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EPÍFITAS VASCULARES EM FLORESTAS ALAGÁVEIS DE VÁRZEAS E IGAPÓS DE ÁGUAS PRETAS DA AMAZÔNIA CENTRAL: PADRÕES DE RIQUEZA, COMPOSIÇÃO, DIVERSIDADE E DISTRIBUIÇÃO DE ESPÉCIES

ADRIANO COSTA QUARESMA

Manaus, Amazonas

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Sinopse:

Estudou-se a assembleia de epífitas vasculares nos dois ecossistemas alagáveis mais representativos da Amazônia: Várzeas e igapós de águas pretas. Foram verificados aspectos como composição, distribuição e diversidade de epífitas, bem como a relação do grupo com a assembleia de árvores.

Palavras-chave: Áreas alagáveis, Epífitas vasculares, Interação

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Epífitas vasculares em florestas alagáveis de várzeas e igapós de águas pretas da Amazônia central: padrões de riqueza, composição, diversidade e distribuição de espécies

Resumo

Epífitas vasculares constituem parte importante do dossel das florestas tropicais, no entanto, estudos com foco no componente epifítico são escassos, sobretudo em florestas alagáveis na Amazônia. Isso dificulta a inclusão desse grupo de plantas em estratégias de conservação e também obscurece o próprio entendimento da dinâmica e funcionamento dos ecossistemas alagáveis. Em florestas de várzeas e igapós da Amazônia central, investigamos 1.121 indivíduos e 242 espécies arbóreas, das quais 343 (30,5%) árvores hospedaram 2.922 indivíduos e 96 espécies de epífitas vasculares, distribuídas em 59 gêneros e 13 famílias. A floresta de várzea foi mais rica e apresentou mais que o dobro de espécies de epífitas que a floresta de igapó. Apenas 15,6 % das espécies foram compartilhadas entre os ambientes, evidenciando que ambientes de várzeas e igapós são contrastantes em sua riqueza e composição de epífitas. As análises de alpha diversidade revelaram que o diâmetro da árvore se correlaciona positivamente com a diversidade de epífitas nos dois ambientes e, ao contrário, a diversidade arbórea não se correlacionou com a diversidade de epífitas. A diversidade beta entre várzea e igapó é gerada principalmente pela substituição das espécies e não pelo aninhamento. Por outro lado, as análises de distribuição mostraram que, na várzea, epífitas se distribuem horizontalmente de acordo com o diâmetro da árvore, ao passo que no igapó, a preferência de epífitas por espécies arbóreas específicas parece exercer maior influência na distribuição horizontal das espécies. As análises de distribuição vertical por zonas ecológicas mostraram que, tanto em várzea como em igapó, a copa interior das árvores apresenta maior riqueza de espécies. Análises de distribuição utilizando a altura da epífita em relação ao solo, junto com o diâmetro da árvore, revelaram grupos de espécies que têm suas distribuições determinadas por esses dois parâmetros, que parecem se relacionar à fisiologia de cada grupo. Nossos achados também mostram que, exclusivamente em florestas de igapó, a inundação influencia grande parte dos padrões de riqueza e distribuição de epífitas, pois limita a ocorrência de espécies na porção onde a árvore é inundada, impedindo a ocorrência de grupos especializados em ocupar a parte basal das árvores. Isto influencia secundariamente a distribuição horizontal, pois determina a distribuição de árvores que são preferidas por epífitas, e parece influenciar a distribuição vertical promovendo um deslocamento da riqueza de epífitas para as partes mais altas das árvores. Argumentamos que a flora epifítica entre várzeas e igapós possui padrões de riqueza similares aos encontrados para a flora arbórea, com uma baixa similaridade de espécies e com a inundação influenciando seus padrões de riqueza e distribuição. Sugerimos que outras pesquisas sejam desenvolvidas em mais áreas de várzeas e igapós para verificar se esses padrões são consistentes ao longo da grande planície de inundação Amazônica. Finalmente, os resultados apresentados esclarecem padrões ecológicos e biogeográficos para epífitas na Amazônia e ajudam em futuros planos de conservação de epífitas e de ecossistemas alagáveis, cada vez mais ameaçados por ações antrópicas.

Vascular epiphytes in várzeas and black-water igapós flooding forests in Central Amazon: richness, composition, diversity, and species distribution patterns

Abstract

Vascular epiphytes are important elements of the canopy of tropical forests, however, studies focused on the epiphytic component are scarce, most of all in Amazonian flooding forests. This hampers the inclusion of such plant group in conservation action plans and obscures the understanding on the dynamics of flooding ecosystems. In várzea and igapó forests in Central Amazon, we investigates 1121 individuals and approximately 242 arboreal species, from which 343 trees hosted 2922 individuals belonging to 96 species of vascular epiphytes, classified into 59 genera and 13 families. The várzea forest was the more diverse and presented more than the double of species found in igapó forests. Only 15.6% of the species were common to both environments, demonstrating that várzea and igapó contrast in their epiphytes richness and composition. The beta diversity in these environments is mainly generated by species turnover instead of nestedness. The analyses of alpha diversity revealed that tree diameter is positively correlated with epiphyte diversity in both environments, meanwhile, the arboreal and epiphytic diversity are not correlated. On the other hand, distribution analysis showed that, in várzea, epiphytes are horizontally distributed according to tree diameter, while in igapó the horizontal distribution of epiphytes seems to be influenced by the preference of epiphytes in colonizing specific tree species. The analyses of vertical distribution by ecological zones showed that in both várzea and igapó, the inner canopy presented higher species richness. Analyses of distribution using epiphyte height in relation to the soil along with tree diameter showed group of species that have their distribution determined by these two factors and that this pattern seems to reflect the physiology of each group. Our discoveries also show that, exclusively in igapó forests, the flooding cycle influences a great part of the patterns of richness and distribution of epiphytes. The flooding limits the occurrence of species where the tree is submerged, hampering specialized species to occupy the basal portion of the tree. Water level also secondarily influences the horizontal distribution of epiphytes in igapó, because it determines the distribution of trees that are preferred by epiphytes, it also seems to influence in the vertical distribution as it promotes a vertical displacement of epiphyte richness to the higher parts of the trees. We discuss that the epiphytic flora in várzea and igapó have richness patterns similar to the arboreal component of these environments, with a low similarity and the flooding influencing patterns of species richness and distribution. We suggest that other studies should be conducted in other várzea and igapó forests to verify if such patterns are consistent along the great Amazonian floodplain. Finally, the results we present here shed light on ecological and biogeographical patterns for epiphytes in the Amazon and will help in future conservation plans of epiphytes and flooding ecosystems, more and more threatened by anthropogenic actions.

Sumário

Lista de figuras

Capítulo 1

Capítulo 2

Capítulo 3

Introdução Geral

As áreas úmidas amazônicas representam cerca de 30% da área de cobertura da região (Junk *et al.* 2011), sendo cerca de 50% desse total áreas alagáveis florestadas, o que equivale a uma extensão superior a 800.000 km² (Melack e Hess 2010). As florestas alagáveis da Amazônia são classificadas em dois grandes grupos com base na físico-química da água, que por sua vez esta relacionada à geomorfologia das áreas de captação (Sioli 1984). Assim, nas margens dos rios com origem andina e pré-andina são encontradas as florestas de várzea, que estão associadas aos rios de águas brancas, relativamente ricas em nutrientes, com alta concentração de sedimentos e minerais dissolvidos, e pH próximo da neutralidade. Por outro lado, nas margens dos rios originados nos escudos erodidos das Guianas e do Brasil Central, são encontradas as florestas de igapó, que são associadas a rios de águas pretas ou claras, pobres em nutrientes. Rios de água preta possuem uma alta quantidade de matéria orgânica diluída, principalmente ácidos húmicos e fúlvicos, e um pH ácido; rios de água clara tem baixa quantidade de matéria orgânica diluída com valores de pH variando (Junk e Furch 1980). Essas diferenças no conteúdo nutricional do solo acarretam grande dissimilaridade da diversidade e composição de espécies arbóreas. De modo geral, as várzeas são mais ricas e diversas que as florestas de igapó e a similaridade de composição arbórea variando entre 20% - 30% (Wittmann et al. 2010, 2012)

Estes ambientes têm extrema importância histórica, cultural e econômica, além de terem funções ecológicas de importância para todo o bioma Amazônia (Junk e Piedade 2005; Junk *et al.* 2011). Não obstante a importância, grande extensão territorial e diversidade tipológica das áreas alagáveis amazônicas, o conhecimento sobre esses ambientes ainda apresenta lacunas, não só de descobrimentos científicos, mas também de soluções para conservação frente ao grande avanço do desmatamento e das mudanças climáticas recentes no ciclo hidrológico, com cheias e secas cada vez mais extremas, cujas consequências ainda são desconhecidas. Trabalhos florísticos e ecológicos para estes ambientes concentram-se majoritariamente nas várzeas, e em todos esses ecossistemas são dirigidos quase que exclusivamente para o componente arbóreo, com poucos estudos dando ênfase a outros grupos vegetais, sobretudo a grupo de epífitas.

Por sua vez, epífitas vasculares são parte integrante do dossel de florestas alagáveis, e se caracterizam por utilizarem durante toda a sua vida, ou parte dela, um suporte mecânico (forófito/árvore hospedeira) apenas como suporte para fixação, sem a retirada direta de nutrientes (Gentry e Dodson 1987; Benzing 1990), e por viverem diretamente sobre troncos e galhos das árvores para obtenção de luz, dispensando a utilização de longos caules (Benzing 1990). Abrangem aproximadamente 10% da flora mundial, em um total de aproximadamente 27.614 espécies inseridas em 913 gêneros e 73 famílias (Zotz 2013). As epífitas vasculares são de importância fundamental na manutenção da diversidade biológica e dos ecossistemas onde são encontradas, pois proporcionam recursos alimentares e microambientes especializados para a fauna de dossel, sendo descrito o uso de epífitas por aves (Nadkarni e Matelson 1989) e por formigas (Schimper 1888), entre outros. Este grupo de plantas serve ainda como refúgio reprodutivo a muitas espécies de animais (Benzing 1986), o que o torna importante elemento na manutenção da biodiversidade.

Por ser o epifitismo uma relação de dependência mecânica das epífitas com a comunidade arbórea, a supressão da vegetação arbórea resulta na exclusão dessas plantas da área afetada (Borgo e Silva 2003, Bartholott *et al*. 2001, Wolf 2005). Desta forma, entender como a assembleia de epífitas é modificada pela assembleia de árvores é extremamente importante em um cenário de crescente aumento do desmatamento, principalmente nas várzeas, e consequente perda de habitat em florestas da Amazônia. Além disso, em florestas alagáveis, mudanças recentes no ciclo hidrológico com cheias e secas cada vez mais extremas e severas, ainda têm suas consequências pouco conhecidas. Já se sabe, por exemplo, que igapós são mais suscetíveis ao fogo e que possuem baixa resiliência a esse impacto (Flores et al. 2012).

Informações sobre epífitas vasculares podem preencher lacunas sobre sua composição, diversidade e distribuição em florestas alagáveis, e elucidar padrões florísticos, ecológicos e biogeográficos para esse grupo na Amazônia. O presente estudo, dividido em três capítulos, foi desenvolvido com esse proposito.

O primeiro capítulo compara a composição, diversidade e estrutura da assembleia de epífitas vasculares entre as duas principais tipologias alagáveis da Amazônia (várzea e igapó de águas pretas), mostrando contrastes entre esses ambientes. O segundo capítulo analisa como o diâmetro das árvores hospedeiras influencia a riqueza, composição e distribuição de epífitas, verifica os processos de beta diversidade entre esses ecossistemas, e apresenta uma abordagem alternativa para verificar a distribuição vertical das espécies, que não categoriza a ocorrência de epífitas em zonas, mais usa a altura da planta até o solo florestal e seu diâmetro para discriminar grupos de distribuição epifítica. O terceiro capítulo é focado na assembleia de epífitas em florestas de igapó de águas pretas, fazendo um paralelo da riqueza desse ambiente com outras florestas na Amazônia e investigando como a composição arbórea e a inundação influenciam a riqueza e a distribuição de epífitas vasculares desse ecossistema.

Objetivos

A tese buscou conhecimentos sobre padrões gerais de riqueza, composição, diversidade e distribuição de epífitas vasculares nos dois ecossistemas alagáveis mais representativos do bioma Amazônia. Esses objetivos estão distribuídos em três capítulos, a saber:

Capítulo 1

1) Analisar a composição, diversidade e estrutura da assembléia de epífitas em florestas de várzea e igapó de águas pretas, identificar similaridades e contrastes entre as florestas e comparar se esses padrões são condizentes com os reportados para árvores.
2) Verificar se a diversidade de árvores influência a diversidade de epífitas vasculares.

Capítulo 2

1) Verificar a influencia do diâmetro das árvores na riqueza, abundância e distribuição de epífitas vasculares em florestas de várzea e igapó de águas pretas.
2) Analisar os processos de turnover e nestedness entre florestas de várzeas e florestas de igapó de águas pretas (beta diversidade) e dentro de cada floresta (alpha diversidade).

Capítulo 3

1) Verificar se florestas de igapó de água preta têm maior riqueza e abundância de espécies epífitas vasculares do que outras florestas amazônicas.
2) Analisar se a distribuição horizontal das epífitas é determinada pela distribuição das espécies arbóreas.
3) Verificar se as inundações influenciam a distribuição vertical e a ocupação das árvores pelas epífitas.

Capítulo 1

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Original Article

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, where only two previous studies were 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 16 25x25 m plots, in each floodplain 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 with only 15.6% of species common to both ecosystems. The two floodplains were also structurally different for most abundant species and those with the highest Epiphytic Importance Value (IVe). The diversity of trees did not influence the diversity of epiphytes in both ecosystems. The forests differ in the composition, diversity and structure of their epiphytic assemblages and this must be taken into account when designing conservation action plans for these ecosystems and for their vascular epiphytes.

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

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 (Schuelttpelz & Trapnell 2006).

In the Brazilian Amazon research on vascular epiphytes is mostly concentrated in upland forests (Irume *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 (Obermuller *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 (ter Steege & Cornelissen 1989; Mari *et al*. 2016)

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 and 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 igapo forests are comparatively species poor (with up to 60 species ha^{-1}) (trees ≥10 cm dbh) (Wittmann *et al*. 2010; Montero *et al*. 2014). 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.

Material 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.

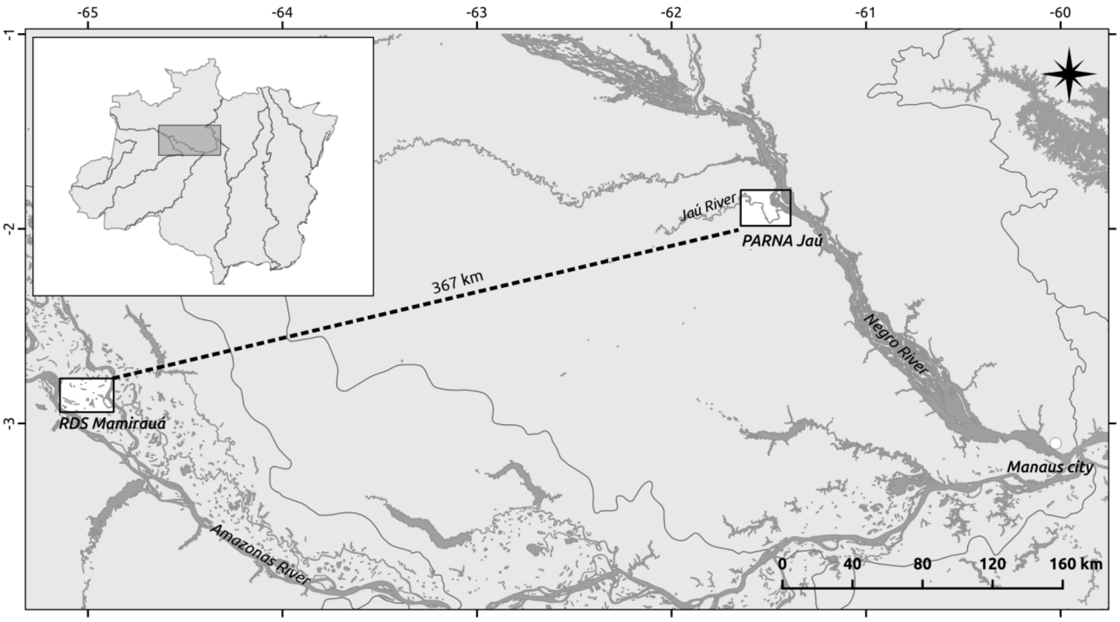

Figure 1. Location map of the study sites in the Reserva de Desenvolvimento Sustentável Mamirauá and Parque Nacional do Jaú.

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; Fundação Victoria Amazônica 2008). 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., *Macrolobium 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 (2º 51’ S, 64º 55’ W). The reserve covers an area of approximately 11,240 km^2 of *várzea* forests and is delimited by the Juruá and Amazon/Solimões Rivers and the Auati-Paraná channel (Management Plan RDS Mamiruá 2014). *Várzea* soils generally have high proportions of silt and fine sand, and often are eutrophic (Irion 1984).

Wittmann *et al*. (2002) sampled four hectares of *várzea* forest in the Mamiraua 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, *Guatteriopsis 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 (Lista de Espécies da 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 & Colwel 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 (FAi, FRi) and on specific host trees (FAj, FRj); the value of epiphytic importance (IVe) was calculated using both types (FRi and FRj) of relative frequency (Waechter 1998), as follows:

$FAi = (Nfi / Nfa).100$

$FRi = (Nfi / \sum Nfi).100$

$FAj = (Sfi / Sfa).100$

$FRj = (Sfi / \sum Sfi).100$

$IVe = (FRi + FRj) / 2$

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 IVe the value of epiphytic importance. These parameters translate the species capacity by means of reproduction and dispersion in the environment (FRi), and their capacity to colonize different substrata (FRj), which in turn express themselves in the ecological importance of each species (IVe) (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 95 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 (8 species, 8.3%) (Table 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 (9 and 5 species) and Polypodiaceae (7 and 3 species).

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**		**Hábito**
		Várzea	**Igapó**	
Araceae	*Anthurium clavigerum* Poepp.	09	-	HM
	Anthurium bonplandii Bunting	45	-	HO
	Anthurium gracile (Rudge) Schott	45	05	HO
	Anthurium pentaphyllum (Aubl.) G. Don	02	05	HM
	Anthurium sp.	03	-	HM
	Philodendron sp.	04	-	HM
	Philodendron acutatum Schott	-	09	HM

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

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

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. 2). 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. 3). In *varzea* and *igapo*, 61.5% and 22.9% of all recorded species were exclusive, while 15.6% of all species were common to both environments. **anosim**

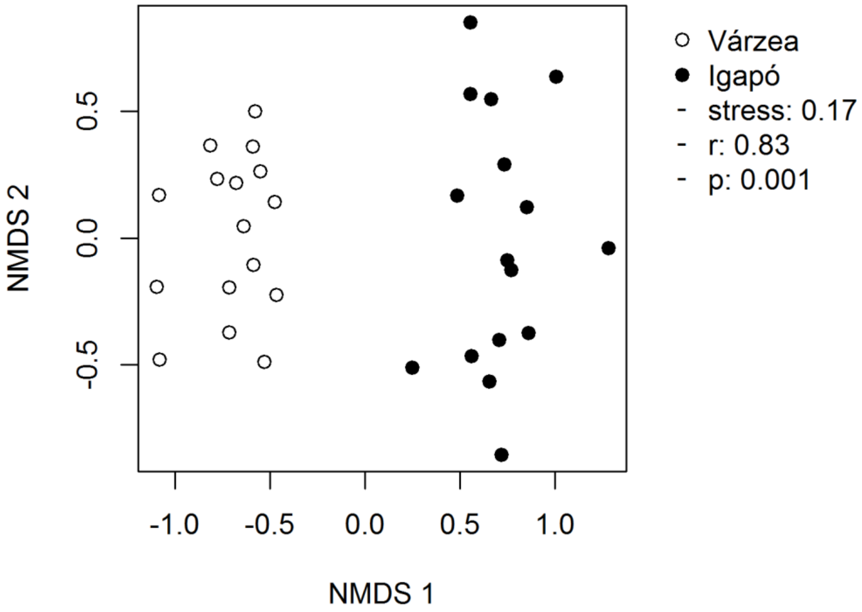

Figure 2.Non-metric Multidimensional Scaling (NMDS) showing the separation of the composition of epiphytic species between the várzea and igapó, floodplain forests indicating the existence of two distinct groups.

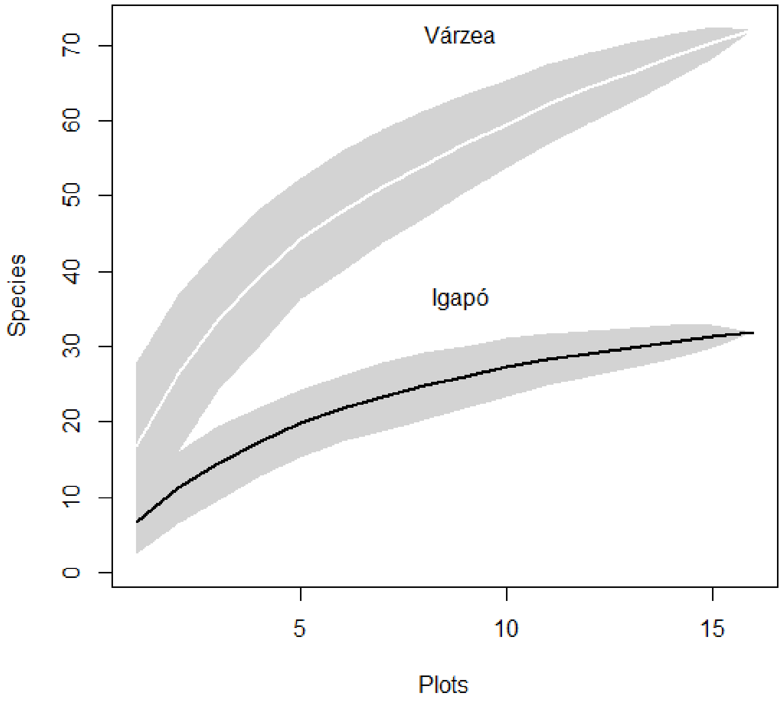

Figure 3. Rarefaction curves showing the sampling sufficiency in each environment.

Holo-epiphytism is the predominant life-form (a total of 85 species, 88.6%, in both environments combined: Table 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 4A). For trees the values were 3.4 ± 25.9 in *igapó* and 5.4 ± 53.2 in *várzea* (Fig 4B). 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. 4C). While in *igapó* forest, though it was not significant (r^2 = -0.01, P = 0.27; Fig. 4D), it did show a trend.

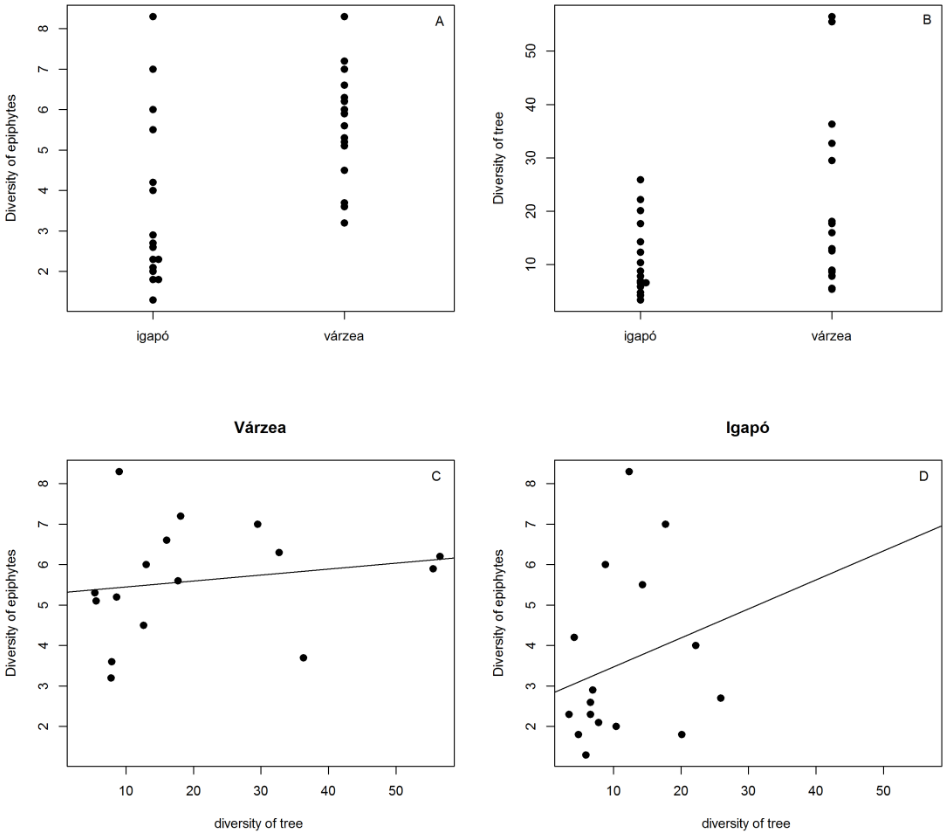

Figure 4. Difference of the diversity of epiphyte assemblages (Fig. 4A) and tree assemblages (Fig. 4B) in plot of varzea and igapó forest. of Central Amazonia. Despite a difference in diversity between the forests, diversity of trees did not influence diversity

Structure

Both environments are dominated by few, very abundant, species, and many species with a low number of individuals that can be considered as rare (Table 2, Fig. 5). Nevertheless, the most abundant species differ between assemblages; among the 15 overall most abundant species, only *Codonanthopsis crassifolia* (H. Focke) Chautems & M. Perret occurred in both forests.

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**
M. reptans	45,26	13,69	59,78	10,54	12,12	*C. crassifolia*	32,12	21,73	53,70	19,34	20,54
P. rotundifolia	33,68	10,19	50,00	8,81	9,50	*P. solimoesensis*	10,30	6,97	20,37	7,34	7,15
C. crassifolia	24,74	7,48	38,04	6,70	7,09	*Philodendron* sp.	15,76	10,66	9,26	3,33	7,00
M. percusa	19,47	5,89	33,70	5,94	5,92	*Orleanesia* sp.	8,48	5,74	16,67	6,00	5,87
P. polypodioides	18,95	5,73	30,43	5,36	5,55	*C. cebolleta*	9,09	6,15	14,81	5,33	5,74
A. bomplantii	14,21	4,30	23,91	4,21	4,26	*E.micronocturnum*	6,06	4,10	16,67	6,00	5,05
A. gracile	10,00	3,03	19,57	3,45	3,24	*Clusia* sp.	6,67	4,51	14,81	5,33	4,92
A. angustifolium	8,95	2,71	17,39	3,07	2,89	*P. stenophylla*	6,67	4,51	12,96	4,67	4,59
H. equitans	10,00	3,03	15,22	2,68	2,85	*G. devoniana*	7,27	4,92	11,11	4,00	4,46
C. micrantun	8,42	2,55	15,22	2,68	2,61	*P. acutatum*	4,85	3,28	14,81	5,33	4,31
C. uncata	8,42	2,55	14,13	2,49	2,52	*E. nocturnum*	4,24	2,87	9,26	3,33	3,10
A. angustifolium	7,37	2,23	15,22	2,68	2,46	*P. concreta*	3,03	2,05	9,26	3,33	2,69
Epiphilum sp.	1,05	0,32	23,91	4,21	2,27	*C. bicornutum*	3,64	2,46	7,41	2,67	2,56
Monstera sp.	7,89	2,39	10,87	1,92	2,15	*V. lineata*	4,24	2,87	3,70	1,33	2,10
Aechmea sp.	6,84	2,07	11,96	2,11	2,09	*C. ulei*	2,42	1,64	5,56	2,00	1,82
E. rigidum	6,84	2,07	11,96	2,11	2,09	*P. vespa*	1,82	1,23	5,56	2,00	1,62
C. angustifolium	5,79	1,75	9,78	1,72	1,74	*A. serratum*	3,64	2,46	1,85	0,67	1,56
E. strobiliferum	5,79	1,75	9,78	1,72	1,74	*C. violacea*	1,82	1,23	3,70	1,33	1,28
Philodendrum sp.	5,26	1,59	7,61	1,34	1,47	*A. setigera*	1,21	0,82	3,70	1,33	1,08
S. spiculifera	4,74	1,43	7,61	1,34	1,39	*B. martiana*	1,21	0,82	3,70	1,33	1,08

Species in the *várzea* had higher absolute and relative abundance than those in *igapó*. In *várzea*, *Cristensonela uncata* (Lindl.) Szlach., Mytnik, Górniak & Śmiszek was the most abundant species (255 individuals), followed by *Microgramma reptans* (Cav.) A.R.Sm. (223 individuals), *Pleopeltis polypodioides* (L.) Andrews & Windham (183 individuals), *Peperomia retundifolia* (L.) Kunth (178 individuals) and *Specklinia picta* (Lindl.) Pridgeon & M.W.Chase (127 individuals). In *igapó* the most abundant species were *C. crassifolia* (205 individuals), *Polysthachya stenophilla* Schltr. (52 individuals), *Epidendrum micronocturnum* Carnevali & G.A.Romero (42 individuals), *Octomeria brevifolia* Cogn. (40 individuals) and *Philodendron solimoesensis* A.C.Sm. (40 individuals).

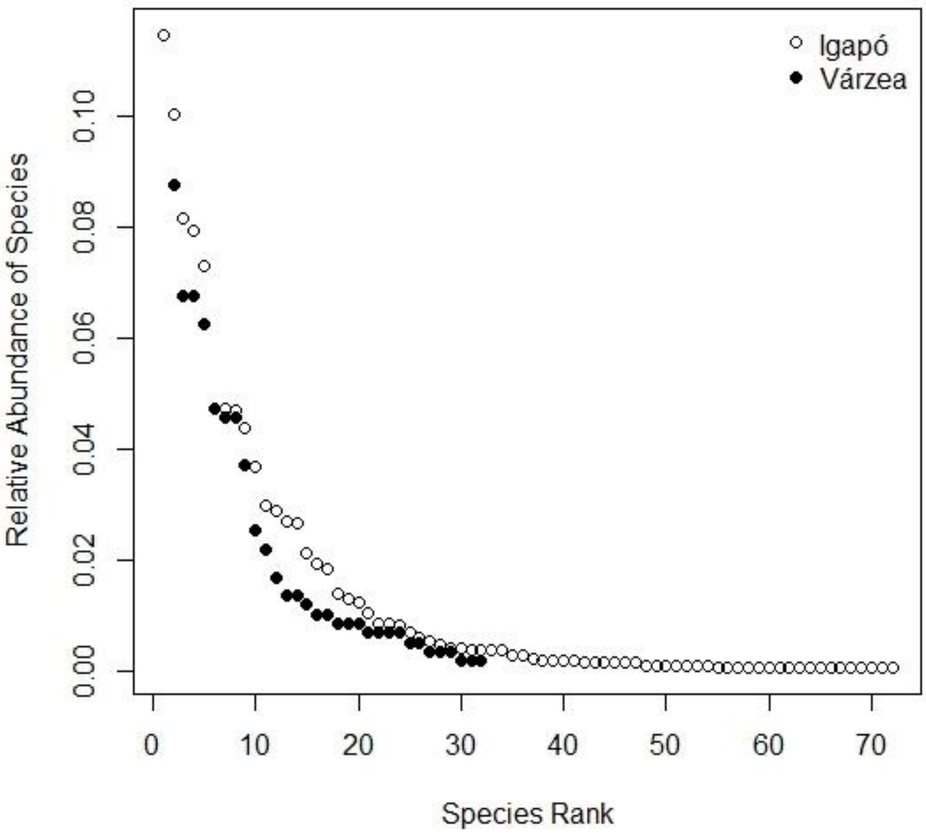

Figure 5. Abundance ranking of epiphyte species found in várzea and igapó forests in Central Amazonia. Black circles represent igapó species and empty circles várzea species.

Analysis of frequencies and species importance values indicates that the structure of *várzea* and *igapó* forests differs considerably (Table 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 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 *igapo* 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 & Garcia-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 families (*i.e.* Laube & Zotz 2003; Wang *et al*. 2016). This tendency has been widely observed in Amazonian forests (Nieder *et al*. 2000; Pos ET & Sleegers 2010; Obermuller *et al*. 2012; Quaresma & Jardim 2014; Boelter *et al*. 2015), except for the study of Irume *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 *et al*. 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 holoepiphyte 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 & Sleegers 2010; Boelter *et al*. 2015,) and coastal forests (*restinga* forests) (Quaresma & Jardim 2014). Holoepiphytes 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 *Philodendrum 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 and colleagues (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*. Irume *et al*. (2013) reported *Guzmania lingulata* (Bromeliaceae) and *Philodendron linnaei* (Araceae) in *terra firme forest* to have an IVe of 27%. While Quaresma and Jardim (2014) recorded *Philodendrun acutatum*, *Anthurium pentaphylum* and *Philodendrum 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 an high beta diversity has been reported in *igapós*, studies in further *várzea* and *igapó* forests may may refine, amplify and finesse the patterns reported in this study.

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Capítulo 2

Quaresma AC, Feitosa YO, Wittmann F, ter Steege H, Piedade MTF. 2017. O diâmetro da árvore influencia a riqueza, abundância, distribuição e padrões de diversidade alpha de epífitas vasculares em florestas alagáveis da Amazônia. Manuscrito em preparação para *Plant Ecology*.

O diâmetro da árvore influencia a riqueza, abundância, distribuição e padrões de diversidade *alpha* de epífitas vasculares em florestas alagáveis da Amazônia

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Resumo

Investigamos como a riqueza, abundância e distribuição de epífitas vasculares é influenciada pela assembleia de árvores nas duas principais florestas alagáveis da Amazônia, para elucidar padrões ecológicos e biogeográficos, essenciais no sentido de delinear medidas de conservação da biodiversidade dessas áreas, particularmente pouco estudas sobre esses aspectos. Amostramos 1 (um) ha em floresta de *várzea* e 1 (um) ha em floresta de *igapó*, totalizando 32 parcelas de 25x25 m onde contabilizamos e identificamos todas as epífitas vasculares, bem como todas as árvores com DAP≥10 cm, com ou sem epífitas. A riqueza e a abundância de epífitas se correlacionam positivamente com o aumento do diâmetro das árvores hospedeiras. A diversidade beta entre várzea e igapó é gerada principalmente pela substituição de espécies (turnover) em vez de aninhamento (nestedness). A diversidade alpha, na *várzea*, ocorre por turnover de epífitas em árvores com diferentes diâmetros que abrigam diferentes assembléias, enquanto no *igapó* árvores com menores diâmetros abrigam um subconjunto de epífitas. A distribuição vertical de espécies, analisada por zonas verticais, demonstrou um maior número de espécies e indivíduos na copa interna das árvores. Quando a análise de

distribuição vertical foi baseada na altura da epífita em relação ao solo em conjunto com o diâmetro das árvores, observamos grupos de distribuição refletindo a fisiologia ecológica de diferentes grupos de espécies. Na várzea, medidas de conservação devem priorizar a manutenção da estrutura florestal, sustentando tanto a diversidade taxonômica como também a diversidade diamétrica das árvores. Por outro lado, em igapós os esforços de conservação para epífitas vasculares, primeiramente devem levar em consideração a identidade taxonômica das árvores hospedeiras e posteriormente seu diâmetro.

Introdução

Determinar os fatores que estruturam a riqueza e a distribuição das assembleias de plantas em florestas alagáveis tem sido objetivo constante em pesquisas ecológicas. Embora avanços significativos sejam observados para as assembleias de árvores (p.ex. Ferreira 1997, Wittmann et al. 2001, 2002, Montero et al. 2012), para outros grupos vegetais isso é menos evidente, sobretudo para epífitas vasculares. Não obstante, epífitas e hemiepífitas vasculares podem ultrapassar um total de 27.600 espécies, 913 gêneros e 73 famílias em todo o mundo (Zotz 2013). Além disto, este grupo de plantas sofre grande pressão antrópica, pois parte significativa da sua composição é perdida pela exploração seletiva de madeira (Barthlott et al. 2001, Mondragon et al. 2014).

Nieder et al. (2000) investigaram epífitas vasculares em uma floresta alagável de igapó, e atribuíram o padrão de distribuição espacial ao substrato disponível para colonização, possivelmente ofertado por árvores com maior diâmetro. Estes mesmos autores evidenciaram que 5,1% das árvores com DAP>20 cm acolheram 57% de todos os indivíduos epifíticos e 7,6% das árvores com DAP<20 agruparam 43% dos indivíduos. Árvores com maiores diâmetros possuem maior superfície e, na maioria dos casos, maior tempo disponível para colonização (Gentry e Dodson 1987, Benzing 1990, Wagner et al. 2015) acarretando em maior diversidade de espécies, o que já foi demonstrado em alguns trabalhos (Callaway et al 2002, Hietz e Hietz-Seifert 1995, Flores-Palacios e Garcia-Franco 2006, Wolf et al. 2009). No entanto, outros trabalhos mostraram uma relação contrária (Koster et al. 2009, Kersten et al. 2009), levando-nos a crer que essa influência não é um padrão geral para a assembleia de epífitas.

A distribuição vertical de epífitas também não é bem estabelecida e parece variar de acordo com o ambiente e entre ambientes semelhantes. Isso é esclarecido quando observamos que em floresta de restinga, Kersten e Silva (2001) relataram maior riqueza nas partes basais das árvores, enquanto Ribeiro (2009) relatou maior riqueza na região dos galhos mais grossos da copa. Outro exemplo, em Floresta Ombrófila Mista, Fraga et al. (2008) encontraram maior riqueza nas partes basais, enquanto Kersten e Silva (2002) relataram maior riqueza na região dos galhos mais grossos. Por outro lado, trabalhos para florestas na Amazônia relatam maior riqueza e abundância de epífitas na região dos galhos mais grossos das árvores (Pos e Sleegers 2010, Quaresma e Jardim 2013, 2014), inclusive para florestas alagáveis amazônicas (Nieder et al. 2000).

Florestas alagáveis de *várzea* e *igapó* perfazem uma extensão superior a 600.000 km² da bacia amazônica (Melack e Hess 2010), sendo os dois ecossistemas alagáveis mais representativos do bioma. Ambas as florestas estão submetidas a um elevado pulso de inundação anual, monomodal e previsível que determina grande parte dos padrões ecológicos subjacentes (Junk *et al*. 1989, Wittmann *et al*. 2010, Junk *et al*. 2011), porém diferem no conteúdo nutricional dos solos aluviais, o que acarreta em grande diferença florística da sua assembleia de árvores (Junk et al. 2011). De modo geral, a quantidade de espécies arbóreas, com DAP≥10 cm, é maior nas várzeas (supeior a 100 espécies ha^{-1}) quando comparadas com os igapós (com até 60 espécies ha^{-1}) (Wittmann *et al*. 2002; 2006; Montero *et al*. 2012) e a similaridade da assembleia de árvores entre essas florestas, na Amazonia Central, é entre 20% - 30% (Wittmann et al. 2010; 2012).

Diferenças de diversidade entre dois ambientes (beta diversidade) podem ser geradas por dois processos antagônicos ou pela combinação deles (Baselga 2010). O primeiro consiste em uma troca de espécies entre duas assembleias (turnover), e o segundo, ocorre quando o conjunto das espécies de ambientes pobres constitui um subconjunto das espécies de ambientes mais ricos (nestedness) (Baselga 2010, Ulrich & Gottelli 2007). Turnover e nestedness já foram documentados como processos que podem gerar a diversidade beta em assembleias arbóreas de florestas tropicais (p. ex. Pitman et al. 2002, Condit et al. 2013, Esquiver-Muelbert et al. 2016), porém, até onde sabemos, esses aspectos nunca foram explorados para assembleias de plantas associadas, sobretudo para epífitas vasculares. Diferenciar esses processos é essencial para melhorar nossa compreensão biogeográfica e ecológica. Além disso, este conhecimento pode ajudar na conservação das espécies (Baselga 2010).

Investigamos a influencia do diâmetro das árvores na riqueza, abundância e distribuição de epífitas vasculares, bem como os processos de turnover e nestedness entre florestas de *várzeas* e florestas de *igapós* (beta diversidade) e dentro de cada floresta (alpha diversidade). Especificamente buscamos responder às seguintes perguntas: I) O diâmetro da árvore hospedeira influencia a riqueza, abundância e a distribuição de epífitas vasculares? II) Qual processo determina a diversidade alpha e beta de epífitas vasculares em florestas alagáveis?

Material e métodos

Áreas de estudo

A pesquisa foi desenvolvida em duas unidades de conservação do Estado do Amazonas (AM) (Figura 1). A primeira área está situada nas florestas de igapó do Parque Nacional (PARNA) Jaú, localizado entre os municípios de Barcelos e Novo Airão, a 220 km da cidade de Manaus. A segunda área encontra-se nas florestas de várzea da Reserva e Desenvolvimento Sustentável (RDS) Mamirauá, localizada na parte ocidental da Amazônia Central, a aproximadamente 70 km do município de Tefé, AM. Junto com a Reserva de Desenvolvimento Sustentável Amanã, essas duas unidades de conservação foram declaradas Herança Natural da Humanidade pela UNESCO em 2000.

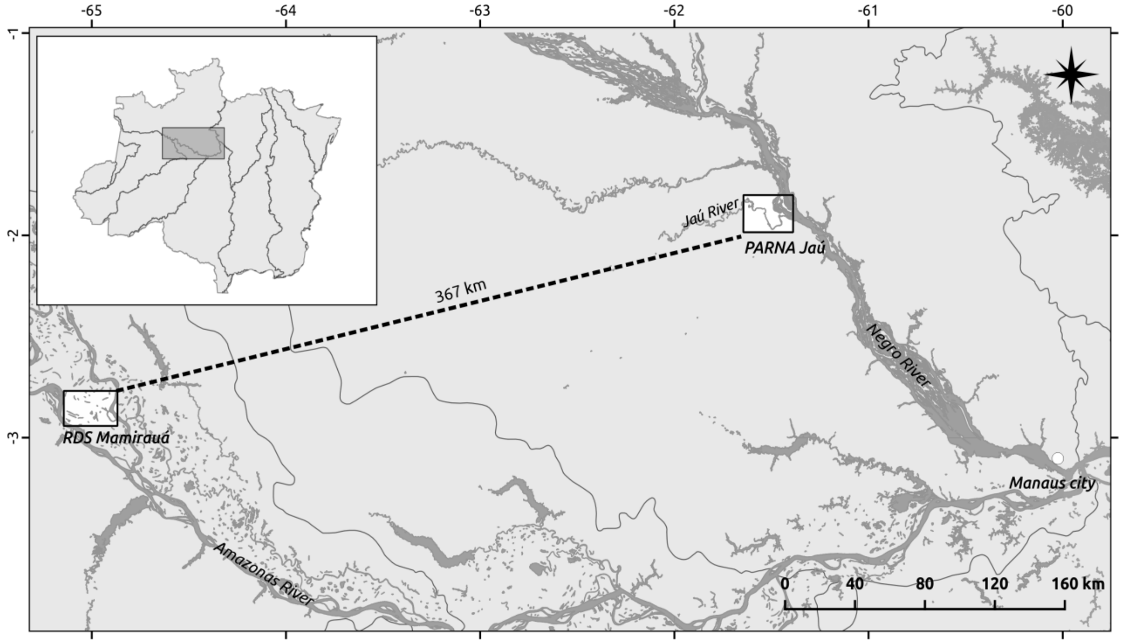

Figura 1. Location map of the study sites in the Reserva de Desenvolvimento Sustentável Mamirauá and Parque Nacional do Jaú.

O PARNA Jaú possui cerca de 2. 272. 000 ha e abrange as bacias hidrográficas dos rios Jaú e Unini, afluentes da margem direita do Rio Negro (Ferreira 2000), ao passo que, a RDS Mamirauá abrange uma área de 1.240.000 ha e está delimitada entre os rios Japurá, Solimões e canal Auati-paraná (Plano de Manejo). O clima nas duas áreas é do tipo tropical úmido. A temperatura média anual nas florestas de igapó é de 26,7 °C, com precipitação média anual de 2300 mm, apresentando uma estação seca de junho a setembro e uma estação chuvosa de dezembro a maio (Ferreira 2000). A máxima temperatura nas áreas de várzea, varia de 30 a 33°C e ocorre nos meses de seca (outubro e novembro), e a mínima oscila entre 21 e 23°C, com pluviosidade média de 2373 mm e valores máximos entre os meses de dezembro a maio.

As florestas estudadas estão sujeitas a um pulso anual e monomodal de inundação, com uma amplitude média anual de 8,3 m (Junk et al. 2015) nos igapós do PARNA Jaú, e de 10,8m na RDS Mamirauá (Andrade 2012). A cheia em ambos ambientes ocorre durante a segunda quinzena de junho e o nível mínimo da água no início de novembro (Agência Nacional de Água – ANA).

Coleta de dados

Seis expedições foram realizadas para as áreas de estudo. As primeiras em junho e julho de 2014 (período de águas altas) para reconhecer as área e coleta prévia de plantas férteis e inférteis. As outras quatro foram realizadas em setembro de 2014, janeiro e setembro de 2015, e setembro de 2016 (período águas baixas). Foram demarcadas 32 parcelas de 25x25 m, totalizando 2 ha amostrados, sendo 1 ha nas florestas de igapó e 1 ha nas florestas de várzea. Nossa amostragem foi realizada apenas em florestas maduras (ver Wittmann et al., 2002, Junk et al., 2015), de modo que a estrutura da floresta foi equivalente em termos estruturais (altura, no. de indivíduos, distribuição de diâmetros). Também padronizamos a marcação de parcelas no mesmo nível de inundação para os dois ambientes (cinco parcelas em níveis de inundação > 3 m; cinco parcelas em níveis de inundação variando de 3.1 m a 5.5 m; e seis parcelas com nível de inundação variando de 5.5 m a 8.0 m). Dentro destas, foram amostradas, contabilizadas e identificadas todas as árvores com DAP≥10 cm, que hospedavam epífitas vasculares.

A amostragem das epífitas foi realizada com auxílio de binoculo e câmera fotográfica, sempre olhando as árvores de dois ângulos opostos para percorrer todo o forófito e para evitar dupla contagem dos espécimes. Amostragens realizadas do solo florestal capturam mais de 90% da ocorrência de epífitas (Burns 2007), entretanto, já foi verificado que observações de epífitas do solo subestimam a ocorrência de plantas (Flores-Palacios e Garcia-Franco 2001). Para corrigir este viés, também escalamos quatro ou mais árvores em cada parcela para observações mais precisas, coleta de amostras, contagem e identificação.

Para verificar a distribuição vertical das epífitas, dividimos a árvore em quatro zonas, adaptando a metologia de Johansson (1974) que dividiu a árvore em cinco zonas. Assim, utilizamos as três primeiras classes, sendo: a parte basal do tronco (JZ I, 0-3 m); o tronco de três metros até a primeira ramificação (JZ II) e; a parte basal dos grandes ramos (JZ III 1/3 do comprimento total do ramo), contudo, as duas últimas zonas foram consideradas como uma única zona (JZ IV), devido há dificuldade de delimitação e baixa ocorrência de espécies.

As espécies epifíticas e arbóreas foram identificadas sempre que possível in loco ao nível de gênero. Espécies em campo eram coletadas e identificadas posteriormente por meio de chaves dicotômicas (Cruz 1994, Cruz & Braga, 1997), livros especializados (Ribeiro et al., 1999, Zuquim et al., 2008), comparações com material de herbário (INPA Herbarium e Herbarium MG) e / ou com a ajuda de especialistas. Amostras estéreis foram cultivadas em estufa até a abertura das flores. As plantas férteis estão em processo de incorporação no herbário INPA. Nós classificamos espécies seguindo APG III (2009) e usamos nomes válidos de acordo com a lista de espécies da flora brasileira (Lista de Espécies da Flora do Brasil 2020).

Para espécies epífitas que produzem indivíduos distintos, consideramos cada grupo distintamente isolado, como rosetas (Bromeliaceae), pseudobulbos, hastes, rizomas (Orchidaceae) e hastes (Araceae e Clusiaceae) como um indivíduo; Para as espécies que ocorrem em colônias (Gesneriaceae e Piperaceae), aglomerados de ramos foram considerados únicos quando distintamente separados de outros indivíduos na árvore hospedeira, então, em ambos os casos consideramos grupos "individuais" separados um do outro (Sanford 1968).

Análise dos dados

Construímos um histograma para visualizar como o número de indivíduos arbóreos em cada classe de diâmetro se relaciona com riqueza e abundância de epífitas. Como o número de árvores em cada classe de diâmetro diferia entre os ambientes, excluímos aleatoriamente algumas árvores para homogeneizar as análises. Em seguida, usando árvores hospedeiras como unidades amostrais (Kersten e Waechter 2011), relacionamos o diâmetro da árvore com a riqueza e abundância de epífitas, através de análise de ANCOVA, usando os ambientes como fator. Verificamos a distribuição horizontal de epífitas em diferentes diâmetros de árvores hospedeiras, dividindo as árvores em seis classes diamétricas (10-20, 20.1-30, 30.1-40, 40.1-50, 50.1-60, >60.1). Devido a pouca representatividade de árvores com DAP>60 cm no igapó, usamos apenas as cinco primeiras classes. Para isso, ordenamos a composição de espécies pelas classes de diâmetro usando Bray-Curtis como medida de distância (Bray e Curtis 1957). Finalmente, construímos gráficos de ordenação para visualizar a influência do diâmetro na distribuição de epífitas em cada ambiente.

Analisamos o padrão de distribuição vertical ordenando as espécies pelas quatro zonas, usando bray-curtis como medida de distância e visualizamos a diferença de composição através de gráficos de ordenação. Por outro lado, medimos a altura das espécies epífitas em relação ao solo, independente das zonas sugeridas por Johansson (1974) e, juntamente com as classes de diâmetros, realizamos uma análise alternativa de distribuição que englobasse as espécies nas zonas verticais e nas classes de diâmetro. Para isso, usamos uma análise de agrupamento (Cluster).

Verificamos a dissimilaridade entre os ambientes através da distância de Sorensen (Sorensen 1948), visualizada por uma análise de NMDS. Para verificar se a assembleia de epífitas entre os ambientes apresentam padrão aninhado, foi utilizado o índice proposto por Baselga (2010) que quantifica o grau de aninhamento entre duas comunidades e, a partir desse índice foi realizado uma análise de NMDS para analisar visualmente se as duas assembleias possuem um padrão aninhado. Para verificar se a as assembleias apresentam um padrão turnover, foi utilizado o índice de Simpson que quantifica o grau de substituição de espécies entre os ambientes (Simpson 1943, Baselga 2010), seguido de uma análise de NMDS para visualizar o padrão. Se uma dessas medidas gerar uma crescente dissimilaridade entre as assembleias, esse será o processo que melhor explica o padrão de beta diversidade (Baselga 2010, Baselga e Orme 2012).

As espécies de epífitas que ocorreram em número inferior a cinco indivíduos e em menos de três árvores hospedeiras foram excluídas das análises, devido à baixa representatividade. Como o número de indivíduos arbóreos amostrados diferia entre os ambientes, homogeneizamos o mesmo número de indivíduos em cada classe de diâmetro nos dois ambientes.

Todas as análises foram desenvolvidas no R (R Development Core Team 2011). As distâncias foram calculadas usando o pacote betapart (Baselga 2012) e metaMDS em vegan foi usado para a análise NMDS. As ordenações foram desenvolvidas através de scripts genéricos. Análise de ANCOVA e de agrupamento (Cluster) foram rodadas pelo pacote vegan (vegan: Community Ecology Package 2016). Rodamos o cluster usando o agrupamento hierárquico pelo critério dos mínimos quadrados (Legendre e Legendre 1998), usando o método 'Ward D' da função hclust (Ward 1963).

Resultados

Verificamos um decréscimo no número de árvores hospedeiras com o aumento do diâmetro nos dois ambientes, e isso gerou dois padrões diferentes para as epífitas. Nas várzeas, mesmo com a diminuição do número de indivíduos arbóreos, o aumento em diâmetro leva a uma elevada abundância e riqueza de epífitas, enquanto que no igapó, a riqueza e abundância está concentrada em árvores menores e o aumento do diâmetro parece ter pouca influencia na riqueza e abundância (Fig. 2).

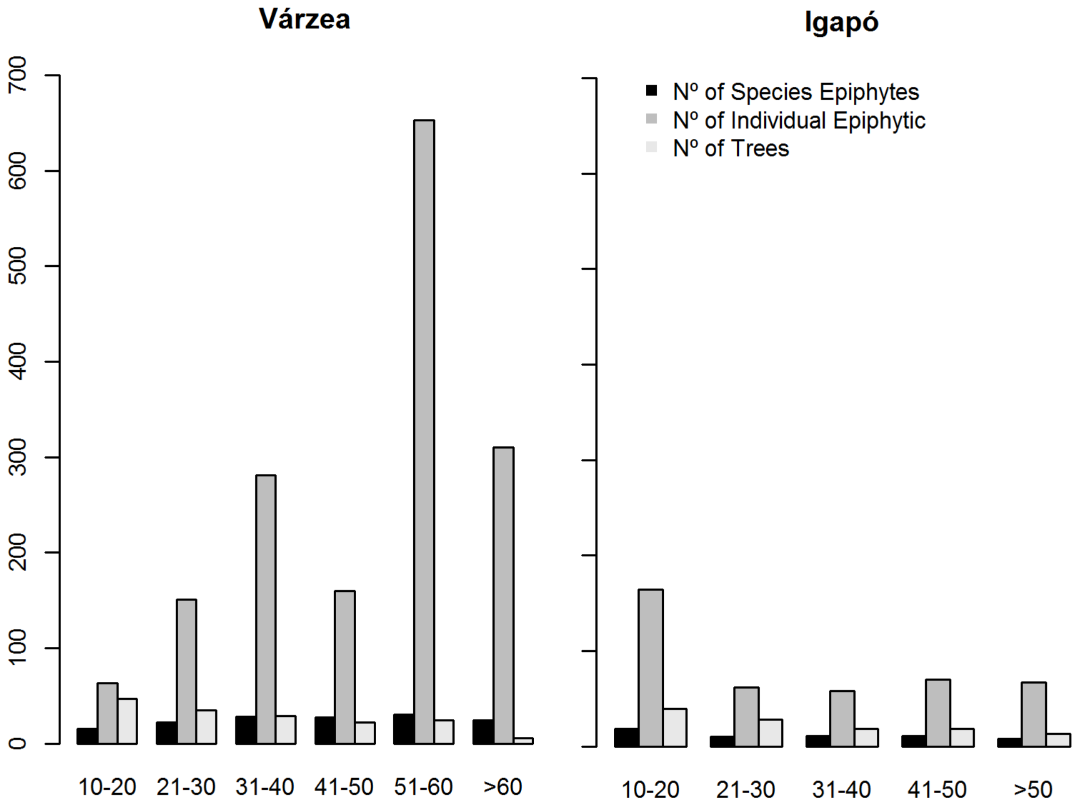

Figura 2. Histograma da relação da riqueza e abundância de epífitas vasculares com a distribuição do número de indivíduos arbóreos por classes de diâmetro. Explicar melhor a metodologia dessa análise

Contudo, a análise de covariância mostrou que apesar da significância estatística, a correlação do diâmetro com a riqueza eundância de epífitas é muito baixa na floresta de várzea (r^2=0.22, P<0.00001; r^2= 0.11, P<0.0001) e na floresta de igapó (r^2=0.14, P<0.001; r^2= 0.10, P<0.001) (Fig.4A, 4C, 4B e 4D, respectivamente).

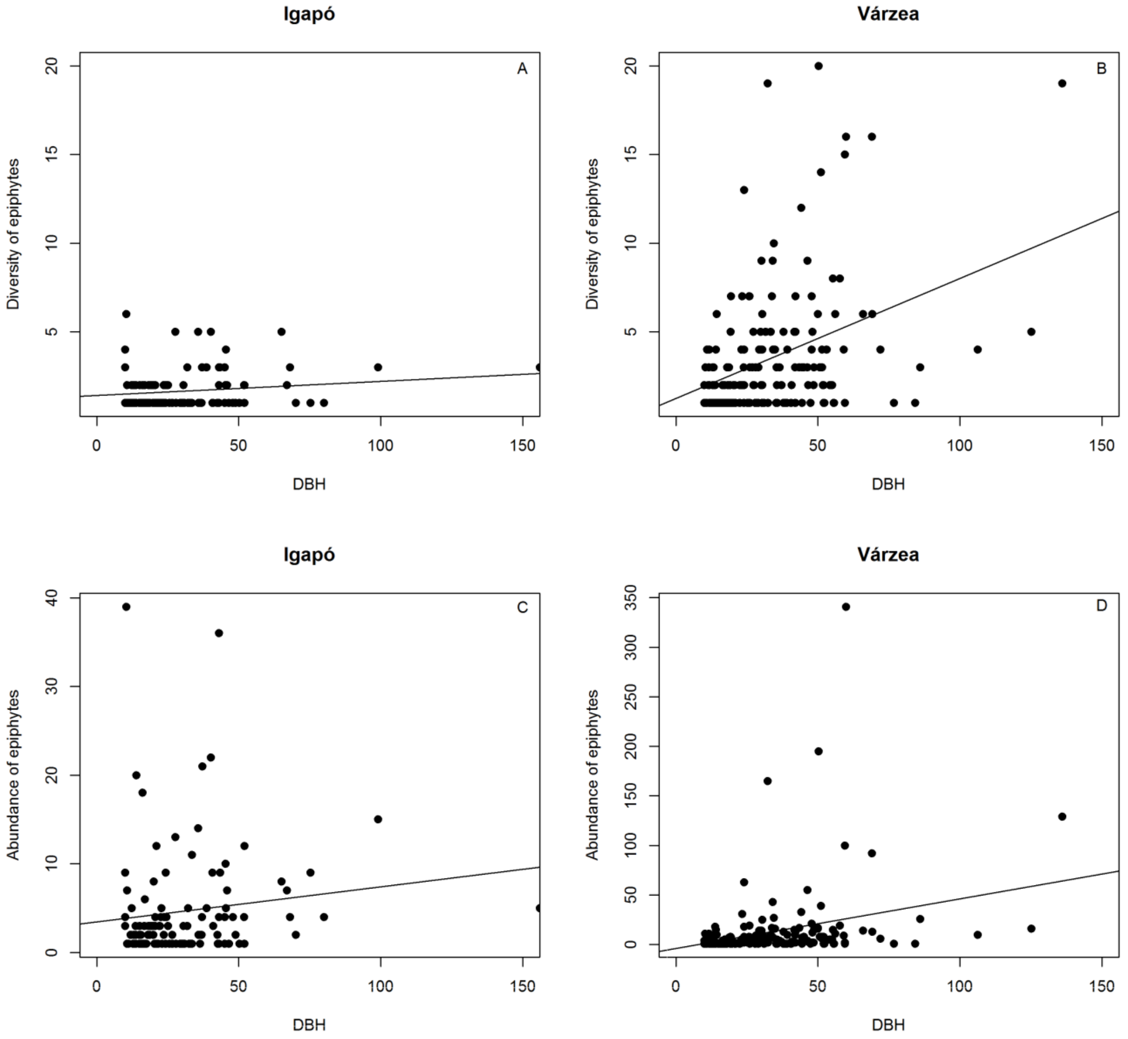

Figura 3. Influência do diâmetro das árvores na diversidade e abundância de epífitas vasculares, utilizando as árvores como unidades amostrais. O aumento do diâmetro reflete um aumento na diversidade e abundancia de espécies na floresta de igapó (Fig 3A e 3C). rever as análises

A diversidade beta entre várzea e igapó é gerada principalmente pelo turnover das espécies em vez de aninhamento (Fig. 4-B e 4-C). Dentro de cada ambiente identificamos dois padrões opostos: na várzea, a alpha diversidade é gerada por um turnover na composição de espécies, ao passo que no igapó, é gerada por um nested de espécies. Ambos os padrões de alpha diversidade foram impulsionados pela variação no diâmetro da árvore suporte. A várzea apresentou uma substituição de espécies ao longo das classes de diâmetro, enquanto no igapó, as espécies que ocorrem em árvores com maiores diâmetros constituem um subconjunto das que ocorrem em árvores com diâmetros menores (Fig. 5).

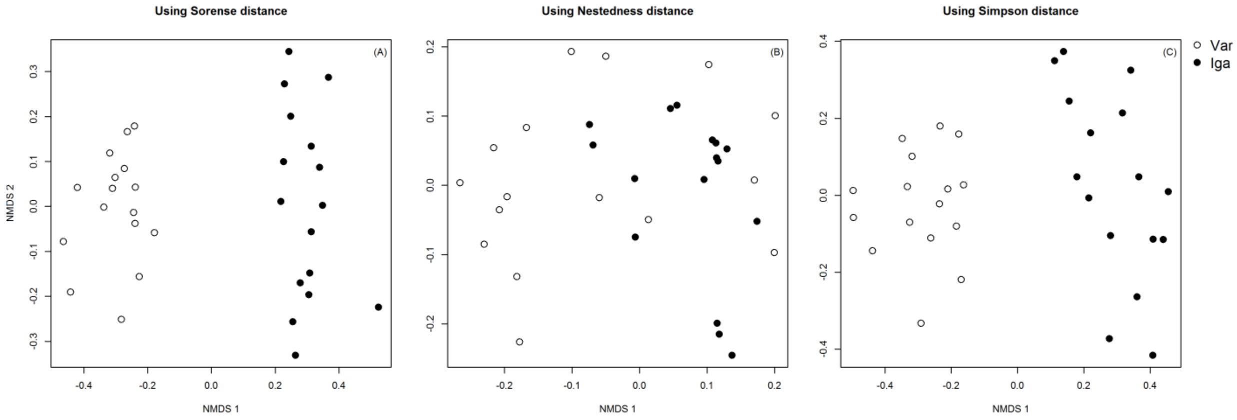

Figura 4. Non-metrical multidimensional scaling (NMDS) using three measures of distance to evaluate differences in the vascular epiphyte composition between várzea and igapó forests. The (A) graph shows the separation of sampling units by the distance of Sørensen's. (B) shows that this separation is not by a standard nested pattern, and (C) indicates the species turnover between forests, using Simpson's distance.

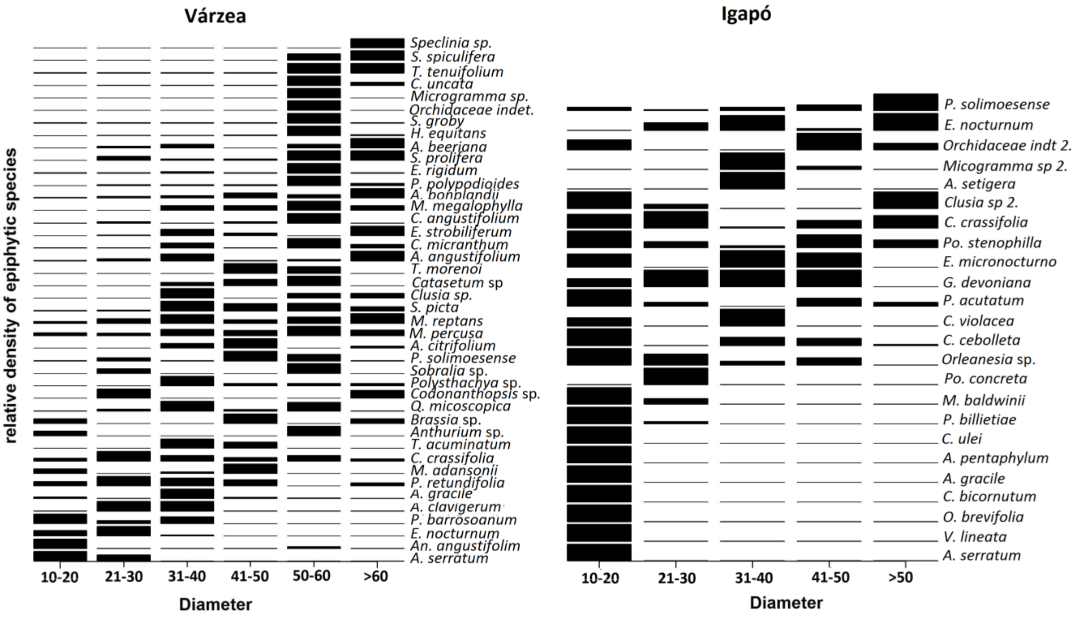

Figura 5. Gráfico de ordenação mostrando o padrão de distribuição das epífitas vasculares nos diferentes diâmetros das árvores em florestas de várzea e Igapó. A várzea apresentou um turnover de epífitas ao longo das classes de diâmetro, enquanto o igapó apresenta um nestedness de epífitas em árvores com menores diâmetros.

Em ambas as florestas a maior riqueza de epífitas ocorre na ZJ III, e a menor riqueza na JZ I (Fig. 6). Por outro lado, pela análise de cluster unindo as alturas de ocorrência com as classes de diâmetro, ocorre a formação de cinco grupos de distribuição de epífitas (Fig. 7).

Alguns desses grupos são facilmente distinguíveis: G1 *várzea* e G5 *igapó*, tratam-se dos grupos formados pelas espécies que estão associadas às menores alturas e menores diâmetros, principalmente as aráceas hemiepífitas *Philodendron barrosoanum*, *P. solimoesense, P. billieteae, Anthurium pentaphyllum, A. gracile, A. clavigerum, Monstera adansonii,* e as samambaias *Asplenium serratum, Microgramma megalophylla, Anetium citrifolium, Ananthacorus angustifolium, Vittaria lineatta;* e G2 *várzea* e G3 *igapó*, tratam-se dos grupos formados pelas espécies generalistas que ocorrem em praticamente todos os diâmetros e alturas, *Peperomia retundifolia, Codonanthopsis crassifolia, Microgramma reptans, M. percusa, Aechmea setigera, Epidendrum nocturno, Philodendron solimoesensis, Clusia* sp2, *Cohniella cebolleta*.

Outros grupos puderam ser distinguidos somente na várzea (G3 e G4). G3 é formado por espécies associadas a grandes diâmetros e alturas intermediárias de 20-30 m, tendo as espécies *Sobralia* sp*., Microgramma* sp*., Specklinia groby*; e G4 por espécies associadas a grandes diâmetros e alturas, principalmente orquídeas e *Clusia* sp. Por fim, algumas espécies formaram grupos que não apresentaram padrões claros (G5 várzea; G1,G2 e G4 igapó).

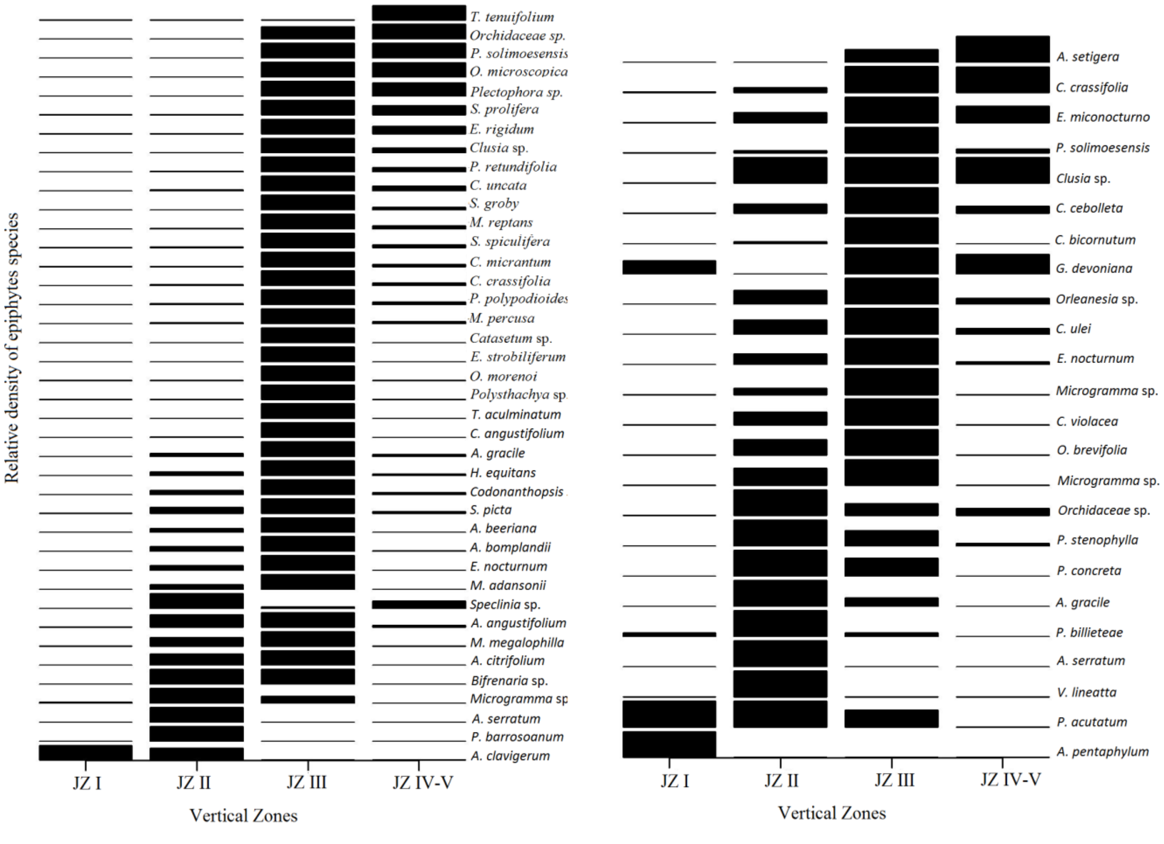

Figura 6. Distribuição das espécies epífitas em zonas verticais. JZI – região da base da árvore até 3 m; JZ II – região de 3 m até a saída do primeiro ramo; JZ III – início dos ramos principais até a metade dos mesmos; JZ IVand V – metade final dos ramos.

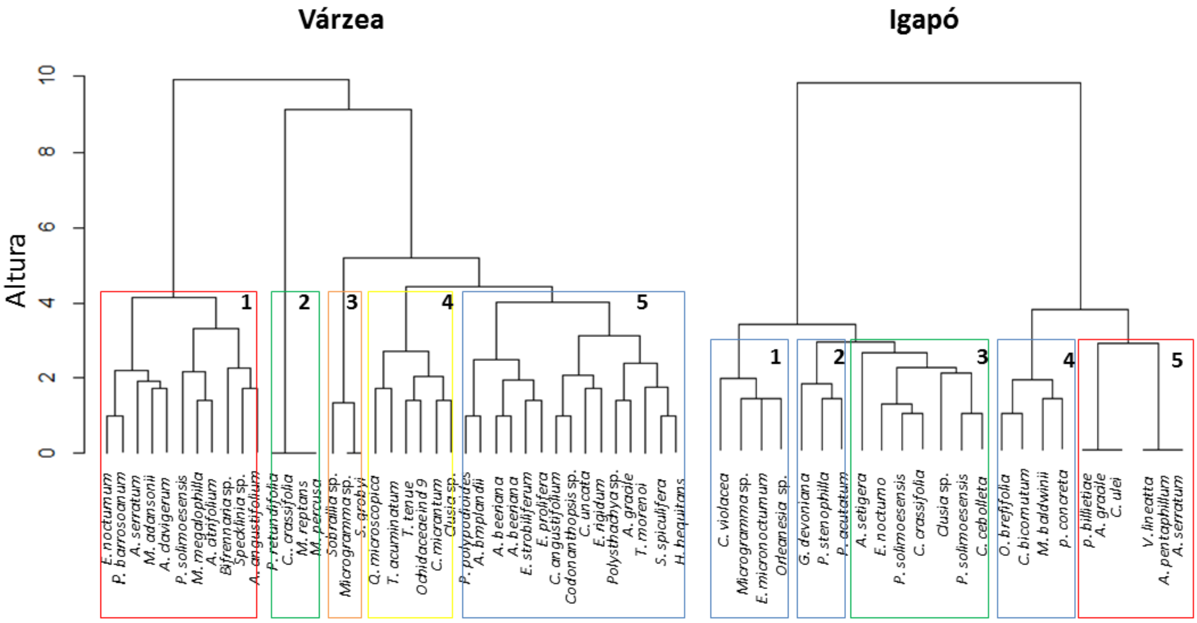

Figura 7. Análise de cluster mostrando o agrupamento de espécies de acordo com sua distribuição em altura e classes de diâmetro em florestas de várzea e igapó

Discussão

O aumento da diversidade e abundância de epífitas com o aumento do tamanho das árvores é uma observação quase onipresente em investigações sobre epífitas vasculares (Johnson 1974, Hietz e Hietz-Seiferd 1995, Callaway et al. 2002, Zotz e Volrath 2003, Flores-Palacios e Garcia-Franco 2006, Wolf et al. 2009). Este fato é relacionado à maior quantidade de substrato e tempo para colonização. Para as florestas de *igapó* esse efeito não foi observado, isso pode estar relacionado ao fato que árvores de igapó com pequeno porte podem atingir idades elevadas mesmo com diâmetros reduzidos (Schöngart et al. 2005), já estando disponíveis há bastante tempo como substratos a serem colonizados. Assim, é possível que, em florestas de igapó, outros aspectos como microclima, rugosidade da casca e utros aspectos estruturais das árvores hospedeiras sejam mais importantes que o diâmetro na estruturação da assembleia de epífitas.

O turnover espacial das espécies já foi observado para as assembleias de árvores em florestas tropicais (Pitman et al., 2002, Tuomisto et al., 2003, Engelbrecht et al., 2007, Condit et al. 2013). Em escala regional, esse padrão parece ser causado por um gradiente climático (Pitman et al., 2002), mesmo que em uma escala maior (neotropical), a precipitação exerce grande influência na distribuição de famílias, gêneros e espécies arbóreas, limitando fisiologicamente a ocorrência em direção a florestas cada vez mais secas, o que leva a um nestedness de espécies em florestas com maiores índices pluviométricos (Muelbert et al. 2016). Como em nossas áreas de estudo os índices pluviométricos são semelhantes, nossos resultados estão de acordo com o relatado para flora arbórea neotropical.

Sabe-se que o turnover das espécies pode ser causado por restrições históricas, seleção de espécies pelo ambiente ou por interações interespecíficas (Quian et al., 2005, Baselga 2008). A história evolutiva pode ser uma importante fonte de variação na diversidade, porém, variações claras na diversidade vegetal ainda não foram esclarecidas com o debate sobre a história paleoclimática da Amazônia (Pitman et al 2002). Por outro lado, interações interespecíficas não aleatórias entre as epífitas vasculares e seus hospedeiros arbóreos, podem explicar o padrão encontrado. A seleção preferencial de arvores por epífitas já foi documentado em alguns trabalhos (Burns & Zotz 2010). Como a composição arbórea entre várzeas e igapós é pouco semelhante (Wittmann et al., 2012), isso pode produzir o padrão aqui descrito, com epífitas ocorrendo de acordo com as singularidades nas assembleias arbóreas em cada ambiente.

Em contraste com o esquema de zonas verticais, sugerido por Johansson (1974), nossos resultados sugerem que uma abordagem baseada na altura exata das espécies em relação ao solo, em conjunto com o diâmetro das árvores, é mais apropriada para detectar padrões de distribuição das espécies epifíticas. A abordagem de Johansson (1974) permite uma fácil aplicação para determinados locais (Zotz 1997), por esta razão é altamente difundida em estudos com epífitas vasculares. Contudo, outros trabalhos não conseguiram distinguir essas zonas (p.exe. ter Steege and Cornelissen 1989, Ek 1997).

O crescimento de espécies ao longo do eixo vertical não pode ser atribuído só ao microclima. Características das árvores como a longevidade e sua disponibilidade espacial para colonização, rugosidade da casca e capacidade de retenção de água diferem na mesma ordem e acabam superando as diferenças causadas por microclima (Zotz 1997).

Na várzea, o turnover de espécies em relação ao diâmetro das árvores e zonas ecológicas é consequência de adaptações morfológicas e fisiológicas para colonizar diferentes substratos e/ou tolerar condições ambientais adversas, o que leva a formação de grupos de espécies com diferentes estratégias de ocupação. Espécies de samambaias epífitas toleram sombra e exigem alta umidade, possuindo tricomas foliares que absorvem umidade atmosférica e incham com saturação de água (Pouig, 2008, Andrade e Nobel, 1997), ao passo que, espécies de aráceas hemiepífitas dependem do solo após a fixação, emitindo raízes adventícias (Zotz 2013). Por estas razões, espécies desses grupos colonizaram alturas mais baixas e árvores com menor diâmetro. No outro extremo ocorrem espécies que toleram grande dessecação por vento e insolação, o que levou a adaptações como estolões e raízes com grande capacidade de armazenamento e absorção de água e nutrientes em orquídeas, tricomas para absorção e controle da perda de água, mecanismo ácido crassuláceo (CAM) e folhas crassuláceas e coriáceas com paredes espessas e cutinizadas com reservas de água (Schimper 1888, Benzing 1990). Entre esses “extremos” encontramos as epífitas mesófilas que podem suportar, ao menos temporariamente, uma atmosfera menos carregada de umidade e insolação, ocupando as partes médias e superiores dos troncos, assim como os galhos mais grossos (Benzing 1990). Por fim, espécies com crescimento reptante, capazes de colonizar substratos recentes, como árvores mais finas e os galhos mais finos das menores e maiores árvores, são espécies generalistas ocorrendo desde árvores pequenas e baixas alturas, até grandes árvores e elevadas alturas, sendo extremamente abundantes nas áreas de várzea estudadas.

Por outro lado, no igapó, o nestedness de espécies em árvores com menores diâmetros pode ser explicado pela preferencia das espécies epífitas por algumas espécies arbóreas (Quaresma et al. in press). Verificamos que essas espécies arbóreas particulares, descritas no trabalho acima citado, ocorreram apenas nas classes de diâmetros menores. Desta forma, o nestedness em árvores com menores diâmetros pode ser um artefato do acolhimento diferencial de epífitas vasculares por espécies arbóreas específicas.

Para epífitas, é a primeira vez que se demostra esses padrões e os processos subjacentes em escala local e regional. Para fins de conservação, a distinção entre os processos de distribuição de espécies (turnover e nestedness) é essencial uma vez que constituem processos antagônicos. Em ambientes estruturados por turnover esforços devem priorizar para a manutenção de diferentes sítios, não necessariamente os mais ricos, enquanto que ambientes estruturados por nestedness devem priorizar a manutenção de um pequeno número de locais mais ricos (Baselga 2010).

Conclusões

O diâmetro da árvore hospedeira influencia os padrões de distribuição espacial de epífitas vasculares em florestas alagáveis, porém explica de forma não satisfatória os padrões de riqueza e abundância. Apesar de não ser um objetivo claro desse trabalho, revisar a metodologia de zonas verticais proposta por Johansson (1974), nossos resultados sugerem que análises baseadas na altura da epífita até o solo, junto com o diâmetro da árvore hospedeira, parecem revelar padrões mais claros sobre a distribuição da assembleia de epífitas e devem ser consideradas em trabalhos posteriores.

Análises da distribuição da assembleia de epífitas revelaram que esforços de conservação devem diferir entre as florestas. Na várzea, medidas de conservação devem priorizar a manutenção da estrutura florestal, sustentando tanto a diversidade taxonômica como também a diversidade diamétrica das árvores. Por outro lado, em igapós os esforços de conservação para epífitas vasculares, primeiramente devem levar em consideração a identidade taxonômica das árvores hospedeiras e posteriormente seu diâmetro. Entender como a composição florística de epífitas é distribuída em suas árvores suporte é fundamental para melhor prever os resultados para a rica biodiversidade da região diante das mudanças cada vez mais intensas decorrentes do processo de desmatamento e de mudanças no ciclo hidrológico em áreas alagáveis.

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Capítulo 3

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Species richness, composition, and spatial distribution of vascular epiphytes in Amazonian black-water floodplain forests: tools for conservation

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Abstract

This study examines the occurrence of vascular epiphytic species in Central Amazonian black-water floodplain forests (*igapó*) and whether their horizontal and vertical distribution is influenced by the flood pulse, as is the case with tree species. The research was conducted in the Jaú National Park; sixteen forest plots where established, each with an area of 25m x 25m, and the epiphytes on all host trees with DBH ≥ 10 cm were identified, as well as their respective host trees. We measured flood height using the watermark left by the last high-water period and then estimated the height relative to the ground of every epiphytic individual. We registered 653 individuals and 37 species distributed on 109 host trees. Only 24.9% of studied trees were occupied by epiphytes: the general low species richness of epiphytes is possibly due to the decreased number of sites available for colonization or trees are unsuitable for colonization. Holoepiphytes predominated, and the combined presence of a flood-pulse, linked to the nutrient-poor soil poor seems to limit the occurrence of nomadic vines. The horizontal distribution of epiphytes followed the distribution of host trees, which in turn followed the flood-level gradient. Epiphytes colonized the vertical gradient differently and flooding interacted strongly with vertical zonation to determine species richness. As already well reported for trees, and unlike reports of epiphytes in other floodplains, flooding strongly influences of the richness and distribution processes of vascular epiphytes in the studied igapó forests.

Keywords: Wetlands; Igapó; Vertical distribution; Horizontal distribution; Flood pulse

Introduction

Amazonian black-water forests (igapó) are areas periodically flooded by nutrient-poor river waters, and characterized by low primary productivity when compared to other Amazonian ecosystems (Furch 1997; Junk et al. 2011; Montero et al. 2012). The periodical flood pulse is the main force affecting the biota and determining the patterns of tree species composition and diversity (Junk et al. 1989; Wittmann et al. 2010; Junk et al. 2015). Tree species are strongly influenced by the flood-level gradient, with species-poor communities at low topographic positions and more species-rich communities at higher topographic positions (Ferreira 1997). Similarly, many tree species from the central Amazonian floodplain forests are strongly zoned across the flood-level gradient (Wittmann et al. 2004, 2010; Targhetta et al. 2015). Tree species distribution in response to flooding may also cause variations in the distribution of the assemblage of associated plants, such as vascular epiphytes (Burns and Zotz 2010). It has been postulated that epiphyte richness in floodplains is not influenced by flood-related stress, but may be influenced indirectly by increased humidity (Leimbeck and Balslev 2001).

Vascular epiphytes are plants that germinate and live upon another plant, don't issue parasitic roots, and do not take nutrients and water from the forest floor for at least a part of their life cycle (Benzing 1990; Flores-Palacios 2016). Moreover, epiphytes are currently considered one of the most threatened groups of plants due to their dependence on the presence/availability of hosts (Flores-Palacios and García-Franco 2008), because despite the abundance of hosts in the Amazon, species widely marketed as wood tend to take a epiphytes load up to three times greater than other trees selected at random (Obermuller et al. 2014), showing that a significant portion of the epiphytic contingent is missed by selective logging (Mondragon et al. 2015).

It has been shown that most epiphytes occupy trees and their vertical strata randomly (Zotz et al. 2014; Flores-Palacios et al. 2015). On the other hand, some studies postulate that vascular epiphytic species are not randomly distributed in host trees and vertical strata. A marked stratification in vertical strata has been recorded by studies conducted in different environments (Schimper 1888; Gentry and Dodson 1987; ter Steege and Cornelissen 1989; Benzing 1990; Nieder et al. 2000; Zotz and Vollrath 2003; Kersten et al. 2009; Zotz 2013). We know, however, much less about the horizontal distribution of epiphytic species among their host trees. Although studies of epiphytes did not often find evidence of epiphytes/host species specificity, some reports state that vascular epiphytes prefer particular host species, so resulting in greater abundance of an epiphyte species on a select number of species (Laube and Zotz 2006; Blick and Burns 2009; Kersten et al. 2009; Vergara-Torres et al. 2010), indicating that the vascular epiphyte assemblage may to some extent be determined by tree species distribution (Burns and Zotz 2010). The distribution of arboreal species in Amazonian black-water forests is directly related to flooding (Ferreira 1997; Junk et al. 2015). However, until this study it was unknown whether the flood pulse also influenced the distribution of vascular epiphytes.

Epiphyte richness is directly correlated with precipitation (Gentry and Dodson 1987), that increases humidity. This may explain the positive relationship between epiphyte richness found in the proximity of small water bodies (Flores-Palacios and Garcia-Franco 2008) and rivers (Leimbeck and Balslev 2001). However, in the Central Amazon floodplains the flooding amplitude and duration are far too intense (up to 200 days and 8 meters, respectively) leading to a decline in the number of tree species near the rivers, indicating that only those adapted to such particular flooding regimes are likely to survive (Ferreira 1997; Wittmann et al. 2002; Junk et al. 2015). Thus, our hypothesis was that the seasonally-flooded areas studied will have a lower richness and abundance of species than other forest environments in the Amazon.

For epiphytes in Amazonian floodplains black-water river, only one comparative study is available, from Surimoni in Venezuela (Nieder et al. 2000), while to the best of our knowledge, there is no study of the species richness, composition, and spatial distribution of vascular epiphytes in a Central Amazon *igapó* floodplain forest. Our research questions were: i) Do *Igapó* floodplain forests have greater richness and abundance of vascular epiphytes species than other Amazonian forests? ii) Is the horizontal distribution of epiphytes determined by the distribution of tree species? And iii) Does flooding influence the vertical distribution and the occupation of trees by epiphytes?

Material and Methods

Study area

We conducted our research in the Jaú National Park, which is part of the Central Amazonian conservation complex and declared a Natural Heritage of Humanity by UNESCO in 2000. The Park is located between the cities of Barcelos and Novo Airão, approximately 220 km North of the city of Manaus, Amazonas State, Brazil. The Park covers an area of approximately 22,720 km^2 and includes the hydrographical basins of the Jaú and Unini Rivers, which are right-hand tributaries of the Negro River (Fig. 1). The mean annual temperature is 26.7 °C, with a mean annual precipitation of approximately 2,300 mm; the dry season lasts from June to September and the rainy season from December to May (Ferreira 2000). The hydrological regime shows a monomodal flood pulse with mean amplitude of 8.3 m (Junk et al. 2015). The peak flooding usually occurs in June with minimum water levels in the beginning of

November [Moura’s hydrological station, 70 km upstream from the Jaú PARNA, data from the National Agency of Waters (Agência Nacional de Águas, ANA)].

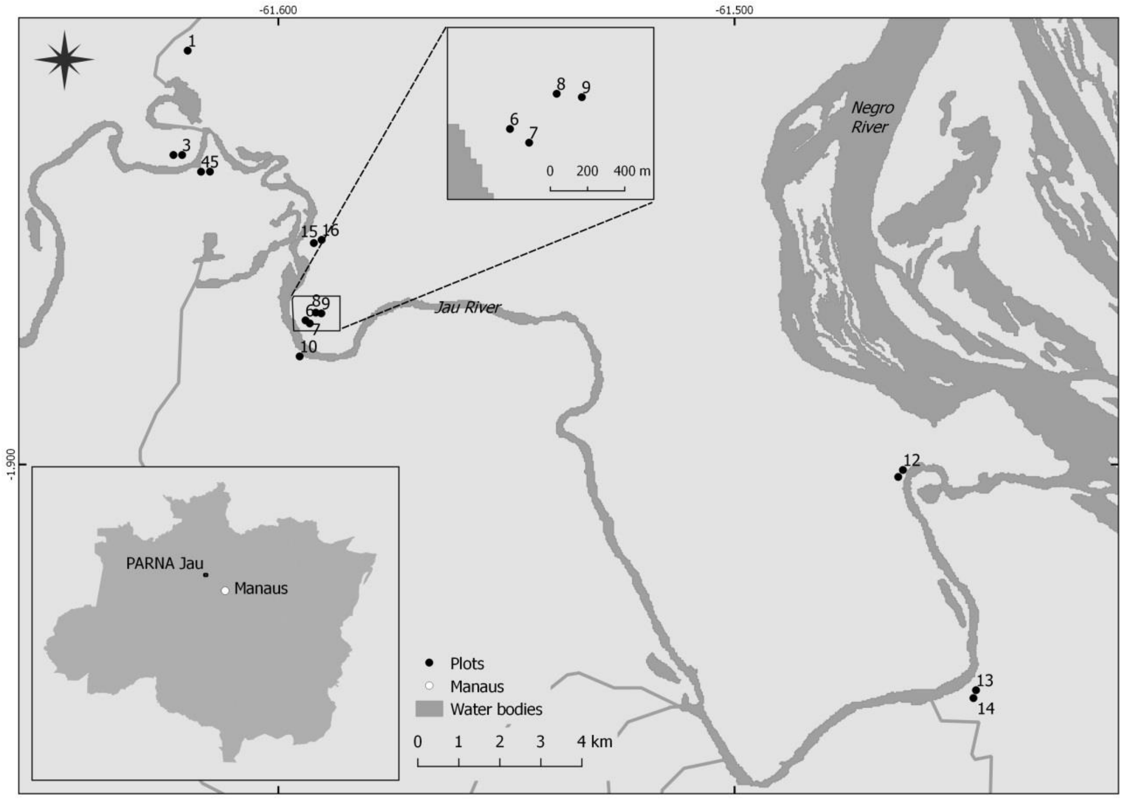

Figure 1. Location of Jaú National Park (Jaú PARNA) showing the 16 plots used for epiphyte sampling.

Data collection

Three expeditions were made to the study area. The first in June 2014 (high water period) to reconnoitre the area and collect fertile and infertile plants. The two following excursions took place in September 2014 and in January 2015, respectively (low water period). In the latter two expeditions, data were collected from sixteen 25 m x 25 m (625 m^2) plots, totaling an inventoried area of 1 ha. The sampled areas formed part of eight 50 m x 200 m (1 ha) forest plots demarcated and inventoried by the PELD MAUA program (Program of Long-term Ecological Research/Programa de Pesquisa Ecológica de Longa Duração – CNPq – Site MAUA “Áreas Úmidas”), and used pre-existing 25 m x 25 m sub-plots. In seven of the nine plots monitored by the program, these sub-plots were the first and last in the series of 50 m x 200 m within in each large plot. The remaining two sampling plots were situated at the extremes of the flood gradient (0.8 m and 7.9 m, respectively), so we could sample the full spectrum of the flood gradient.

For the current study, we divided the sixteen selected plots into three different flood levels based on Wittmann et al. (2002) and Junk et al. (2015). Six plots occurred in areas of low topography (flood level >5.5 m), five in intermediate topography (flood level > 3 m < 5.5 m), and five plots in high topography area (flood level <3 m).

We measured the maximum flood height in the vertices and center of each plot using a 10 m measuring bar, taking as a basis the maximum height of the mark left on the tree trunks by the inundation from the previous year. We identified and quantified all vascular epiphytes, as well as trees with DBH≥10 cm regardless of the presence of epiphytes. We used binoculars for the visualization and counting of the epiphytes on the trees, looking at the host tree on two opposite angles to improve the observation and avoid double counting. Although ground-looking samplings may capture more than 90% of the occurrence of epiphytes (Burns 2007), some studies affirm that observations of epiphytes from the forest floor underestimate the frequency of plants (Flores-Palacios and Garcia-Franco 2001). For correct this bias, we also climbed two or more trees in each plot for more accurate observations, collecting samples, counting and identifying.

For epiphyte species with vegetative reproduction we considered as an individual every group distinctively isolated, as rosettes (Bromeliaceae), pseudobulbs, stems, rizhomes (Orchidaceae) and stems (Araceae and Clusiaceae), colonies distinctly separated (Gesneriaceae) (Sanford 1968). We classified the species according to APG III (2009) and validated species names consulting the list of species of the Brazilian flora (List of Species of the Brazilian Flora, 2015).

For the classification of epiphyte habits we followed the classification of Benzing (1990), and replaced the term “secondary hemi-epiphyte” by “nomadic vine” as suggested by Zotz (2013). We classified the epiphytes as: characteristic holo-epiphytes (normally sprout and grow on other plants); facultative holo-epiphytes (may grow both as terrestrial and epiphyte); accidental holo-epiphytes (usually terrestrial, but may also develop as epiphytes); hemi-epiphytes (germinate on other plants and later establish contact with the ground) and nomadic vines (germinate on the ground and, as they make contact with the host trees the basal part of the radicular/shoot system degenerates, even though the plant still maintains contact with the ground through adventitious roots).

Fertile or sterile samples of epiphyte species were collected for posterior identification using dichotomous keys, specialized books, taxonomists skilled in the groups, and through comparison with exiccates from the herbaria at the Instituto Nacional de Pesquisas da Amazônia (INPA) and Emilio Goeldi Museum, Pará (MG). To achieve the post complete list possible of vascular epiphytes in the study region, we also surveyed trees around the plots for a qualitative assessment. Sterile samples were maintained in a greenhouse until they flowered, and could be used for full species identification.

Epiphyte abundance and richness by within-tree height were calculated and compared with five from the ground to canopy height zones, as proposed by Johansson (1974). We divided each tree into the following Johansson Zones: the basal parts of the trunk (JZ I, 0-3 m); the trunk from three meters to the first ramification (JZ II); the basal part of the large branches (JZ III 1/3 of the total length of the branch); the middle part of the large branches (JZ IV 1/3 of the total length of the branch); the outer part of the large branches (JZ V). However, we considered zones IV and V as a single zone, due to the difficulty of delimitation and because of the low occurrence of epiphyte species in both of them.

Data analysis

We tested for spatial autocorrelation, using a floristic distance matrix and a spatial distance matrix with a Mantel spatial correlogram for Moran's method I. We used the print function to display the correlogram results because it allows for correction of the p values for multiple testing. In a correlogram, a test is performed for each lag (distance class), so that without correction, the overall risk of type I error is greatly increased. The Holm (1979) correction was applied at this point. We used a rarefaction method to test for adequacy of sampling size (Gotelli and Colwel 2010).

Ordination was also used to analyze the horizontal distribution of vascular epiphytes and host trees, using Horn-Morisita distance (Horn 1966), and a significance level of 5%. The first epiphyte ordination involved plot flood level, followed by relation to host trees and then inundation level. The flooding gradient was formed from the weighted average (WA) of measured flood heights in each plot. To confirm the observed pattern, we performed a regression analysis of the first axis of the non-metric multidimensional scaling (NMDS) by flood gradient. Finally, we used a Mantel test to assay the significance of the association between the correlation matrix host trees x flood with the correlation matrix epiphytes x flood.

We performed a regression analysis to test whether the percentage occupancy of trees by epiphytes differed across the flood gradient. We tested the interaction between the flood levels and the vertical distribution of the epiphytes by two-way analysis of variance (ANOVA Two-Way, Sokal and Rohlf 1995).

All analyses were carried out only with epiphytes host trees with a total abundance greater or equal five individuals. All analyses were performed in R (R

Development Core Team 2011). Ordination analysis was performed through generic scripts. Analysis of variance and regression were conducted in the vegan package (vegan: Community Ecology Package 2016); metaMDS in vegan was also used for the NMDS analysis.

Results

Host trees: species composition and occurrence of epiphytes

We checked 662 individual trees, of which 165 (24.9%) had at least one vascular epiphytic. The arboreal individuals were distributed in 111 species, and among these, 52 (47%) hosted epiphytes. The tree species that were colonized by more species and individuals are shown in Table 1.

Table 1. Host trees, and respective richness and abundance of vascular epiphytes. NI – Number of single trees registered with or without vascular epiphytes within the permanent sample plots; NIH – Number of those single trees with vascular epiphytes ; RE – Richness of epiphytes; AE – Abundance of epiphytes.

Host Trees	**N**	**NIH**	**RE**	**AE**
Leopoldinia pulchra Mart.	56	49	11	52
Erythroxylum spruceanum Peyr.	20	06	11	34
Macrolobium acaciifolium (Benth.) Benth.	34	07	09	62
Aldina latifolia Spruce ex Benth.	19	04	08	70
Amanoa oblongifolia Müll. Arg.	39	07	07	11
Pouteria elegans (A.DC.) Baehni	62	05	06	23
Diospyros vestita Benoist	07	05	06	33
Swartzia polyphylla DC.	23	05	06	19
Tachigali sp.	41	12	05	53
Hevea spruceana (Benth.) Müll. Arg.	13	04	05	11
Hydrochorea marginata (Benth.) Barneby & J.W.Grimes	08	01	05	08
Ternstroemia candolleana Wawra	12	05	04	28
Micropholis humboldtiana (Roem. & Schult.) T.D.Penn.	10	03	04	49
Eugenia latifolia Aubl.	02	02	04	04
Licania apetala (E.Mey.) Fritsch	05	03	03	04

Ormosia excelsa Benth.	10	03	03	03
Leptolobium nitens Vogel	01	01	03	05
Couepia sp.	01	01	03	05
Miconia pubipetala Miq.	01	01	03	03
Andira micrantha Ducke	06	02	02	05
Buchenavia ochroprumna Eichler	16	02	02	02
Byrsonima punctulata A.Juss.	10	02	02	07
Elvasia quinqueloba Spruce ex Engl.	24	02	02	02
Licania hypoleuca Benth.	08	02	02	02
Mabea nitida Spruce ex Benth.	05	02	02	07
Marila laxiflora Rusby	03	02	02	02
Simaba obovata Spruce ex Engl.	06	02	02	03
Vatairea guianensis Aubl.	06	02	02	06
Zygia latifolia (L.) Fawc. & Rendle	04	02	02	03
Calophyllum brasiliense Cambess.	03	01	02	04
Dialium guianense (Aubl.) Sandwith	01	01	02	03
Elaeoluma nuda (Baehni) Aubrév.	02	01	02	08
Homalium racemosum Jacq.	04	01	02	07
Micropholis guyanensis (A.DC.) Pierre	10	01	02	09
Myrcia gigas McVaugh	04	01	02	03
Parkia discolor Spruce ex Benth.	01	01	02	04
Xylopia aromatica (Lam.) Mart.	04	01	02	03
Sacoglottis guianensis Benth.	08	02	01	18
Aspidosperma spruceanum Benth. ex Müll.Arg.	03	01	01	40
Calyptranthes sp.	02	01	01	01
Chaunochiton kappleri (Sagot ex Engl.) Ducke	01	01	01	02
Couma utilis (Mart.) Müll.Arg.	06	01	01	01
Elaeoluma schomburgkiana (Miq.) Baill.	04	01	01	02
Eschweilera sp.	06	01	01	01
Laetia suaveolens (Poepp.) Benth.	01	01	01	01

Lecythis chartacea O.Berg	03	01	01	01
Marlierea umbraticola (Kunth) O.Berg	01	01	01	01
Nectandra amazonum Nees	03	01	01	02
Qualea sp.	01	01	01	01
Sloanea floribunda Spruce ex Benth.	01	01	01	02
Swartzia laevicarpa Amshoff	19	01	01	02
Xylopia neglecta (Kuntze) R.E.Fr.	07	01	01	02

We found 257 individual trees belonging to 31 species at lower elevations, 229 individuals of 46 species at intermediate elevations, and 202 individuals of 65 species at highest elevations within the trees. The highest percentage of individuals and tree species occupied by epiphytes were found at intermediate elevations (26.1±73.9 and 31.5±56.2, respectively). The lowest percentage of epiphyte occupancy on individual trees occurred at the lowest elevations (8.9±23.2), while the lowest percentage of tree species occupied by epiphytes occurred at higher elevations (20±29.1) (Table 2).

Table 2. Percentage of occupation (% Occupation) of individuals and species of trees by vascular epiphytes in higher, intermediate and low flood level. AT - Abundance of Tree. RT - Richness of Tree.

	Flooding (M)	AT	% Occupation	RT	% Occupation
Higher flood level	0.8	54	14.8	23	26.0
	0.9	42	28.5	23	29.1
	1.2	37	16.2	20	20.0
	1.5	30	20.0	20	25.0
	2.0	39	17.9	22	22.7
Intermediate flood level	3.1	23	73.9	13	53.8
	3.6	47	29.9	15	40.0
	4.4	42	26.1	15	53.3
	5.1	71	29.5	19	31.5
	5.5	46	41.3	16	56.2

Low flood level	5.6	56	8.9	25	16.0
	5.7	47	21.0	13	46.1
	5.9	27	22.2	08	50.0
	6.4	56	23.2	10	50.0
	7.4	42	11.9	06	33.3
	7.9	29	13.7	06	50.0

Vascular epiphytes: species composition and habits

We recorded 653 individual epiphytes belonging to 37 species, 21 genera and nine families. The rarefaction curve for same sample effort trended to a stabilization around 37 species (Figure 2), indicating that sampling was highly representative. Orchidaceae was the most species-rich family (19), representing 51.3% of our sample. Araceae had five species, followed by Bromeliaceae and Polypodiaceae, both with three species. *Codonanthopsis crassifolia* (Gesneriaceae), *Polystachya stenophylla*, *Octomeria brevifolia*, *Epidendrum micronocturnum* (Orchidaceae) and *Philodendron fragrantissimum* (Araceae) were the species with most individuals recorded (Table 3). Combined, these species comprised 58% of all sampled individuals; 13 species were represented by only one individual, and comprised 2.5% of all recorded individuals.

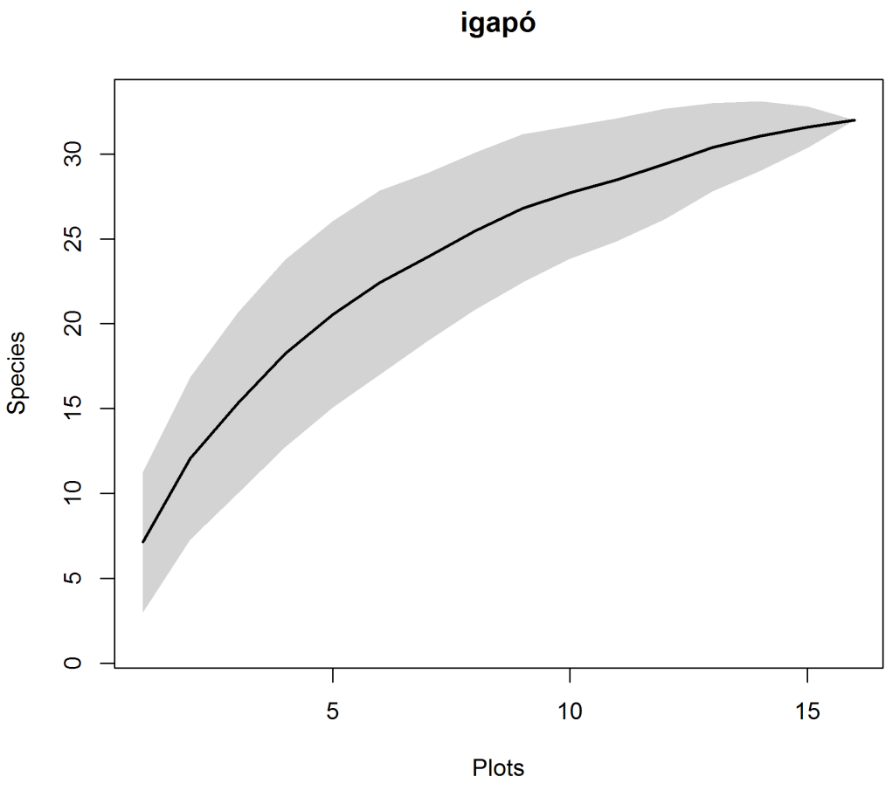

Figure 2. Species accumulation curves for vascular epiphytes in igapó floodplain forest. Average species richness based on 50 randomizations. Displaying the sampling sufficiency with the curve beginning to reach asymptote.

Table 3. Species of vascular epiphytes recorded in the igapó forests of Jaú PARNA, Amazonas State, Brazil, organized by families. N – number of individuals. H – habit. CH – characteristic holoepiphyte. HM – hemiepiphyte. NE – Not found * Species recorded outside of the parcels.

Families/Species	**N**	**H**
Araceae		
Anthurium gracile (Rudge) Lindl.	05	CH
Anthurium pentaphyllum (Aubl.) G.Don	01	HM
Philodendron acutatum Schott	09	HM
Philodendron solimoesensis (Hook.) G.Don	40	HM
Philodendron billietiae Croat	27	HM
Aspleniaceae		
Asplenium serratum L.	06	CH
Bromeliaceae		

Aechemea mertensii **(G.Mey.) Schult**. & Schult.f.*	01	CH
Aechmea setigera Mart. ex Schult. &Schult.f.	02	CH
Araeococcus micranthus Brongn.*	01	CH
Cactaceae		
Epiphyllum sp.	01	CH
Clusiaceae		
Clusia sp.	13	HM
Gesneriaceae		
Codonanthopsis crassifolia (H. Focke) Chautems & Mat. Perret	205	CH
Codonanthopsis ulei Mansf.	11	CH
Orchidaceae		
Aganisia cyanea (Schltr.) Rchb.f.*	01	CH
Brassavola martiana Lindl.	02	CH
Caularthron bicornutum (Hook.) Raf.	02	CH
Cattleya violacea (Kunth) Rolfe	05	CH
Cohniella cebolleta (Jacq.) Christenson	35	CH
Dichaea ancoraelabia C. Schweinf.	03	CH
Epidendrum micronocturnum Carnevali & G.A.Romero	42	CH
Epidendrum nocturnum Jacq.	15	CH
Epidendrum rigidum Jacq.	08	CH
Galeandra devoniana M.R.Schomb. ex Lindl.	13	CH
Octomeria brevifolia Cogn.	40	CH
Octomeria sp.	01	CH
Orchidaceae sp1.	10	CH
Orchidaceae sp2.	13	CH
Orchidaceae sp3.	01	CH
Orleanesia sp.	23	CH
Polystachya concreta (Jacq.) Garay& Sweet	28	CH
Polystachya stenophylla Schltr.	52	CH
Prosthechea vespa (Vell.) W.E.Higgins	04	CH

Rudolfiella aurantiaca (Lindl.) Hoehne	01	CH
Polypodiaceae		
Microgramma megalophylla (Desv.) de la Sota	01	CH
Microgramma baldwinii Brade	19	CH
Microgramma sp.	01	CH
Pteridaceae		
Vittaria lineata (L.) Sm.	12	CH

Only three epiphyte habits were recorded, the holo-epiphytes being the most common with 86.5% of all observed species, and hemiepiphytes they added (13.8%). The Mantel correlogram analysis found no spatial autocorrelation between the sample units (Appendix 1).

Horizontal distribution

Direct gradient analysis showed that the epiphytic species were distributed according to the flood-level gradient (Figure 3-A). Inundation seemed to play a secondary role in the horizontal distribution of epiphytes, since, when the host trees were ordinated by the flood level, a similar and stronger correlation was found (Figure 3-B). This was confirmed by a Mantel test which found a significant relationship between the distribution of epiphytes and host trees (r=0.28, p=0.011; Figure 4).

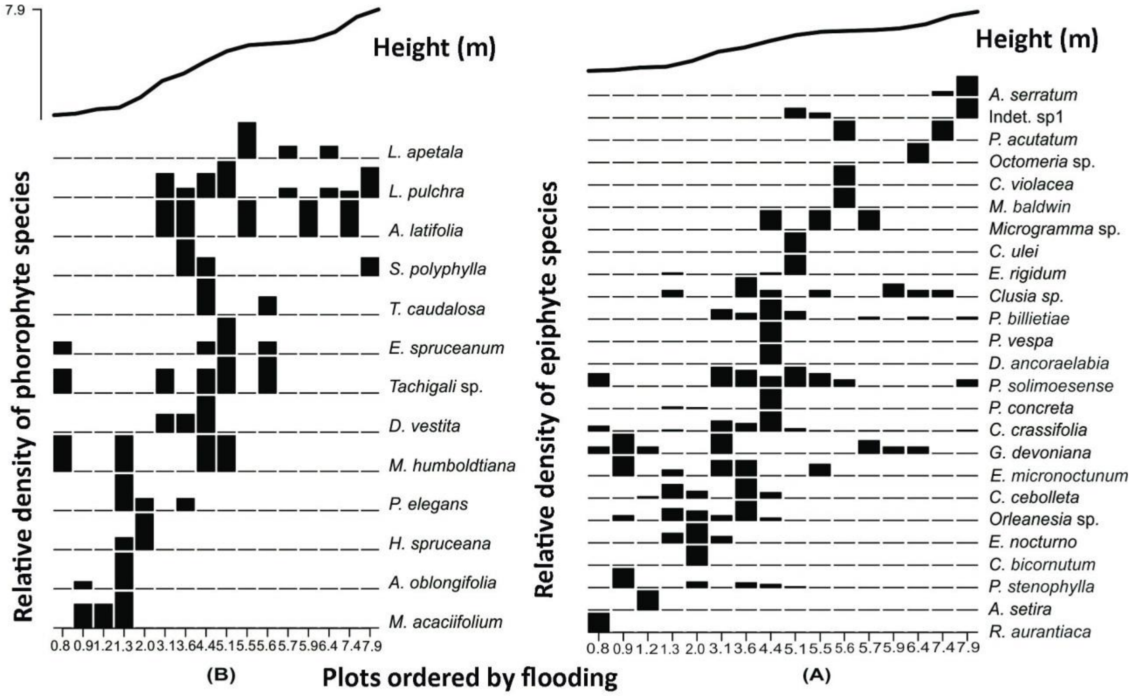

Figure 3. Ordination analysis showing the distribution patterns of the phorophytes (A) and epiphytes (B) according to the flooding gradient in the plots, pointed in superior part of the figure.

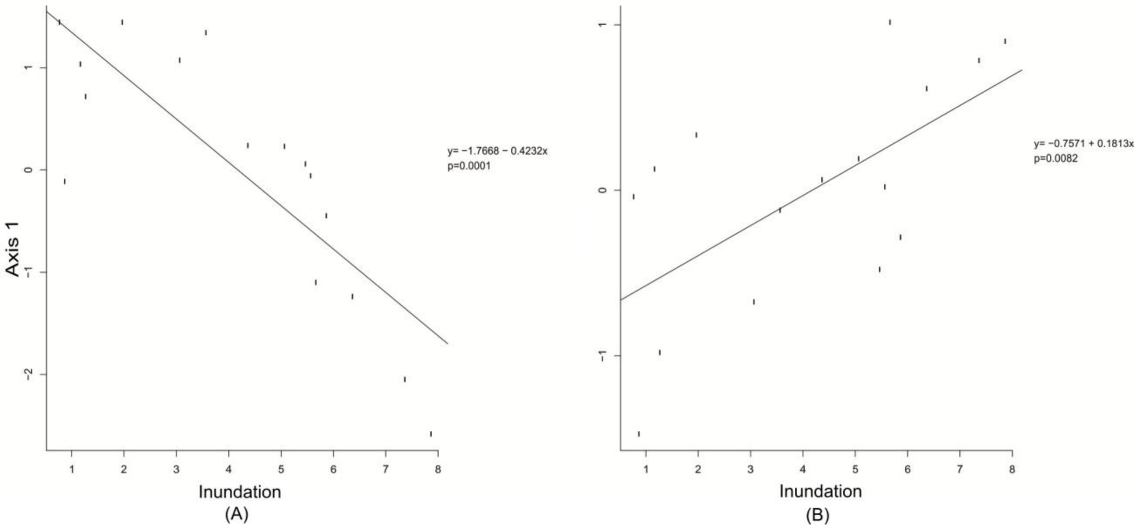

Figure 4. Regression analysis using the first axis NMDS (metaMDS in Vegan) to confirm the distribution pattern displayed in Figure 4, A – host trees and B – vascular epiphytes.

Polysthachya stenophilla, *E. rigidum*, *C. cebolleta*, and *A. serratum* were strongly associated with their phorophytes (Tab. 4), whose distribution responded to the flooding gradient (*M. acaciifolium*, *A. guianensis*, *P. elegans*, *L. pulchra*). The distribution of the majority of epiphytes was not related to the distribution of tree species, but their abundance differed among host tree species. Two species (*Asplenium serratum* and *Vittaria lineata*) occurred only on the palm *L. pulchra*. Two other epiphytic species (*Philodendron* sp. and *Galeandra devoniana*) did not occur exclusively on *L. pulchra*, but showed higher abundance on this species in comparison to its occurrence on other host species (Table. 4).

Table 4. Epiphytic species occurring on host trees with more than five individuals and highlighting in bold the epiphytes that occurred in only one host tree species or with high abundance.

	H. spruceana	*L apetala*	*A. latifolia*	*Tachigali sp.*	*T .candollean*	*D. vestita*	*P. elegans*	*S. polyphylla*	*L. pulchra*	*M. acaciifolium*	*humboldtiana*	*A. oblongifolim*	*E. spruceanum*
C. crassifolia	0	1	24	24	25	18	2	10	6	0	26	0	7
C. ulei	0	0	0	0	0	0	0	0	5	0	0	0	0
G. devoniana	0	1	1	1	0	0	0	0	5	3	0	1	0
P. solimoesensis	0	0	12	16	0	0	0	2	0	0	0	0	2
Clusia sp.	0	0	6	0	0	0	0	2	1	0	0	1	0
A. setigera	0	0	0	0	0	0	0	0	0	5	0	0	0
C. violacea	0	0	0	0	0	0	0	0	0	0	0	0	4
Microgramma sp.	0	2	0	0	0	1	0	0	2	0	0	0	0
M. baldwinii	0	0	0	11	0	0	0	0	0	0	0	0	0
C. bicornutum	0	0	0	0	0	0	0	0	0	3	0	2	0
C. ceboleta	3	0	9	0	1	3	7	0	0	3	8	0	0
Orleanesia sp.	4	0	2	0	0	2	4	3	0	3	1	2	1
E. micronocturnum	1	0	14	0	0	8	2	0	0	10	0	0	0
E. nocturnum	0	0	2	0	0	0	2	0	0	6	0	2	0
E. rigidum	0	0	0	0	0	1	0	0	0	0	0	1	13
P. acutatum	0	0	0	0	1	0	0	0	2	0	0	0	0
P. billietiae	0	0	0	1	0	0	0	1	22	0	1	0	0
P. concreta	1	0	0	0	1	0	0	0	0	0	22	1	0
P. stenophylla	0	0	0	0	0	0	6	0	1	31	0	0	4

A. serratum	0	0	0	0	0	0	0	0	6	0	0	0	0
V. lineata	0	1	0	0	0	0	0	0	**7**	0	0	0	0
P. vespa	0	0	0	0	0	0	0	2	0	0	0	0	2
Octomeria sp.	0	**1**	0	0	0	0	0	0	0	0	0	0	0
D. ancoraelabia	0	0	0	0	0	0	0	0	0	0	0	0	3
R. aurantiaca	0	0	0	0	0	0	0	0	0	0	0	0	1

Vertical distribution

Mean canopy height was 14.6 ± 27.4 m, with maximum and minimum of 35 m and 5 m, respectively. The majority of epiphytic species occupied intermediate heights between 6-16m, JZ II and III (23 species, 523 individuals) (Figure 5). Species richness differed among the vertical zones ($r^2=0.72$; $P=0{,}001$, Figure 6), with fewer species and individuals occurring in JZ I (13 species, 63 individuals), on the basal part of the host trees (e.g., *A. gracile*, *A. serratum* and Orchidaceae sp3, one individual each), and on upper branches of the canopy between 17-24 m, JZ IV and V (8 species, 67 individuals, e.g., *Clusia* sp., *E. nocturnum*, *C. crassifolia*). Epiphytes did not occur on parts of host trees that were flooded and the ANOVA showed a strong interaction between the food level and the vertical zones ($F=3.2$; $P=0.01$), suggesting that flooding promotes a vertical structuring of epiphyte species richness (Figure 6).

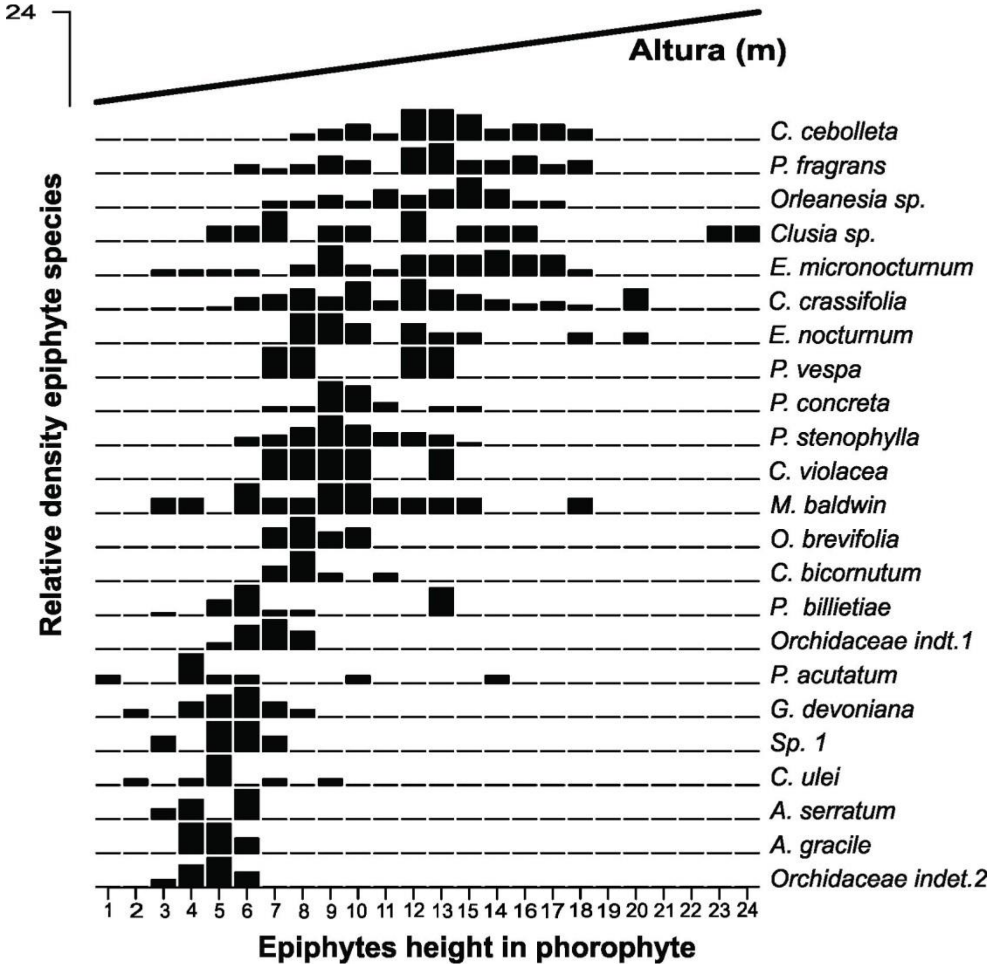

Figure 5. Ordination showing the pattern of vertical distribution of epiphytes on host trees. Species are ordered by host tree height gradient. This varies from 1-24m, but with a notable predominance in intermediate zone.

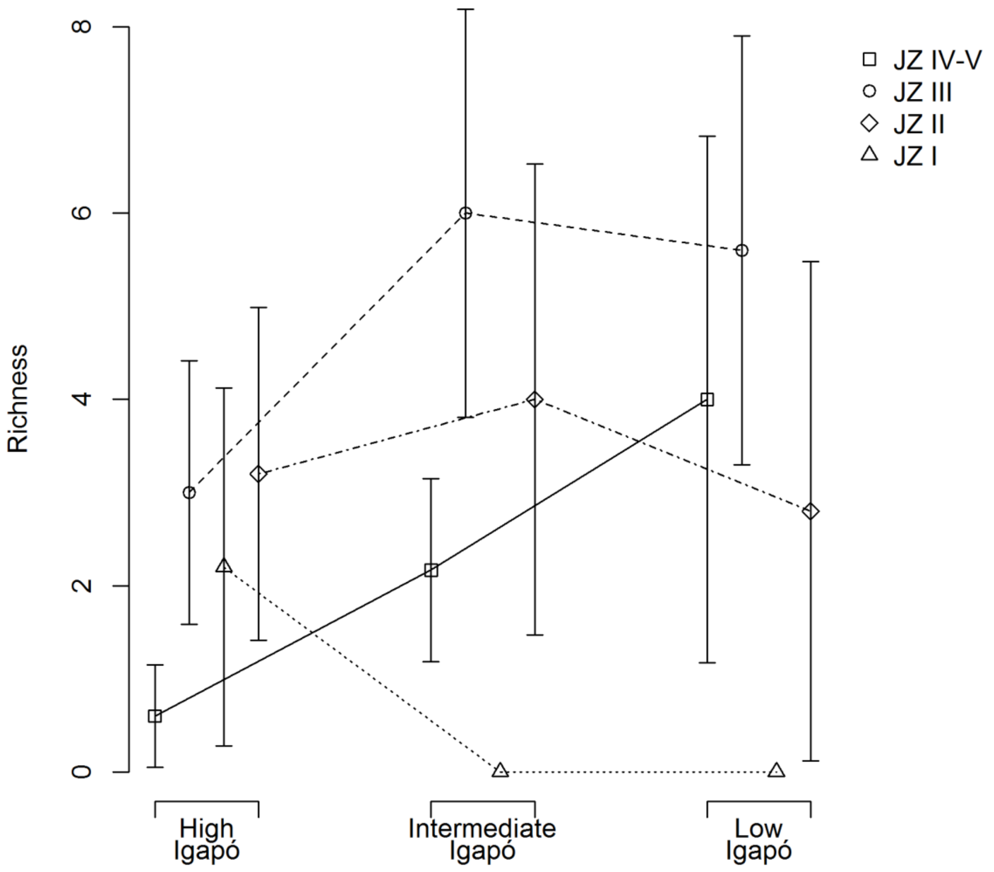

Figure 6. Two-way analysis of variance (ANOVA) showing the difference in richness between floodlevels and between vertical zones, as well as the interaction between flood level and the vertical distribution of species richness. JZ I - Basal parts of the trunk; JZ II - Trunk from three meters up to the first ramification; JZ III - Basal part of the large branches; JZ IV and V - Outer part of the large branches.

Discussion

Orchidaceae, Araceae and Polypodiaceae were, as found earlier, the most prominent epiphyte families. These families most successfully colonize the epiphytic environment, by means of adaptations such as storage of water inside pseudobulbs, velame, mechanism CAM (orchids) and on the development of roots that make contact with the ground (majority of Araceae) or the development of unconventional photoreceptors that are found in eupolipods ferns (Gentry and Dodson 1987; Benzing 1990; Zotz 2013). The fact is that, different adaptations appear to have conferred an evolutionary advantage for each these epiphytic groups to colonize empty niches formed by the emergence of angiosperms in the Cretaceous forests, as suggested for diversifications ferns groups at the end of the Cretaceous (Schneider et al. 2004).

A high percentage of orchids, as recorded in our study (51.3%) was already expected, and results similar were obtained by Freiberg (1996) (50% of orchids), per ter Steege and Cornelissen (1989) (52.9% of orchids) in Guyana, and Nieder et al. (2000) (35.9% of orchids) in flooded forests in Venezuela. However, we expected a higher number of Araceae, as found in other studies (Triana-Moreno et al. 2003; Benavides et al. 2005; Pos and Sleegers 2010; Obermüller et al. 2012). The low percentage of Araceae may be a consequence of environmental restraints for this taxon since many of its species are nomadic vines (Zots 2013), which occupy the ground in their early development. Therefore, the combination of nutrient-poor-soil (Furch 1997), and a short non-flooded period for establishment and initial growth of seedlings (Ferreira 2000; Parolin et al. 2003, 2004), may restrict the number of nomadic vines species in periodically flooded *igapó* forest.

Compared to other Amazonian forests, the low richness and abundance of epiphytes in *igapó* forests is surprising and confirms our hypothesis that *igapó* floodplains forests are poor in epiphytes species. For example, in Amazonian terra firme forests Pos and Sleegers (2010) found 476 individuals from 60 species; Obermüller et al. (2012) 77 species; Irume et al. (2013) 3,528 individuals from 164 species; Boelter et al. (2014) 21,000 individuals from 121 species. In *Campinarana* forests Mari et al. (2016) reported 6,490 individuals from 68 species, and Leimbeck and Balslev (2001) in white-water floodplain forests that registered 57 species of aroids alone (compared to the five aroids species in this study). On the other hand, the only other available study for other *igapó* floodplain forests (Nieder et al. 2000, for the Surimoni River, a tributary of the Orinoco River, Venezuela), reported similar values to the current study, with 778 individuals and 53 species in 1.5 ha. These results may indicate a general pattern of low epiphytic richness in Amazonian igapó floodplain forests, although more studies are needed to support such an affirmation.

Igapó forests are environments poor in tree species, compared to other Amazonian forest types (Junk et al. 2015). The low alpha-diversity and beta-diversity (locally) of trees in *igapó* forests, associated with stable dynamics of the forest, combined with a slow erosion/sedimentation processes (Montero et al. 2012), may restrict the number of niches available for colonization. Gentry and Dodson (1987) suggested that there is evidence for a lower abundance and diversity of vascular epiphytes on the poorer soils of the Central Amazon. The forests studied by ter Steege and Cornellisen (1989) in Guyana also had poor soils, but were richer in species compared to our forests, however they did not experience flooding.

The presence of substances in the tree's bark lower the germination, limiting the occurrence of epiphytes in tropical dry forests, where 12% of the trees were limiting for epiphytes (Vergara-Torres et al. 2010). Studies in white-water floodplain forests of the Ecuadorian (Leimbeck and Balslev 2001) and Colombian Amazon (Benavides et al. 2011), have reported high percentage of tree occupancy (98% and 20-70%, respectively). The low occupation of trees by epiphytes reported in our study(24.9%), reinforces the idea that most trees limit the occurrence of epiphytes, as already reported from other forests where epiphyte richness is low (Vergara-Torres et al. 2010).

Another aspect that we observed was the dominance of a few species and a high number of rare species (one individual), pattern characteristic not just of epiphytic communities (Kersten and Waechter 2011), but also of the Amazon trees community (ter Steege et al. 2013). Only five species made up 58% of all individuals we recorded, while 13 species represented 2.5% of the total. Nieder et al. (2000) recorded four species (*Anthurium gracile*, *Philodendron deflexum*, *Aechmea tillandsioides*, *Codonanthe calcarata*) in flooded areas as distinguished elements of the community, representing 51% of all recorded individuals. The authors attributed this notable abundance to the association of those species with “ant gardens” present in their sampled plots. This explanation may be suitable at least for the most abundant species in our study (*Codonanthopsis crassifolia*) that we also observed associated with ant gardens. This association favors the epiphytes because they are nourished and have their seeds dispersed, furthermore both epiphyte and host trees benefit through the associated protection against herbivores (Kaufmann and Maschwitz 2006).

The majority of species in our study (86.5%) were holo-epiphytes, corroborating data in the available literature on the relative abundance of epiphytes life-forms (see Zotz 2013). We did not observe any facultative or accidental holo-epiphytes. It is likely that inundation and nutrient-poor soils are factors that restrain the development of these types of epiphytes on the ground, favoring the holo-epiphytic life-form in *igapós*. The lack of oxygen and high levels of iron and aluminum toxicity in flooded soils may hamper the germination of seeds of epiphyte species that germinate in the soil (Benavides et al. 2011). Many species also reproduce vegetatively and standing water can be a barrier for growth (Benavides et al. 2011).

Horizontal distribution

Inundation drives the distribution of host tree species, which in turn, determines the distribution of the associated epiphytes. We have shown that the epiphytic assemblage is structured in concordance with the arboreal assemblage; a pattern already suggested by studies in non-flooded environments (Johansson 1974; Bennet 1986; ter Steege and Cornellisen 1989; Dejean et al. 1995; Kernan and Fowler 1995; Callaway et al. 2002; Burns and Zotz 2010; Wagner et al. 2015).

Hietz and Hietz-Seifert (1995) postulated that if a vascular epiphyte shows a preference for any arboreal species, this trait would be shared for the majority of epiphytic species, which suggests that there is a general adequacy of a phorophyte to the colonization by epiphytes. Species such as *A. latifolia*, *M. acaciifolium*, *E. spruceanum* have low number of host trees individuals but a high number of species and epiphytic individuals.

The non-parasitic nature of epiphytism imposes an unique series of constraints on the plants that adopt it, including a dependence on a living organism with different characteristics, and this dependence greatly affects spatial and biological dynamism of epiphytic species and may lead to a closer relationship between epiphyte and host trees, as reported by Burns and Zotz (2010). In this context, we recorded the species *A. serratum* and *Vittaria lineata* exclusively on the host species *L. pulchra*. Though the distribution of the majority of the epiphytes species was not linked to that of the tree species, for particular epiphyte species the number of individuals was much higher on certain tree host species (ter Steege and Cornelissen 1989; Bernal et al. 2005; Laube and Zotz 2006; Kersten et al. 2009; Blick and Burns 2009). The greater richness and abundance of various epiphytes species on the palm tree *L. pulchra* is notable. Characteristics vary little between individuals with stems generally being five to six meters in height, and five to six centimeters in diameter with a covering of persistent old leaf-sheaths. Such factors might facilitate the aggregation and settlement of epiphyte seeds and thus may act as a determining factor in the apparent preference of epiphytes for this tree species.

Our results suggest that epiphytes occupy a higher proportion of host trees in areas of intermediate flooding. If on the one hand the humidity decreases in less flooded areas (Leimbeck and Balslev 2001), the extended inundation in highly-flooded areas physically reduces the substrate area that can be occupied by epiphytes. Accordingly, epiphytes appear to achieve maximum abundance between the extremes of the flooding. However, these patterns should be the subject of further studies

Vertical distribution

The greatest concentration of species and individuals was observed in the intermediate heights of the host trees (JZ III). Two factors may explain the higher epiphyte abundance in this part of the canopy: i) at intermediate heights, tree branches are thicker, bryophytes are more common, there is an accumulation of detritus on the branches, so that arriving epiphyte seeds might have more extensive support mechanisms, and even simply greater traction (ter Steege and Cornelissen 1989; Kersten 2006); ii) this height interval has an intermediate light climate and a high current of circling air, reducing humidity and leading to an ameliorated nutrient uptake (ter Steege and Cornelissen 1989; Kersten 2010).

Contrary to the finds for epiphytes in floodplains of the Ecuadorian Amazon (Leimbeck and Balslev 2001), in our study area flooding appears to hinder the development of epiphytes on the submerged parts of trees; individuals growing on the basal portion of host trees were only observed where flooding is episodic and of low duration. However, outside the plots, we found individuals of the epiphytic orchid *G. devoniana* fully submerged while growing on the palm *L. pulchra*. On the trunk of this palm tree persistent leaf-bases form a network of fibers that forms an irregular matrix in which seeds can establish. This is has sufficient depth and complexity that plants can root into the matrix and resist the force of the current of the river during periods of flood, allowing both their establishment and persistence. This combination does not occur in other host trees in igapó, thus diminishing epiphyte recruitment opportunities.

Our results suggest that flooding promotes a shift of species richness to the higher parts of host trees. Humidity near rivers or in areas with high soil moisture is higher as indicated by extensive formations of mist in the early morning hours in the Ecuadorian Amazon (Leimbeck and Balslev 2001), what is commonly observed in our study area (pers. obs.). Higher humidity in more flooded areas can mean that epiphytes on trees in floodplain forests are less likely to suffer desiccation that those growing in other habitats. Additionally, the lower areas of the landscape are more protected from winds and desiccation (Leimbeck and Balslev 2001), allowing more species to occupy higher positions in the vertical gradient.

According to ter Steege and Cornelissen (1989) the light level and the subsequent humidity on the vertical strata from the base to the top of trees are the main determinant in the vertical distribution of epiphytes. Notwithstanding, along the different areas of the vertical gradient other aspects other than microclimate also influences epiphytes occurrence (Zotz 2007). For instance, intrinsic factors of the species are also important in the distribution of vascular epiphytes in a given habitat. Among them the tolerance to drought, capacity of protection against desiccation, capacity of water absorption and of retaining nutrients directly from the atmosphere are important traits that also influence patterns of vertical distribution (Gentry and Dodson 1987; Benzing 1990).

Conclusions

Igapó floodplain forests have much lower richness and abundance of vascular epiphytes species than other Amazonian forests. Possibly this reflects the limitation of available sites for colonization or the bark of their trees possess characteristics that make them poor hosts limiting the occurrence of epiphytes. The distribution of host trees determined the horizontal distribution of epiphytes, since several species of epiphytes showed occurrence preference for specific host trees. On the other hand, flooding determines the distribution of these specific host trees. Flooding also influences the occupation of trees by epiphytes, as well as interacts with vertical zonation to determine species richness.

Our results suggest that Amazonian ecosystems with low diversity of tree species associated with flooding and nutrient-poor soil are also poor in epiphytes. As already well-reported for trees, and contrary to the proposal that epiphytes are not stressed by flooding (Leimbeck and Balslev 2001), our results show a direct effect of flooding on the vertical distribution of species, in the dominance of characteristic holo-epiphytes, and an indirect effect on the pattern of horizontal distribution of vascular epiphytes.

By establishing a relationship with their hosts, vascular epiphytes are affected when these hosts are removed from the forest environments (Borgo and Silva 2003; Barthlott et al. 2001). In the *igapó* forest, certain host trees species have great richness and abundance of epiphytes than others, indicating that removal of individuals of those species can disproportionately affect the vascular epiphyte assemblage by removing the most highly-preferred hosts. Future action plans for biodiversity conservation should take into account this aspect of differential occupation of tree species by epiphytes.

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Síntese

Investigando os dois principais ecossistemas florestais alagáveis da Amazônia (várzea e igapó de águas pretas), a presente tese elucida padrões e direciona questões relacionadas à composição, padrões de diversidade e distribuição de epífitas vasculares em uma escala local e regional. Nossos resultados revelaram que: 1) árvores de florestas de igapó de águas pretas parecem limitar a ocorrência de espécies fazendo com que esse ambiente seja particularmente pobre em epífitas vasculares; 2) epífitas se distribuem preferencialmente em algumas espécies arbóreas específicas e isso determina sua distribuição horizontal; e 3) a inundação tem um papel crucial na riqueza (limitando a ocorrência de espécies nas partes inundadas), na distribuição horizontal (pois determina a distribuição das árvores que são preferidas por epífitas) e na distribuição vertical (parece promover um deslocamento da riqueza de espécies para áreas mais altas das árvores); 4) a composição de espécies difere consideravelmente entre os dois ecossistemas com uma similaridade menor do que a relatada para a assembléia de árvores; 5) a diversidade de espécies epifíticas é maior na floresta de várzea, mas em nenhum dos ambientes estudados a diversidade de árvores influenciou a diversidade de epífitas; 6) o diâmetro da árvore hospedeira determina a riqueza, abundância, composição e distribuição de epífitas, principalmente em florestas de várzea.

Os resultados desta tese elucidam por primeira vez alguns padrões e processos ecológicos e biogeográficos para epífitas vasculares em florestas alagáveis da Amazônia Central, que até o presente concentrava-se em estudos do componente arbóreo. Dada a grande abrangência e diversidade tipológica de áreas alagáveis, os resultados sobre a vegetação epifítica podem esclarecer estimativas da biodiversidade vegetal para o bioma e servir como base para trabalhos biogeográficos e evolucionários para a Amazônia e para os Neotropicos. Os resultados contidos neste trabalho podem ainda contribuir para a tomada de decisões sobre conservação da biodiversidade dessas áreas e seus múltiplos componentes vegetais.

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BRASIL
GOVERNO FEDERAL

ATA DA DEFESA PÚBLICA DA TESE DE DOUTORADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

Aos 28 dias do mês de julho do ano de 2017, às 14:00 horas, no Auditório do Programa LBA, Campus II, INPA/ALEIXO. Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Rodrigo de Andrade Kersten**, da Pontifícia Universidade Católica do Paraná - PUCPR, o(a) Prof(a). Dr(a). **Charles Eugene Zartman**, do Instituto Nacional de Pesquisas da Amazônia - INPA, o(a) Prof(a). Dr(a). **Veridiana Vizoni Scudeller**, da Universidade Federal do Amazonas - UFAM, o(a) Prof(a). Dr(a). **Rafael Leandro de Assis**, do Instituto Nacional de Pesquisas da Amazônia - INPA, o (a) Prof(a). Dr(a). **Jochen Schöngart**, do Instituto Nacional de Pesquisas da Amazônia – INPA, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública do trabalho de **TESE DE DOUTORADO** de **ADRIANO COSTA QUARESMA**, intitulado **"Epífitas vasculares em florestas alagáveis de várzeas e igapós de águas pretas da Amazônia Central: Padrões de riqueza, composição, diversidade e distribuição de espécies"**, orientado pelo(a) Prof(a). Dr(a). Maria Teresa Fernandez Piedade, do Instituto Nacional de Pesquisas da Amazônia - INPA.

Após a exposição, o(a) discente foi argüido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☒ APROVADO(A) ☐ REPROVADO(A)

☒ POR UNANIMIDADE ☐ POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). Rodrigo de Andrade Kersten

Prof(a).Dr(a). Charles Eugene Zartman

Prof(a).Dr(a). Veridiana Vizoni Scudeller

Prof(a).Dr(a). Rafael Leandro de Assis

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