DOES THE SIZE OF THE TREES DETERMINE THE RICHNESS AND DISTRIBUTION OF VASCULAR EPIPHYTES IN AMAZONIAN FLOODPLAIN FORESTS?

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Abstract: Vascular epiphytes (VE) are among the most threatened group of plants due to the extraction of trees (phorophytes). Yet, surveys and ecological information on vascular epiphytes are rather scarce particularly in wetlands. To understand the effect of tree assemblage on the occurrence of VE and in order to elucidate ecological patterns of distribution and composition, 16 (25 x 25 m) permanent plots were sampled in an oligotrophic floodplain forest (*igapó* - PELD MAUA) and compared to the same amount and size of plots in a nutrient-rich floodplain (*várzea* - RDS Mamirauá), both in Central Amazon. All trees and associated VE were counted and identified. The diversity in *várzea* is driven by the turnover of epiphytes in trees with different diameters, while in *igapó* there is a pronounced concentration of VE in trees with smaller diameters. Conservation actions in *várzea* forests should prioritize the maintenance of forest structure, sustaining taxonomic diversity in all diameter classes of trees. In *igapó* forests efforts to conserve epiphytes must first consider the taxonomic identity and, after, size of trees in the community. The comparison of our results with those of other PELDs in wetlands and other ecosystems will enhance our knowledge on the biogeographic patters and constrains on the distribution of this important botanical component.

Keywords: wetlands; várzea forest; igapó forest; turnover; nestedness.

INTRODUCTION

Ecological knowledge on bioindicator groups in different habitats is fundamental for monitoring biodiversity, to detect threatened species or environments and to guide preventive conservation actions. There were significant advances regarding the factors that structure the patterns of richness and distribution of plant groups in Amazonian upland forests (Pezzini *et al.* 2012), which is essential for long term ecological monitoring (Tundisi 2013).

However, in Amazonian wetlands such advances occurred mostly for tree assemblages (e.g. Ferreira 1997, Wittmann *et al.* 2002, 2010, Montero *et al.* 2014). Nevertheless, other plant groups remain poorly known, especially for vascular epiphytes.

The world-wide species count of vascular epiphytes and hemiepiphytes might be greater than 27,600 (Zotz 2013). This group of plants is under severe anthropogenic pressure, as a significant part of its species composition is lost due to selective logging of large trees (Barthlott *et*

al. 2001, Mondragón *et al.* 2015). Monitoring the epiphytic component is no trivial task as these plants occupy the forest canopy, making them difficult to sample and survey. This is particularly challenging for wetlands where the inundation (Junk et al. 1989) pulse adds up methodological complexity to surveys, given the shifting in water levels between dry and rainy season. Notwithstanding, it is known that trees with greater diameters support more diversity and abundance of epiphytes (Callaway *et al.* 2002, Hietz & Hietz-Seifert 1995, Flores-Palacios & Garcia-Franco 2006, Wolf *et al.* 2009). This normally occurs because larger trees have more surface and, in most cases, more time available for colonization by epiphytes (Gentry & Dodson 1987, Benzing 1990, Wagner *et al.* 2015). Still, this relationship can not be generalized for all environments because some studies did not find a positive relationship between tree diameter and epiphyte richness and abundance (Köster *et al.* 2009, Kersten *et al.* 2009).

Analysing the tree diameters in Amazonian wetlands might elucidate patterns of distribution and richness of epiphytes along time, assuming that, in most cases, the dimeter is a proxy of the time of establishment of a tree (Schöngart *et al.* 2005). In an area nearby the Surumori River (a blackwater river), Colombia, Nieder *et al.* (2000) sampled 139 trees and observed that 56 trees with DBH > 20 cm hosted 57 % of all epiphytic individuals. On the other hand, 83 trees with DBH < 20 cm supported 43 % of the epiphytic individuals, corroborating that the time of establishment of the phorophyte is important to the colonization by epiphytes. Therefore, emphasizing the maintenance of large trees in floodplains.

White-Water *várzea* forests and black-water *igapó* forests (sensu Prance 1979) comprise an extension of more than 750,000 Km^2 of the Amazon Basin (Melack & Hess 2010, Wittmann & Junk 2016), these are the most representative wetland ecosystems of this biome. Both forests are subjected to an annual predictable monomodal inundation pulse, which determines most the patterns of distribution and diversity of trees (Junk *et al.* 1989, Wittmann *et al.* 2010, Junk *et al.* 2011) and vascular epiphytes (Quaresma *et al.* 2018). However, *várzeas* and *igapós* differ in their chemistry and geology of their floodplains, *várzeas* have greater fertility than *igapós*. This translates into a great floristic

difference on the assemblage of trees of these two ecosystems (Junk *et al.* 2011) and likely influences the epiphyte floristic diversity as well (Quaresma *et al.* 2017). The quantity of tree species with DBH ≥ 10 cm is greater in *várzeas* (up to 150 species x ha^{-1}) when compared to *igapós* (up to 80 species x ha^{-1}; Wittmann *et al.* 2006, Montero *et al.* 2014). In addition, the arboreal floristic similarity between the two types of forests is less than 20 % (Wittmann *et al.* 2006, Wittmann 2012). Trees in *igapó* forests grow 2 to 3 times slower than in *várzeas* due to the differences in the edaphic conditions of their alluvial soil (Schöngart *et al.* 2006). In Central Amazon the richness of epiphytes is also higher in *várzeas* (73 species) than in *igapós* (37 species) and the similarity between these two environments is only 15.6 % (Quaresma *et al.* 2017).

Differences in the diversity between these two ecosystems might be driven by two distinct processes or by a combination of those (Baselga 2010). The first consists in a change of species between two assemblages (species turnover), and the second occurs when just a small set of species from the poorer environment constitutes a subset of species present in the richer environment (nestedness) (Baselga 2010, Ulrich & Gottelli 2007). Turnover and nestedness have been documents as processes that promote beta diversity in tropical arboreal assemblages (e.g. Pitman *et al.* 2002, Condit *et al.* 2013, Esquiver-Muelbert *et al.* 2016). To our knowledge these aspects are still to be studied for the assemblages of other associated plants, especially for vascular epiphytes. Differentiating these processes is essential for improving our understanding of epiphyte ecology, biogeography and will help to solve matters on species conservation, like to prioritize conservation units in richer sites (Baselga 2010).

Processes that regulate the diversity of the epiphytic component and their relationship phorophyte age are poorly known for Amazonian wetlands (Quaresma *et al.* 2018). In order to fill this gap, we investigated the influence of tree diameter (as a proxy of age) on the richness, abundance and distribution of vascular epiphytes. In addition, we studied the effect of turnover and nestedness processes between *várzea* and *igapó* (i.e., beta diversity) as well as inside each forest (i.e., alpha diversity). Specifically, we aimed to answer the following questions: I) There is a

positive relationship between diameter to richness and abundance? II) What is the structure of the alpha and beta diversities of vascular epiphytes in wetlands?

MATERIAL AND METHODS

Study area

Our field research was conducted in an *igapó* forest of the Jaú National Parque (PARNA) in permanent plots of Long-Term Ecological Research Program - PELD MAUA, and in an *várzea* forest in the Mamirauá Reserve of Sustainable Development (RDS) (Figure 1). The Jaú PARNA is located between the towns of Novo Airão and Barcelos, 220 km from the Manaus (Capital of Amazonas State, Northern Brazil). The Mamirauá RDS is set in Central Amazon, about 70 km away from the town of Tefé (Amazonas State). Mamirauá and Amanã RDS's (Central Amazon Conservation Complex) were declared Natural Heritage of Humanity by UNESCO in 2000.

The Jaú PARNA has an extension of about 2,272,000 ha and covers the basins of the Jaú and Unini Rivers, tributaries of the Negro River's right margin (Ferreira 2000). Meanwhile, the Mamirauá RDS extends through 1,240,000 ha and is delimited by the Japurá and Amazon Rivers, and by the Auati-

Paranã channel (Plano de Gestão 2010). Both sites have a tropical humid climate. The mean annual temperature is close to 26.7 ºC, mean annual rainfall is 2,300 mm, the dry season goes from June to September and the rainy period from December to May (Ayres 1993, Ferreira, 2000).

The study areas are subjects to a monomodal inundation pulse, the mean annual amplitude in the Jaú PARNA is 8.3 m (Junk *et al.* 2015) and 10.8m in the Mamirauá RDS (Junk *et al.* 2012). The highest waters in both forests occurs in the second fortnight of June and the lowest in early November (Junk *et al.* 2012, 2015).

Data collection

We conducted three field expeditions to each field site between 2014 and 2016 as part of the PELD MAUA project. The first two, in June and July 2014 (highwater period), aimed to recognize field sites and for collecting epiphytes and botanic samples of trees (fertile and unfertile). The remaining four expeditions were carried out in September 2014, January and September of 2015, and September 2016 (low water period). We demarcated 16 25 x 25 m plots in each site, sampling 2 ha in total. We only collected data in forests on late stages of succession (see Wittmann *et al.* 2002, Junk *et al.* 2015).
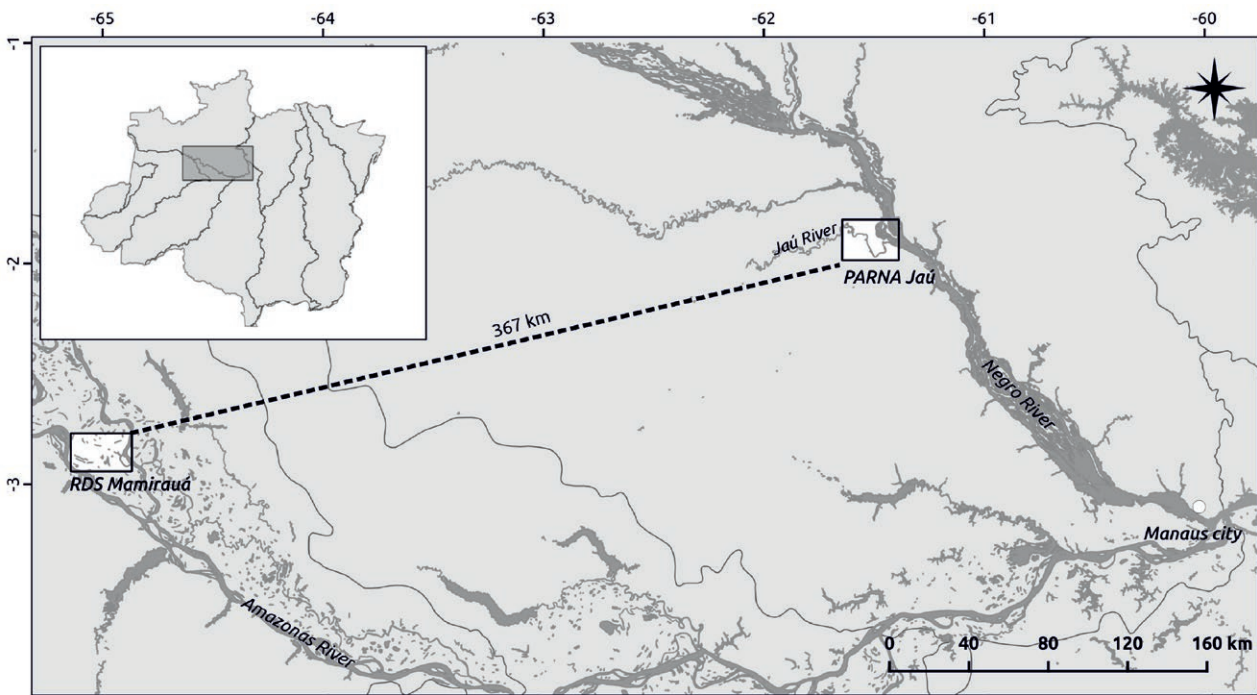
Figure 1. Location of the study sites: the Jaú National Park and the Mamirauá Reserve of Sustainable Development.

Plots were located at least 150 m from each other. Plots across field sites were demarcated in the same inundation level, for example, if plot was demarcated in the *igapó* at an inundation level of 2.5 m another plot was demarcated at the same level in the *várzea* forest. These plots were used as sample units in the beta diversity analysis. Inside each plot we sampled, counted and identified all epiphytes, and trees with DBH ≥ 10 cm that hosted vascular epiphytes (phorophytes). We divided phorophytes into five diametric classes (10-20; 20.1-30; 30.1-40; 40.1-50 and > 50.1). Because the number of arboreal individuals differed between the field sites, we homogenized the same number of phorophytes by randomly selecting the same quantity of trees in each class (Table 1).

Epiphyte survey was conducted using binoculars and photographic cameras, always looking on the phorophytes from two distinct angles as to avoid double counting of individual epiphytes. According to Burns (2007), counting from the forest ground captures up 90 % of epiphytes diversity. Nevertheless, Flores-Palacios & Garcia-Franco (2001), verified that counting from the forest ground underestimate the occurrence of several plant species. Therefore, we climbed four or more trees in each plot in order to account for this bias. We usually climbed trees on the four corners of the plot for a more precise data collection.

If possible, we identified the epiphyte and phorophyte species *in loco* with the help of a parataxonomist experienced in the identification of Amazonian plants. Species that could not be identified in the field were later diagnosed using dichotomic keys, specialized books, comparison with herbarium specimens and/or the help of

experts. For the epiphyte species with vegetative reproduction we considered an individual each cluster of plants distinctively isolated (e.g. rosettes (Bromeliaceae), pseudobulbs, stems, rhizomes (Orchidaceae), stem (Araceae and Clusiaceae), and separated colonies (Gesneriaceae and Piperaceae) (Sanford 1968).

Epiphytes with no flowers during surveys were collected and cultivated in green houses until blooming. Specimens that were too small and unidentifiable such as micro-orchids, aroids and piperaceous were not included in the analysis. In our classification we adopted the APGIII (2009), the valid names on the list of species of the Brazilian flora (Lista de Espécies da Flora do Brasil, 2020) and the International Plant Names Index (www.ipni. org, 2015). We held permits for our activities under SISBIO 45538-2.

Data analysis

We plotted a histogram to visualize the distribution of epiphytes abundance and richness across different diametric classes of phorophytes. Then, we used an Analysis of Covariance (ANCOVA) with standardized data using Log10 to evaluate the relationship between the phorophyte dimeter and the abundance and richness of epiphytes in the two types of forest (*várzea* and *igapó*); with the trees as sample units. To verify how epiphytes are distributed in different dimeter classes of the host tree we applied an ordination analysis, using Bray-Curtis distance as a similarity measure. The epiphyte species represented by less than five individuals were excluded from the ANCOVA and ordination analysis for presenting low representation. Finally, we plotted the ordination graph to visualize the

Table 1. Number of species and individual phorophytes in each diametric class, in *várzea* (Mamirauá RDS) and *igapó* (Jaú PARNA) forests, Central Amazon.

DBH Classes	Várzea		Igapó	
	Phorophyte Species	Phorophyte Individuals	Phorophyte Species	Phorophyte Individuals
10 – 20	36	41	26	41
21,1 – 30	28	28	17	28
31,1 – 40	19	19	13	19
41,1 – 50	20	21	12	21
> 50	25	16	11	16
Total		**125**		**125**

influence of phorophyte diameter in epiphyte composition of both forests.

We measured the dissimilarity between environments (beta diversity) using the Sørensen distance, because it is well known that this measure incorporates both, true spatial turnover and differences in richness (Koleff *et al.*, 2003, Baselga 2010), and visualized it through a NMDS. In order to verify if dissimilarity of epiphyte assemblages between field sites was driven by nestedness we applied the index proposed by Baselga (2010), which quantifies the degree of nestedness between two communities. The values of this index in each forest were then compared through a NMDS. To verify if the dissimilarity between *várzea* and *igapó* was promoted by species turnover we used the Simpson's index that measures the degree of species substitutions between the two areas (Simpson 1943, Baselga 2010). Similarly, we compared these values using a NMDS. We tested the NMDS significance by ANOSIM analyses, which calculates a ratio between within-group and between-group dissimilarities. The process which leads to a greater dissimilarity between assemblages is the one that better explains the beta diversity pattern (Baselga 2010, Baselga & Orme, 2012).

All analyses were conducted in R version 3.5.2 (R Development Core Team 2011). The similarity distances were calculated using the package betapart (Baselga 2012). Ordinations of epiphytes by DBH were developed using generic scripts. The metaMDS, ANOSIM, and ANCOVA analysis were performed using the vegan package (Oksanen *et al.* 2016).

RESULTS

In the *várzea* forest we observed 132 species of phorophytes, on which we found 2968 individuals of vascular epiphytes belonging to 96 species. Twenty species of phorophytes supported 69.5 % of individuals and 63.4 % of all epiphyte species in this environment (Table 2). In the *igapó* forest we identified 111 species of phorophytes, and 653 individuals of epiphytes classified into 37 species. Twenty phorophyte species hosted 72.8 % of individuals and 67 % of the species of epiphytes in this site (Table 2).

Table 2. Twenty main phorophytes and their related richness and abundance of vascular epiphytes. RE – Richness of epiphytes; AE – Abundance of epiphytes; NIH – Number of those single trees with vascular epiphytes. Host trees were ordered according to the associated epiphytes richness.

Várzea's Phorophyte Species	RE	AE	NIH	Igapó's Phorophyte Species	RE	AE	NIH
Leopoldinia pulchra Mart.	11	52	49	*Chrysophyllum argenteum* Jacq.	24	184	06
Erythroxylum spruceanum Peyr.	11	34	06	*Pouteria* sp.	21	182	04
Macrolobiumacaciifolium (Benth.) Benth.	09	62	07	*Tapura guianensis* Aubl.	20	201	02
Aldina latifolia Spruce ex Benth.	08	70	04	*Eschweilera parviflora* (Aubl.) Miers	19	193	02
Amanoa oblongifolia Müll. Arg.	07	11	07	*Hura crepitans* L.	19	128	03
Pouteria elegans (A.DC.) Baehni	06	23	05	*Maquira coriacea* (H.Karst.) C.C. Berg	16	109	01
Diospyros vestita Benoist	06	33	05	*Piranhea trifoliata* Baill.	13	68	07
Swartzia polyphylla DC.	06	19	05	*Pouteria elegans* (A.DC.) Baehni	13	76	11
Tachigali sp.	05	53	12	*Handroanthus barbatus* (E.Mey.) Mattos	13	92	07
Hevea spruceana (Benth.) Müll. Arg.	05	11	04	*Tapura juruana* (Ule) Rizzini	12	37	01

Table 1. ...Continued

Várzea's Phorophyte Species	RE	AE	NIH	Igapó's Phorophyte Species	RE	AE	NIH
Hydrochorea marginata (Benth.) Barneby & J.W.Grimes	05	08	01	*Discocarpus essequeboensis* Klotzsch	11	28	02
Ternstroemia caudalosa Wawra	04	28	05	*Eschweilera ovalifolia* (DC.) Nied.	10	36	04
Micropholis humboldtiana (Roem. &Schult.)	04	49	03	*Micropholis egensis* (A.DC.) Pierre	10	39	02
Eugenia latifolia Aubl.	04	04	02	*Cedrela odorata* L.	09	59	02
Licania apetala (E.Mey.) Fritsch	03	04	03	*Oxandra riedeliana* R.E.Fr.	09	32	03
Ormosia excelsa Benth.	03	03	03	*Glycidendrum* sp.	08	19	01
Leptolobium nitens Vogel	03	05	01	*Ocoteacym barum* Kunth	08	22	02
Couepia sp.	03	05	01	*Attalea phalerata* Mart. Ex Spreng.	07	49	07
Miconia pubipetala Miq.	03	03	01	*Cordia* sp.	07	11	01
Andira micranta Ducke	02	05	02	*Coussapoa nítida* Miq.	07	11	02

In both sites we found more phorophytes (36 %) in the minor diametric class (10-20 cm) in comparison with phorophytes with larger diameters (12,8 % in > 50 cm in diameter; see Table 1). In *várzea*, the richness and abundance of epiphytes was higher in phorophytes with larger diameters, even though there were less individuals observed in this class. Meanwhile, in *igapó* epiphytes were more abundant and richer in phorophytes with smaller diameters (Figure 2). This pattern was confirmed by the ANCOVA which revealed that phorophyte diameter influences positively the richness and abundance of epiphytes in the *várzea* forest (R^2 = 0.23, p = 0.00001 and R^2 = 0.17, p = 0.0001; Figs. 3C and 3D respectively), but not in the *igapó* forest (R^2 = 0.04, p = 0.5 and R^2 = 0.02, p = 0.1; Figs. 3A and 3B respectively).

In each environment, the patterns of alpha diversity were driven by the diameter of the host tree. In the *várzea* forest, there is a species turnover across diameter classes. In the *igapó* forest the species that occur in larger diameters are a subset of species present in smaller diameters (Fig. 4). Beta diversity between *várzea* and *igapó* is mainly structured by the species turnover rather than nestedness (Fig. 5-B e 5-C).

DISCUSSION

Our results for *várzea* forests support the hypothesis that more epiphyte species are found in trees with bigger diameters. Larger trees, possibly the older ones (Schöngart *et al.* 2005, Schöngart 2008), play a key role on the richness and composition of epiphytes in *várzea* forest, and this was also reported in studies conducted in different environments (Johanson 1974, Hietz & Hietz-Seiferd 1995, Callaway *et al.* 2002, Zotz & Volrath 2003, Flores-Palacios & Garcia-Franco 2006, Wolf *et al.* 2009, Wang *et al.* 2017). Nevertheless, this hypothesis was not supported by the results for the *igapó* forest, where the diameter of trees did not influence the richness and composition of epiphytes. In the present study, the diameter of phorophytes varies greatly among species in the same environment and between different ones. Considering that trees in *igapós* grow 2-3 times slower than in *várzeas* the contrast among phorophyte diameters between environments is even more pronounced.

In *igapó* forests trees might reach an old age maintaining a reduced diameter. This increases the time that a tree can serve as substratum and its availability for colonization. Schöngart *et al.* (2005) used dendrochronological analysis to study the tree *Macrolobium acaciifolium* in *várzea* and *igapó* forests. These authors observed that trees with similar diameters presented pronounced age difference, 500 years in *igapó*, while no individuals had more than 200 years in *várzea*. Moreover, trees in *igapó* forests are not "good hosts", because only
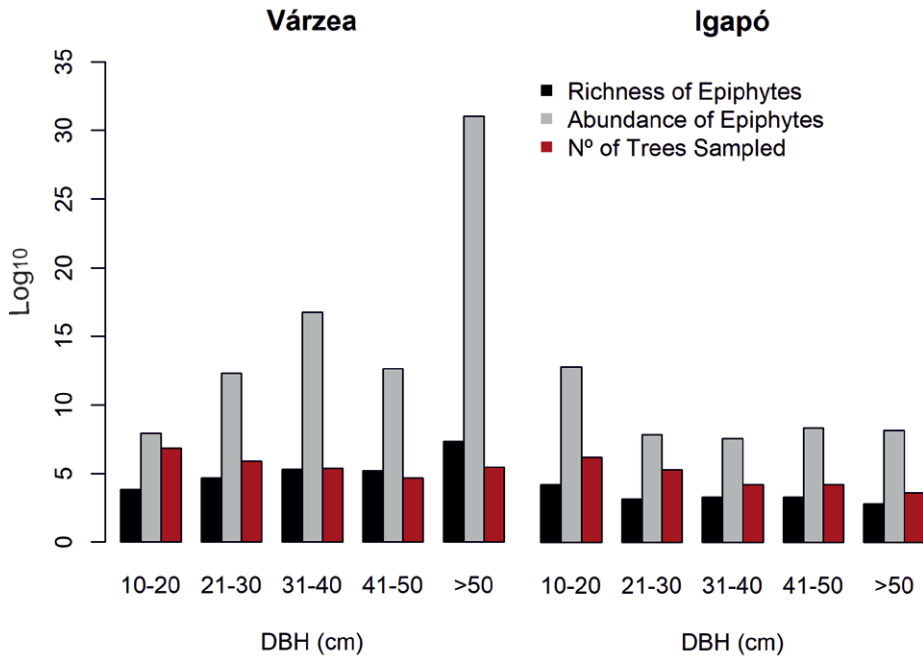
Figure 2. Histogram of the relationship of richness and abundance of vascular epiphytes with the distribution of the number of tree individuals by diameter classes. Richness, abundance and number of trees were standardized by Log10.
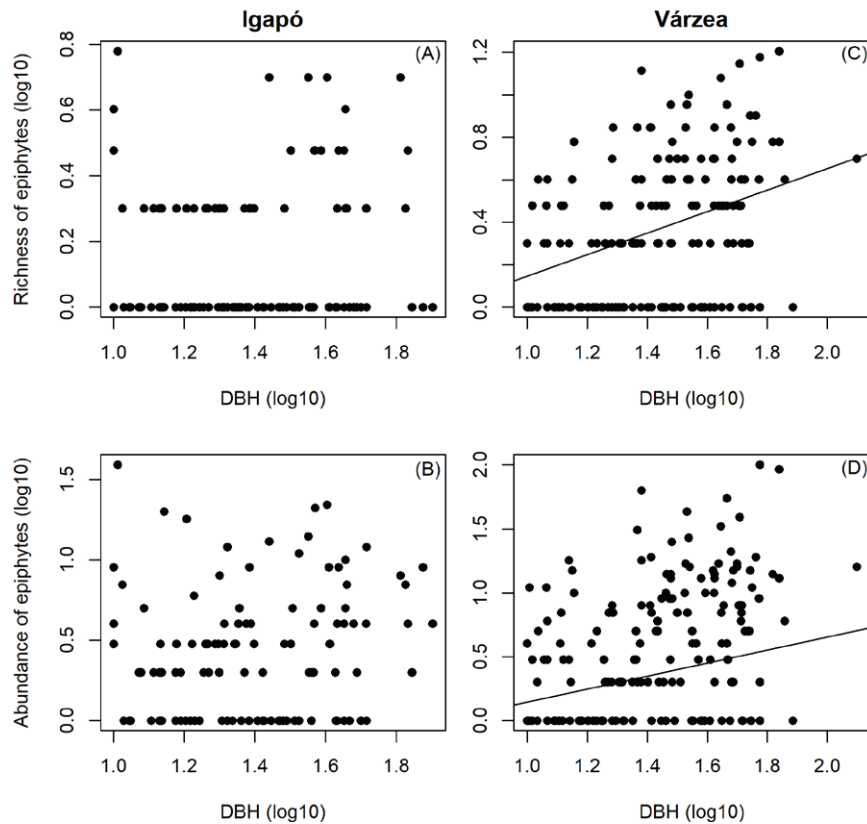
Figure 3. Influence of tree diameter on the richness and abundance of vascular epiphytes, using phorophytes as sample units. The increase in diameter promotes higher epiphyte richness and abundance in the *várzea* forest (Fig. 3C and 3D). No significant correlations were found in the *igapó* forest. Richness and abundance were standardized by Log10.
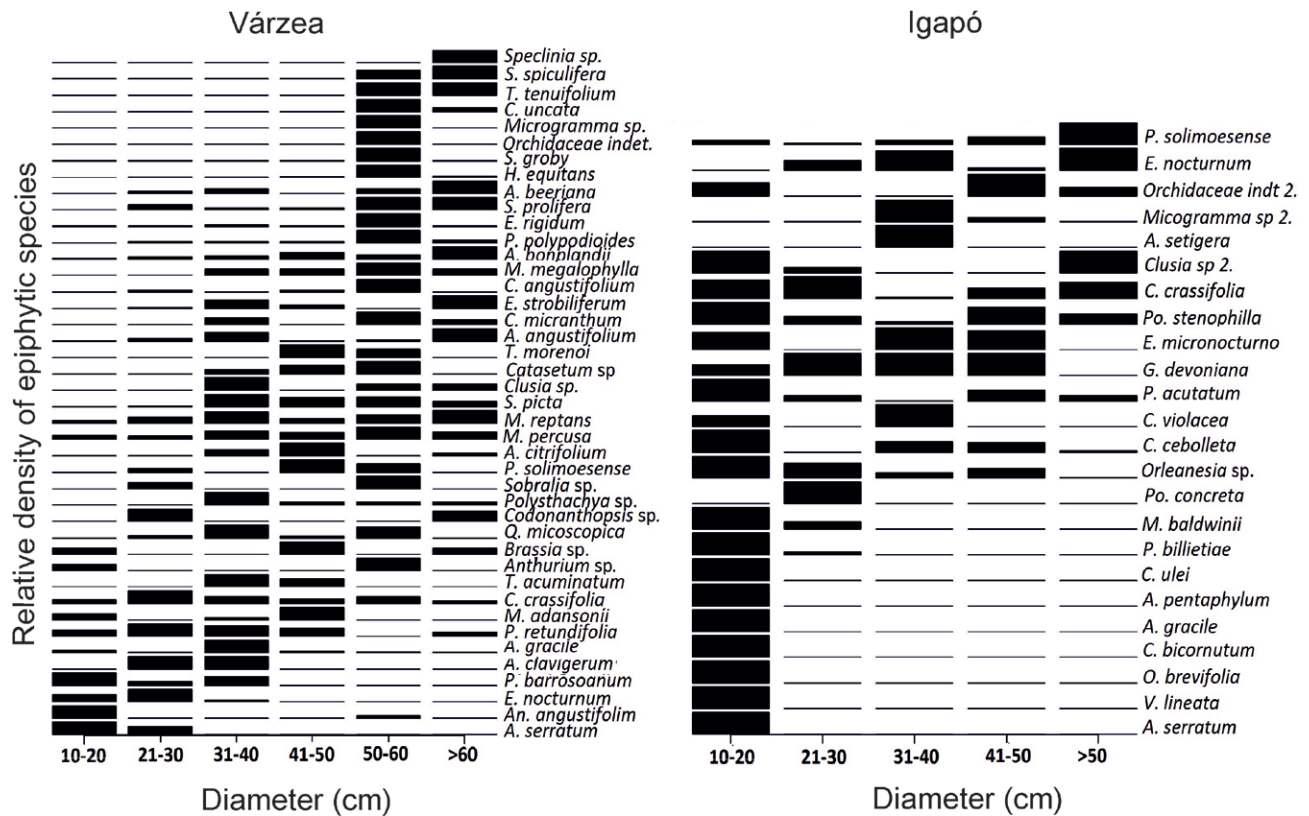
Figure 4. Ordination graph displaying distribution patterns of vascular epiphytes across diametric classes of phorophytes in *várzea* and *igapó* forests. *Várzea* presented species turnover along diameter classes, while *igapó* presented nestedness of epiphytes in trees with smaller diameters.

24.9 % of the individuals and 53 % of the tree species were colonized to epiphytes (Quaresma *et al.* 2018). Also, some epiphyte species show preference for certain phorophytes (13 species, 11.7 %; Quaresma *et al.* 2018), which makes the preferred colonization pattern more important than phorophyte diameter.

The species turnover in várzea is possibly correlated with light gradients, variations in relative air humidity and canopy temperature. Therefore, epiphytes with adaptations to colonize substratum with different establishment times and/or tolerate adverse conditions tend to form groups with different occupation strategies. This is evident in our results for várzea, where ferns (e.g. *A. serratum, A. angustifolium* and *P. barrosoano*), that tolerate shadows and demand high humidity (Pouig 2008, Andrade & Nobel 1997), and hemiepiphytes, that depend on the soil after fixation secondary roots (Zotz 2013), colonized trees with smaller diameters and, likely, with unconsolidated substratum, given they are trees in development. On the other hand, species that tolerate desiccation by wind or sunlight (e.g. *S. spiculifera, T. tenuifolium* and *C. uncata*), occupied large trees, likely with a firm substratum, as they are older trees (Schimper 1888, Benzing

1990). Finally, generalist species with fast growth, able to colonize recent substrata such as smaller trees, occurred in all the range of diameters and are abundant in the studied várzea forest.

Meanwhile, the canopy of igapó forests is less tall and less stratified in comparison with upland forests, resulting in more homogeneous conditions of microclimate, which is usually drier (Resende *et al.* 2014, Almeida *et al.* 2016) and likely drier than várzeas as well (Resende *et al.* 2014, Almeida *et al.* 2016). Epiphytes in igapós also have preference for certain species of trees like *L. apetala, A. latifolia, S. polyphylla, T. caudalosa, E. spruceanum, Tachigali sp., D. vestita, M. humboldiana, P. elegans, H. spruceana, A. oblongifolia* and *M. acaciifolium* (Quaresma *et al.* 2018). We verified that most of these arboreal species belong to minor diameter classes. Thus, nestedness in trees is likely an artefact of differential colonization by vascular epiphytes; on preferred species of phorophytes or due to the environment structure itself.

The spatial species turnover has been previously observed for tree assemblages in tropical forests (Pitman *et al.* 2002, Tuomisto *et al.* 2003, Engelbrecht *et al.* 2007, Condit *et al.* 2013). For
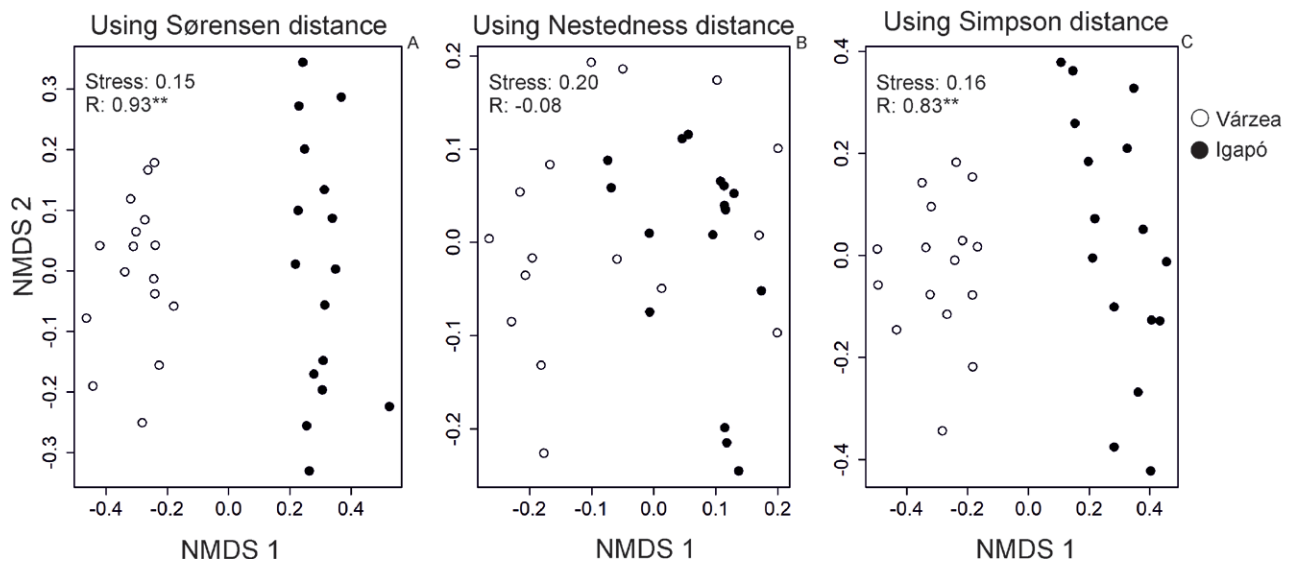
Figure 5. Non-metrical multidimensional scaling (NMDS) using three measures of distance to evaluate differences in the vascular epiphyte composition between *várzea* and *igapó* forests. The (A) graph shows the separation of sampling units by the distance of Sørensen's. (B) shows that this separation is not by a standard nested pattern, and (C) indicates the species turnover between forests, using Simpson's distance. Significance was carried out using ANOSIM analysis. **p-value < 0.005.

epiphytes in a regional scale, was demonstrated that this pattern seems to be driven by an altitudinal gradient (Kuper et al. 2004). As our study area has similar pluviometric indexes (2330 mm/year), our results are in accordance with what was reported for the regional arboreal flora. In a larger (neotropical) scale, rainfall has great influence over the distribution of arboreal species (Muelbert *et al.* 2016). The occurrence of tree species is physiologically limited towards drier environments, leading to species nestedness in forests with higher rainfall (Muelbert *et al.* 2016). Because epiphytes are strongly limited by rainfall (Benzing 1990, Zotz 2016), we believe that species nestedness is the process that explains the beta diversity patterns in a broader geographical scale.

Previous studies have shown that species turnover might occur due to species selection by the environment, interspecific interactions or historical restrictions (Quian *et al.* 2005, Baselga 2008). Non-random interspecific interactions between epiphytes and their host trees might explain the turnover pattern between *igapó* and *várzea*. Preferred selection of trees by epiphytes has been previously documented (Burns & Zotz, 2010). Due to the little similarity between the composition of tree species from *igapó* and *várzea* (Wittmann 2012), the species turnover might be the predominant mechanism, with epiphytes occurring accordingly to singularities of arboreal

assemblages in each environment.

The diameter of the phorophyte, and possibly the time it has been available for colonization, positively influence the richness, abundance and the distribution of epiphytes composition in *várzea*. In *igapó* forests, the diameter was not a predictor of the richness, abundance and distribution of epiphytes. This difference must be addressed by survey methods. In *várzea*, the diameter can be used as a proxy to observe changes of richness and composition of epiphyte species along time, because there is a strong relationship between age and growth. Nonetheless, in *igapós* we suggest that surveys must be directed to some arboreal species that are the preferred sites for epiphytes. This knowledge can assist long-term monitoring projects by directing them to tree species that have greater richness and abundance of epiphytes in these wetland ecosystems.

This is the first time a distinction is made between turnover and nestedness processes for vascular epiphytes in a local and regional scale of the Amazon region. For conservation purposes, the distinction between species distribution process is essential, since they are distinct from each other (Baselga 2010). Conservation efforts should also take into account the difference between *igapó* and *várzea* forests. Even though both forest floodplains are subject to similar rainfall and flood pulses, the patterns that structure epiphytic communities in

our study sites have proved to be very different, with important conservation implications. While in the *várzeas* the maintenance of larger tree species, target of logging, is essential for epiphytic communities, in *igapós* all the diametric classes are of great importance and must be maintained.

Understanding how the floristic composition of epiphytes is distributed along their phorophytes is fundamental to direct future long-term monitoring work focusing on tree species that are key-phorophytes for the composition and diversity of epiphytes. These tree species should be chosen as priority sites following taxonomic and diameter criteria. Additional long-term monitoring can confirm important patterns of distribution and diversity of epiphytes presented in this study and help to predict alterations resulting from deforestation and changes in the hydrological cycle in Amazonian floodplains. In addition, considering that several of the PELD sites are in wetlands, our results point to the relevance of encouraging studies in other ecosystems, to broaden our understanding of the important epiphytic component on a national scale.

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