp. 2	L	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-