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LUCIO ROYER TRUJILLO RODRIGUEZ

INFLUÊNCIA DA ESTRUTURA DA COPA SOBRE A DISTRIBUIÇÃO E COMPOSIÇÃO DE EPÍFITAS VASCULARES DE GRANDE PORTE NO EXTREMO NORTE DA AMAZÔNIA

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Dissertação/Tese apresentada ao Programa de Pós-Graduação em Biodiversidade Tropical (PPGBIO) da Universidade Federal do Amapá, como requisito parcial à obtenção do título de Mestre em Biodiversidade Tropical.

Orientador: Dr. Jose Julio Toledo

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combustible e impulsaron mis sueños, e
hicieron mi vida más agradable. Gracias.
“tomas una decisión basada en el amor, nunca
basada en el miedo, con amor todos ganan”.

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RESUMO

Influência da estrutura da copa sobre a distribuição e composição de epífitas vasculares de grande porte no extremo norte da Amazônia. Macapá, 2019. Dissertação (Mestrado em Biodiversidade Tropical) – Programa de Pós-graduação em Biodiversidade Tropical – Pró-Reitoria de Pesquisa e Pós-Graduação - Universidade Federal do Amapá.

Organismos dependentes estruturais como epífitas vasculares tem uma contribuição importante na biodiversidade sobre tudo em ambientes neotropicais, onde a informação sobre o seu estabelecimento, distribuição, e ecologia é ainda pouco conhecida. O objetivo principal deste estudo foi analisar se a forma da copa das árvores hospedeiras têm influência nas epífitas vasculares, tanto em relação à distribuição interna como nos componentes da sua diversidade no extremo nordeste da Amazônia, Brasil. Foram registrados indivíduos de epífitas vasculares com altura maior que 10cm em 124 árvores, em diferentes faixas de DBH, distribuídas em 20 parcelas em uma área de 25km^2 de floresta de terra firme. Os gradientes de volume, profundidade: largura e distancia (5 estratos) foram utilizados como preditores de abundância, riqueza e composição de epífitas. Foram encontrados 800 indivíduos de 49 espécies e 11 famílias de epífitas. Os grupos mais abundantes encontrados foram Cyclanthacea, Araceae, Bromeliaceae e Pteridophytas. As regressões dos modelos lineares mostraram que a riqueza e a abundância das epífitas aumentam em copas volumosas e menos profundas, e em estratos próximos à base da copa. O volume e a forma da copa afetaram a composição das epífitas. Espécies de substituição foram mais importantes em relação às de aninhamento para a beta diversidade, apesar de aninhamento ter um papel significativo na diversidade beta de Bromeliaceae. Os resultados sugerem que a estrutura da copa pode ser uma ferramenta para estimar assembléias e distribuição de epífitas, e que o tempo de estabelecimento é mais importante que a disponibilidade de substrato na distribuição interna, devido a sua maior incidência próxima à base da copa.

Palavras-chave: Diversidade beta, forma da copa, heterogeneidade da copa, largura da copa, profundidade da copa, volume da copa.

ABSTRACT

Influence of crown structure on distribution and composition of large vascular epiphytes in the extreme northeast Amazonia. Macapá, 2019. Dissertação (Mestre em Biodiversidade Tropical) – Programa de Pós-graduação em Biodiversidade Tropical – Pró-Reitoria de Pesquisa e Pós-Graduação - Universidade Federal do Amapá.

Structural dependent organisms such as vascular epiphytes have an important contribution to biodiversity especially in neotropical environments, where information about their establishment, distribution, and ecology is still poorly understood. The main objective of this study was to analyse if the crown shape of host trees has influence on the vascular epiphytes both in relation to the internal distribution and in the components of its diversity in the extreme northeast of the Amazon, Brazil. Individuals of vascular epiphytes with height greater than 10cm were registered in 124 trees, in different DBH ranges, distributed in 20 plots in an area of 25km^2 of terra firme forest. The volume, depth:width and distance gradients (5 strata) were used as predictors of abundance, richness and epiphyte composition. There were 800 individuals from 49 species and 11 families of epiphytes. The most abundant groups were Cyclanthacea, Araceae, Bromeliaceae and Pteridophytas. Regressions of linear models showed that the richness and abundance of the epiphytes increase in voluminous and wider crowns, and in strata near the base of the crown. The volume and shape of the crown affected the composition of the epiphytes. Substitution species were more important in relation to nestedness for beta diversity, although nestedness plays a significant role in the beta diversity of Bromeliaceae. The results suggest that the crown structure may be a tool for estimating assemblies and distribution of epiphytes, and that establishment time is more important than the availability of substrate in the internal distribution, due to its higher incidence near the base of the crown.

Keywords: Beta-diversity, crown depth, crown heterogeneity, crown shape, crown volume, crown width.

SUMÁRIO

1 INTRODUÇÃO GERAL

Epífitas vasculares representam aproximadamente 10% de todas as espécies de plantas vasculares conhecidas, com 27 614 espécies, 913 gêneros e 73 famílias (Zotz 2013a). Em florestas tropicais podem chegar a mais de um terço (35%) das espécies de plantas vasculares e quase a metade (49%) dos indivíduos (Gentry and Dodson 1987,Kelly et al. 1994). A maioria das espécies de epífitas estão nos neotrópicos (55%) (Madison 1977), embora existam números similares de gêneros e famílias em outras regiões (por exemplo, 43 famílias no paleotrópicos e 42 no neotrópico), a especiação explosiva deste grupo de plantas foi dramaticamente intensa no Neotrópico resultando numa maior diversidade (Gentry & Dodson 1987). Epífitas têm um maior número de gêneros nos neotrópicos do que nos paleotrópicos (Croat, 1988) constituindo um componente importante de muitos ecossistemas diferentes, incluindo florestas tropicais, florestas de montanha e florestas nubladas e savanas (Putz & Holbrook 1986). Apesar de contribuir com 31% da diversidade de epífitas na Amazônia Central (Boelter et al. 2014) e 37% no Sudeste da Amazônia (Obermüller et al. 2012), este grupo de plantas é bem pouco estudado. Epífitas são importantes no funcionamento do ecossistema, pois fornecem abrigo e alimento para insetos e vertebrados (Madison 1977, Goetghebeur et al. 1998, Vieira and Izar 1999, Gibernau et al. 2007), ajudam na retenção de água da chuva e nutrientes (Clark et al. 1998, Díaz et al. 2010, Stanton et al. 2014) e atuam como indicadores do estado de conservação dos ecossistemas (Triana-Moreno et al. 2003).

O ciclo de vida natural das plantas hemiepifitas inclui uma fase epífita e uma terrestre ao contrário das holoepifitas que não possuem a fase terrestre (Barkman 1958). As hemiepifitas compreendem duas categorias principais, os hemiepífitos primários, que iniciam seu ciclo de vida como epífitas e posteriormente estabelecem contato com o solo através de cumpridas raízes descendentes e as hemiepífitas secundárias, que germinam no solo e escalam usando raízes aderentes, tornando-se epífitas após a perda do contato do solo (Putz & Holbrook 1986). Zotz (2013b) sugeriu o termo de lianas nômades para a categoria de hemiepífitas secundárias.

Epífitas vasculares são influenciadas pelas características estruturais da copa das suas arvores hospedeiras ou forófitos (Orihuela & Waechter 2010). É conhecida a relação do diâmetro da árvore com a abundância e riqueza de epífitas, porém as relações com variáveis de tamanho e forma da copa são conceitos baseados em evidência indireta.

A copa pode ser altamente determinante na presença de espécies de epífitas, pois cerca de 80% delas ocorre no dossel dos trópicos (Benzing 1990; Wolf & Alejandro 2003). Ao longo do gradiente vertical, estratos baixos mostram pouca incidência de luz e menos disponibilidade de substrato embora apresentem alta umidade (Steege & Cornelissen 1989). Devido às diferenças microclimáticas na copa e no tronco, a maioria das espécies são mais sensíveis quando estão mais longe do dossel. Isso poderia exercer uma força na distribuição vertical de epífitas, assim como indivíduos hemiepíficos que buscam níveis fotônicos apropriados e são mais abundantes neste estrato (Nieder et al. 2000). A disponibilidade de nutrientes no solo também mostrou influenciar a distribuição das comunidades epífitas em escalas locais (A H Gentry & Dodson 1987; Boelter et al. 2014; Orihuela et al. 2014). No entanto, a distribuição horizontal também pode desempenhar um papel importante na distribuição de epífitas na árvore hospedeira (Woods 2017).

Explicações competitivas do tamanho da copa geralmente se referem à largura da copa e sua relação com a competição horizontal pela luz. A competição na dimensão vertical também é possível e pode ocorrer para luz difusa e reduzida, resultando em maior plasticidade na profundidade da copa do que na largura dela (Poorter et al. 2006).

A existência de um *tradeoff* geral entre investimento em crescimento e altura versus extensão lateral da copa tem algum apoio (Archibald & Bond 2003; Poorter et al. 2006; Pretzsch & Dieler 2012). Espera-se que a largura da copa imponha maiores demandas ao suporte mecânico do que a profundidade da copa e, portanto, espera-se que seja escalonada independentemente do diâmetro do caule e da ontogenia (Blanchard et al. 2016; Jucker et al. 2017). Copas largas têm maior pressão mecânica em sua arquitetura (Jucker et al. 2017), isso somado à presença de epífitas, acelera o dinamismo de uma floresta ao quebrar ramos, reforçando a importância das epífitas (Sarmento Cabral et al. 2015). Sterck e Bonger (1998) descobriram que as copas das árvores se tornaram relativamente mais largas, uma vez que se deslocaram para a parte superior, apesar do aprofundamento no início da ontogenia. Alves e Santos (2002) encontraram uma maior variabilidade no formato da copa de espécies emergentes e de dossel em comparação com espécies de menor estatura, atribuindo essa variabilidade à reduzida competição por luz e espaço. A estratificação horizontal pode não estar claramente definida, no entanto, essas duas magnitudes da copa juntas deveriam ser capazes de explicar melhor a composição das epífitas (Martinez-Melendez et al. 2008; Wang 2016).

Árvores maiores foram disponíveis como hospedeiras por um período de tempo maior e geralmente têm mais área de superfície do que árvores menores (Flores-Palacios & García-Franco 2006; Laube & Zotz 2006). Portanto, espera-se que a base da copa contenha uma maior quantidade de epífitas, e a borda uma menor, seguindo a linha de crescimento "radial" característica da ramificação da árvore (Hallé et al. 1978). De acordo com essa forma de desenvolvimento da copa da árvore, a base da copa atua como um vaso de flores, retendo a matéria orgânica e fornecendo um habitat adequado para o desenvolvimento de epífitas (Woods et al. 2015). Essa característica poderia influenciar mais do que a disponibilidade de substrato no restante da copa, pois a base da copa representa aproximadamente 4% do volume total dela, em este estudo.

As epífitas foram estudadas verticalmente ao longo de copas (Graham & Andrade 2004; Krömer et al. 2007; Ruiz-Cordova et al. 2014; Petter et al. 2016), porém, essa estratificação desconsidera o formato esférico da copa (Horn 1971; Johansson 1974; Hallé et al. 1978). No entanto a distribuição das epífitas depende da estrutura da copa (Johansson 1974; Zotz 2007) e a composição epifítica pode mudar em diferentes camadas dela. Esta distribuição também pode ser evasiva e vagamente definida. Usando medidas quantitativas de distância em relação ao seu "centroide" (base da copa) espera-se que os padrões de distribuição e composição da diversidade se tornem mais evidentes.

A diversidade beta foi definida como a variação temporal ou espacial na composição das comunidades ao longo de gradientes de habitat ambiental. Koleff et al. (2003) descreve a diversidade beta como a mudança na composição da comunidade que pode ser medida por similaridade/dissimilaridade entre os sítios (Baselga 2010). A diversidade beta tem dois componentes diferentes que demonstram complementaridade: a substituição de espécies (turnover) e o aninhamento (nestedness) (Harrison et al. 1992, Baselga et al. 2007, 2017). O aninhamento pode acontecer quando os locais têm poucas espécies e são subconjuntos de sítios com uma maior riqueza (Wright and Reeves 1992, Ulrich and Gotelli 2007). Isso pode refletir na perda de espécies como resultado de qualquer processo ecológico que promove diminuição de espécies e a desagregação de comunidades biológicas. O turnover de espécies representa a substituição de espécies por outras de um local a outro (Qian et al. 2005) e pode ser o resultado do ganho ou perda delas devido à seleção ambiental, restrições históricas e competição. Estes componentes da diversidade beta são importantes para compreender melhor questões centrais de biogeografia, ecologia e conservação (Baselga 2010). A diversidade beta pode depender de muitos processos, gradientes ambientais, dispersão de espécies e conectividade espacial entre os locais, moldando os componentes de aninhamento e turnover da diversidade beta.

Espera-se que a diversidade beta seja maior em copas maiores e mais profundas devido à disponibilidade de espaço e à estratificação vertical (Nieder et al. 1999; Nieder et al. 2001; Zotz 2007; Barbosa et al. 2015). Também se espera maior diversidade beta em estratos afastados da base da copa, pois a comunidade com menor proteção da copa fica mais instável, devido às mudanças frequentes no habitat que geram perdas e substituição de espécies (Limberger & Wickham 2012; Myers et al. 2015). Assim, espera-se um aninhamento alto de espécies em copas grandes e perto da base, considerando o tempo de estabelecimento e retenção de matéria orgânica (substrato) (Benzing 2004).

O extremo nordeste da Amazônia é uma região diversa, dominada por uma exuberante floresta de terra firme. A diversidade de epífitas é alta, com 129 espécies de hepáticas e uma espécie de antocero registrada nas florestas nevoadas da Guiana francesa (Gradstein 2006). Nas Restingas do estado de Belém foram registradas 37 espécies de orquídeas (Medeiros & Jardim 2011), oito espécies de Bromélias em floresta de várzea (Quaresma & Jardim 2012) e 11 espécies entre orquídeas e aráceas (Quaresma & Jardim 2014). No entanto, há uma escassez de informação sobre a distribuição e diversidade, especialmente no que se refere ao grupo das hemiepífitas. Apenas estudos sobre taxonomia e registros esporádicos foram realizados na região (Cantuária et al. 2014), mas há uma grande diferença entre os padrões de diversidade e composição e a associação com as características da copa e distribuição interna de epífitas.

2 HIPÓTESES

- Abundância e riqueza aumentarão em copas com maior volume devido ao maior tempo de estabelecimento e também à maior disponibilidade de substrato. Copas com um formato mais esférico e menor heterogeneidade terão mais epífitas pois encontram-se melhor protegidas do exterior. Uma copa com maior abertura de dossel terá mais epífitas pela disponibilidade de luz, mas poderá alcançar o clímax rapidamente. A composição de espécies variará devido a um gradiente diferencial entre copas pequenas e grandes pela disponibilidade maior de substrato. Copas mais profundas também terão uma variação da composição mais acentuada do que em copas largas devido à estratificação vertical. A composição em árvores com alta heterogeneidade da copa será mais complexa por apresentar maior variação. Copas com uma abertura de dossel alta terão uma pobre definição da composição pela preferência de certas espécies nestes ambientes de alta luminosidade. A comunidade será mais aninhada em copas grandes e uma alta substituição de espécies ocorrerá em copas mais profundas e heterogêneas. Em copas com abertura de dossel maior ocorrerá um alto aninhamento.

- Quanto mais próximo da base da copa maior será: (1) a abundância e riqueza pelo maior tempo de estabelecimento e estabilidade; (2) a composição diferenciada em cada distancia da base da copa pela disponibilidade de substrato diferenciado e (3) o aninhamento de espécies e a porcentagem de substituição em distancias maiores da base da copa.

3 OBJETIVOS

3. 1 GERAL

Analisar a influência da copa sobre a abundância, riqueza e distribuição interna de epífitas vasculares de grande porte em uma floresta do extremo nordeste da Amazônia.

3. 2 ESPECÍFICOS

- Testar se abundância, riqueza, composição e diversidade beta de epífitas vasculares é influenciada pelo volume, forma, heterogeneidade e abertura de dossel da copa.
- Testar se abundância, riqueza, composição e diversidade beta de epífitas vasculares é influenciada pela distância dentro da copa, tomando como referência a base da copa.

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5 ARTIGO CIENTÍFICO

Influence of crown structure on distribution and composition of large vascular epiphytes in the extreme northeast Amazonia

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Influence of crown structure on distribution and composition of large vascular epiphytes in the extreme northeast Amazonia

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Abstract

Background: Tree crowns structure can influence epiphytic assemblages, but these concepts have been little explored and are generally based on indirect evidence.

Aims: Here we test the direct influence of crown structure on epiphytes assemblages in a forest in the extreme northeast Amazon.

Methods: We assessed if volume, shape, heterogeneity, canopy openness and relative distance of epiphytes to crown base affect, abundance, richness and composition of epiphytes using three-dimensional data.

Results: Epiphytes showed a significant relationship with volume and at less extent to crown shape. Volume and crown shape affected the composition of epiphytes and species turnover was more important than nestedness for beta diversity, though nestedness has a significant role on beta diversity of Bromeliaceae. Epiphytes were clumped near the crown base, demonstrating that age and quality of substrate are determinants for within-crown distribution of epiphytes.

Conclusions: Results suggest that the crown structure can be a tool to estimate assemblages and distribution of epiphytes, and that establishment time is more important than availability of substrate in the internal distribution, due to its higher incidence near the crown base.

Keywords: beta-diversity, crown depth, crown heterogeneity, crown shape, crown volume, crown width.

Introduction

The ecological knowledge about determinants of distribution and diversity of vascular epiphytes in Brazilian Amazon is currently still incipient, with a modest number of studies (Irume et al. 2013; Boelter et al. 2014; Magalhães & Lopes 2015). Epiphytic plants are important components of the tropical forest ecosystem and understanding their relationship with the environment, including tree hosts, may help to predict their occurrence and to plan their conservation.

The complex appearance of tropical rainforests is largely due to the many structurally dependent plants (Richards et al. 1996). Epiphytes may be particularly prominent, accounting for a large proportion of the vascular species at a given site (A H Gentry & Dodson 1987; Kelly et al. 1994b). Despite their high local diversity and abundance, vascular epiphytes grow very slowly; available information suggests the greater availability of substrate increases the probability of establishment (Callaway et al. 2001; Zotz & Vollrath 2003; Magalhães & Lopes 2015).

Structural characteristics of the phorophyte crowns have influence on vascular epiphytes (Orihuela & Waechter 2010).It is known that tree diameter is related to the abundance and richness of epiphytes, but relations with other variables such as crown size and crown shape are assumed based almost entirely on indirect evidence

Crown can be highly determinant in the presence of epiphytes because almost 80% of the epiphytic species in tropics occur in the upper canopy (Benzing 1990; Wolf & Alejandro 2003) .Along the vertical gradient, lower strata show lower light incidence and less substrate availability, although higher humidity (ter Steege & Cornelissen 1989). Due to the microclimatic differences between crown and trunk, species are more sensitive to desiccation the more far from the canopy. This could exert a force in the vertical distribution of epiphytes, as well as hemiepiphytic individuals seeking appropriate photic levels and are more abundant in this stratum (Nieder et al. 2000). Soil nutrient availability has also been shown to influence epiphyte community distribution at local scales (A H Gentry & Dodson 1987; Boelter et al. 2014; Orihuela et al. 2014). However, horizontal distribution could also play an important role in the distribution of epiphytes in the host tree.

Competitive explanations of crown size usually refer to crown width and its relationship with horizontal competition for light. Competition in the vertical dimension is also possible(Poorter et al. 2006)and may occurs for diffuse and reduced light, resulting in greater plasticity in crown depth than crown width.

The existence of a general tradeoff between investment in height growth versus lateral crown extension has some support (Archibald & Bond 2003; Poorter et al. 2006; Pretzsch & Dieler 2012). Crown width is expected to place higher demands on mechanical support than crown depth, and is therefore expected to scale independently of stem diameter and ontogeny (Blanchard et al. 2016; Jucker et al. 2017). Wide crowns have greater mechanical pressure in their architecture (Jucker et al. 2017), this added to the presence of epiphytes to these crowns, would reinforce the concept of epiphytes accelerate the dynamism of a forest, breaking branches (Sarmento Cabral et al. 2015). Sterck and Bonger (1998) found that tree crowns became relatively wider once they moved into the overstory, despite deepening earlier in ontogeny. Alves and Santos (2002) found a greater variability in crown shape of emergent and canopy species compared to smaller-statured species, attributing this variability to reduced competition for light and space. Horizontal stratification may not be clearly defined, however, these two magnitudes of the crown together, should be able to better explain the composition of epiphytes (Martinez-Melendez et al. 2008; Wang 2016).

Larger trees are available as hosts for a longer period of time and usually have more surface area than smaller trees (Flores-Palacios & García-Franco 2006; Laube & Zotz 2006). Therefore, it is expected that the base of the crown contains a greater amount of epiphytes, and the edge a smaller one, following the line of "radial" growth characteristic of the branching of the tree (Hallé et al. 1978).

According to the form of development of the tree crown, crown base acts as a flowerpot, retaining organic matter and providing a suitable habitat for the development of epiphytes (Woods et al. 2015). this characteristic could influence the availability of substrate in the rest of the crown, since it occupies 4% of the entire crown volume.

Regarding the distribution of epiphytes within the crown, epiphytes were studied vertically along crowns (Graham & Andrade 2004; Krömer et al. 2007; Ruiz-Cordova et al. 2014; Petter et al. 2016), however, this stratification disregards the spherical format of the crown (Horn 1971; Johansson 1974; Hallé et al. 1978). suggesting that epiphytes distribution depend of its crown structure (Johansson 1974; Zotz 2007) and epiphytic composition can change into different layers of the crown. However, this distribution can also be elusive and vaguely defined, using quantitative measures of distance in reference to their "centroid" (crown base), we hope that patterns of distribution and composition of diversity become more evident.

Beta diversity is the change in community composition and can be measured through similarity/dissimilarity between sites (Koleff et al. 2003; Baselga 2010). Beta diversity may be divided into two different components, turnover and nestedness (Harrison et al. 1992). Nestedness can appears when sites of poor species are subsets of sites with higher richness (Ulrich & Gotelli 2007) while turnover represents the substitution of species by other species (Qian et al. 2005).

The extreme northeastern Amazonia is a diverse region dominated by exuberant terra firme forest. Diversity of epiphytes is high with 129 species of liverworts and one hornwort species recorded (S. R. Gradstein 2006), 37 species of orchids (Medeiros & Jardim 2011). However, there is a lack of information on the species distribution and diversity. Only studies about taxonomy and sporadic records were made in the region (Cantuária de Castro et al. 2014), but there is a large gap to be filled about the patterns of diversity and composition and the association with host characteristics, forest structure and environmental constraints. Characteristics of the crown can be useful for predicting epiphytic assemblage, along with characteristics such as the internal distribution of epiphytes can be a great tool in the detection and best estimate of richness, abundance and composition of epiphytes .Therefore, we studied epiphytes in a representative tract of terra firme forest and inventoried tree crowns to (1) test if epiphyte community is influenced by crown variables and distances to the crown base, and (2) to determine how composition, beta diversity and its components (turnover and nestedness) vary with crown volume and shape and distance of crown base.

Materials and methods

Study area

The study site spans an area of 25 km^2 of tropical terra firme forest within the Amapá National Forest (ANF) (**Fig. 1**) which is located in the extreme northeast of the Brazilian Amazon, in the Guiana Shield, in the core of Amapá state (0°55’29”N, 51°35’45”W). ANF is part of a large ecological corridor known as Amapá Biodiversity Corridor, a group of protected areas that account for more than 70% of the state's total area (Albernaz and Souza 2007). The regional climate is classified by Köppen-Geiger as Am (Equatorial monsoon) (Kottek et al. 2006). The temperature varies between 22°C and 32°C, and annual rainfall is around 2,284 mm with a rainy season from December to July and dry season from August to November, but precipitation often exceeds 60 mm in dry months (ICMBio 2014). The topography is slightly undulated with altitudes varying between 100 and 200 m and inclination around 7% on slopes. The ultisols are predominant and chemical fertility is low. The vegetation consists of continuous tropical rainforest vegetation, predominantly non-flooded closed canopy ‘‘terra firme” forest (ICMBio 2014). Canopy trees typically reach a height of 25–35 m interspersed with frequent emergent trees reaching up to 50 m (ICMBio 2014). Most abundant tree families in the area are Lecythidaceae, Fabaceae, Sapotaceae, Burseraceae and Annonaceae, and the most important species are *Voucapoua americana* Aubl., *Eschweilera ovata* (Cambess.) Miers, *Eschweilera coriacea* (DC.) S.A. Mori, *Lecythis chartacea* O. Berg and *Eugenia cupulata* Amshoff (ICMBio 2014).

Data sampling

Epiphytes and Phorophytes

The epiphytes were surveyed in 122 host trees distributed in 20 permanent plots out of 30 plots that were established following the guidelines of RAPELD method (Rapid Assessment for Long-Term Ecological Research) (Magnusson et al. 2005) along the east-west trails of a trail system installed by the Brazilian Program for Biodiversity Research (PPBio) in the southern part of the ANF (Fig. 1). Sampling of host trees was conducted in order to include at least one tree per plot of previously established diameter size-classes (DBH: ≥1-<10, ≥10-<20, ≥20-<30, ≥30-<40, ≥40-<50, ≥50-<60, ≥60-<70, ≥70-<80, ≥80-<90 and ≥90 cm).

Phorophytes were surveyed for large vascular epiphytes (>10 cm of length) from March 2017 to June 2018 utilizing binoculars (Bushnell Nature view 10 × 22mm), hypsometer (TRUEpulse 360B) and by naked eye. Taller trees were climbed with single rope technique to access the canopy (Wolf et al. 2009). Most of the vascular epiphytes were identified using the guides of flora of Ducke reserve (Ribeiro et al. 2002) and Amazonian ferns fromZuquim et al. (2017). When it was not possible to identify the species in the field, botanical vouchers were collected for taxonomic identification by comparison with material deposited in the HAMAB herbarium at Institute of Scientific Research and Technology of Amapá. Fertile material is in process of deposition in this herbarium. For circumscription of fern families, we followed Smith et al. (2006) and for the flowering plants we used the APGIII and APG IV (Angiosperm Phylogeny Group 2016).

Crown variables

Using a hypsometer (TRUEpulse 360B), 12 three-dimensional points of the edge of the crown were taken; 1 point of the crown base (point 0, 0, 0) where branches of first order (coarse branches) begin to form the crown, 1 point of the highest part of the crown (total height point) and 10 points of the most extreme lateral edges according to the shape of the crown (Figure 2a), generating a cloud of points in a three-dimensional space. Each three-dimensional point contains 3 data in spherical coordinates: Azimuth (Az), horizontal distance (HD) and vertical distance (VD) (Figure 2a), which were converted into the three-dimensional Cartesian system (X, Y, Z) for further calculations.

The centroid of the cloud of points was calculated and the distance between the centroid and each one of the 12 external points (radii) were also calculated, providing 12 radii measures per crown, including those in relation to crown base and in relation to the highest point of the crown (total height point) (Figure 2d). The average radius of the 12 distances (Rm) was used in a sphere volume formula ($4/3 \times \pi \times Rm^2$) to provide the volume of the crown.

Most trees presented a cone-shaped crown, convex at the base (spherical sector). However, there were also spherical, spheroidal and tubular crowns although in a minimal proportion. Because the volume of the crown can vary widely according to the estimation method (Nelson 1997; Boudon & Godin 2011) the same method was used for all crowns.

We calculated the ratio between crown depth and crown width as an index of crown shape. The higher values of this index indicate deeper crowns and the smaller values indicates wider crowns. Crown depth was calculated as the vertical distance between the crown base and the highest point of the crown (VDch) (Figure 2a) in meters and the crown width was calculated as the average of all horizontal distance values (HDaverage) in meters measured at10 points at the extreme lateral edges (LP) in relation to the base of crown (Figure 2a).

$$\text{Depth: width crown ratio} = \text{VDth} / \text{HDaverage} \times 2$$

Crown heterogeneity was estimated as the variability (standard deviation) of the 12 radii obtained between extreme lateral points and the crown centroid.

We also estimated canopy openness using hemispherical photographs of the crowns taken with a smartphone (Xiaomi Redmi Note 4) in the application GLAMA version 3.0 (Tichý 2014). For the calculation of canopy openness, we selected only the target crown putting a circle of approximate size of the crown to separate it from all the crowns which appeared in the photograph **(**Fig. **S3)**

Relative distance of epiphytes to crown base

We selected three nearest lateral edge points of the crown (LP), including ever the highest point (CH), of each epiphyte and calculated the average distance of these points to crown base (CB) and also we determined the centroid of these points into the three-dimensional Cartesian system. The centroid was used to set the right three-dimensional position of a straight line which represents the averaged distance between crown base and lateral edge points. Thus, it was possible to drawn two segments of arch between the highest point position of the crown (CH) and the other two nearest lateral edge points. The segments of arch passed obligatory through the position of the average distance of crown base to lateral edge points set using the centroid. We calculated the distance of the epiphyte to a projected edge of the crown drawing a straight line between the epiphyte point position (EP) and the crown edge (CE) generated using the two segments of arch (Figure 2b). Thus, the relative distance of each epiphyte to crown base was calculated dividing the distance of CB - EP by CB- CE. All these calculations were made in Geogebra version 6.0.451.0 (Hohenwarter 2018).

Relative Volume of within crown layers

Distances from crown base (CB) to crown lateral edges (LP) (Figure 2c) were multiplied by five proportional boundary line values (0.2, 0.4, 0.6, 0.8 and 1), which represent the boundary line between layers into the crown. It produced distance values (in meters) for each boundary line. The distances of each boundary were used to calculate averages, which represent radii of five different spheres into a crown. The volume of these five spheres were calculated for each crown and five constants (0.04, 0.12, 0.20, 0.28 and 0.36), which represent the proportional volumes of corresponding crown layers (0 - 0.2, 02 - 0.4, 04 - 0.6, 06 – 0.8 and 08 – 1, respectively), were calculated by subtracting the volumes of one sphere from another and by dividing the results by the total volume of the sphere. By multiplying the constants by the crown volume (calculated as described in the section of crown variables) it was possible to calculate the volume of each layer of each crown.

Data analysis

Species richness per crown was estimated using Chao estimator, which considers the number of rare species that are found in a sample as a way of calculating how likely rare species are to be undiscovered (Chao 1984). We calculate the Chao Index for all the epiphytes and for the most abundant groups (Araceae, Bromeliaceae and Pteridophyta) for all the analyzes

Due to a large number of crowns and crown layers without epiphytes or groups of epiphytes, the models were performed with zero inflated correction (Zuur et al. 2009) for abundance data using Poisson or negative binomial distribution families. The values of Chao Index were rounded to the nearest integer to fit into Poisson distribution and the zero inflated correction was also performed. Zero inflated models have well controlled type I errors, higher power, better goodness of fit measures, and are more accurate and efficient in the parameter estimation (Xu et al. 2015).

We tested if four characteristics of crown structure (volume, shape as depth: width ratio, heterogeneity as radii variability and canopy openness) affect species abundance and richness of epiphytes using zero-inflated general linear models. We also tested for the influence of distance to the crown base (using the mid class value of each crown layer) and volume of crown layer on abundance and richness using linear mixed-effect models also with zero-inflated correction. Distance to the crown base and volume layer were placed as fixed effect factors and crown was placed as random effect factor.

Total height of the phorophyte was not included as predictive variable because it was highly correlated to crown volume ($r^2 = 0.77$) showing a high variance inflation factor in the models (VIF > 4).

We tested if epiphyte composition of all epiphytes and its main abundant groups was affected by crown structural characteristics (volume, depth: width ratio, crown variability and canopy openness) and if distance to crown base influence composition within crown through Permutational Multivariate Analysis of Variance (PERMANOVA) using Bray Curtis dissimilarity as distance. The significant predictive variables (crown volume and depth:width ratio) were divided into 10 discrete size classes, keeping at least 12 crowns within each class, and the number of epiphytes within these classes was calculated for further beta partitioning analysis. These news classes were compared with the beta diversity of epiphytic species, multivariate analysis continued to be significant with compositions of representative groups.

We analyzed the contribution of turnover and nestedness for beta diversity of all epiphytes and for most abundant epiphyte groups through the classes of crown volume and crown heterogeneity (Baselga 2010; Baselga 2017b). For qualitative data the overall beta diversity was estimated by the multiple-site dissimilarity of Sorensen (βsor), while the turnover component was calculated using Simpson dissimilarity (βsim) and the nestedness component (βsne) was calculated as the resultant fraction βsor - βsim (Baselga 2010). For partitioning of beta diversity using abundance data, the abundance-based multiple-unit Bray-Curtis dissimilarity index (βbc) was calculated and split into turnover (abundance-balanced variation – βbc.bal) and into nestedness (abundance gradient - βbc.gra) using the relation βbc.bal= βbc.bal+ βbc.gra.

We performed all analyses using the R platform version 3.4.2 (R Core Team, 2017). Pscl 1.5-2 (Jackman et al. 2017) and glmmADMB 0.6-5 (Bolker, 2012) packages were used to run the models with zero inflated correction. The vegan 2.4-4 (Oksanen et al. 2013) package was utilized to run PERMANOVA and betapart 1.4-1 (Baselga 2017b) package was used for partitioning of beta diversity.

Results

A total of 800 individuals of large vascular epiphytes distributed in 49 species, 24 genera and 12 families were recorded in 122 phorophytes crowns. The most abundant groups were Cyclanthaceae (50.25%), Araceae (16.25%), Bromeliaceae (15%) and Pteridophyta (12%). Araceae was the most rich group of epiphytes with 15 species, followed by Bromeliaceae with 8 species, Pteridophyta with 7 and Cyclanthaceae with only 2 species. Dicotyledon epiphytes were represented by Clusiaceae with 3 species, and by Ericaceae, Gesneriaceae and Piperaceae, each one with 2 species. The four most abundant vascular epiphyte species were *Ludovia lancifolia* Brongn. (399 individuals), *Guzmania* sp1 (52), *Anthurium jenmanii* Engl. (35) and *Tilandsia anceps* G. Lodd. (32), which together represent 64% of all the individuals recorded in the study. Holo-epiphytes have 33 species accounting for 90.9% of all individuals while hemi-epiphytes were represented by 16 species which contributed only to 9.1% of all individuals (Table S1)

The sampling effort was able to detect 74% of the expected species (Figure S1) since Chao estimator predicted 66±10 species (mean ± standard deviation).Crown volume varied from 1.75 m^3 to 11409 m^3 (1168.5 ± 1481), crown depth:width ratio varied between 0.15 to 4.14 (1.44 ± 0.66), crown heterogeneity between 0.1 m to 15.8 m (2.12 ± 1.66) and Canopy openness between 0.21 to 27.94 (8.31 ± 5.67).

Effect of crown structure on epiphytes

Crown volume affected positively the abundance and richness of all epiphytes ($b > 0.3$ and $p < 0.001$ for abundance and richness), Araceae ($b > 0.4$ and $p < 0.001$), Bromeliaceae ($b > 0.3$ and $p < 0.001$), but not for Pteridophyta ($p > 0.05$) (Table 1), which may indicate that the amount of substrate for colonization may not be determinant for all groups of epiphytes. Depth:width ratio influenced negatively the abundance of all epiphytes ($b = -0.24$, $p < 0.01$), which indicates that wide crowns have more epiphytes than deep crowns. However, depth:width ratio did not affect any epiphyte group separately ($p > 0.05$) and also did not influence richness ($p > 0.05$). Crown heterogeneity and canopy openness had no effect on abundance and richness ($p > 0.05$) (Table 1).

The PERMANOVA applied on quantitative (abundance) and qualitative (presence/absence) data (**Table 2**) indicated a strong effect of crown volume ($F = 4.21$, $p<0.001$ and $F=3.73$, $p<0.001$, respectively for quantitative and qualitative data) on composition of all epiphytes, indicating significant changes in composition along the gradient of crown size. Depth:width ratio also affected composition of all epiphytes ($F=2.14$, $p<0.05$ and $F=1.87$, $p<0.05$ respectively), demonstrating that a crown shape influences the composition of species. The composition of Pteridophyta was significantly related to volume ($F=3.68$, $p<0.01$ and $F=4.47$, $p<0.01$ respectively for quantitative and qualitative data) and depth:width ratio ($F=2.58$, $p<0.05$ and $F=2.94$, $p<0.05$ respectively). Bromeliaceae was related only to crown volume ($F=3.04$, $p=0.05$ and $F=3.11$, $p=0.05$ respectively) and Araceae had no relationship either with volume nor with depth:width ratio ($p > 0.05$). Crown variability and canopy openness did not show significant effect on composition (**Table 2**).

Across the gradient of crown volume, the turnover accounted for most of beta diversity for all epiphytes (85% in presence/absence and 73% in abundance data), for Araceae (80.7% and 71% respectively) and for Pteridophyta (85.7% and 77.5% respectively), indicating that species replacement determines beta diversity along the gradient of crown volume. However, Bromeliaceae presented a higher percentage of nestedness (69.3% in presence/absence and 74.5% in abundance data) indicating the existence of subsets of species along the gradient of crown volume. Along the gradient of crown shape (depth:width ratio) turnover represented most variation in beta diversity for all epiphytes (92% in presence/absence and 85.6% in abundance data), for Araceae (85.2% and 78.2% respectively) and for Pteridophyta (76.2% and 68,1 respectably), but for Bromeliaceae nestedness accounted for half (49.7% in presence/absence and 54,1% in abundance data) of beta diversity, indicating the existence of subsets associated to crown shape.

Epiphyte distribution and composition within crowns

The slopes of the model in fixed effects showed a negative relation of epiphytes abundance and richness (**Table 3**) with relative distance to crown base in all epiphytes (-1,85 ± 0.31 and -1.84 ± 0.3 to abundance and richness respectably), Araceae (-2.64 ± 0.51) and Bromeliaceae (-1.46 ± 0.45), with an except for Pteridophyta (-1.03 ± 0.64), indicated an increment of individuals and species closer to the crown base (**Fig. 5**). The influence of distance to crown base was not dependent on availability of substrate since volume of crown layer was not significantly related to abundance or richness (**Table 3**). Standard deviation in random effects applicate to distance did not show any significant relationship neither with abundance nor with richness.

The PERMANOVA indicated an effect of relative distance to crown base on epiphyte composition for qualitative data (F=1.96, p<0.05) but not for qualitative data (F=1.12, p>0.1). Separately by epiphyte group, only Pteridophyta showed prominent differences in composition related to crown distance (F=6.86, p<0.01 and F=34.16, p<0.001 for quantitative and qualitative data respectively). The effect of the phorophyte was significant for all epiphytes, indicating differences among crowns for both abundance and presence/absence (F=1.61, p<0.001 and F=1.74, p<0.001 respectively). Separately, Araceae (F=1.70, p<0.05 and F=1.73, p<0.05 respectively) and Pteridophyta (F=18.33, p<0.001 and F=83.26, p<0.001) show effect of the phorophytes, only Bromeliaceae did not present any effect of the phorophyte (F=1.18, p>0.1 and F=1.21, p>0.1 respectively) The interaction Phorophyte/Distance was only significant for Pteridophyta both in abundance (F=8.3, p<0.001) and presence / absence (F=31.79, p<0.001) data, indicating that the effect of distance depends on the phorophyte. Volume of each crown layer did not show significant effect on composition (**Table 4**).

Across the gradient of distance of the crown base to edges (five layers), the turnover accounted for most of beta diversity for all epiphytes (79% both in presence/absence and abundance data), for Bromeliaceae (67.3% and 67.5% respectively) and for Araceae (68% and 69% respectively), indicating that species replacement determines beta diversity along the gradient of crown volume. However, Pteridophyta presented a medium percentage of nestedness (42.1% in presence/absence and 38% in abundance data) indicating the existence of subsets of species along the gradient of distance of crown base to edges.

Discussions

This determined the dependence of epiphytes on crown structure and revealed different patterns of within-crown distribution of epiphytes. Abundance and richness were low in this study compared to studies carried out in Amazonia (Nieder et al. 2000; Küper et al. 2004; Pos & Sleegers 2010; Benavides et al. 2011; Irume et al. 2013; Boelter et al. 2014; Magalhães & Lopes 2015). However, it is probably because we included only epiphytes greater than 10 cm and possible several species of epiphytes, especially small orchids and some ferns, were not detected (Johansson 1974). Large epiphytes are easier to detect and feasible for mapping inside crown by an observer on ground level, but small epiphytes would require a new approach to allow the mapping from the canopy level to increase detectability. However, large epiphytes are useful to reveal general patterns distribution related to crown structure since these epiphytes are expected to be strongly influenced by crown structure (Johansson 1974; Benzing 1990; Zotz 2007). The inclusion of small epiphytes would reveal different patterns as the dependence of substrate may be related to epiphyte size and should be subject for further investigation.

As expected according to the biogeographical principle, a greater area for colonization allows the establishment of more individuals and species. Abundance and richness increase according to crown volume indicating that availability of substrate for colonization is a strong predictor of epiphytes. However, Pteridophyta did not follow this pattern, possibly due to the sensitivity of this group to water stress (Benavides et al. 2011; Petter et al. 2016). Since larger trees, mainly emergent, have crowns positioned over the average canopy level, these trees are regularly more exposed to direct light (Alves & Santos 2002), which may level off the quantity of suitable substrate independently of crown size.

The depth:width ratio, which is a measure of crown shape, may be determined by genetic expression and by competition with other crowns (Sterck & Bonger 1998). Crown shape may be influenced by competition for light and space, according to adaptive geometry (Horn 1971; Hallé et al. 1978). Wide crowns are more exposed to direct light, while vertical crowns are more specialized in receiving diffuse light. Our results suggest that epiphytes are more abundant in relatively wide crowns probably because of a predilection for direct light. However, since the relation between abundance and canopy openness was absent, epiphytes could also be more frequent in wide crowns due to orientation of branches, which are horizontally oriented and may allow more water retention than vertical oriented braches (Sarmento Cabral et al. 2015). These findings show that crown shape is a strong predictor of epiphytes and that inter and intraspecific variability of crowns modelled by genotype and competition with other trees are important factors to explain the abundance of epiphytes in tropical forests.

The distribution of epiphytes within crowns was clumped near the crown base (except for ferns). Most individuals of different epiphytes may find a suitable substrate near the crown base. At the crown base branches are thicker and organic matter often accumulates in the branch bifurcations providing nutrients and humidity for establishment of epiphytes. As the branches become thinner far from the crown base probably the quantity of organic matter accumulated decreases and so the humidity of the substrate also becomes lower. Near the crown edges most large epiphytes are less frequent because of unsuitable substrate but also due to a microclimate more variable.

Epiphytes composition changed along the gradient of distance to crown base Branch age may influence the distribution of epiphytes because branches are older near the crown base (Woods et al. 2015)and the substitution of species may follow a temporal sequence of colonization where species which arrive first near the crown base are replaced by other species and become more abundant at younger branches, but the most probable is that the first colonizers remains and facilitate the establishment of late colonizers (Benzing 2008; Zotz 2013c; Boelter et al. 2014; Magalhães & Lopes 2015).

Hemiepiphytes represented only 9.1% of the total of individuals with 16 species and most epiphytes were holo-epiphytes. Holo-epiphytes are less influence by soil (Benzing 1990) and are affected at a greater extent by the structure of crown. Furthermore, a study carried out in the same area, demonstrates that soil nutrients (K, Na, sum of bases) did not determines the presence of hemiepiphytes (Clemente Arenas 2018).

Compositions of Araceae and Bromeliaceae were not affected by distance to crown base probably because their species have general requirements which are encompassed at different positions within crowns. Bromeliaceae shows greater efficiency in the use of water and photosynthetic capacity (Petter et al. 2016). Also, the low substitution of Bromeliaceae species in this study agrees with Ruiz-Cordova (2014) indicating a high stochastic distribution of this family to different environments within the crown (Benzing 1990; Woods et al. 2015).

The differentiation of the spatial turnover and nestedness components of beta diversity is crucial for improving our understanding of central biogeographic, ecological and conservation issues (Baselga 2010). The turnover of species was preponderant process of beta diversity and this variation evidences that epiphyte community is different in the size, shape and interior of the crown. For example, species of hemiepiphyte Araceae had more frequency in less voluminous crowns and Pteridophyta and Bromeliaceae species had more frequency in voluminous crowns. Similarly, epiphytes such as *Tilandsia anceps* G. Lodd. were established more frequently in less deep crowns. Also species as *Bromeliaceae sp2* and *Philodendron melinonii* Brongn. ex Regel were only observed in layers close to crown base, while genus *Clusia* and *Bromeliaceae sp3* were only observed in layers away from the crown base. Epiphytes succession in the crown shows that the process of species accumulation persists while more microhabitats are formed as tree crowns increase in size. The increase in microhabitats on larger crowns enable the accumulation of species with replacement, so we recommend measuring the density of branches to have an accurate estimate in this aspect. The increase of species turnover (and decreasing of nestedness) in voluminous crowns shows that available substrate may implies that epiphyte (except Bromeliaceae) community will be hierarchically organized (Woods et al. 2015; Marí et al. 2016). In the same way, the higher percentage of turnover in Araceae and Pteridophyta in deeper cups reinforces their preference for more humidity and indirect lightand vertical distribution specially in Pteridophyta, since it had no influence from distance. Increase of nestedness in Bromeliaceae respect to shape crown, confirmed the stochastic distribution of this family.

This is the first study that directly evaluated the volume as a measure of substrate availability, and quantitative distances within the crown to explain the richness, abundance and composition and distribution of epiphytes and found influence of crown structure in this group of plants.

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Tables with captions

Table 1.Influence of structure of the phorophytes crown on richness and abundance of epiphytes.The values are slopes of zero inflated models.

	Volume	Depth/Width	Crown Heterogeneity	Canopy Openness
Abundance				
All Epiphytes	0.46***	-0.24***	0.004	0.012^{+}
Araceae	0.56***	0.091	-0.079	0.019
Bromeliaceae	0.32***	0.149	0.059	-0.015
Pteridophyta	-0.001	-0.304	0.008	-0.038
Richness				
All Epiphytes	0.32***	0.138^{+}	-0.025	0.016^{+}
Araceae	0.43***	0.171	-0.054	0.007
Bromeliaceae	0.36***	0.286	0.049	-0.017
Pteridophyta	0.16	-0.091	0.003	-0.038

***$p<0.001$ **$p<0.01$ *$p<0.05$ †$p<0.1$

Table 2. Influence of crown structure on floristic composition (Abundance and Presence/absence) of all epiphytes and representative families and group. F-value for the permutations in every variable of crown.

	Df	Volume F(R^2)	Depth:Width F(R^2)	Crown Heterogeneity F(R^2)	Canopy Openness F(R^2)
Abundance					
All Epiphytes	95	4.21(0.043)***	2.14(0.021)*	0.43(0.004)	0.70(0.007)
Araceae	54	1.20(0.022)	1.43(0.026)	1.10(0.020)	0.64(0.011)
Bromeliaceae	57	3.04(0.051)*	0.78(0.013)	1.59(0.027)	0.76(0.013)
Pteridophyta	45	3.68(0.075)**	2.58(0.052)*	0.51(0.010)	0.96(0.019)
Presence/Absence					
All Epiphytes	95	3.73(0.038)***	1.87(0.019)*	0.36(0.003)	0.92(0.009)
Araceae	54	1.42(0.026)	1.43(0.026)	1.10(0.020)	0.51(0.009)
Bromeliaceae	57	3.11(0.053)*	0.48(0.008)	1.62(0.027)	0.45(0.007)
Pteridophyta	45	4.47(0.089)**	2.94(0.059)*	0.39(0.008)	0.99(0.020)

***$p<0.001$ **$p<0.01$ *$p<0.05$ †$p<0.1$

Table 3. Results of the model using linear-mixed models (LMM) with random and fixed effects with zero-inflation modification with abundance (up) and richness (down); ‘Poisson’ family in all epiphytes, Bromeliaceae and Pteridophyta, only Araceae with ‘Negative binomial’ family. explaining the epiphytic abundance in the crowns trees with the ‘*Distance*’ to base crown and ‘*Volume*’ of layer variables. ‘*a*’ is the intercept and ‘*b*’ is the slope with the standard error and standard deviation for the intercept and distance of the random effects.

		fixed effects		*Random effects* (standard deviation)	
Abundance	*a*	*b Distance*	*b Volume*	*a*	*Distance*
All epiphytes	1.179±0.123***	-1.846±0.312***	-0.00028±0.00029	0.7303	2.120
Araceae	0.269±0.176	-2.640±0.510***	0.00062±0.00311	0.0018	0.611
Bromeliaceae	0.274±0.214	-1.455±0.447**	0.00015±0.00025	0.0003	0.009
Pteridophyta	-0.005±0.229	-1,030±0.628	0.00097±0.00064	0.0003	0.963

Richness	*a*	*b Distance*	*b Volume*	*a*	*Distance*
All epiphytes	0.832±0.117***	-1.84±0.296***	-0.00074±0.00022	0.5386	0.988
Araceae	0.269±0.176	-2.640±0.510***	0.00062±0.00311	0.0018	0.611
Bromeliaceae	0.274±0.214	-1.455±0.447**	0.00015±0.00025	0.0003	0.009
Pteridophyta	-0.005±0.229	-1,030±0.628	0.00097±0.00064	0.0003	0.963

Table 4. Influence of relatives distances, volume contained in each distance layer, crown and interaction Crown:distance on floristic composition distribution (Abundance and Presence/absence) of all epiphytes and representative families and group. F-value for the permutations in every variable.

	Df	Distance F(R^2)	Volume F(R^2)	Phorophyte F(R^2)	Phorophyte:Distance F(R^2)
Abundance					
All Epiphytes	252	1.96(0.006)*	0.68(0.021)	1.61(0.482)***	1.10(0.25)
Araceae	88,	0.65(0.005)	0.66(0.005)	1.70(0.754)*	0.87(0.178)
Bromeliaceae	82	1.80(0.020)	1.42(0.016)	1.18(0.737)	0.85(0.140)
Pteridophyta	66	6.86(0.007)**	0.59(0.001)	18.33(0.865)***	8.30(0.123)**
Presence/Absence					
All Epiphytes	252	1.12(0.003)	0.85(0.003)	1.74(0.498)***	1.13(0.248)$^{+}$
Araceae	54	0.63(0.005)	0.62(0.005)	1.73(0.765)*	0.82(0.168)
Bromeliaceae	57	1.94(0.021)	1.51(0.016)	1.21(0.747)	0.79(0.128)
Pteridophyta	45	34.16(0.008)***	2.26(0.001)	83.26(0.885)***	31.79(0.105)***

***p<0.001 **p<0.01 *p<0.05 †p<0.1

Figures captions

Fig. 1 Location of the Amapá National Forest (ANF) and the trail system (5 × 5 km) of the Brazilian Program for Biodiversity Research (PPBio) showing the sampled plots (black points), (B) Amapá state in (C) South America.

Fig. 2a) Three-dimensional representation of points of the crown, lateral edges (LP1:LP10), total height (CH), and their horizontal and vertical distances to the crown base. The vertical distance of CH (VDch) was used as crown Depth and average horizontal distances of LP1:LP10 was used as crown Width; b) Estimation of relative distance of epiphytes (EP) to crown base; c) Estimation of relative distance of lateral edges (LP) to crown base; d) centroid of the cloud of points and their radii, used for the calculation of the volume.

Fig. 3 Regressions (generalized linear model) results for volume and depth:width ratio crown on abundance and richness of epiphytes with zero-inflation. Relations of volume versus abundance (A) and richness (C), and depth:width ratio versus abundance (B) of epiphytes.

Fig. 4 Species-level abundance “total” histograms for epiphytic species in relation to: a) relative distance to crown base (five distances layers into the crown), b) volume in cubic meters and c) depth: Width crown. Species of the Bromeliacea family appear in blue color, Araceae in green and Pteridophyta in yellow.

Fig.5 Histograms of abundance in all epiphytes and tree representative groups, based in the epiphytes distances to the base of the crown. where 0 is close and 1 is away from the crown base.

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Fig. 1

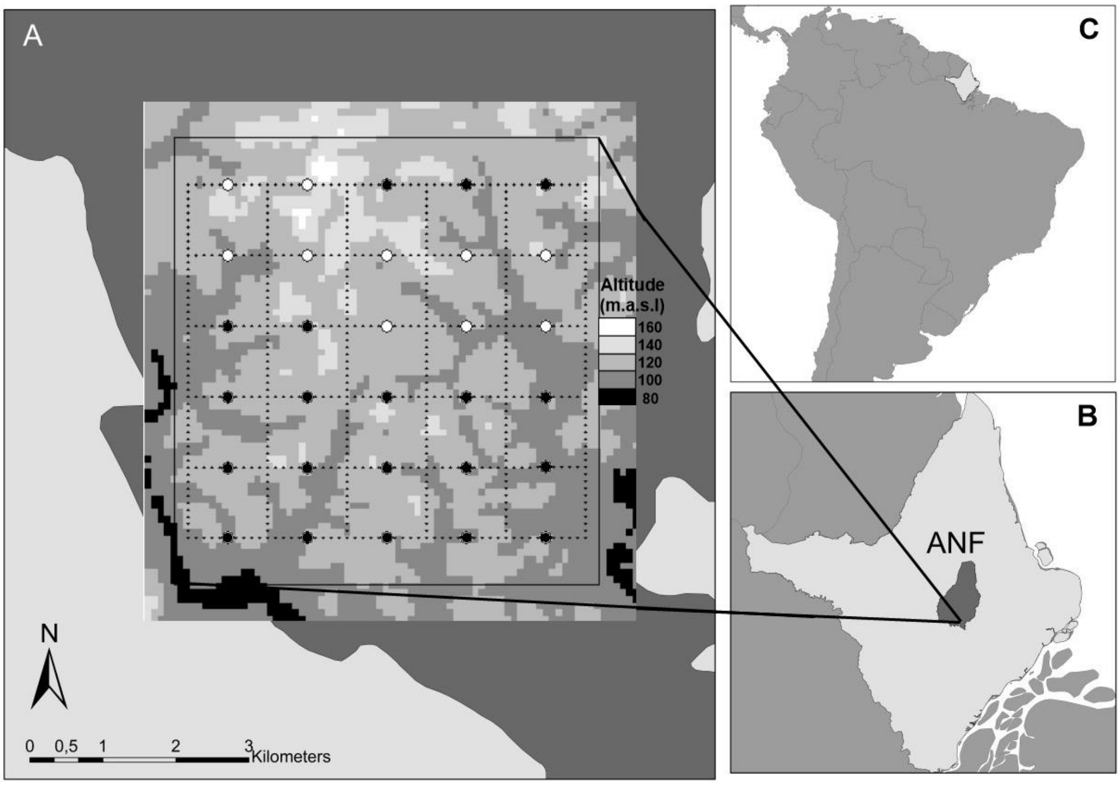


Fig 2.

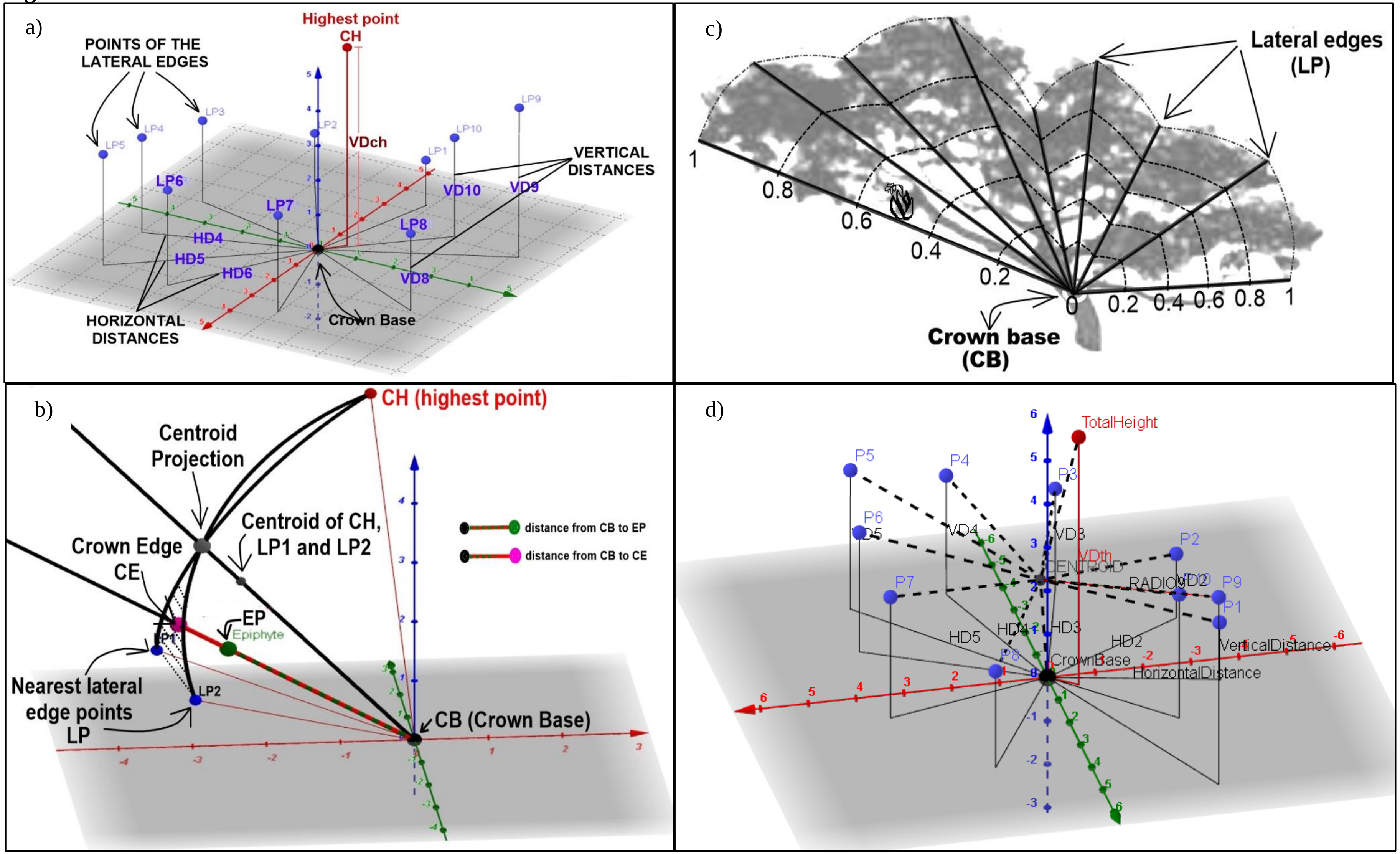

a)
POINTS OF THE LATERAL EDGES
Highest point CH
LP5
LP4
LP3
LP2
VDch
LP1
LP10
LP9
VERTICAL DISTANCES
LP6
LP7
LP8
VD10
VD9
HD4
HD5
HD6
VD8
HORIZONTAL DISTANCES
Crown Base
c)
Lateral edges (LP)
1
0.8
0.6
0.4
0.2
0
0.2
0.4
0.6
0.8
1
Crown base (CB)
b)
CH (highest point)
Centroid Projection
Centroid of CH, LP1 and LP2
Crown Edge CE
EP
Epiphyte
LP1
LP2
Nearest lateral edge points LP
CB (Crown Base)
distance from CB to EP
distance from CB to CE
d)
TotalHeight
P5
P4
P3
P6
P2
P7
P9
P1
P8
VD4
VD3
VD5
VDth
CENTROID
RADIO
VD2
HD5
HD4
HD3
HD2
CrownBase
VerticalDistance
HorizontalDistance

Fig. 3

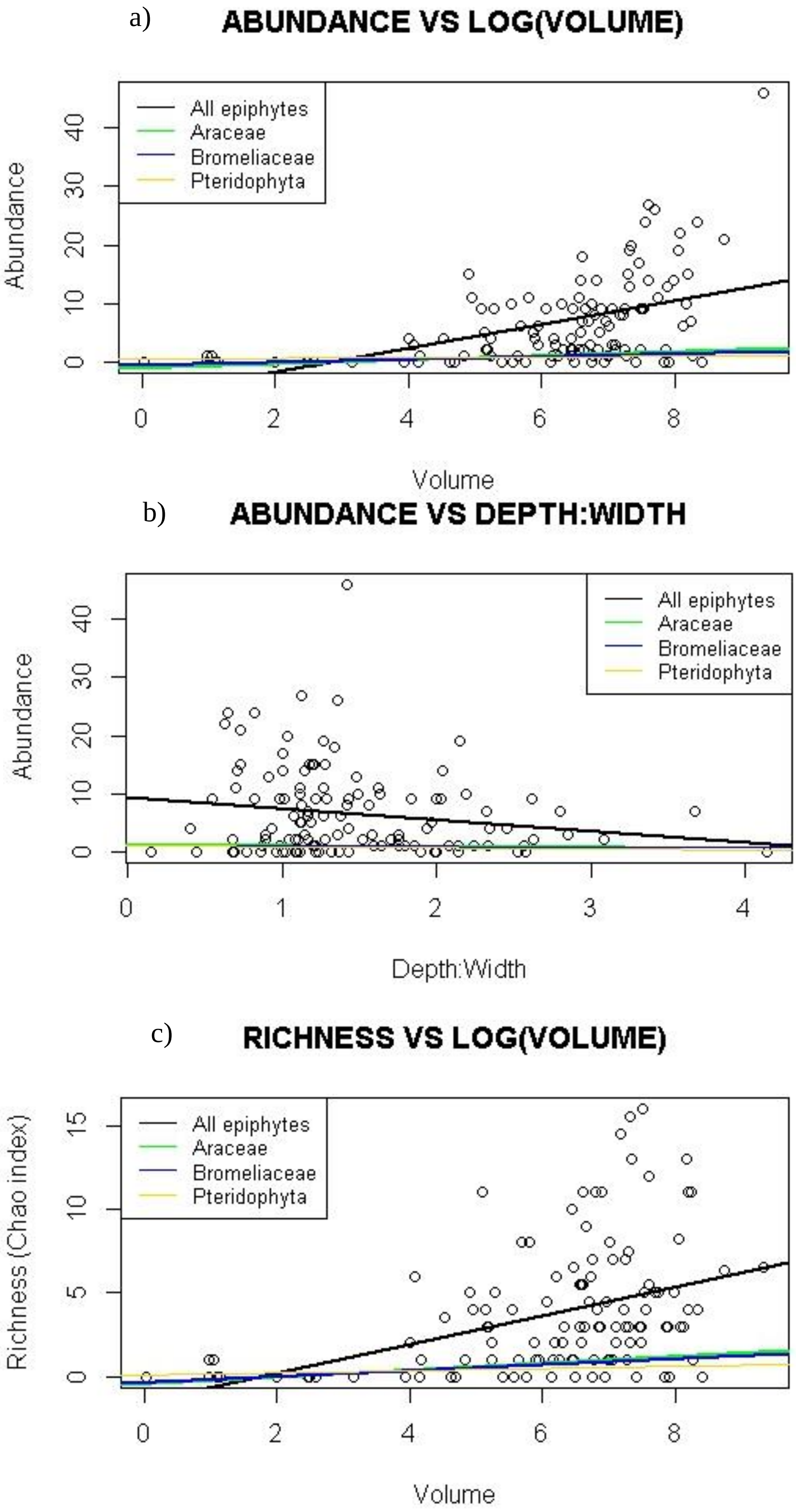

a)
ABUNDANCE VS LOG(VOLUME)
All epiphytes
Araceae
Bromeliaceae
Pteridophyta
Abundance
0
10
20
30
40
0
2
4
6
8
Volume
b)
ABUNDANCE VS DEPTH:WIDTH
All epiphytes
Araceae
Bromeliaceae
Pteridophyta
Abundance
0
10
20
30
40
0
1
2
3
4
Depth:Width
c)
RICHNESS VS LOG(VOLUME)
All epiphytes
Araceae
Bromeliaceae
Pteridophyta
Richness (Chao index)
0
5
10
15
0
2
4
6
8
Volume

Fig. 4

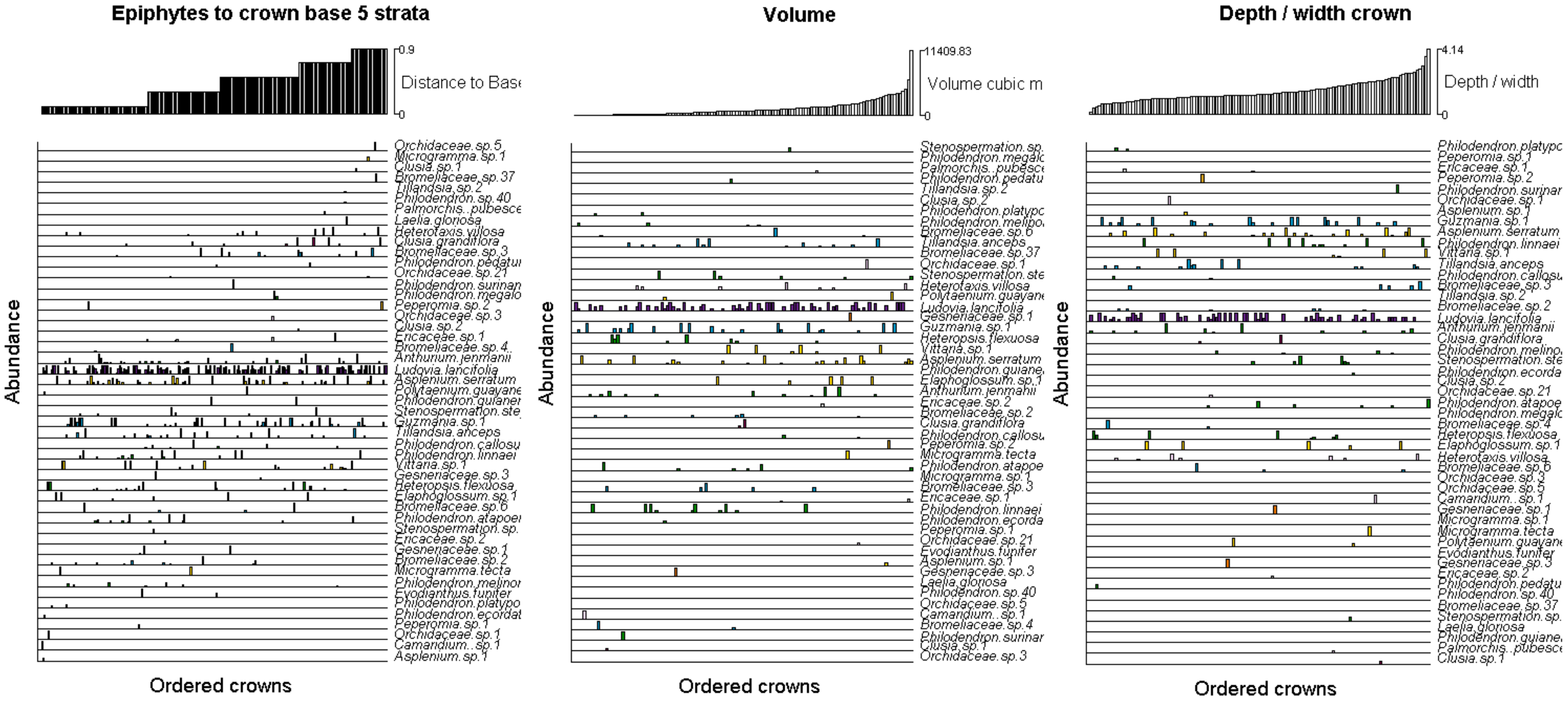
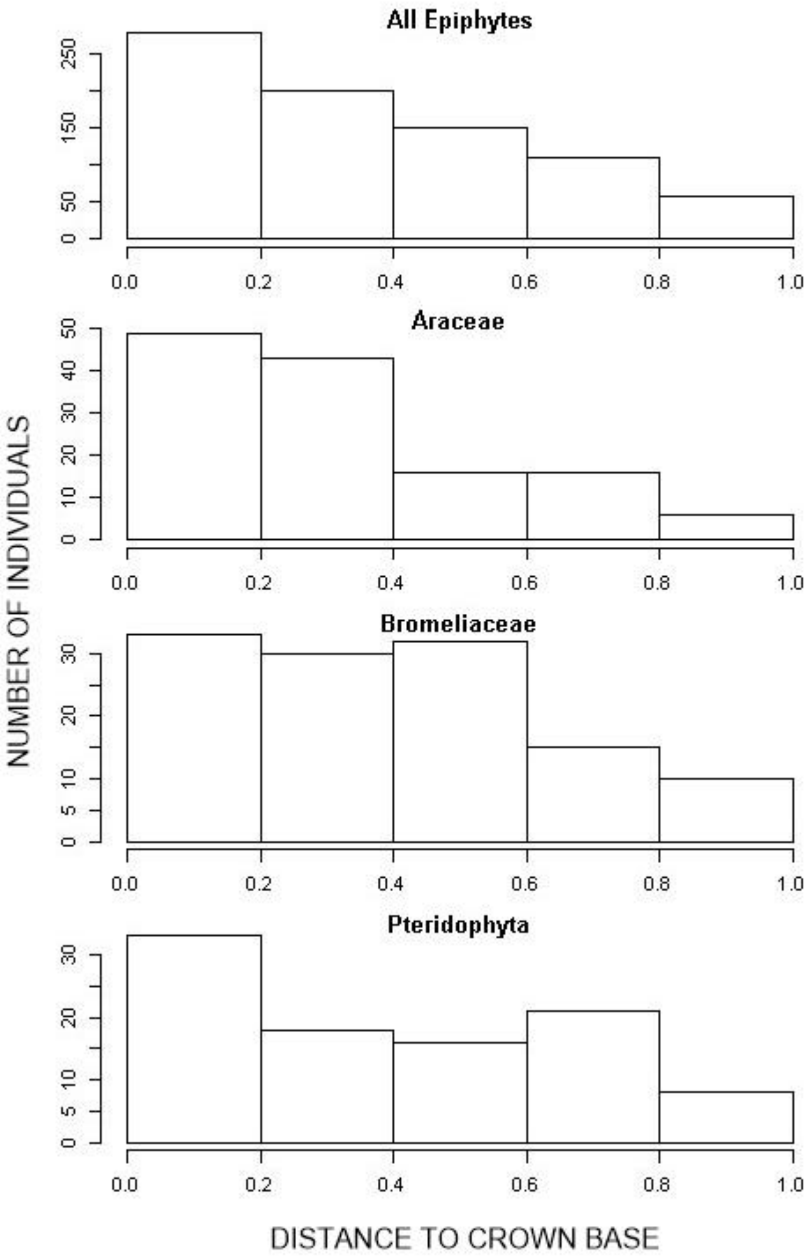

Epiphytes to crown base 5 strata
0.9
Distance to Bas
0
Orchidaceae.sp.5
Microgramma.sp.1
Clusia.sp.1
Bromeliaceae.sp.37
Tillandsia.sp.2
Philodendron.sp.40
Palmorchis..pubesce
Laelia.gloriosa
Heterotaxis.villosa
Clusia.grandiflora
Bromeliaceae.sp.3
Philodendron.pedatu
Orchidaceae.sp.21
Philodendron.surinan
Philodendron.megalo
Peperomia.sp.2
Orchidaceae.sp.3
Clusia.sp.2
Ericaceae.sp.1
Bromeliaceae.sp.4
Anthurium.jenmanii
Ludovia.lancifolia
Asplenium.serratum
Polytaenium.guayane
Philodendron.guianer
Stenospermation.ste
Guzmania.sp.1
Tillandsia.anceps
Philodendron.callosu
Philodendron.linnaei
Vittaria.sp.1
Gesneriaceae.sp.3
Heteropsis.flexuosa
Elaphoglossum.sp.1
Bromeliaceae.sp.6
Philodendron.atapoe
Stenospermation.sp.
Ericaceae.sp.2
Gesneriaceae.sp.1
Bromeliaceae.sp.2
Microgramma.tecta
Philodendron.melinor
Evodianthus.funifer
Philodendron.platypo
Philodendron.ecordat
Peperomia.sp.1
Orchidaceae.sp.1
Camaridium..sp.1
Asplenium.sp.1
Abundance
Ordered crowns
Volume
11409.83
Volume cubic m
0
Stenospermation.sp.
Philodendron.megalo
Palmorchis..pubesce
Philodendron.pedatu
Tillandsia.sp.2
Clusia.sp.2
Philodendron.platypo
Philodendron.melino
Bromeliaceae.sp.6
Tillandsia.anceps
Bromeliaceae.sp.37
Orchidaceae.sp.1
Stenospermation.ste
Heterotaxis.villosa
Polytaenium.guayane
Ludovia.lancifolia
Gesneriaceae.sp.1
Guzmania.sp.1
Heteropsis.flexuosa
Vittaria.sp.1
Asplenium.serratum
Philodendron.guiane
Elaphoglossum.sp.1
Anthurium.jenmanii
Ericaceae.sp.2
Bromeliaceae.sp.2
Clusia.grandiflora
Philodendron.callosu
Peperomia.sp.2
Microgramma.tecta
Philodendron.atapoe
Microgramma.sp.1
Bromeliaceae.sp.3
Ericaceae.sp.1
Philodendron.linnaei
Philodendron.ecorda
Peperomia.sp.1
Orchidaceae.sp.21
Evodianthus.funifer
Asplenium.sp.1
Gesneriaceae.sp.3
Laelia.gloriosa
Philodendron.sp.40
Orchidaceae.sp.5
Camaridium..sp.1
Bromeliaceae.sp.4
Philodendron.surinar
Clusia.sp.1
Orchidaceae.sp.3
Abundance
Ordered crowns
Depth / width crown
4.14
Depth / width
0
Philodendron.platypo
Peperomia.sp.1
Ericaceae.sp.1
Peperomia.sp.2
Philodendron.surinar
Orchidaceae.sp.1
Asplenium.sp.1
Guzmania.sp.1
Asplenium.serratum
Philodendron.linnaei
Vittaria.sp.1
Tillandsia.anceps
Philodendron.callosu
Bromeliaceae.sp.3
Tillandsia.sp.2
Bromeliaceae.sp.2
Ludovia.lancifolia
Anthurium.jenmanii
Clusia.grandiflora
Philodendron.melino
Stenospermation.ste
Philodendron.ecorda
Clusia.sp.2
Orchidaceae.sp.21
Philodendron.atapoe
Philodendron.megalo
Bromeliaceae.sp.4
Heteropsis.flexuosa
Elaphoglossum.sp.1
Heterotaxis.villosa
Bromeliaceae.sp.6
Orchidaceae.sp.3
Orchidaceae.sp.5
Camaridium..sp.1
Gesneriaceae.sp.1
Microgramma.sp.1
Microgramma.tecta
Polytaenium.guayane
Evodianthus.funifer
Gesneriaceae.sp.3
Ericaceae.sp.2
Philodendron.pedatu
Philodendron.sp.40
Bromeliaceae.sp.37
Stenospermation.sp.
Laelia.gloriosa
Philodendron.guiane
Palmorchis..pubesce
Clusia.sp.1
Abundance
Ordered crowns

Fig. 5


All Epiphytes
0
50
150
250
Araceae
0
10
20
30
40
50
Bromeliaceae
0
5
10
20
30
Pteridophyta
0
5
10
20
30
0.0
0.2
0.4
0.6
0.8
1.0
NUMBER OF INDIVIDUALS
DISTANCE TO CROWN BASE

Appendices

Table S1: Table representing species epiphytes and their abundances in North Amazon Forest, Amapá, Brazil.

Epiphytes vascular species	Individuals
Angiospermae/Eudicots	**25**
Clusiaceae	**11**
Clusia grandiflora Splitg.	9
Clusia sp.1	1
Clusia sp.2	1
Ericaceae	**6**
Ericaceae sp.1	5
Ericaceae sp.2	1
Gesneriaceae	**5**
Gesneriaceae sp.1	3
Gesneriaceae sp.3	2
Piperaceae	**3**
Peperomia sp.1	1
Peperomia sp.2	2
Angiospermae/Monocotyledons	**679**
Araceae	**130**
Anthurium jenmanii Engl.	35
Heteropsis flexuosa (Kunth) G.S. Bunting	19
Philodendron atabapoense G.S. Bunting	15
Philodendron callosum K. Krause	16
Philodendron ecordatum Schott	1
Philodendron guianense Croat & Grayum	2
Philodendron linnaei Kunth	16
Philodendron megalophyllum Schott	3

Philodendron melinonii Brongn. ex Regel	8
Philodendron pedatum (Hook.) Kunth	2
Philodendron platypodum Gleason	2
Philodendron sp.40	1
Philodendron surinamense (Miq.) Engl.	1
Stenospermation sp.1	1
Stenospermation steyermarkii G.S. Bunting	8
Bromeliaceae	**120**
Bromeliaceae sp.2	11
Bromeliaceae sp.3	17
Bromeliaceae sp.37	1
Bromeliaceae sp.4	2
Bromeliaceae sp.6	4
Guzmania sp.1	52
Tillandsia anceps G. Lodd.	32
Tillandsia sp.2	1
Cyclanthaceae	**402**
Evodianthus funifer (Poit.) Lindm.	3
Ludovia lancifolia Brongn.	399
Orchidaceae	**27**
Camaridium sp.1	1
Heterotaxis villosa (Barb. Rodr.) F. Barros	16
Laelia gloriosa (Rchb. f.) L.O. Williams	2
Orchidaceae sp.1	1
Orchidaceae sp.21	4
Orchidaceae sp.3	1
Orchidaceae sp.5	1
Palmorchis pubescens Barb.Rodr.	1

Pteridophyta	**96**
Aspleniaceae	**63**
Asplenium serratum L.	62
Asplenium sp.1	1
Dryopteridaceae	**7**
Elaphoglossum sp.1	7
Polypodiaceae	**5**
Microgramma sp.1	3
Microgramma tecta (Kaulf.) Alston	2
Pteridaceae	**21**
Polytaenium guayanense (Hieron.) Alston	2
Vittaria sp.1	19
Total individuals	**800**

APG IV 2016 to angiosperms and Smith et al. 2006/PPG I 2016 to Pteridophytes

Table S2: Table representing species phorophytes in North Amazon Forest, Amapá, Brazil.

Andira micrantha Ducke
Astronium graveolens Jacq.
Brosimum guianense (Aubl.) Huber
Carapa guianensis Aubl.
Couepia guianensis Aubl.
Couepia robusta Huber
Couratari guianensis Aubl.
Dialium guianense (Aubl.) Sandwith
Dinizia excelsa Ducke
Duguetia cadaverica Huber
Enterolobium schomburgkii (Benth.) Benth.
Eperua sp.1

Eschweilera coriacea (DC.) S.A. Mori
Eschweilera ovata (Cambess.) Miers
Eschweilera sp.1
Eugenia cupulata Amshoff
Guarea humaitensis T.D. Penn.
Hirtella rodriguesii Prance
Inga alba (Sw.) Willd.
Lecythis chartacea O. Berg
Lecythis poiteaui O. Berg
Mabea piriri Aubl.
Manilkara huberi (Ducke) Standl.
Micropholis guyanensis (A. DC.) Pierre
Minquartia guianensis Aubl.
Neea ovalifolia Spruce ex J.A. Schmidt
Ocotea cinerea van der Werff
Ocotea floribunda (Sw.) Mez
Ocotea percurrens A. Vicentini
Ocotea rhynchophylla (Meisn.) Mez
Ormosia sp.1
Pourouma tomentosa Mart. ex Miq.
Pouteria campanulata Baehni
Pouteria elegans (A. DC.) Baehni
Pouteria pallens T.D. Penn.
Pradosia cochlearia (Lecomte) T.D. Penn.
Protium nitidifolium (Cuatrec.) Daly
Pseudopiptadenia suaveolens (Miq.) J.W. Grimes
Qualea paraensis Ducke
Roucheria punctata (Ducke) Ducke

Sextonia rubra (Mez) van der Werff
Simaba cedron Planch.
Siparuna decipiens (Tul.) A. DC.
Siparuna monogyna Jangoux, Jacques Ivan G.
Sloanea excelsa Ducke
Sterculia peruviana (D.R. Simpson) E.L. Taylor ex Brako & Zarucchi
Swartzia polyphylla DC.
tachigali myrmecophila (Ducke) Ducke
Talisia allenii Croat
Tapura amazonica Poepp.
Tetragastris altissima (Aubl.) Swart
Thyrsodium spruceanum Benth.
Trichilia schomburgkii C. DC.
Vouacapoua americana Aubl.
Xylopia amazonica R.E. Fr.

APG IV 2016 to angiosperms

Fig. S1. Species accumulation curve of epiphytes in Amapá National Forest

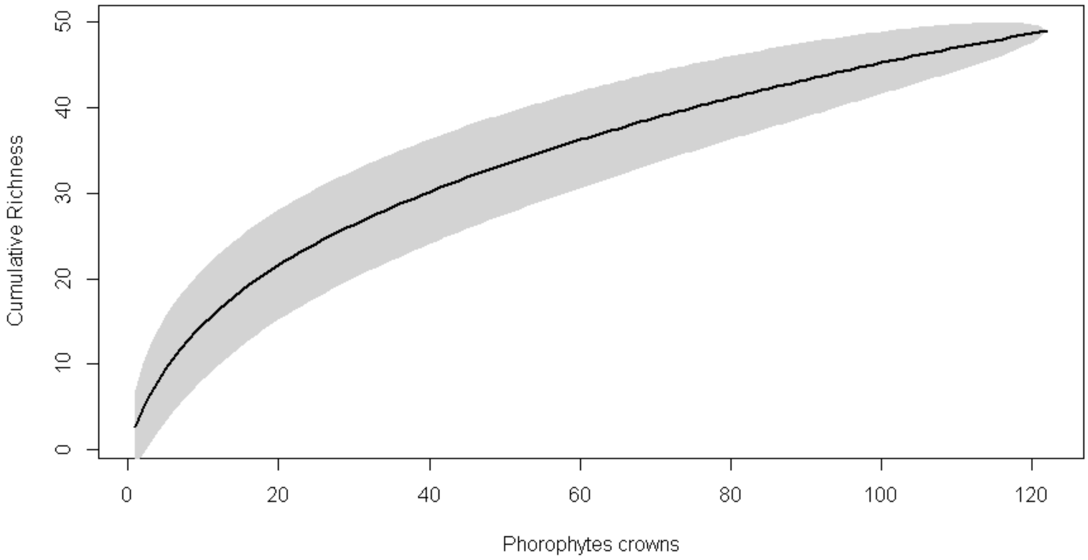


Fig. S2. Family/ Groups-level presence/absence histograms for epiphytic in relation to distance to crown base (five distances layers into the crown).

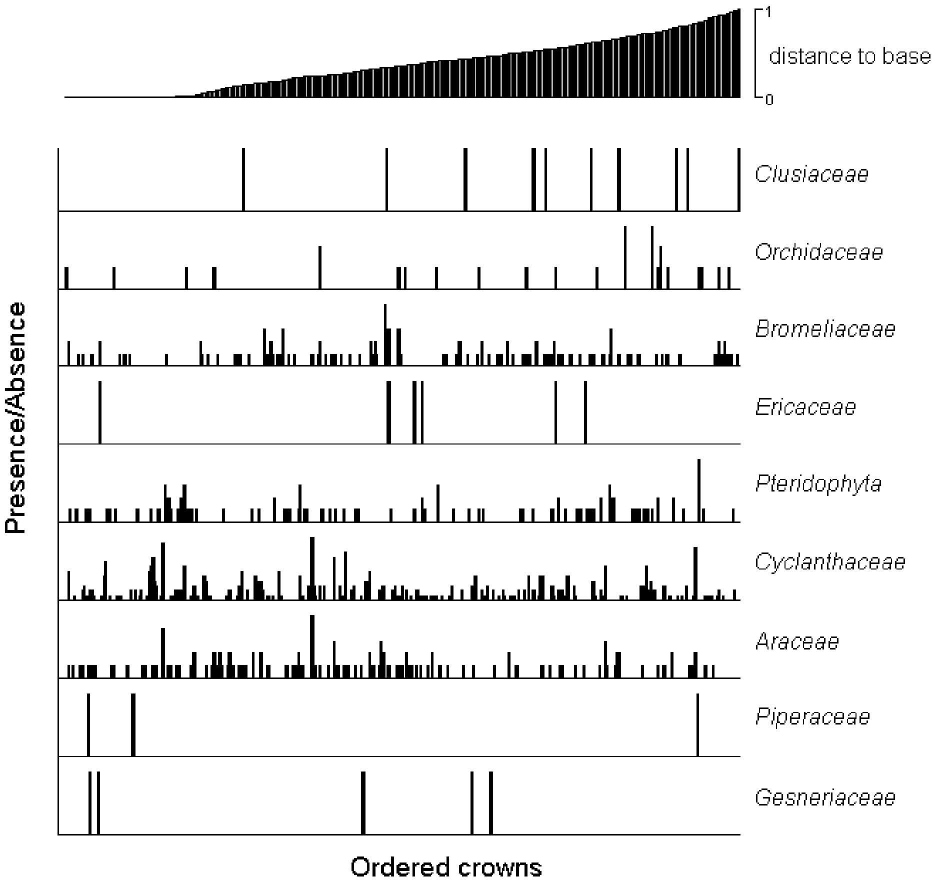
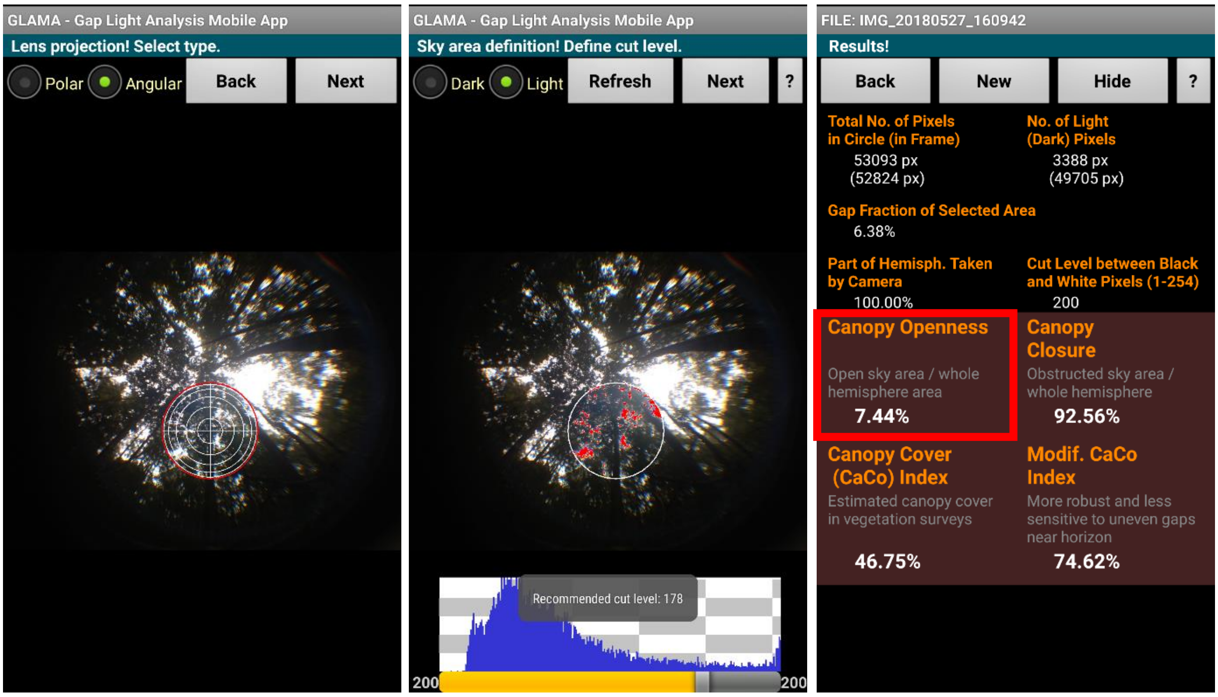


Fig. S3. Estimation method of 'Canopy Openness' of the crowns, with the GLAMA 3.0 application to smartphone.



GLAMA - Gap Light Analysis Mobile App

Lens projection! Select type.

○ Polar ● Angular

GLAMA - Gap Light Analysis Mobile App

Sky area definition! Define cut level.

○ Dark ● Light

Recommended cut level: 178

FILE: IMG_20180527_160942

Results!

Total No. of Pixels in Circle (in Frame): 53093 px (52824 px)

No. of Light (Dark) Pixels: 3388 px (49705 px)

Gap Fraction of Selected Area: 6.38%

Part of Hemisph. Taken by Camera: 100.00%

Cut Level between Black and White Pixels (1-254): 200

Canopy Openness: Open sky area / whole hemisphere area: 7.44%

Canopy Closure: Obstructed sky area / whole hemisphere: 92.56%

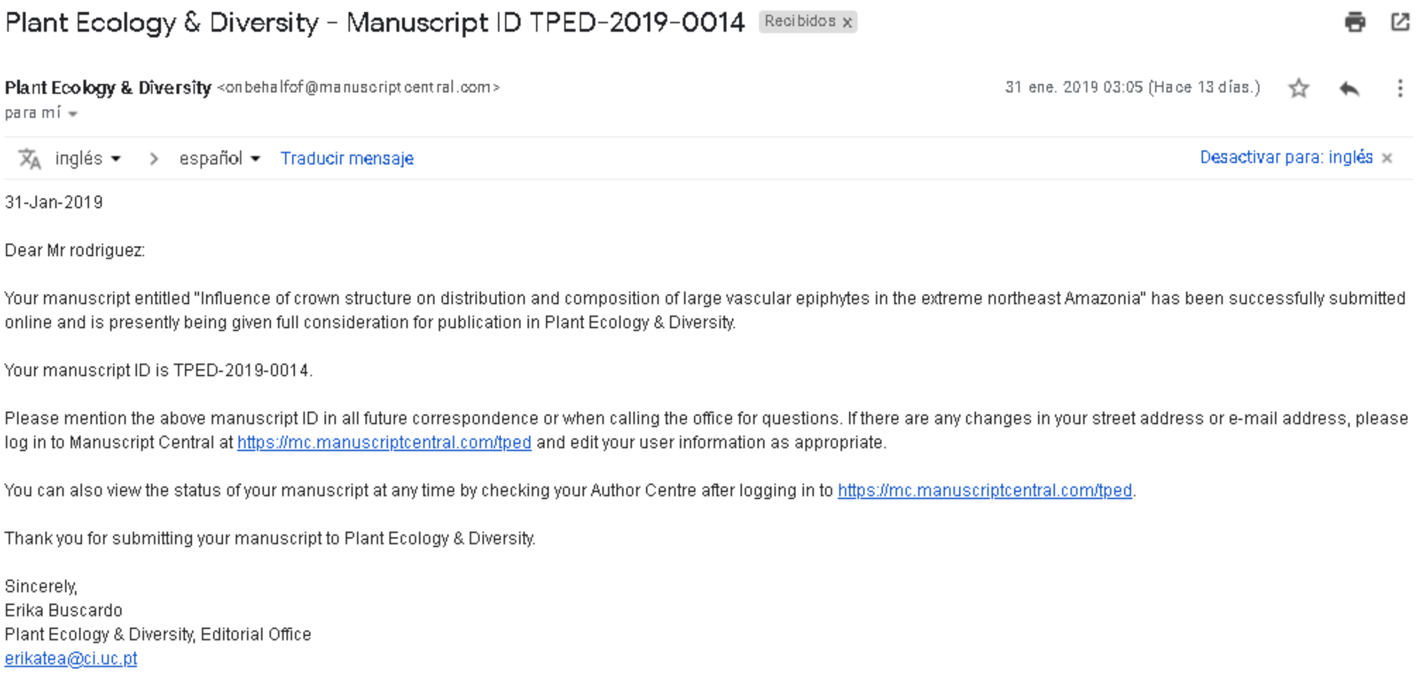
Canopy Cover (CaCo) Index: Estimated canopy cover in vegetation surveys: 46.75%

Modif. CaCo Index: More robust and less sensitive to uneven gaps near horizon: 74.62%

6 CONCLUSÕES

Resultados sugerem que copas maiores e menos profundas são melhores hospedeiras de epífitas. A composição muda ao longo do gradiente de tamanho (volume) e forma das copas. Famílias/grupos de epífitas não tiveram o mesmo comportamento na diversidade beta indicando uma separação de grupos. Resultados da distribuição de epífitas na copa sugerem que a estrutura da copa pode ser uma ferramenta para estimar assembleias e distribuição de epífitas e que o tempo de estabelecimento e a quantidade de substrato são importantes na distribuição interna.

ANEXO 1. Submission confirmation for Plant Ecology and Diversity



Plant Ecology & Diversity - Manuscript ID TPED-2019-0014

Plant Ecology & Diversity <onbehalfof@manuscriptcentral.com>

31 ene. 2019 03:05 (Hace 13 días.)

31-Jan-2019

Dear Mr rodriguez:

Your manuscript entitled "Influence of crown structure on distribution and composition of large vascular epiphytes in the extreme northeast Amazonia" has been successfully submitted online and is presently being given full consideration for publication in Plant Ecology & Diversity.

Your manuscript ID is TPED-2019-0014.

Please mention the above manuscript ID in all future correspondence or when calling the office for questions. If there are any changes in your street address or e-mail address, please log in to Manuscript Central at https://mc.manuscriptcentral.com/tped and edit your user information as appropriate.

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Thank you for submitting your manuscript to Plant Ecology & Diversity.

Sincerely,
Erika Buscardo
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erikatea@ci.uc.pt