



Composition, diversity and structure of vascular epiphytes in two contrasting Central Amazonian floodplain ecosystems

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ABSTRACT

Research focusing on assemblages of vascular epiphytes in the Amazon are scarce. This is especially true for Amazonian floodplain forests, for which only two previous studies have been published. We compared composition, richness and structure of epiphyte assemblages in white-water and black-water floodplains (*várzea* and *igapó*) in Central Amazonia in order to close knowledge gaps concerning the distribution and richness of epiphytes. We established sixteen 25x25 m plots in each forest type, and counted and identified all species of vascular epiphytes occurring on trees with a diameter at breast height (DBH) ≥ 10 cm. We observed a clear distinction in epiphytic species composition ($r^2=0.83$, $p=0.001$) and diversity ($t=3.24$, $P=0.003$) between the two environments, with 61.5 % of species being restricted to *várzea*, 22.9 % restricted to *igapó* and only 15.6 % common to both ecosystems. The floodplains were also structurally different for the most abundant species and those with the highest Epiphytic Importance Value (IVE). The diversity of trees did not influence the epiphyte diversity in either ecosystem. The forests were found to differ in the composition, diversity and structure of their epiphytic assemblages, which must be taken into account when designing conservation action plans for these ecosystems and for their vascular epiphytes.

Keywords: Amazon, biodiversity, floodplains, *igapó* forests, *várzea* forests

Introduction

Vascular epiphytes are characterized by using a mechanical host only for support and to reach areas with higher levels of solar radiation. Consequently, they are independent from the soil in terms of physical support, water and nutrient uptake, either during their entire life (holoepiphytes) or during part of it (hemiepiphytes) (Mueller-Dombois & Ellenberg 1974; Benzing 1990; Zotz 2013). Globally, there are some 27,614 known species of epiphytes, with a notably greater diversity in the tropical Americas (Zotz 2013), where more than 100 species can

be found on a single host tree (Schuettpelez & Trapnell 2006).

In the Brazilian Amazon research on vascular epiphytes is mostly concentrated in upland forests (Irumé *et al.* 2013; Boelter *et al.* 2014). However, even in these environments, vascular epiphytes are neglected in conservation action plans, which mostly focus on arboreal species (Obermüller *et al.* 2012). Epiphytes are also poorly sampled in other Amazonian environments, including savannas (Gottsberger & Morawetz 1993), coastal forests (Quaresma & Jardim 2014) and white-sand forests (Steege & Cornelissen 1989; Mari *et al.* 2016)

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While vascular epiphytes are visually highly abundant in Amazonian floodplain forests, to the best of our knowledge there are only two studies that investigated species composition and richness. Nieder *et al.* (2000), in 1.5 ha of a *igapó* forest along of the Suromoni River, Venezuelan Amazon, reported 778 individuals belonging to 53 epiphyte species, where orchids (19 species) and aroids (15 species) were the most abundant families. In another study conducted in 0.3 ha of *várzea* of Colombian Amazon, Benavides *et al.* (2011) also found orchids and aroids to be the most representative families. This scarcity of studies hampers proper management and conservation measures for forestry ecosystems and their epiphyte assemblages. But it is much more serious, because it hampers our understanding of ecosystem functioning.

White-water floodplain forests (*várzea*) and black-water floodplain forests (*igapó*) (*sensu* Prance 1979) cover more than 600,000 km² in the Amazon (Melack & Hess 2010) and are classified based on the physical-chemical features of their waters. *Várzeas* are flooded by river waters with high concentrations of nutrients, while *igapós* are flooded by river waters of low concentration of minerals (Sioli 1984). The difference in fertility is mirrored by tree species richness; in Central Amazonia, *várzea* forests are comparatively species rich (with up to 100 species ha⁻¹), while *igapó* forests are comparatively species poor (with up to 60 species ha⁻¹) (trees ≥ 10 cm dbh) (Wittmann *et al.* 2010; Montero *et al.* 2012). However, these environments are similar in that both are seasonally flooded during the high water (aquatic) phase, and are seasonally dry during the low water (terrestrial) phase (Junk *et al.* 1989). This flood pulse is generally regarded as the main driving force determining patterns of tree species composition in these forests (Junk *et al.* 1989; 2011; Wittmann *et al.* 2004; 2006).

Though there have been several floristic inventories and ecological analyses of Central Amazonian floodplain forests (collated in Junk *et al.* 2010), none inventoried epiphytes. Tree species similarity between *igapó* and *várzea* is low due, mainly, to differences of soil nutrients (Wittmann *et al.* 2010). Each tree species is, in theory, a potentially different niche for epiphytes colonization, because of its size, architecture, chemistry, bark roughness, and phenology. On the other hand, the majority of epiphytes are not connected to the soil as are their arboreal hosts. So, we hypothesize that the epiphyte assemblages will show much higher similarity between ecosystems than do trees.

In this study, we compare the composition, diversity and structure of epiphyte assemblages in two contrasting floodplain ecosystems (*várzea* and *igapó*) in the Central Amazon, in order to verify whether the patterns of similarity of vascular epiphyte and trees are concordant, and also to analyze if the tree diversity influences the diversity of epiphytes. *Várzea* and *igapó* are the most extensive

seasonally-flooded ecosystems in the Amazon, nevertheless, they have long been under anthropogenic pressure from housing construction direct clearance and timber extraction, plant and animal husbandry and illegal logging.

Materials and methods

Study Area

We conducted our study in a *várzea* forest at the Mamirauá Reserve for Sustainable Development (RDS) and an *igapó* forest in Jaú National Park (Parna) (Fig. 1). We selected these study areas because both have well-conserved floodplain forests and reliable inventories for their arboreal species (≥ 10 cm dbh) were available in the database of the INPA-Max Planck project and PELD MAUA Amazonian Humid Areas program.

Jaú National Park (Parna) - *igapó* forest

The Jaú National Park (1°90'S-3°00'S 61°25'W±63°50'W) covers an area of approximately 22,720 km², and is drained by the Jaú and Unini rivers, which are right bank tributaries of the Rio Negro (Ferreira 2000). Mean annual temperature is 26.7 °C, and mean annual precipitation amounts to 2,300 mm. The rainy season occurs from December to May and the dry season from June to September. The flooding cycle is monomodal, with a mean annual amplitude of 8.17 m; highest water levels occur in June and July, and lowest in October and November (Ferreira 2000). The soil is derived from ancient tertiary sediments, with high levels of kaolinitic clay soils and large areas covered by white sands (podzols) (Junk *et al.* 2015).

Aguiar (2015) inventoried nine hectares in *igapó* forests of the Jau River and recorded 6,992 tree individuals ≥ 10 cm dbh, belonging to 193 tree species. The most common tree species in climax stage were: *Pouteria elegans* (A.DC.) Baehni, *Amanoa oblongifolia* Müll. Arg., *Macrobium acaciifolium* (Benth.) Benth., *Elvasia quinqueloba* Spruce ex Engl., *Burdachia* sp., *Eschweilera tenuifolia* (O.Berg) Miers, *Duroia velutina* Hook.f. ex K.Schum., *Swartzia polyphylla* DC., *Hevea spruceana* (Benth.) Müll. Arg. and *Erythroxylum spruceanum* Peyr.

Mamirauá Sustainable Development Reserve (SDR) - *Várzea* forest

Mamirauá SDR is located in the western part of the Central Brazilian Amazon, approximately 30 km NW of the city of Tefé (2°51'S 64°55'W). The reserve covers an area of approximately 11,240 km² of *várzea* forests and is delimited by the Juruá and Amazon/Solimões Rivers and the Auati-Paraná channel (Plano de Gestão 2014). *Várzea* soils generally have high proportions of silt and fine sand, and often are eutrophic (Irion 1984).



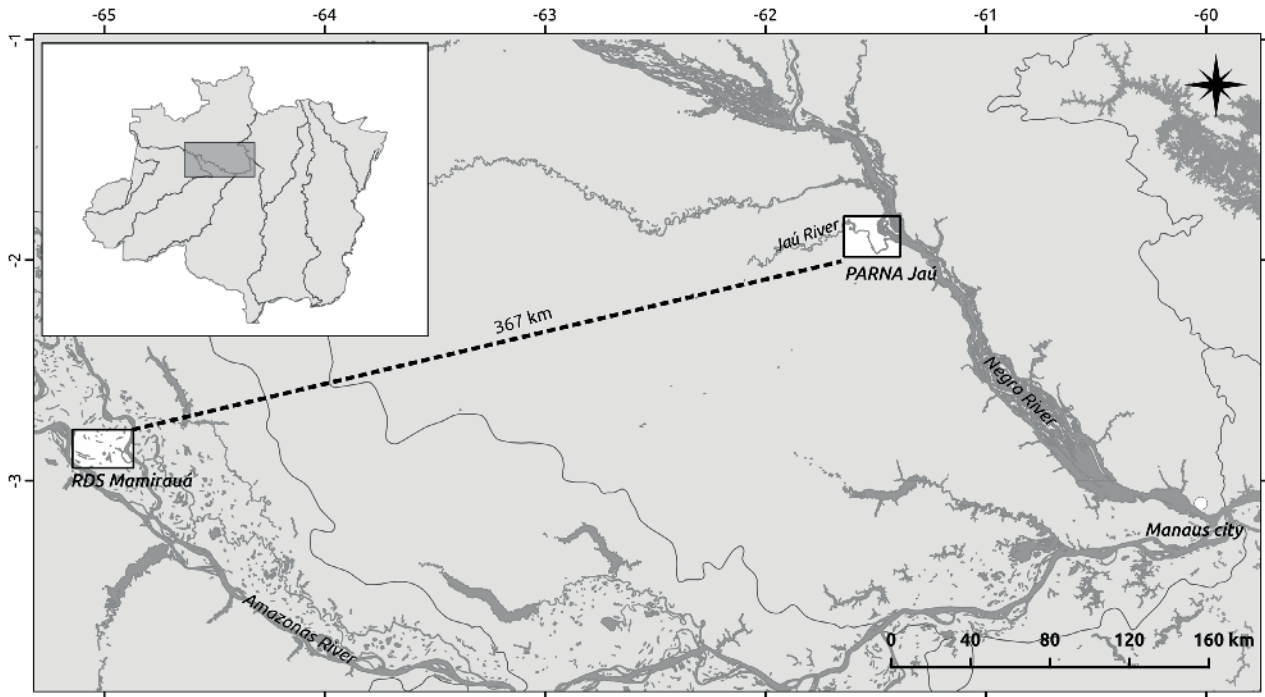


Figure 1. Location map of the study sites in the Reserva de Desenvolvimento Sustentável Mamirauá and Parque Nacional do Jaú.

Wittmann *et al.* (2002) sampled four hectares of *várzea* forest in the Mamirauá SDR and recorded 2,080 individuals from 226 tree species. The most common in the climax stage were *Cecropia latiloba* Miq., *Pouteria procera* (Mart.) K. Hammer, *Oxandra riedeliana* R.E. Fries, *Pouteria polyphleba* Diels (R.E. Fries), *Tabebuia barbata* (E. Mey.) Sandwith, *Mabea nitida* Spruce ex. Benth., *Hevea spruceana* Muell. Arg., *Crataeva benthamii* Eichl., *Malouetia tamaquariana* A.D.C., *Aspidosperma riedelii* Muell. Arg., *Gutteriopsis paraensis* R.E. Fries.

Data collection

For epiphyte inventories, we selected 16 plots of 25 x 25 m within forest plots previously established in each ecosystem - for an inventoried area total of 1 ha in size. Sampling was conducted only in climax forest (see Wittmann *et al.* 2002; Junk *et al.* 2015), so that the forest structure was similar. Also, we standardized marking of plots at the same flood level in both environments.

We sampled, counted and identified all individuals of all vascular epiphyte species occurring on trees ≥ 10 cm DBH. We conducted our sampling with the help of binoculars and a digital camera, searching each host tree from two opposite angles, to avoid counting specimens twice. We also climbed at least four host trees per plot. When possible we climbed the four largest host trees within the plot, to facilitate specimen visualization, count and collecting of epiphytes in the largest possible number of surrounding trees.

For epiphyte species that produce distinct individuals we considered each distinctively isolated group, such as rosettes

(Bromeliaceae), pseudobulbs, stems, rizhomes (Orchidaceae) and stems (Araceae and Clusiaceae) as one individual; for species that occur in colonies (Gesneriaceae and Piperaceae), “clusters of branches” were considered unique when distinctly separated from other individuals on the host tree. So, in both cases have we considered “individuals” groups that were separated from each other (Sanford 1968).

When possible the species were identified *in loco*, samples fertile or sterile of species were collected for posterior identification using dichotomous keys (Cruz 1994; Cruz & Braga 1997), specialized books (Ribeiro *et al.* 1999; Zuquim *et al.* 2008), comparisons with herbarium material (INPA Herbarium and Herbarium MG) and/or with the help of experts. For a more complete list of vascular epiphytes, we also surveyed trees around the plots for a qualitative assessment. Samples sterile were grown in a greenhouse until the opening of the flowers. Fertile plants are in the process of being incorporated in the INPA Herbarium. We classified species following APG III (2009) and used valid names according to the species list of the Brazilian flora (Flora do Brasil 2020).

The variety of life-form classifications for epiphytes (Benzing 1990) has the potential to confuse (see Zotz 2013). Consequently, we opted to divide epiphytes into ecological life-forms, and classified epiphytes, and classified epiphytes, through literature and also in field observations, as: 1) holo-epiphytes; species that sprout and grow on other plants and never have permanent contact with the soil, and hemi-epiphytes; species that sprout and grow on other plants but subsequently maintain contact with the soil by means of secondary

roots. In this study we followed Fontoura *et al.* (2009) and considered species with only two individuals or less per hectare (low abundance) or that only occupies up to two trees (low distribution) rare, and considered species with five or more individuals or groups on trees abundant.

Data analysis

We used a rarefaction method to compare the number of species found and estimate sampling sufficiency in the two forests (Gotelli & Colwell 2010). We calculated similarity as the percentage of species exclusive to each environment and the percentage of species that were common to both environments. In order to evaluate the epiphytic composition between the two environments we used a non-metric multidimensional scaling (NMDS), using Bray-Curtis distance for species abundance. We tested the NMDS significance using Analysis of Similarity (ANOSIM).

Alpha diversity of the each epiphyte and tree assemblage was calculated using Fisher's coefficient of diversity (Fisher *et al.* 1943), including all individuals and species per plot, including distinguishable morpho-species. The Student t test was applied to compare the diversity between two environments. We tested the influence of tree diversity on epiphyte diversity with ANCOVA analysis, using the environments as factor.

We used a rank graph to test the distribution of species abundances in the two assemblages. A quantitative evaluation of epiphyte species was conducted using absolute and relative frequencies on individual host trees (FA_i, FR_i) and on specific host trees (FA_j, FR_j); the value of epiphytic importance (IV_e) was calculated using both types (FR_i and FR_j) of relative frequency (Waechter 1998), as follows:

$$\begin{aligned} \text{FA}_i &= (\text{Nfi} / \text{Nfa}).100 \\ \text{FR}_i &= (\text{Nfi} / \sum \text{Nfi}).100 \\ \text{FA}_j &= (\text{Sfi} / \text{Sfa}).100 \\ \text{FR}_j &= (\text{Sfi} / \sum \text{Sfi}).100 \\ \text{IV}_e &= (\text{FR}_i + \text{FR}_j) / 2 \end{aligned}$$

where, Nfi is the number of host trees occupied by the epiphyte species *i*; Nfa the total number of host trees species in the sample; Sfi the number of host trees occupied by the epiphyte species *i*; Sfa= the total number host trees species in the sample; and IV_e the value of epiphytic importance. These parameters translate the species capacity by means of reproduction and dispersion in the environment (FR_i), and their capacity to colonize different substrata (FR_j), which in turn express themselves in the ecological importance of each species (IV_e) (Waechter 1998).

We conducted all analyses in R (R Development Core Team 2011). Anosim and ANCOVA were conducted in the vegan package (vegan: Community Ecology Package 2016); metaMDS in vegan was also used for the NMDS analysis.

Results

Composition and diversity

In total and from both environments, we recorded a total of 2,922 individuals, belonging to 96 species, 59 genera and 13 families of epiphytes. Fifty-six (59.3 %) of these were Orchidaceae. Other important families were Araceae (11 species, 11.4 %) and Polypodiaceae (eight species, 8.3 %) (Tab. 1). In the *várzea* forest, we recorded 459 individuals from 132 tree species, of which 181 had 2,968 individuals and 96 species of vascular epiphytes (Fisher's alpha = 18.97), belonging to 13 families, 47 genera and 73 species. In the *igapó* forest we recorded 662 individuals from 111 tree species, of which 165 trees hosted 653 epiphyte individuals belonging to 9 families, 21 genera and 37 species (Fisher's alpha = 8.6). Orchidaceae dominated in both *várzea* and *igapó* (39 and 19 species, respectively), followed by Araceae (nine and five species) and Polypodiaceae (seven and three species).

The rarefaction shows that for the same sample effort, the curve in *igapó* forest tends to stabilize around 37 species. However, for the *várzea* forest that sampling effort seemed inadequate and even with a great number of species recorded for the area the rarefaction curve did not tend to stabilization (Fig. 2). In *várzea* and *igapó*, 61.5 % and 22.9 % of all recorded species were exclusive, while 15.6 % of all species were common to both environments.

Holo-epiphytism is the predominant life-form (a total of 85 species, 88.6 %, in both environments combined: Tab. 1), while 11 (11.4 %) hemi-epiphyte species were found. Holo-epiphytes represented 86.4% of species in *várzea* forest and 91.9 % of species in *igapó* forest. On the other hand, hemi-epiphytes represented 13.6 % of species in *várzea* forest and 8.1 % in *igapó* forest.

Fisher's Alpha for epiphytes varied from 1.3 ± 8.3 in *igapó* and 3.2 ± 8.3 in *várzea* (Fig. 3A). For trees the values were 3.4 ± 25.9 in *igapó* and 5.4 ± 53.2 in *várzea* (Fig. 3B). Forests differed in the diversity of both their epiphyte ($t=3.24$, $P=0.003$) and tree ($t=2.03$, $P=0.05$) assemblages. However, tree diversity did not explain the diversity of vascular epiphytes in *várzea* forest ($r^2 = -0.03$, $P = 0.4$, Fig. 3C). While in *igapó* forest, though it was not significant ($r^2 = -0.01$, $P = 0.27$; Fig. 3D), it did show a trend.

Structure

Results show a clear compositional distinction of vascular epiphytes between *várzea* and *igapó* forests ($r^2=0.83$, $p<0.001$), as indicated in the first NMDS displaying two well-defined groups (Fig. 4). Both environments are dominated by few, very abundant, species, and many species with a low number of individuals that can be considered as rare (Tab. 2, Fig. 5). Nevertheless, the most abundant species differ between



Table 1. Floristic composition and life-form of vascular epiphyte assemblages of várzea and igapó forests in Central Amazonia. HM – Hemiepiphytes. HO – Holoepiphytes.

Family	Species	Habitat		Life form
		Várzea	Igapó	
Araceae	<i>Anthurium clavigerum</i> Poepp.	09	-	HM
	<i>Anthurium bonplandii</i> Bunting	45	-	HO
	<i>Anthurium gracile</i> (Rudge) Schott	45	05	HO
	<i>Anthurium pentaphyllum</i> (Aubl.) G. Don	02	05	HM
	<i>Anthurium</i> sp.	03	-	HM
	<i>Philodendron</i> sp.	04	-	HM
	<i>Philodendron acutatum</i> Schott	-	09	HM
	<i>Philodendron billietiae</i> Croat	02	27	HM
	<i>Philodendron solimoesense</i> A.C.Sm.	07	40	HM
	<i>Philodendron barrosoanum</i> G.S.Bunting	26	-	HM
Aspleniaceae	<i>Monstera adansonii</i> Schott	23	-	HM
	<i>Asplenium angustifolium</i> Michx	51	-	HO
Bromeliceae	<i>Asplenium serratum</i> L.	68	06	HO
	<i>Aechmea beeriana</i> L.B.Sm. & M.A.Spencer	19	-	HO
	<i>Aechmea mertensii</i> (G.Mey.) Schult. & Schult.f.*	01	01	HO
	<i>Aechmea setigera</i> Mart. ex Schult. & Schult.f.	-	02	HO
Cactaceae	<i>Araeococcus micranthus</i> Brongn*	-	01	HO
Clusiaceae	<i>Epiphyllum</i> sp.	04	01	HO
Cyclantaceae	<i>Clusia</i> sp.	05	13	HM
Gesneriaceae	<i>Cyclantaceae</i> ind.	01	-	HM
Orchidaceae	<i>Codonanthesis crassifolia</i> (H. Focke) Chautems & M. Perret	114	205	HO
	<i>Codonanthesis ulei</i> Mansf.	08	11	HO
	<i>Codonanthesis</i> sp1	05	-	HO
	<i>Aganisia cyanea</i> (Schltr.) Rchb.f.*	-	01	HO
	<i>Bifrenaria</i> sp.	05	-	HO
	<i>Brassia</i> sp.	02	-	HO
	<i>Brassavola martiana</i> Lindl.	-	02	HO
	<i>Caularthron bicornutum</i> (Hook.) Raf.	-	02	HO
	<i>Camaridium micranthum</i> M.A. Blanco	105	-	HO
	<i>Catasetum</i> sp.	01	-	HO
	<i>Cattleya violacea</i> (Kunth) Rolfe	03	05	HO
	<i>Cohniella cebolleta</i> (Jacq.) Christenson	-	35	HO
	<i>Christensonella uncatata</i> (Lindl.) Szlach., Mytnik, Górniak & Śmiszek	255	-	HO
	<i>Dickeya</i> sp.	02	-	HO
	<i>Dichaea ancoraelabia</i> C. Schweinf.	-	03	HO
	<i>Epidendrum coronatum</i> Ruiz & Pav.	02	-	HO
	<i>Epidendrum micronoctrinum</i> Carnevali & G.A.Romero	-	42	HO
	<i>Epidendrum nocturnum</i> Jacq.	09	15	HO
	<i>Epidendrum schlechterianum</i> Ames	02	-	HO
	<i>Epidendrum</i> sp.	04	-	HO
	<i>Epidendrum strobiliferum</i> Rchb. f.	31	-	HO
	<i>Epidendrum rigidum</i> Jacq.	64	08	HO
	<i>Galeandra devoniana</i> M.R.Schomb. ex Lindl.	-	13	HO
	<i>Heterotaxis equitans</i> (Schltr.) Ojeda & Carnevali	82	-	HO
	<i>Maxillaria</i> sp.	01	-	HO
	<i>Trichocentrum morenoi</i> (Dodson & Luer) M.W.Chase & N.H.Williams	05	-	HO
	<i>Octomeria brevifolia</i> Cogn.	-	40	HO
	<i>Octomeria</i> sp.	-	01	HO
	Orchidaceae 1	-	10	HO
	Orchidaceae 2	-	13	HO
	Orchidaceae 3	-	01	HO
	Orchidaceae 4	01	-	HO



Table 1. Cont.

Family	Species	Habitat		Life form
		Várzea	Igapó	
Orchidaceae	Orchidaceae 5	01	-	HO
	Orchidaceae 6	01	-	HO
	Orchidaceae 7	01	-	HO
	<i>Orleanesia</i> sp1	-	23	HO
	<i>Orleanesia</i> sp2	01	-	HO
	<i>Plectrophora iridifolia</i> (Lodd. ex Lindl.) H.Focke	01	-	HO
	<i>Pleorothalis</i> sp.	66	-	HO
	<i>Polystachya</i> sp1	07	-	HO
	<i>Polystachya</i> sp2	01	-	HO
	<i>Polystachya concreta</i> (Jacq.) Garay & Sweet	-	28	HO
	<i>Polystachya stenophylla</i> Schltr.	-	52	HO
	<i>Prosthechea vespa</i> (Vell.) W.E.Higgins	-	04	HO
	<i>Prosthechea fragrans</i> (Sw.) W.E.Higgins	01	-	HO
	<i>Rudolfiella aurantiaca</i> (Lindl.) Hoehne	-	01	HO
	<i>Queketia</i> sp.	05	-	HO
	<i>Quekettia microscopica</i> Lindl.	57	-	HO
	<i>Scaphyglottis prolifera</i> (R.Br.) Cogn.	20	-	HO
	<i>Laelia gloriosa</i> (Rchb.f.) L.O.Williams	01	-	HO
	<i>Sobralia</i> sp.	13	-	HO
	<i>Aspasia variegata</i> Lindl.	01	-	HO
	<i>Specklinia picta</i> (Lindl.) Pridgeon & M.W.Chase	127	-	HO
	<i>Specklinia spiculifera</i> (Lindl.) Pridgeon & M.W.Chase	99	-	HO
	<i>Specklinia grobyi</i> (Batem. ex Lindl.) F.Barros	23	-	HO
	<i>Specklinia</i> sp.	21	-	HO
	<i>Stelis</i> sp.	10	-	HO
	<i>Trigonidium acuminatum</i> Batem. ex Lindl.	01	-	HO
<i>Trigonidium tenue</i> Lodd.	07	-	HO	
Piperaceae	<i>Peperomia rotundifolia</i> (L.) Kunth	178	-	HO
Polypodiaceae	<i>Peperomia urocarpa</i> Fisch. & C.A.Mey.	02	-	HO
	<i>Campyloneurum angustifolium</i> (Sw.) Fée	48	-	HO
	<i>Campyloneurum phyllitidis</i> (L.) C. Presl	01	-	HO
	<i>Microgramma</i> sp.	16	01	HO
	<i>Microgramma baldwinii</i> Brade	-	19	HO
	<i>Microgramma megalophylla</i> (Desv.) de la Sota	08	01	HO
	<i>Microgramma percussa</i> (Cav.) de la Sota	105	-	HO
	<i>Microgramma reptans</i> (Cav.) A.R.Sm.	223	-	HO
<i>Pleopeltis polypodioides</i> (L.) Andrews & Windham	183	-	HO	
Pteridaceae	<i>Anetium citrifolium</i> (L.) Splitg.	21	-	HO
	<i>Vittaria lineata</i> (L.) Sm.	-	12	HO
Lomariopsidaceae	<i>Ananthacorus angustifolius</i> (Sw.) Underw. & Maxon	01	-	HO
	<i>Nephrolepis</i> sp.	02	-	HO
Lycopodiaceae	<i>Phlegmariurus</i> sp.	01	-	HO
	Unknown Lycophyte	01	-	HO
	Total	2268	654	

assemblages; among the 15 overall most abundant species, only *Codonanthopsis crassifolia* occurred in both forests. Species in the várzea had higher absolute and relative abundance than those in igapó. In várzea, *Cristensonela uncatata* was the most abundant species (255 individuals), followed by *Microgramma reptans* (223 individuals), *Pleopeltis polypodioides* (183 individuals), *Peperomia rotundifolia* (178 individuals) and *Specklinia picta* (127 individuals). In igapó the most abundant

species were *C. crassifolia* (205 individuals), *Polystachya stenophylla* (52 individuals), *Epidendrum micro nocturnum* (42 individuals), *Octomeria brevifolia* (40 individuals) and *Philodendron solimoesensis* (40 individuals).

Analysis of frequencies and species importance values indicates that the structure of várzea and igapó forests differs considerably (Tab. 1). Only *C. crassifolia* showed high importance values in both environments, while among



the 20 most important species, 19 were exclusive to one of the two habitats. The 20 most important species were responsible for 86.7 % of the IVE in *várzea* and 95 % of the IVE in *igapó*, indicating that few species have high importance in terms of abundance and colonization of host trees in these forest types.

Discussion

Composition and diversity

Studies in Central Amazon floodplain forests have already shown that the number and diversity of tree and herbaceous species are higher in *várzea* forests than in *igapó* (i.e. Prance 1979; Ayres 1993; Haugaassen & Peres 2006; Inuma 2006). This was the case in the present work for

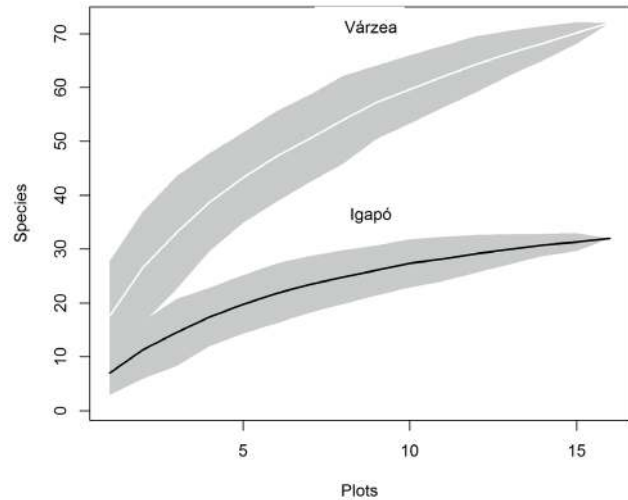


Figure 2. Rarefaction curves showing the sampling sufficiency in each environment.

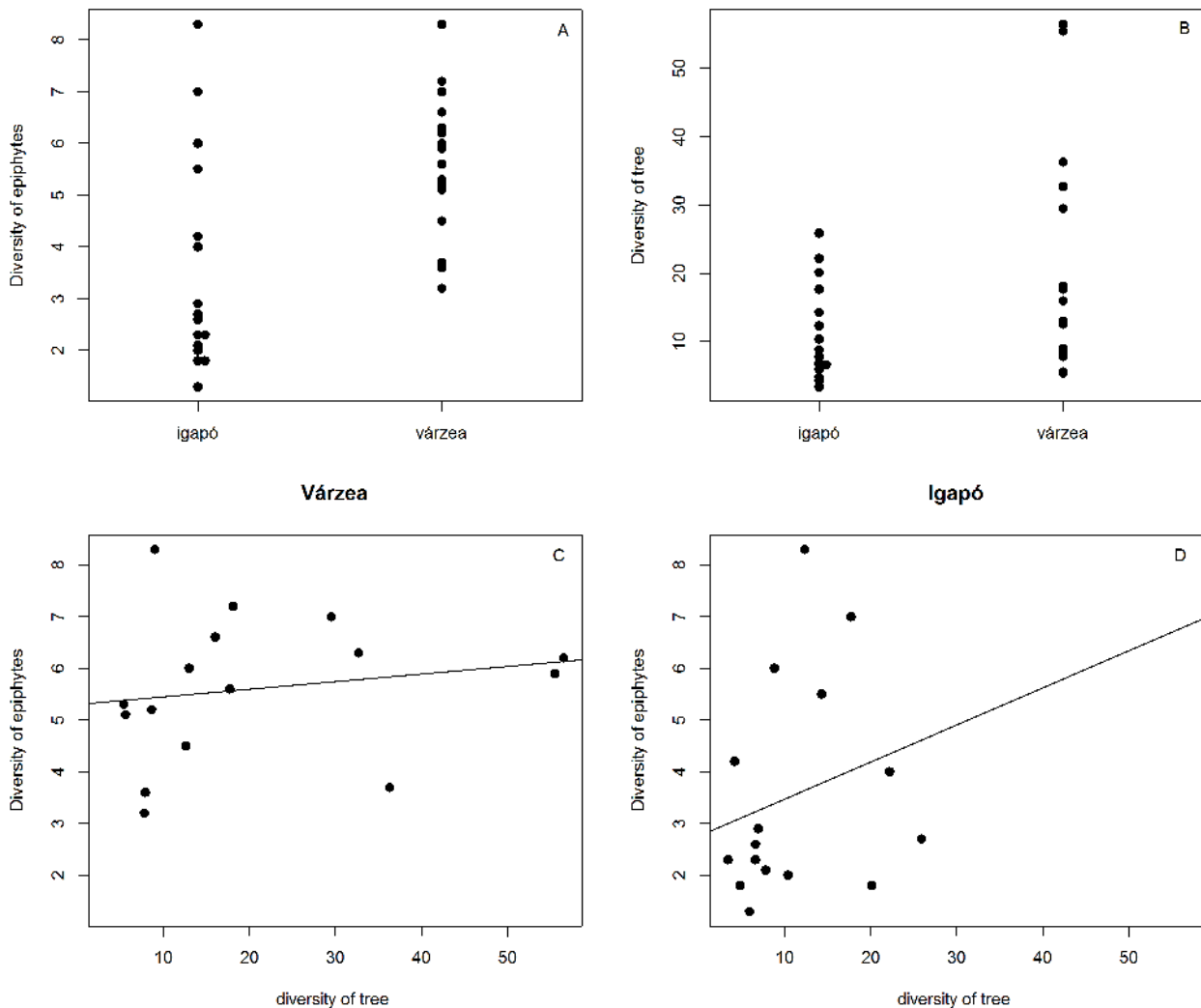


Figure 3. Difference of the diversity of epiphyte assemblages (A) and tree assemblages (B) in plot of *várzea* and *igapó* forest of Central Amazonia. Despite a difference in diversity between the forests, diversity of trees did not influence diversity of epiphytes in the studied forests (C-D).

the trees and vascular epiphyte. *Várzea* environments are characterized by relatively high nutritional richness and river dynamics that provide high habitat heterogeneity and proportionate higher diversity when compared to nutrient poor and low dynamic of the *igapó* river systems (Wittmann *et al.* 2012; Junk *et al.* 2015).

Differences in epiphyte diversity may be associated with differences in tree diversity between environments. Epiphytes are dependent on support structure, and they evolved a variety of ways to colonize various tree species and avoid competition. Consequentially, structural host preference of particular epiphytes means that the composition of local tree assemblages can potentially have a strong influence on epiphyte species assemblage composition, (Laube & Zotz 2006; Burns & Zotz 2010). This was shown by Zotz *et al.* (2014) who investigated canopy of a montane forest in Panama, and found that epiphytes cease to occupy certain habitats not because of climatic adversity, but due to the lack of adequate substrate for colonization. Other supporting evidence comes from observations that epiphyte diversity decreased in areas that suffered a reduction in the tree diversity of primary forest species, and where secondary forests dominated (Bartholott *et al.* 2001; Wolf 2005).

While vascular epiphytes are not attached to the soil, Gentry & Dodson (1987) suggest that their richness and composition vary according to soil fertility, as occurs with other plant groups such as trees. In support of this, Boelter *et al.* (2014) demonstrated that soil phosphorus (P) concentration was the most important factor in explaining the vascular epiphyte richness of in Central Amazonian *terra firme* forest. Even though the differences in P levels between *várzea* and *igapó* forests are small, the proportion of this nutrient available to be passed from soil to trunk, branches and leaves is higher in *várzea* (Furch 1997). Of the 41kg/ha⁻¹ of phosphorus present in *igapó*, only 4 kg/ha⁻¹ (9.7 %) is passed to the above-ground plant biomass. In contrast, out of the 49 kg/ha⁻¹ P in *várzea* soil, 24 kg/ha⁻¹ (49.9 %) is passed to the above-ground plant biomass (Furch 1997). Thus, it is expected that a greater amount of this nutrient is absorbed by epiphytes through lixiviation of rainwater passing along host tree stem and branches and/or by the accumulation of humus in-between branches, which may explain the higher epiphyte species richness in *várzea* environment.

Nutrients might also be carried from the soil to the canopy by animals, especially invertebrates that perform vertical movements to avoid inundation (Adis & Messer 1997). Martius (1997) observed that the canopy is the habitat most used by termites in *várzea* forests. All the trees we climbed in *várzeas* were occupied by termites or ants or both, while this is much less common in *igapó* trees. These animals use, at least as passageway, epiphyte species and thus might contribute carrying nutrients from the soil.

Vascular epiphytes occur at greater richness and abundance on trees with bigger diameters, because those have more substratum available for colonization (Flores-Palacios & García-Franco 2006). *Várzea* forests have twice as much of wood and bark biomass as *igapó* (7.4 t/ha⁻¹ in *várzea* and 3.4 t/ha⁻¹ in *igapó*) (Furch 1997), and consequently twice as much substratum available for epiphyte colonization. Large tree species unique in *várzea* such as *Hura creptans*, *Piranea trifoliolata* and *Crisophyllum argenteum* may increase the number of specific microhabitats available for colonization for epiphytes.

The family composition in the two environments followed a pantropical trend, with Orchidaceae dominant over other

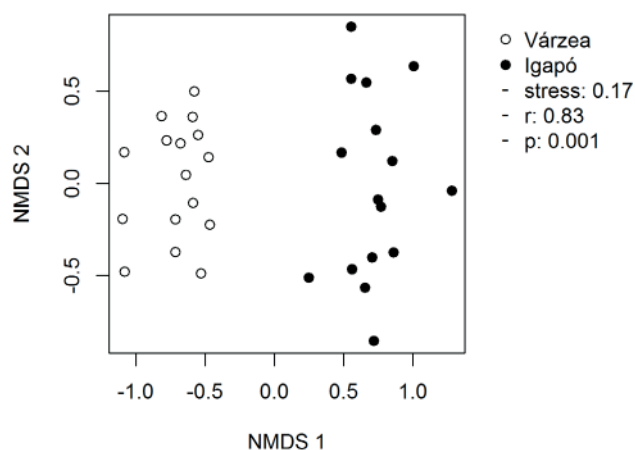


Figure 4. Non-metric Multidimensional Scaling (NMDS) showing the separation of the composition of epiphytic species between the *várzea* and *igapó*, floodplain forests indicating the existence of two distinct groups.

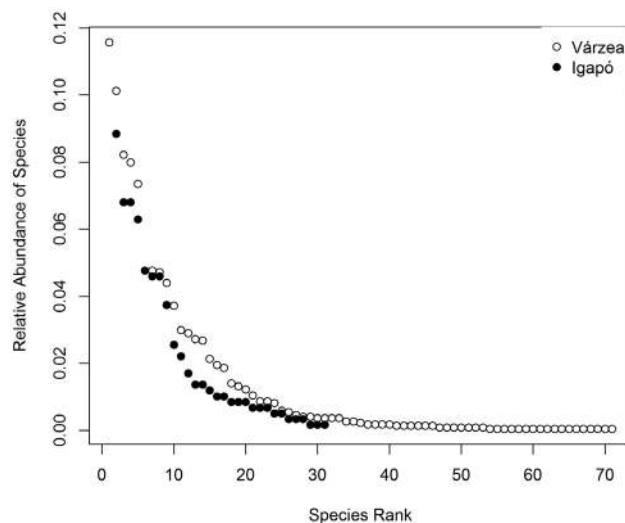


Figure 5. Abundance ranking of epiphyte species found in *várzea* and *igapó* forests in Central Amazonia. Black circles represent *igapó* species and empty circles *várzea* species.

Table 2. Structural parameters of the 20 main vascular epiphyte species from *várzea* and *igapó* forests in Central Amazonia. Fai – absolute frequency of epiphyte species on individual host trees; FRi – relative frequency of epiphyte species on individual host trees; FAj – absolute frequency of epiphyte species on specific host trees; FRj – relative frequency of epiphyte species on specific host trees; IVe – value of epiphytic importance.

VÁRZEA						IGAPÓ					
Species	Fai	FRi	FAj	FRj	IVe	Species	Fai	FRi	FAj	FRj	IVe
<i>M. reptans</i>	45.26	13.69	59.78	10.54	12.12	<i>C. crassifolia</i>	32.12	21.73	53.70	19.34	20.54
<i>P. rotundifolia</i>	33.68	10.19	50.00	8.81	9.50	<i>P. solimoesensis</i>	10.30	6.97	20.37	7.34	7.15
<i>C. crassifolia</i>	24.74	7.48	38.04	6.70	7.09	<i>Philodendron</i> sp.	15.76	10.66	9.26	3.33	7.00
<i>M. percusa</i>	19.47	5.89	33.70	5.94	5.92	<i>Orleanesia</i> sp.	8.48	5.74	16.67	6.00	5.87
<i>P. polypodioides</i>	18.95	5.73	30.43	5.36	5.55	<i>C. cebolleta</i>	9.09	6.15	14.81	5.33	5.74
<i>A. bomplantii</i>	14.21	4.30	23.91	4.21	4.26	<i>E. micronocturnum</i>	6.06	4.10	16.67	6.00	5.05
<i>A. gracile</i>	10.00	3.03	19.57	3.45	3.24	<i>Clusia</i> sp.	6.67	4.51	14.81	5.33	4.92
<i>A. angustifolium</i>	8.95	2.71	17.39	3.07	2.89	<i>P. stenophylla</i>	6.67	4.51	12.96	4.67	4.59
<i>H. equitans</i>	10.00	3.03	15.22	2.68	2.85	<i>G. devoniana</i>	7.27	4.92	11.11	4.00	4.46
<i>C. micrantun</i>	8.42	2.55	15.22	2.68	2.61	<i>P. acutatum</i>	4.85	3.28	14.81	5.33	4.31
<i>C. uncata</i>	8.42	2.55	14.13	2.49	2.52	<i>E. nocturnum</i>	4.24	2.87	9.26	3.33	3.10
<i>A. angustifolium</i>	7.37	2.23	15.22	2.68	2.46	<i>P. concreta</i>	3.03	2.05	9.26	3.33	2.69
<i>Epiphilum</i> sp.	1.05	0.32	23.91	4.21	2.27	<i>C. bicornutum</i>	3.64	2.46	7.41	2.67	2.56
<i>Monstera</i> sp.	7.89	2.39	10.87	1.92	2.15	<i>V. lineata</i>	4.24	2.87	3.70	1.33	2.10
<i>Aechmea</i> sp.	6.84	2.07	11.96	2.11	2.09	<i>C. ulei</i>	2.42	1.64	5.56	2.00	1.82
<i>E. rigidum</i>	6.84	2.07	11.96	2.11	2.09	<i>P. vespa</i>	1.82	1.23	5.56	2.00	1.62
<i>C. angustifolium</i>	5.79	1.75	9.78	1.72	1.74	<i>A. serratum</i>	3.64	2.46	1.85	0.67	1.56
<i>E. strobiliferum</i>	5.79	1.75	9.78	1.72	1.74	<i>C. violacea</i>	1.82	1.23	3.70	1.33	1.28
<i>Philodendron</i> sp.	5.26	1.59	7.61	1.34	1.47	<i>A. setigera</i>	1.21	0.82	3.70	1.33	1.08
<i>S. spiculifera</i>	4.74	1.43	7.61	1.34	1.39	<i>B. martiana</i>	1.21	0.82	3.70	1.33	1.08

families (*i.e.* Laube & Zotz 2003; Wang *et al.* 2016). This tendency has been widely observed in Amazonian forests (Nieder *et al.* 2000; Pos & Slegers 2010; Obermüller *et al.* 2012; Quaresma & Jardim 2014; Boelter *et al.* 2015), except for the study of Irueme *et al.* (2013) in upland forests (*terra firme* forests), where Araceae was the most speciose family recorded. The development of velamen, pseudobulbs for water storage and the CAM metabolic pathway (Benzing 1990; Zotz 2004) are some of the adaptations given as the reasons for the success of orchids in colonizing tropical trees, which make them the epiphyte family with the highest number of species (Zotz 2013). Albeit highly diverse, orchid species were not abundant (see appendix), and the most abundant species were concentrated in few phorophyte species. This aggregated distribution is possibly linked to the dispersal limitations of many orchid species (Mondragon *et al.* 2012), or to the preference for specific tree species, as it is commonly registered for epiphyte assemblages (Burns & Zotz 2010).

The holoeiphyte life-form, dominant in the studied areas, was also reported as predominant for tropical forests canopies (*i.e.* Kersten 2010; Zotz 2013), including Amazonian *terra firme* (Pos & Slegers 2010; Boelter *et al.* 2015) and coastal forests (*restinga* forests) (Quaresma & Jardim 2014). Holoeiphytes are also dominant in forests of the Venezuelan and Colombian Amazon (Nieder *et al.* 2000; Benavides *et al.* 2011, respectively).

It is likely that seasonal inundation creates conditions of high humidity (Benavides *et al.* 2011). This fact, associated with a rapid propagation due to the extensive production

of anemochoric seeds (Cascante-Marin 2006), may greatly facilitate holo-epiphyte establishment and growth. On the other hand, hemi-epiphytes produce fewer seeds (Benzing 1990), and often depend on other dispersers, especially birds and bats, to carry them to suitable germination sites. Annual inundation is also a factor that may limit the occurrence of hemi-epiphytes in both environments as, their post-germination roots subsequently reach the soil and capture nutrients. The greater number of hemi-epiphytes species in *várzea* than *igapó* is probably related to the higher nutrient richness of soils in this ecosystem. Thus, even though inundation may be a limiting factor, our hypothesis is that the occurrence of species able to develop secondary roots would be advantageous, given the nutrient-rich soil.

Structure

The majority of locally rare species are almost always more abundant in another geographical area (Murray & Lepschi 2004; Zotz 2007), making the concept of “rarity” and “abundant” somewhat arbitrary. An example from our study involves two aroid species (*Philodendron billietiae* and *Philodendron solimoesensis*) which are very abundant in *igapó*, but which had only few individuals registered in *várzea*. Distinguishing species that are rare in all their distribution from species that are locally rare is fundamental for ecological studies that aim to assist conservation (Hercos *et al.* 2012).



Of the species we recorded, 42% can be considered “rare”, and 27% “abundant”. The presence of many rare and few abundant species is a frequently reported pattern for vascular epiphyte assemblages (i.e., Nieder *et al.* 2000; Zotz 2007; Zotz & Bader 2011), and is in accord with what Pitman *et al.* (2001) called the “homogeneity hypothesis”. These authors stated that forests are dominated by a small number of species that form compositional “oligarchies” that are relatively constant across large geographical areas. The occurrence of oligarchic species in the arboreal assemblages has already been documented for other life-forms (Pitman *et al.* 2001; Vormisto *et al.* 2004), including trees in *várzea* (Wittmann *et al.* 2006) and *igapó* forests (Montero *et al.* 2012). Oligarchies of species seem to be present in epiphyte assemblages in Amazonian forests, even so it is noteworthy that testing the homogeneity hypothesis was not the objective of this study. Nonetheless, future researches that aim specifically to verify the composition of epiphyte assemblages within great river basins may confirm this hypothesis.

Although the Orchidaceae had the greatest number of species, we found that species with the highest IVE were not orchids, but Gesneriads and Aroids in *igapó*, and Polypoids, Piperacids and Gesneriads in *várzea*. Irumé *et al.* (2013) reported *Guzmania lingulata* (Bromeliaceae) and *Philodendron linnaei* (Araceae) in *terra firme* forest to have an IVE of 27 %. While Quaresma & Jardim (2014) recorded *Philodendron acutatum*, *Anthurium pentaphyllum* and *Philodendron muricatum* (Araceae) densities that together summed to almost 90 % of all IVE in Amazonian *restinga* forests. Therefore, the results found for *várzea* and *igapó* may be part of a broader general pattern for Amazonian forests, where species orchids are more diverse. However, species from other families have a fundamental role, as their species, in addition to contributing large numbers of individuals, have broad distribution in the environment, so that they are involved in a large number of ecological interactions.

Species with high IVE are, according to Waechter (1998), are characterized by a high capacity for dispersal and colonization of different environments, strata, individuals and species of phorophytes. In this context, *C. crassifolia* had very high values for both forest types. The species has a number of adaptive strategies including fleshy leaves, mesophyll with water storing cells, and waxy cuticle for protection from the sun in the upper canopy, plus a high reproductive capacity that comes from perennial production of flowers and fruits (Kleinfeldt 1978) to enable a broad and successful colonization of the epiphytic environment. Additionally, this species is commonly found associated with ant gardens in the study area, and ants disperse *C. crassifolia* seeds to suitable germination sites, as well as increasing the species vegetative growth rates (Kleinfeldt 1978).

Microgramma reptans and *Peperomia retundifolia* also had elevated IVE values in *várzea*. These species have rhizomatous

growth and a strong capacity for colonizing small branches in the forest (Zotz 2007). *Philodendron solimoesensis*, the species with second highest IVE in *igapó*, have a highly-developed pollination capacity, being visited by beetles that fly 50-300m between plants (Gibernal *et al.* 1999). Nonetheless, apart from a scattering of such studies, little is known about the species and populations recorded in this study, which hampers the formation of viable inferences concerning the dominance of some species over others. Future studies on autoecology of Amazon floodplain epiphyte species are essential such questions are to be answered successfully.

Conclusion

Central Amazonian *várzea* and *igapó* forests are environments with vascular epiphyte assemblages of distinct composition, diversity and structure. Like the trees these habitats, their epiphytic flora show low similarity between ecosystems. *Várzea* forests have a considerably larger number of species and individual epiphytes than *igapó*, with the assemblage being so diverse that the sampling effort of this study was not enough to fully assay the composition and richness of this component of *várzea* ecosystem. In contrast, *igapó* is lower so that our sampling effort was satisfactory. As recorded for trees, where a high beta diversity has been reported in *igapós*, studies in further *várzea* and *igapó* forests may refine, amplify and finesse the patterns reported in this study.

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