Universidade Federal do Amapá
Pró-Reitoria de Pesquisa e Pós-Graduação
Programa de Pós-Graduação em Biodiversidade Tropical
Mestrado e Doutorado
UNIFAP / EMBRAPA-AP / IEPA / CI-Brasil

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Quais são os determinantes da comunidade de hemiepífitas em uma floresta do extremo nordeste da amazônia? Efeitos do tamanho do hospedeiro, solo e estrutura da floresta

MACAPÁ, AP
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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. José Julio Toledo

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Aprovada em 09 de março de 2018, Macapá, AP, Brasil

Dedicado a mis padres por todo su apoyo incondicional,

a mi mamá Irene por todo su cariño y confianza,

a mi papá Donato por enseñarme que nada es imposible en la vida

y a Lucio por todo su amor y apoyo en este objetivo alcanzado.

AGRADECIMENTOS

À Universidade Federal de Amapá e ao Programa de Pós-Graduação em Biodiversidade Tropical – PPGBIO, por me receberestes dois anos e me ensenar muito.

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES pela bolsa recebida.

Ao Laboratório de Ecologia Labeco por proporcionar os equipos e materiais que precisei durante este trabalho.

Ao professor Julio Toledo meu orientador por ter me guiado com a maior paciência e dedicação .

Ao Professor Marcelimo Carneiro Guedes por me prestar os equiposnecessários nesta pesquisa

A Lucio Trujillo meu companheiro de vida e de ciencia quem trabalho ao meu lado durante estes dos anos nesta pesquisa por toda sua paciência no trabalho de campo e seu apoio no trabalho de laboratório.

A todas essas lindas pessoas que conheci nesta cidade que foram na minha família aqui por seu apoio e carinho.

RESUMO

Clemente Arenas, Edith Rosario. Quais são os determinantes da comunidade de hemiepífitas em uma floresta do extremo nordeste da amazônia? Efeitos do tamanho do hospedeiro, solo e estrutura da floresta. Macapá, 2018. Dissertação (Mestre em Biodiversidade Tropical) – Programa de Pós-graduação em Biodiversidade Tropical–Pró-Reitoria de Pesquisa e Pós-Graduação - Universidade Federal do Amapá.

As hemiepífitas são um grupo de plantas com uma grande distribuição no neotropico, onde ainda se tem desconhecidos muitos aspectos ecológicos. O objetivo principal deste estudo foi analizar os determinantes da comunidade de hemiepífitas numa floresta do extremo nordeste da Amazônia, Brasil. Indivíduos de hemiepífitas foram registrados em todas as árvores hospedeiras (forófitos) com DBH ≥ 1 cm distribuídos em 110 subparcelos circulares (6 m de raio) alocadas em11 parcelas de floresta de terra firme. Os gradientes de solo (textura e fertilidade) e estrutura da floresta (tamanho da árvore edistribuição da densidade do tamanho das árvores) foram utilizados como preditores de diversidade e composição de hemiepifitas. Encontramos 4878 indivíduos de hemiepífitas que representam 50 espécies, 11 gêneros e 7 famílias distribuídas em 3385 (38,9%) forófitos. A família Araceae representou 84% das espécies e 88,5% de todos os indivíduos de hemiepífitas. Os modelos lineares de efeito misto mostraram que a riqueza e a diversidade das hemiepífitas aumentaram em forófitos maiores, enquanto o solo não teve influência. A composição das hemiepífitas mudou significativamente ao longo do gradiente do tamanho do hospedeiro e da textura do solo. A diversidade beta, turnover e a heterogeneidade da comunidade diminuíram ao longo do gradiente do tamanho do hospedeiro e da estrutura da floresta (representada pela distribuição da densidade dos tamanhos das árvores), evidenciando uma convergência para maior similaridade e homogeneidade das comunidades hemiepifíticas em grandes forófitos e em manchas de floresta com uma maior proporção de árvores grandes. O tamanho dos forófitos e a estrutura da floresta foram preditores significativos das propriedades da comunidade hemiepifítica. A textura do solo foi um preditor importante da composição das hemiepífitas, indicando que o tipo de solo pode agir como um filtro, principalmente para as lianas nômades, as quais estão conectadas ao solo nos primeiros estágios de vida. Uma alta diversidade alfa foi encontrada nos árvores grandes provavelmente devido a uma maior disponibilidade de substrato e tempo para a colonização de hemiepífitas. No entanto a diminuição da diversidade beta, o turnover e a heterogeneidade das espécies sugerem que a comunidade de hemiepífitas atinge um clímax com uma maior similaridade de espécies em árvores maiores e em manchas de floresta madura.

Palavras-chave: hemiepifitas; textura do solo; fertilidade do solo; tamanho do hospedeiro; substituição; aninhamento; diversidade beta; forófito.

ABSTRACT

Clemente Arenas, Edith Rosario. What matters for hemiepiphytes in northeastern Amazonian forest? Effectsof host size, soil and forest structure. Macapá, 2018.Dissertação (Mestre em Biodiversidade Tropical) – Programa de Pós-graduação em Biodiversidade Tropical – Pró-Reitoria de Pesquisa e Pós-Graduação - Universidade Federal do Amapá.

Hemiepiphytes are a group of plants with a wide distribution in the Neotropics, where many ecological aspects are still unknown. The main objective of this study was to analyze the determinants of the hemiepiphytic community in a forest in the extreme northeast of Amazonia, Brazil. Individuals of hemiepiphytes were recorded in all host trees (phorophytes) with DBH ≥1 cm found in 110 circular subplots (6m of radius) distributed in 11 1-ha plots of terra firme forest. Gradients of soil (texture and fertility) and forest structure (tree size and tree size-density distribution) were used as predictors for hemiepiphytic diversity and composition. We found 4878 individuals hemiepiphytes representing 50 species, 11 genera and 7 families distributed in 3385 phorophyte trees (38.9% of the trees total survey). The family Araceae represented 84% of the species and 88.5% of all individuals of hemiepiphytes. Linear mixed-effect models showed that richness and diversity of hemiepiphytes was greater in larger phorophytes, with no soil influence detected. Composition of hemiepiphytes changed significantly along the gradient of host size and the soil texture. Beta diversity, as well as the contribution of species turnover and community heterogeneity, decreased along the gradient of host size and forest structure (represented by tree size-density distributions), evidencing a convergence to higher similarity and homogeneity of hemiepiphytic communities in larger phorophytes and forest stands with a higher proportion of larger trees.Tree host size and forest structure were significant predictors of hemiepiphytic community properties. Soil texture was an important predictor of hemiepiphytes composition, indicating that soil type may act a filter, mainly for nomadic vines which are still connected to the soil in early stages of their life-cycle. Higher alpha diversity was found on larger phorophytes probably due to more availability of substrate and time for hemiepiphytes colonization. However, lower beta diversity, species turnover and heterogeneity suggests that hemiepiphytic communities reach a climax with higher species similarity on larger trees and in mature forest stands.

Keywords: hemiepiphytes; soil texture; soil fertility; host size; turnover; nestedness; beta diversity; phorophyte.

SUMARIO

1. INTRODUÇÃO GERAL

Epífitas vasculares representam aproximadamente 10 % de todas as espécies de plantas vasculares conhecidas, com 27614 especies, 913 generos e 73 familias (Zotz 2013a). Nas 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 no neotrópico (55%) (Madison 1977), embora existam números similares de gêneros e famílias em outras regiões (por exemplo, 43 famílias no paleotrópicos e 42 no neotropico), a especiação explosiva deste grupo de plantas foi intensa no Neotrópico resultando em uma maior diversidade (Gentry and Dodson 1987a). As hemiepífitas 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, florestas nubladas e savanas (Putz and Holbrook 1986). Este grupo de plantas é bem pouco estudado e contribui com 31% da diversidade de epífitas na Amazônia Central (Boelter et al. 2014) e 37% no Sudeste da Amazônia (Obermüller et al. 2012), esta diversidade é devido a uma organização vertical com uma maior abundancia no meio do dossel (Kelly 1985). Vários estudos na Amazônia já reportaram a preponderância da família Araceae nas hemiepífitas (Irume et al. 2013, Boelter et al. 2014), sendo que a maioria das espécies pode ser classificada como lianas nômades.

Além da diversidade, as hemiepífitas são importantes para o funcionamento dos ecossistemas, fornecendo abrigo e alimento para insetos e vertebrados (Madison 1977, Goetghebeur et al. 1998, Vieira and Izar 1999, Gibernau et al. 2007), retendo água da chuva e nutrientes, que servem de reserva para outras espécies de plantas e animais (Clark et al. 1998, Díaz et al. 2010, Stanton et al. 2014). Ademais, as hemiepífitas podem servir como indicadores do estado de conservação dos ecossistemas (Triana-Moreno et al. 2003).

O ciclo de vida natural das plantas hemiepífitas inclui tanto uma fase epifítica como uma terrestre ao contrário das holoepífitas que não possuem a fase terrestre (Barkman 1958). As hemiepífitas compreendem duas categorias principais, as hemiepífitas primárias, que iniciam seu ciclo de vida como epífitas e posteriormente estabelecem contato com o solo através de 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 and Holbrook 1986). Zotz (2013b) sugere o uso do termo lianas nômades para a categoria de hemiepífitas secundárias.

Em contraste com as hemiepífitas primárias, as hemiepífitas secundárias são plantas de tamanho pequeno que são capazes de colonizar hospedeiros de vários tamanhos, iniciando seu ciclo de vida no solo da floresta sombreada (Orihuela and Waechter 2010). Tendo em vista que o início do ciclo de vida ocorre no solo, os nutrientes especialmente fósforo e nitrogênio podem ser determinantes da estrutura da comunidade de hemiepífitas (primárias) e lianas nômades (Boelter et al. 2014). Espera-se que a riqueza de espécies aumente em relação à concentração de nutrientes do solo e à umidade do solo (Pausas 1994). A disponibilidade de nutrientes do solo também têm mostrado influência na estrutura da comunidade de epífitas nas escalas locais, especialmente entre as lianas nômades do sub-bosque que estão enraizadas no solo (Gentry and Dodson 1987a, Orihuela et al. 2014).

Diversidade beta foi definida por (Whittaker 1960) como a variação temporal ou espacial na composição das comunidades ao longo de gradientes ambientais. 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 demostram complementariedade, 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), que pode refletir na perda de espécies como resultado de qualquer processo ecológico que promove disminuicão de espécies e a desagregação de comunidades biológicas (Baselga 2010), enquanto o turnover de espécies representa a substituição de espécies por outras espécies de um local a outro (Qian et al. 2005) e pode ser o resultado do ganho ou perda de espécies devido à selecção ambiental, restrições históricas e competição (Baselga 2010). Estes componentes da diversidade beta são importantes para compreender melhor questões centrais de biogegrafia, ecologia e conservação (Baselga 2010). Tonkin et al (2015) propôs que os gradientes ambientais, a dispersão de espécies e a conectividade espacial entre os locais moldam os componentes de aninhamento e turnover da diversidade beta.

O tamanho do forófito pode influenciar a estrutura da comunidade de epífitas (Zotz 2007, Zhao et al. 2015, Marí et al. 2016), mas o efeito sobre as hemiepífitas foi pouco investigado. Fórofitos maiores podem fornecer mais substrato e diferentes microhábitats para suportar uma maior diversidade (Taylor and Burns 2015, Woods et al. 2015, Woods 2017). As florestas perturbadas com maiores quantidades de árvores pequenas podem abrigar uma menor diversidade de epífitas do que as florestas não perturbadas (Werner and Gradstein 2009, Barthlott et al. 2001). Espera-se que a diversidade beta seja maior nas florestas perturbadas, visto que a comunidade esta exposta a um ambiente mais dinâmico que contribui para a substituição de espécies (Limberger and Wickham 2012, Myers et al. 2015). Uma comunidade arbórea de uma floresta em regeneração é composta principalmente por àrvores pioneiras e árvores de sucessão secundária que possuem traços específicos (tal como um baixo potencial de água na casca) (Huc et al. 1994), o que pode restringir a colonização por hemiepifitas e manter uma menor diversidade alfa, enquanto a diversidade beta pode aumentar (Plowden et al. 2003). Espera-se que as florestas maduras com árvores grandes tenham maior diversidade alfa de hemiepífitas (Barthlott et al. 2001, Flores-Palacios and García-Franco 2008, Boelter et al. 2014), já que o tempo para a colonização abrange centenas de anos eo substrato e microhábitat são abundantes num forófito grande. No entanto, espera-se que a diversidade beta seja reduzida devido ao longo tempo disponível para que as hemiepífitas se dispersarem e colonizar as árvores maiores na área.

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 registradas nas florestas da Guyana francesa (Gradstein 2006), 37 espécies de orquídeas (Jardim and Medeiros 2011), oito espécies de Bromelias em florestas de várzea (Quaresma and Jardim 2012) e 11 especies de orquídeas e aráceas em restingas do Pará (Quaresma and Jardim 2014). No entanto, há uma falta 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 não houve um investigação dos padrões de diversidade e composição e a associação com as características do hospedeiro, estrutura florestal e restrições ambientais.

2. HIPÓTESES

- A diversidade alfa aumenta nas árvores grandes devido ao maior tempo, alta disponibilidade de substrato e microhabitats para colonização. A diversidade alfa também aumentará nos solos arenosos, pois este tipo de solo é associado a condições húmidas, e também será elevada nos solos férteis pois as hemiepífitas dependem parcialmente de recursos do solo.
- Haverá mudanças na comunidade de hemiepífitas ao longo do gradiente de tamanho dos hospedeiros e do solo (textura e nutrientes) porque estes fatores podem restringir a ocorrência espécies.
- A diversidade beta será baixa nas árvores grandes e nas florestas com uma alta proporção de árvores grandes, pois a sustituição de espécies diminuirá nos forófitos mais velhos e florestas maduras.

3. OBJETIVOS

3.1. GERAL

Analisar os determinantes da comunidade de hemiepífitas em uma floresta do extremo nordeste da Amazônia.

3.2. ESPECÍFICOS

- Testar se a comunidade de hemiepifitas é influenciada pelo tamanho do hospedeiro e propriedades edáficas (textura e fertilidade).
- Determinar como a diversidade beta de hemiepifítas e seus componentes (substituição de especies e aninhamento) variam de acordo com o tamanho do hospedeiro e estrutura da floresta.

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4. CAPITULO 1

What matters for hemiepiphytes in northeastern Amazonian forest? Effects of host size, soil and forest structure.

Artigo submetido ao periódico "Journal of Vegetation Science"

What matters for hemiepiphytes in northeastern Amazonian forest? Effects of host size, soil and forest structure.

Running head: What determines hemiepiphytic communities?

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Funding information

Federal University of Amapá (UNIFAP) which has provided transportation and financial support through PAPESQ/UNIFAP (Nº 015/2015). National Council for Scientific and Technological Development (CNPq Universal Nº 447432/2014-1)

Abstract

Questions: How do host size, soil texture, and fertility influence hemiepiphytic community's attributes? How does forest structure affect the beta diversity of hemiepiphytes?

Location: Amapá National Forest, Northeastern Amazonia, Brazil.

Methods: Individuals of hemiepiphytes were recorded in all host trees with DBH ≥1 cm found in 110 circular subplots (radius 6m) distributed 11 1-ha plots of terra firme forest. Gradients of soil (texture and fertility) and forest structure (tree size and tree size-density distribution) were used as predictors for hemiepiphytic diversity and composition.

Results: We found 4878 individuals hemiepiphytes representing 50 species, 11 genera, and 7 families distributed in 3385 phorophyte trees (38.9% of trees total survey). The family Araceae represented 84% of the species and 88.5% of all individuals of hemiepiphytes. Linear mixed-effect models showed that richness and diversity of hemiepiphytes was greater in larger phorophytes, with no soil influence detected. Composition of hemiepiphytes changed significantly along the gradient of host size and the soil texture. Beta diversity, as well as the contribution of species turnover and community heterogeneity, decreased along the gradient of host size and forest structure (represented by tree size-density distributions), evidencing a convergence to higher similarity and homogeneity of hemiepiphytic communities in larger phorophytes and forest stands with a higher proportion of larger trees.

Conclusions: Tree host size and forest structure were significant predictors of hemiepiphytic community properties. Soil texture was an important predictor of hemiepiphytes composition, indicating that soil type may act a filter, mainly for nomadic vines which are still connected to the soil in early stages of their life-cycle. Higher alpha diversity was found on larger phorophytes probably due to more availability of substrate and time for hemiepiphytes colonization. However, lower beta diversity, species turnover and heterogeneity suggest that hemiepiphytic communities reach a climax with higher species similarity on larger trees and in mature forest stands.

Keywords: hemiepiphytes, soil texture, soil fertility, host size, turnover, nestedness, beta diversity, phorophyte.

INTRODUCTION

More than a third (35%) of vascular plant species and almost half (49%) of the individual plants in tropical rain forests are epiphytes (Gentry & Dodson 1987; Kelly et al. 1994). Most epiphytes species are from the Neotropics (55%), though there are similar numbers of genera and families in others regions (e.g. 43 families in Paleotropics and 42 in Neotropics) (Madison, 1977). The explosive speciation of this plant group was dramatic in the Neotropics resulting in higher diversity (Gentry & Dodson 1987). Hemiepiphytes constitute an important component of many different ecosystems, including the tropical rain forests, upper montane and cloud forests and savannas (Putz & Holbrook 1986). Although the hemiepiphytes group is poorly studied, it contributes to around 31% of diversity of epiphytes in Central Amazonia (Boelter et al. 2014) and 37% in the southwestern Amazonia (Obermüller et al. 2012). It is important to ecosystem functioning, providing shelter and food for insects and vertebrates (Madison 1979; Vieira & Izar 1999; Gibernau et al. 2007), retaining rainwater and nutrients (Clark et al. 1998; Stanton et al. 2014) and indicating of the state of conservation of ecosystems (Triana-Moreno, Garzón-Venegas, Sánchez-Zambrano, & Vargas, 2003).

The natural life cycle of hemiepiphytic plants includes both epiphytic and a terrestrial phases, unlike the holoepiphytes which lack a terrestrial phase (Barkman, 1958). Hemiepiphytes comprise two major categories, primary hemiepiphytes, which begin their life cycle as epiphytes and later establish soil contact through long descendent roots, and secondary hemiepiphytes, which germinate in the soil and climb up using adherent roots, to eventually become epiphytes after losing soil contact (Putz & Holbrook 1986). Zotz (2013) suggests using the term nomadic vines for secondary hemiepiphytes.

In contrast to primary hemiepiphytes, secondary hemiepiphytes are small-sized plants which are able to colonize hosts of varied sizes, and start their life cycle in shady forest soils (Orihuela & Waechter 2010). A starting of life-cycle in the soil, can to significate that the nutrients (especially phosphorus and nitrogen) may be determinants of community structure of primary hemiepiphytes and nomadic vines (Boelter et al., 2014). Species richness is expected to increase and saturate in relation to soil nutrient concentration and soil moisture (Pausas, 1994). Soil nutrient availability has also been shown to influence epiphytic community structure at local scales, especially nomadic vines (Gentry & Dodson 1987; Orihuela et al. 2014).

Beta diversity is the spatial change in community composition and can be measured through similarity/dissimilarity between sites (Baselga 2010). Beta diversity may be divided into two different components, turnover and nestedness that are antithetic processes (Baselga et al. 2007, 2017). Nestedness occurs when sites with fewer species are subsets of sites with higher richness (Wright & Reeves 1992; Ulrich & Gotelli 2007) while turnover represents the substitution of one species by another species (Qian, Ricklefs, & White, 2005).

Phorophyte size may influence the structure of epiphytic communities (Zhao et al. 2015; Mari et al. 2016), but the effect on hemiepiphytes is poorly investigated. Larger phorophytes may provide more substrate and different microhabitats which would support higher diversity (Taylor & Burns 2015; Woods et al. 2015, Woods 2017) and disturbed forests with larger quantities of smaller trees, and hence higher heterogeneity, may harbor a lower diversity of epiphytes than undisturbed forest (Werner & Gradstein 2009; Barthlott et al. 2001). Beta diversity is expected to be higher in disturbed forests since communities are instable because frequent changes in habitat can drive loss and/or substitution of species (Limberger & Wickham 2012; Myers et al. 2015). The tree community of a regenerating forest is composed mainly by smaller pioneers and secondary successional trees which have their own specific traits (such low water potential and wood density) which may constrain colonization by hemiepiphytes (Huc et al. 1994; Chen et al. 2017). This would keep alpha diversity low, while beta diversity may be greater (Plowden, Uhl, & de Assis Oliveira, 2003). Considering that substrate and microhabitat are abundant on large phorophytes, mature forests with large trees are expected to have a higher alpha diversity of hemiepiphytes (Barthlott et al. 2001; Boelter et al. 2014) since the time available for successful colonization spans hundreds of years. However, beta diversity is expected to be reduced because hemiepiphytes have time to disperse and colonize all larger trees in an area.

The extreme northeastern Amazonia is a diverse region of terra firme forest. Diversity of epiphytes is high with 129 species of liverworts and one hornwort species recorded (Gradstein, 2006), 37 species of orchids (Jardim & Medeiros 2011), 8 species of bromeliads in várzea forest (Quaresma & Jardim, 2012) and 11 species between orchids and aroids sandbank of Belém state (Quaresma & Jardim, 2014). However, there is a lack of information on species' distributions and diversities, especially regarding the hemiepiphytic group, and all of studies was about taxonomy and sporadic records (Cantuária, Freitas, Lima, & Cantuária, 2014) were made in the region, for which there is a large gap to be filled about patterns of diversity and composition and associations with host characteristics, forest structure and environmental constraints. Therefore, we inventoried thousands of phorophyte trees for hemiepiphytes in a representative tract of terra firme forest to (1) test if the hemiepiphytic community is influenced by host size and soil properties (texture and fertility), and (2) to determine how hemiepiphytes´ beta diversity and its components of turnover and nestedness vary with host size and forest structure.

We hypothesize that alpha diversity will be greater on larger trees due to a longer time for colonization and a higher availability and range of substrates and microhabitats. Alpha diversity is expected to increase on sandy soils since this soil type is associated to humid conditions and we also expect that fertile soils will support higher diversity since hemiepiphytes are partially or truly connected to the soil. Changes in hemiepiphytic communities are also expected along gradients of host size and soil, because these factors may constrain the occurrence of several species. Yet, we hypothesize that beta diversity will be lower on larger trees and in forest stands with a higher proportion of large trees since the turnover of species is expected to decrease on older phorophytes and mature forests.

METHODS

Study area

The study site spans an area of 25 km^2 of terra firme forest within the Amapá National Forest (ANF) which is located in the extreme northeast of the Brazilian Amazon, in the Guiana Shield, state of Amapá (0°55’29”N, 51°35’45”W) (Fig. 1). Situated in the core of the state, ANF is part of a large ecological corridor known as the Amapá Biodiversity Corridor, a group of protected areas that account for more than 70% of the state's total area (Albernaz & Souza, 2007)

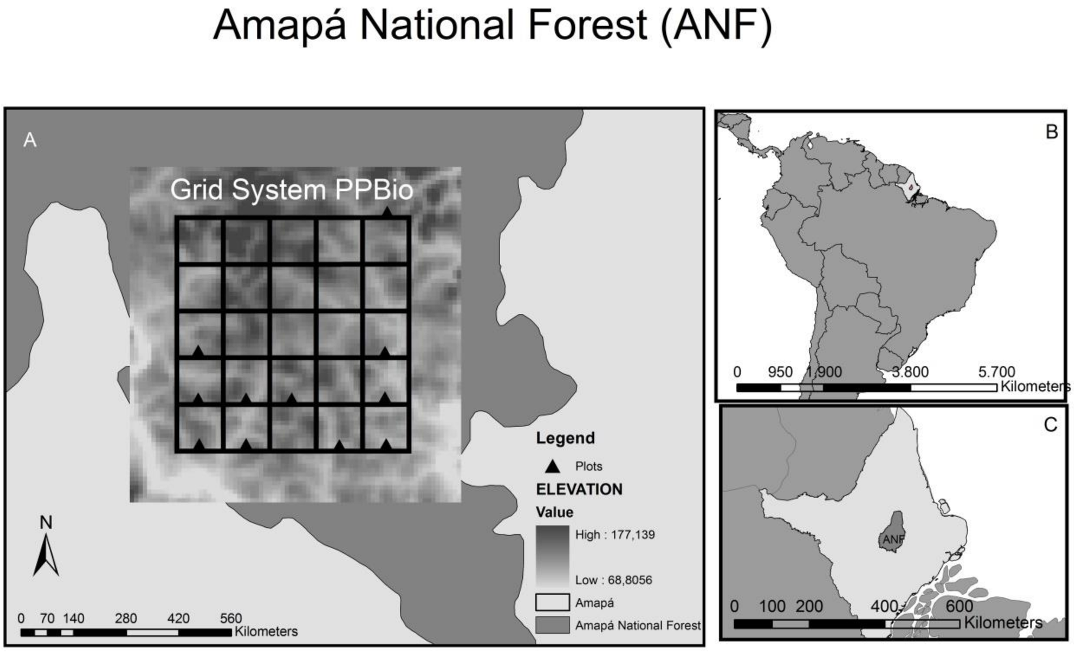

Fig. 1: Map of the study area A) 11 plots distributed on research grid (5x5 km), B) South America and C) Amapá state.

The regional climate is classified by Köppen-Geiger as Am (Equatorial monsoon) (Kottek, Grieser, Beck, Rudolf, & Rubel, 2006). Mean annual temperature varies between 22°C and 32°C, and average annual rainfall is around 2284 mm with a rainy season from December to July and a dry season from August to November. Nevertheless, precipitation often exceeds 60 mm per month even in the driest months (ICMBio, 2014). The topography is slightly undulating, and varying between 100 and

200 m in altitude, and inclination around 7° on slopes. Ultisols are predominant and chemical fertility is low. The vegetation consists of continuous closed canopy “terra firme” tropical rainforest, predominantly never-flooded (ICMBio, 2014). Canopy trees typically reach a height of 25–35 m interspersed with frequent emergent trees reaching up to 50 m (ICMBio, 2014). The most abundant tree families in the area are Lecythidaceae, Fabaceae, Sapotaceae, Burseraceae and Annonaceae, and the most important species are *Vouacapoua americana*, *Eschweilera ovata*, *Eschweilera coriacea*, *Lecythis chartacea* and *Eugenia cupulata* (unpublished data).

Data sampling

The hemiepiphytes surveys were conducted in 11 out of the 30 plots previously established in the ANF according to the guidelines of the RAPELD method (Rapid Assessment for Long-Term Ecological Research) (Magnusson et al., 2005) which is applied by the Brazilian Program for Biodiversity Research (PPBio). Each plot was defined by a 250 m central line that followed topographic isoclines and was 10 m wide on each side. Each plot was divided into 10 sections (50 X 20 m) to allow systematic sampling of trees. Starting from the beginning of each section, we selected always the third tree with DBH (Diameter at Breast Height) greater than 30 cm to be the centre of a smaller circular subplot with 6 m of radius (113 m^2) for each section in total 10 per plot.

From March to September 2017 we sampled all the trees with a minimum DBH of 1 cm within each subplot, totaling 10 187 trees, and recorded all the individuals of primary hemiepiphytes and nomadic vines that grew above 0.3 m from the ground (4878 individuals). We noted whether the hemiepiphytes were connected to the soil in order to classify them as primary hemiepiphytes or nomadic vines. Phorophyte DBH (1.3 m above ground) was measured using a caliper for the small trees (<5cm DBH) and using a diameter tape for larger trees.

Most of the phorophytes were visually surveyed from ground level but the taller trees were climbed with single rope technique to access the canopy (Anderson et al. 2015).

Most were identified using guides (Ribeiro et al. 2002; Zuquim et al. 2008). When it was not possible to identify the species in the field, botanical vouchers were collected for comparison with material deposited in the HAMAB herbarium. For circumscription of fern families we followed Smith et al. (2006) and for the flowering plants we used the APG IV(Angiosperm Phylogeny Group, 2016)

A superficial (0-5 cm deep) soil sample was collected at six points every 50 m along the plot's central line to make a composite sample. Soil analyses were conducted to the soil laboratory of the Brazilian Agricultural Research Corporation (EMBRAPA) of Amapá to be analyzed according to the methodology of EMBRAPA (1997). The soil was oven-dried and passed through a 2 mm sieve. Clay was determined by the hydrometer method as the percentage by volume of particles < 0.002 mm. Atomic absorption spectroscopy was employed to measure K^+ and Na^+ after extraction by 1 Molar Mehlich solution and Ca^{2+} and Mg^{2+} after extraction by 1N KCL solution reagent. Cations were summed for calculated the sum of bases of the soil.

Data analysis

Species richness was estimated using Chao 1 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). Diversity was estimated by the α parameter of Fisher's logarithmic series (Fisher, Corbet, & Williams, 1943) which is recommended for samples with a small proportion of abundant species and a large proportion of "rare" species (Magurran, 2004), as occurs with the hemiepiphytes community. We calculated Fisher’s alpha for 155 phorophytes, taking into account that Fisher’s alpha cannot be calculated when the ratio of number of individuals by richness is smaller than 1.44 (Magurran, 2004).

We tested if percentage of clay, sum of bases and host size (DBH) affect species richness and diversity of hemiepiphytes using linear mixed-effect models (LMM). In a first model, we controlled for the effect of plot by placing it as a random factor and tree diameter as the fixed effect. In a second model where we have the soil variables (clay and sum of bases) as fixed effects, we controlled for the effect of diameter by placing diameter as a random effect. We tested if composition of hemiepiphytic comunities was affected by clay, sum of bases and host size by a Permutational Multivariate Analysis of Variance (PERMANOVA) using Bray Curtis dissimilarity as the distance metric. The mixed models were run at level of the individual phorophyte while PERMANOVA was run at the subplot level since the multivariate analysis did not converge using the matrix of phorophytes probably due to its size or large frequency of zeros.

We analyzed beta diversity and the contribution of its components (turnover and nestedness) in the hemiepiphytes' community by calculating three multiple-site dissimilarity indexes (Baselga 2010, 2007). For qualitative data the overall beta diversity was estimated by the multiple-site dissimilarity of Sorensen (β_{sor}), while the turnover component was calculated using Simpson dissimilarity (β_{sim}) and the nestedness component (β_{sne}) was calculated as β_{sor} - β_{sim}(Baselga, 2010). To partition beta diversity using abundance, we estimated the total abundance-based multiple-unit Bray-Curtis dissimilarity index (β_{BC}) and separated the dissimilarity into turnover (abundance balanced variation, $\beta_{BC.BAL}$) and into abundance gradient (or subset; $\beta_{BC.GRA}$) using the relation $\beta_{BC} = \beta_{BC.BAL} + \beta_{BC.GRA}$ (Baselga, 2017). We used the dissimilarity matrices of Sorensen (β_{sor}) and Bray Curtis (β_{BC}) to calculate the mean of Euclidean distances between objects and centroids of groups of each diameter class, (after reducing the original distances from PCoA Principal Coordinates Analyses) to estimate community heterogeneity. Non-Metric Multidimensional Scaling (nMDS) was used to generate axes to represent hemiepiphytic community composition.

Community properties were calculated at the plot level by pooling the phorophyte data into different classes of diameter (DBH: 1-10, 10.1-20, 20.1-30, 30.1-40, 40.1-50, 50.1-60, 60.1-70, ≥70.1 cm) and at subplot level. The estimates of community properties only can do them like groups (diameter class) and not to each phorophytes, allowing the description of variation within different phorophyte sizes at plot level. For each subplot we fitted a linearized scaling function (Log10 N = a + b * log10 DBH; N is density of individuals of one diameter class) to the tree size-density distribution and extracted the scaling exponent (b) to describe forest structure. A high negative value of this coefficient indicates that the forest has a larger proportion of smaller trees while less negative values reflect a forest stand with a higher proportion of large trees. Linear regressions were used to test if phorophyte size (represented by diameter class midpoint) and forest structure (represented by the scaling coefficient) affect beta diversity (and its components), and composition of hemiepiphytic community.

We performed all analyses using the R platform version 3.4.2. The V*egan* 2.4-4 (Oksanen et al., 2013) package was used to estimate alpha diversity, perform ordination analyses, PERMANOVA and to calculate distances from centroids. The *Betapart* 1.4-1 (Baselga, 2017) package was used for partitioning of beta diversity.

RESULTS

We found 4878 individuals of hemiepiphytes on 3385 phorophytes trees (38.9% of sampled trees ≥ 1cm DBH). The hemiepiphytes were from 50 species, 11 genera, and 7 families (Appendix S1). The family Araceae was the most important, being 84% of the species and 88.5% of the individuals of hemiepiphytes. Almost the whole community was composed of nomadic vines (49 species) and only one species (*Clusia grandiflora*) was a primary hemiepiphyte. The most abundant species were *Heteropsis flexuosa* (n=1034), *Philodendron platypodum* (917) *Philodendron surinamense* (361), *Philodendron ecordatum* (338) and *Evodianthus funifer* (327), which together represent 61.02 % of all recorded individuals.

The sampling effort apparently was enough to collect most representative species of hemiepiphytes because it has an asymptote (Appendix S2).

Effects of host size and soil on alpha diversity and composition.

Richness (LMM: t=8.4, p=0.00) and diversity (t=2.64, p=0.0092) were greater at larger phorophyte size (Appendix S3 and S4, Table 1), indicating that availability of substrate and time for colonization are determinants of hemiepiphytes diversity. Soil texture (t=0.23, p=0.82) and fertility (t=-1.36, p=0.17) did not affect richness. Likewise, diversity was not affected by soil fertility (t=1.58, p=0.12) or texture (t=-0.23, p=0.82).

Composition was highly related to phorophyte size (Permanova: *F*=14.5, *p*=0.001; Appendix S4g), shown by turnover of species along the gradient of tree diameter (Fig. 2a). Seven species occurred exclusively on large trees (*Philodendron melinonii, P. megalophyllum, P. solimoesense, P. atabapoense, P. callosum, Marcgravia* sp.3 and *Clusia grandiflora,* the last two being rare species), while 11 species were found only in smaller trees, namely *Anthurium pentaphyllum, A. sinuatum,* Araceae sp.47, *Philodendron toshibae, P. quinquelobum, Heteropsis* sp.3, *Syngonium podophyllum, S. hastiferum,* Araceae sp.48, Araceae sp.49, *Anthurium* sp.9, the last 8 species being rare species. Soil texture also affected community composition (*F*=3.6, *p*=0.001; Appendix S4h), only one species (Araceae sp.47) being exclusive to clayey soil, while 9 species (*Philodendron solimoesense, Lomagramma guianensis, P.* cf. *rudgeanum, Anthurium* sp.6, *A. sinuatum, P. quinquelobum, Marcgravia* sp.3, *Clusia grandiflora*, and *Anthurium* sp.9, the last four being rare species) were restricted to soils with lower clay content (Fig. 2b). Fertility did not affect composition of hemiepiphytic community (*F*=1.1, *p*=0.33), though 9 species appear only on sites with a lower content of sum of bases (Fig. 2c).

Table 1: Results of the linear mixed-effect models (LMM) for diversity (Fisher´s Alpha) and species richness (Chao Index) of hemiepiphytes related to host size (DBH), texture (clay) and fertility (sum of bases). DBH was considered a random effect in models 1 for diversity and richness, while soil characteristics (clay and sum of bases) were assigned as random effects in models 2. Marginal R^2 values consider only fixed effects, and conditional R^2 includes both fixed and random effects. The relative contribution of predictors is given by the standardized coefficients of the LMMs. The probability for each predictor is shown in parentheses.

Dependent variables	Models	Relative contribution of predictors					
		R^2 marginal	R^2 conditional	Intercept	Diameter	Clay	Sum of bases
Diversity	1	0.0433	0.0433	0.409	0.0016 (0.009)		
	2	0.0159	0.0159	0.0066		-0.0015(0.818)	0.6857(0.117)
Richness	1	0.0206	0.0317	1.5687	0.0189 (0.00)		
	2	0.0002	0.5262	2.7886		-0.0019(0.822)	-0.6443(0.174)

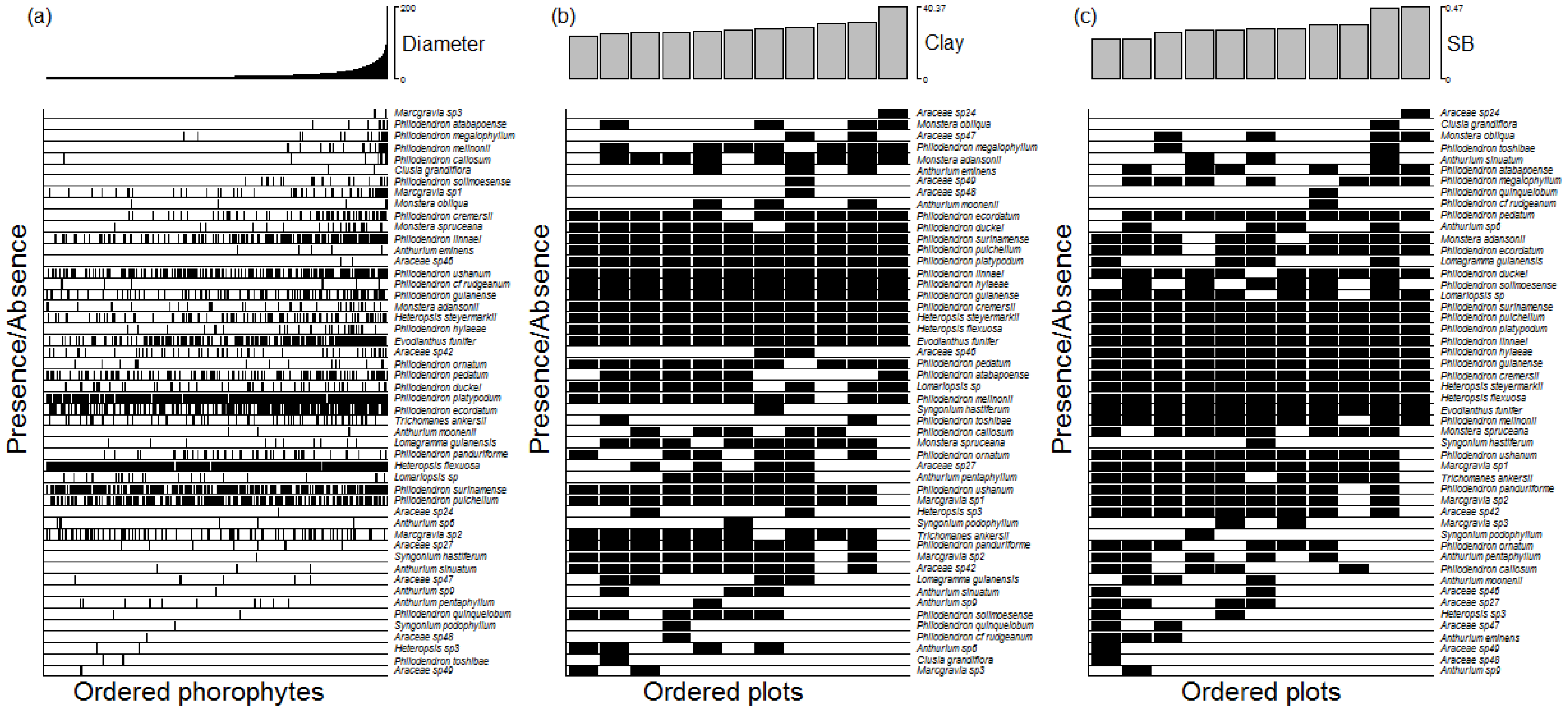

Fig. 2: Species-level presence/absence histograms for the gradients of (a) host size (diameter) for at phorophyte level, and (b) soil texture (clay) and (c) soil fertility (sum of bases) at plotlevel.

Effects of host size and forest structure on beta diversity (turnover and nestedness) and community heterogeneity.

Overall hemiepiphytic beta diversity was high (β_{sor}=0.99) and all variation was due to turnover (β_{sim}=0.99) while nestedness had no importance (β_{nes}=0.00), indicating that species' replacement determines beta diversity at mesoscale. Using abundance data, total abundance-based dissimilarity was also high (β_{BC}=0.99) and balanced variation in abundance accounted for all variation ($\beta_{BC.BAL}$=0.99) while the abundance gradient had no importance ($\beta_{BC.GRA}$=0.00). This shows that a decrease in the abundance of a group of species is counterbalanced by an increase in abundance of another group. At plot and subplot-scales the patterns of beta diversity were the same observed at the mesoscale for both qualitative data (averages: β_{sor}=0.99, β_{sim}=0.98 and β_{nes}=0.01 and β_{sor}=0.93, β_{sim}=0.90 and β_{nes}=0.03, respectively for plot and subplot scales) and for abundance-based dissimilarity (β_{BC}=0.99, $\beta_{BC.BAL}$=0.98 and $\beta_{BC.GRA}$=0.01 and β_{BC}=0.93, $\beta_{BC.BAL}$=0.90 and $\beta_{BC.GRA}$=0.03, respectively).

Beta diversity (t=-4.34, p<0.001), turnover (t=-4.20, p<0.001) and heterogeneity (t=-5.37, p<0.001) were negatively related to host size (Fig. 3), indicating low substitution of species and higher similarity of species among large trees. Forest structure represented by a scaling exponent of tree size-density distribution, affected negatively beta diversity (t=-2.18, p=0.032), turnover (t=-3.09, p=0.003) and heterogeneity (t=-2.12, p=0.036) (Fig. 4), suggesting a lower substitution of species and lower heterogeneity of the hemiepiphytic community at forest stands with a higher proportion of larger trees. The results based on abundance data show the same patterns observed for qualitative data. The total abundance-based dissimilarity (t=-3.82, P<0.001), abundance balanced variation (t=-3.91, P<0.001), and community heterogeneity (t=-5.07, p<0.001) decreased sharply along the gradient of host size (Appendix S5). Also, forest structure affected negatively the abundance-based dissimilarity (t=-1.75, p=0.082), abundance balanced variation (t=-3.07, p=0.003), and community heterogeneity (t=-2.09.75, p=0.039) (Appendix S6). The average number of species per small tree (< 10 cm DHB) was only 1.2, while the number of species per large trees (≥ 30 cm DBH) was 2.3.

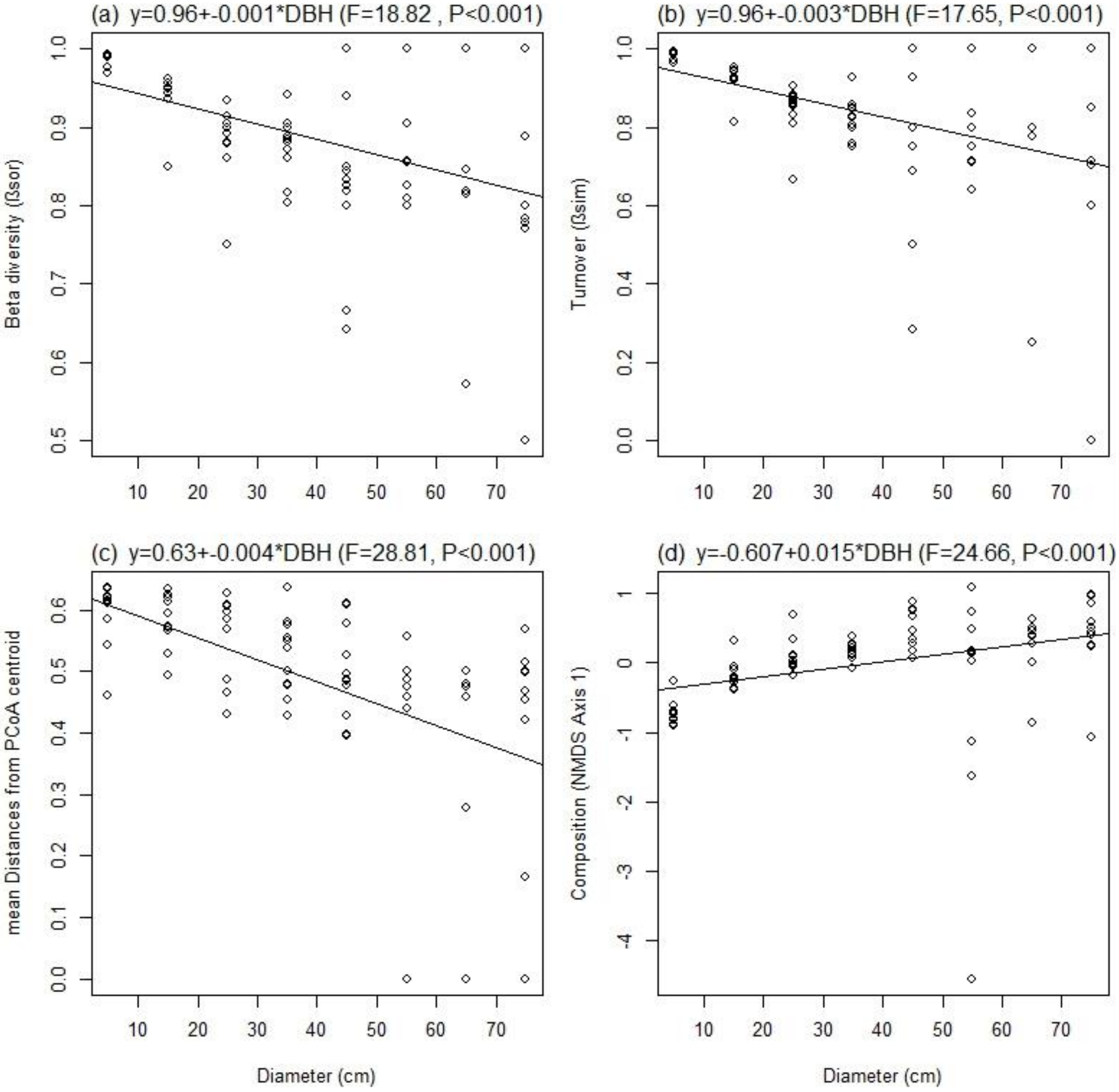

Fig. 3: Effects of tree host size (diameter in cm) at plot level on (a) beta diversity (β_{sor}), (b) turnover (β_{sim}), (c) community heterogeneity represented by mean distance from PCoA centroid based on presence/absence data and (d) composition represented by the first axis of an ordination (nMDS) based on abundance (nMDS did not converged using presence/absence data). The midpoints of size-class bins were used in regressions. Lines denote significant linear regressions.

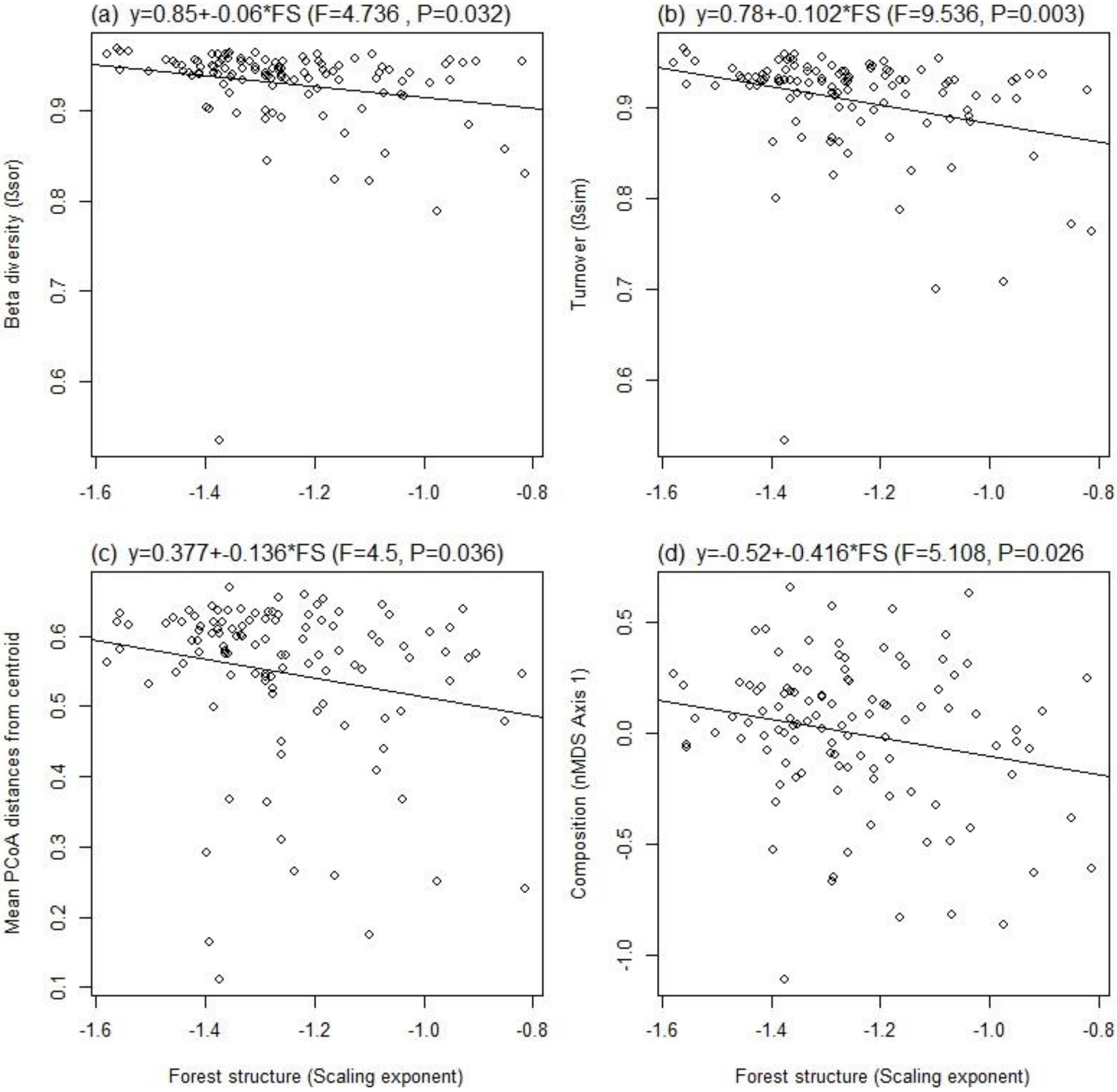

Fig. 4: Effects of forest structure represented by the scaling exponent of tree size-density distribution (FS) calculated at subplot level on (a) beta diversity (β_{sor}), (b) turnover (β_{sim}), (c) community heterogeneity represented by mean distance from PCoA centroid and (d) composition represented by the first axis of an ordination (nMDS) based on presence/absence data. Less negative values of the scaling exponent (Forest structure) indicate higher proportion of larger trees. Lines denote significant linear regressions

Changes in composition along the gradients of host size (*t*=4.97, *p*<0.001 for abundance data; Fig. 3) and forest structure (*t*=-2.26, *p*=0.026 for qualitative, and *t*=2.61, *p*=0.0103, for abundance data; Fig. 4 and Appendix S6) were driven mainly by species substitution.

DISCUSSION

The family Araceae was the main component of the hemiepiphytes' community as previously reported in others studies (Irume et al. 2013; Boelter et al. 2014; Orihuela et al. 2014; Orihuela & Waechter 2010). Nomadic vines were the richest group as recorded for central Amazonia (Boelter et al., 2014) and Atlantic forest in southern Brazil (Orihuela & Waechter, 2010).

As for Orihuela and Waechter (2010), we found nomadic vines distributed along the whole gradient of host size (1 to 200 cm of DBH), probably because these plants have smaller sizes, which allows them to colonize a wider range of phorophyte sizes, starting their life cycle in the shady forest soil and being able to colonize most available phorophytes in their first life stages (Orihuela at al 2014).

Species richness, diversity, and composition of hemiepiphytes were influenced by host size (DBH) indicates that availability of substrate and age are essential for establishment of a higher number of species (Wagner et al. 2015; Zhao et al. 2015; Woods, 2017). The heterogeneity of microhabitats created in large phorophytes is higher (Woods et al. 2015), allowing several hemiepiphyte species to coexist on the same host (Nieder, Engwald, Klawun, & Barthlott, 2000). The coexistence may be possible due to abundance of microhabitats and niche partitioning among hemiepiphyte species. For example, Marí et al. (2016) found differences in epiphyte composition between trunk and crown. Niche partitioning may occur at a yet finer scale, with compositional distinction even inside the crown (Wang et al. 2016; Woods 2017). Age may also determine hemiepiphytes alpha diversity, since the chanced of a phorophyte being colonized may increase with time of exposure of the phorophyte. Experimentally using the same species of phorophyte, several studies demonstrated that composition and diversity vary distinctly along with tree age (e.g. Marí et al. 2016, Woods 2017).

Clay affected the composition of hemiepiphytes demonstrating the substitution of species along a gradient of texture. The Amazonia basin is geologically old, and there is considerable heterogeneity of soil types in tropical lowlands (Williams et al., 2002). Soil heterogeneity is potentially important, with the texture as an influential characteristic because it affects the ability of soils to retain water, nutrients and carbon (Silver et al., 2000). A great number of studies has shown the effects of soil texture on diversity and composition of several plant groups at local- to meso-scales (e.g. Costa et al. 2005, 2009). In the critical early phase of their life-cycles several species depend on soil type to germinate and establish (Balcázar-Vargas, Peñuela-Mora, van Andel, & Zuidema, 2012). As most species were common in sandy soils, probably higher humidity (due to the proximity of sandy soils to water courses) may increase the probability of a phorophyte being colonized by hemiepiphytes. Obregon et al. (2011) found higher epiphyte diversity in wetter sites in French Guiana due to fog.

Forest structure is also dependent on soil texture (Clark & Clark, 2000). Sandy soils, which are nutrient-poor and prone to waterlogging, show higher plant mortality and therefore higher abundance of pioneer species and lower biomass (Toledo, Castilho, Magnusson, & Nascimento, 2017). These factors together may influence both the availability of phorophytes and environmental factors such as light and humidity which are decisive for hemiepiphytes. This especially applies to nomadic vines during the critical early stages of their life-cycle, when they are still connected to the soil and depend on nutrient and water availability to enhance their survival (Boelter et al. 2014; Orihuela et al. 2014).

The differentiation of the spatial turnover and nestedness components of beta diversity is important for understanding important biogeographic, ecological and conservation issues (Baselga, 2010). Lower beta diversity on larger phorophytes indicates that the hemiepiphyte community reaches a climax level on larger trees. Species turnover was the preponderant component of beta diversity and its decrease with DBH show that hemiepiphytes are more similar on larger trees. The reduction of beta diversity in larger trees and mature forest shows a tendency for the community to stabilize, probably due to saturation of spatial niche on large trees. Woods et al. (2015) showed that in epiphyte succession in tree crowns, species accumulate while more microhabitats are formed as the crowns increase in size, conducting to a decrease in turnover and increase of nestedness component the community of large phorophytes. The high hemiepiphyte turnover in forest stands with higher proportion of small trees shows that a host hierarchical structure may not necessarily imply that hemiepiphyte community will be hierarchically organized as expected (Woods et al. 2015; Marí et al. 2016). Numerous large trees in highly diverse forests are apparently able to prevent hierarchical structure of hemiepiphytes probably providing enough and differentiated substrates because the community of hemiepiphytes on smaller phorophytes is a subset of that of larger phorophytes. Increase of hemiepiphytes turnover in forest stands with higher proportion of small trees indicates that other properties of the tree community such as trait functional diversity may act as a determinant of hemiepiphyte community structure. A trait structure of bark type or water potential may cause a hierarchical structure of hemiepiphytes, by hosting a higher diversity on the hosts with the most common trait. Indeed, trees with higher bark water retention are able to host higher species diversity of epiphytes than barks with lower water retention (Callaway, Reinhart, Moore, Moore, & Pennings, 2002) although, epiphyte species are not structurally organized at species- or family-level according to bark type (Boelter et al. 2014).

Lower heterogeneity of hemiepiphytes communities in stands with a higher proportion of larger trees indicates that mature forest will host a stable hemiepiphytes community with high similarity (as seen by lower beta diversity). Abundance and diversity of epiphytes are considerably reduced in disturbed sites (Barthlott et al., 2001), i.e., in forest stands with lower quantity of larger trees. However, there is evidence that in sites with more heterogeneous forest structure due to harvesting of large trees possibly by forest management, the old, large trees may act as ‘stepping stones’ for epiphyte dispersal, increasing the rate of colonization, and reducing extinctions (Ruchty, Rosso, & McCune, 2001). Heterogeneity may be driven by a lack of time and space for smaller trees to host high richness of hemiepiphytes. .

This is the first study to report that hemiepiphytic diversity (alpha and beta) can be predicted by host size, forest structure, and soil properties. Moreover, turnover was the main component of beta diversity and changes according to host size and forest structure, thus describing a tendency to a climax of community in mature forest stands of large-size and probably long-lived trees. Future research on the effect of species composition and functional traits of phorophytes, such as bark type, water and nutrient content in the barks, and branching structure can help to increase the predictability of presence of hemiepiphytes.

Acknowledgements

We acknowledge the Coordination for the Improvement of Higher Education Personnel (CAPES) for supporting E.C.A. with a scholarship to undertake her Master´s thesis in Tropical Biodiversity. We also thanks, Chico Mendes Institute for Biodiversity Conservation and all staff of Amapá National Forest for logistical support and Federal University of Amapá (UNIFAP) which have provided transportation. We also thank Hamilton Silva for valuable help in field work.

Author Contributions

E.C. and J.T. designed the research and wrote the manuscript with support from R.H. and C.Z.; E.C. and L.T. collected the data; R.H. did field work logistic; E.C. and J.T. performed statistical analyses; all authors discussed the results and commented on the manuscript.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Table representing species of hemiepiphytes and their abundances.

Appendix S2. Species accumulation curve of hemiepiphytes.

Appendix S3. Table of results of partial regressions testing the effects of host size, soil texture and soil fertility on diversity, richness, and composition of hemiepiphytic communities.

Appendix S4. Partial regressions testing the effects of host size, soil texture and fertility on diversity, richness and composition of the hemiepiphytic communities.

Appendix S5. Effects of host size at plot level on beta diversity, turnover and community heterogeneity based on abundance data.

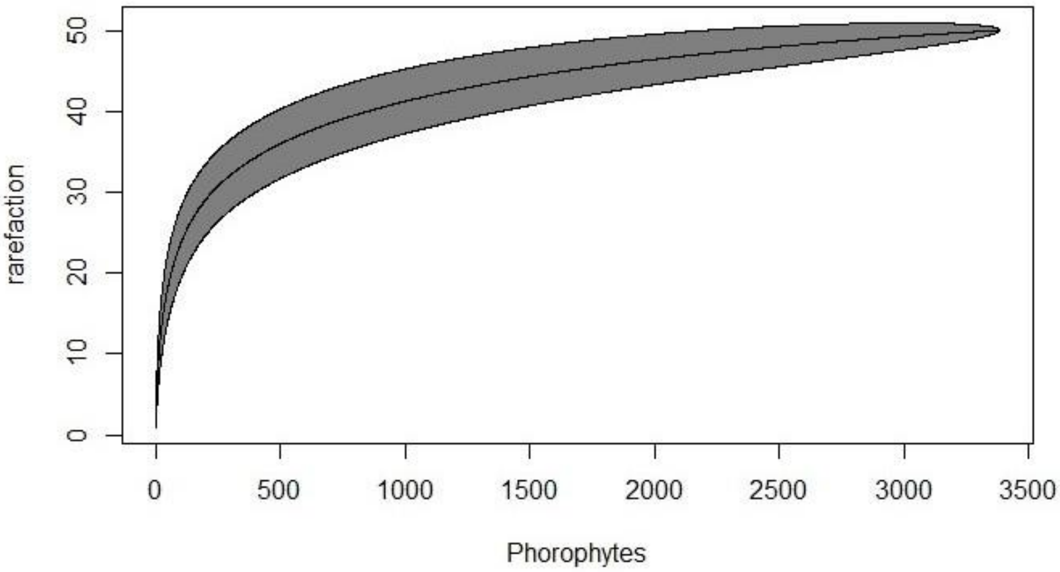
Appendix S6. Effect of forest structure on beta diversity, turnover, community heterogeneity and composition based on abundance data.

Supporting Information to the paper Clemente-Arenas, E. et al. What matters for hemiepiphytes in northeastern Amazonian forest? Effects of host size, soil and forest structure. Journal of Vegetation Science.

Appendix S1. Table representing species of hemiepiphytes

Family/Species	Abundance
Araceae	4314
Anthurium eminens	5
Anthurium moonenii	3
Anthurium pentaphyllum	10
Anthurium sinuatum	4
Anthurium sp.6	5
Anthurium sp.9	1
Heteropsis flexuosa	1034
Heteropsis steyermarkii	104
Heteropsis sp.3	2
Monstera adansonii	38
Monstera obliqua	5
Monstera spruceana	23
Philodendron atabapoense	12
Philodendron callosum	9
Philodendron cfrudgeanum	7
Philodendron cremersii	69
Philodendron duckei	45
Philodendron ecordatum	338
Philodendron guianense	102
Philodendron hylaeae	34
Philodendron linnaei	278
Philodendron megalophyllum	22
Philodendron melinonii	33
Philodendron ornatum	15
Philodendron panduriforme	48
Philodendron pedatum	137
Philodendron platypodum	917
Philodendron pulchellum	303
Philodendron quinquelobum	2

Philodendron solimoesense	21
Philodendron surinamense	361
Philodendron toshibae	2
Philodendron ushanum	258
Syngonium hastiferum	1
Syngonium podophyllum	1
Araceae sp.24	1
Araceae sp.27	7
Araceae sp.42	48
Araceae sp.46	2
Araceae sp.47	5
Araceae sp.48	1
Araceae sp.49	1
Clusiaceae	2
Clusia grandiflora	2
Cyclanthaceae	327
Evodianthus funifer	327
Marcgraviaceae	142
Marcgravia sp.1	53
Marcgravia sp.2	87
Marcgravia sp.3	2
Lomariopsidaceae	25
Lomariopsis sp.	25
Hymenophyllaceae	57
Trichomanes ankersii	57
Dryopteridaceae	11
Lomagramma guianensis	11
Total	4878

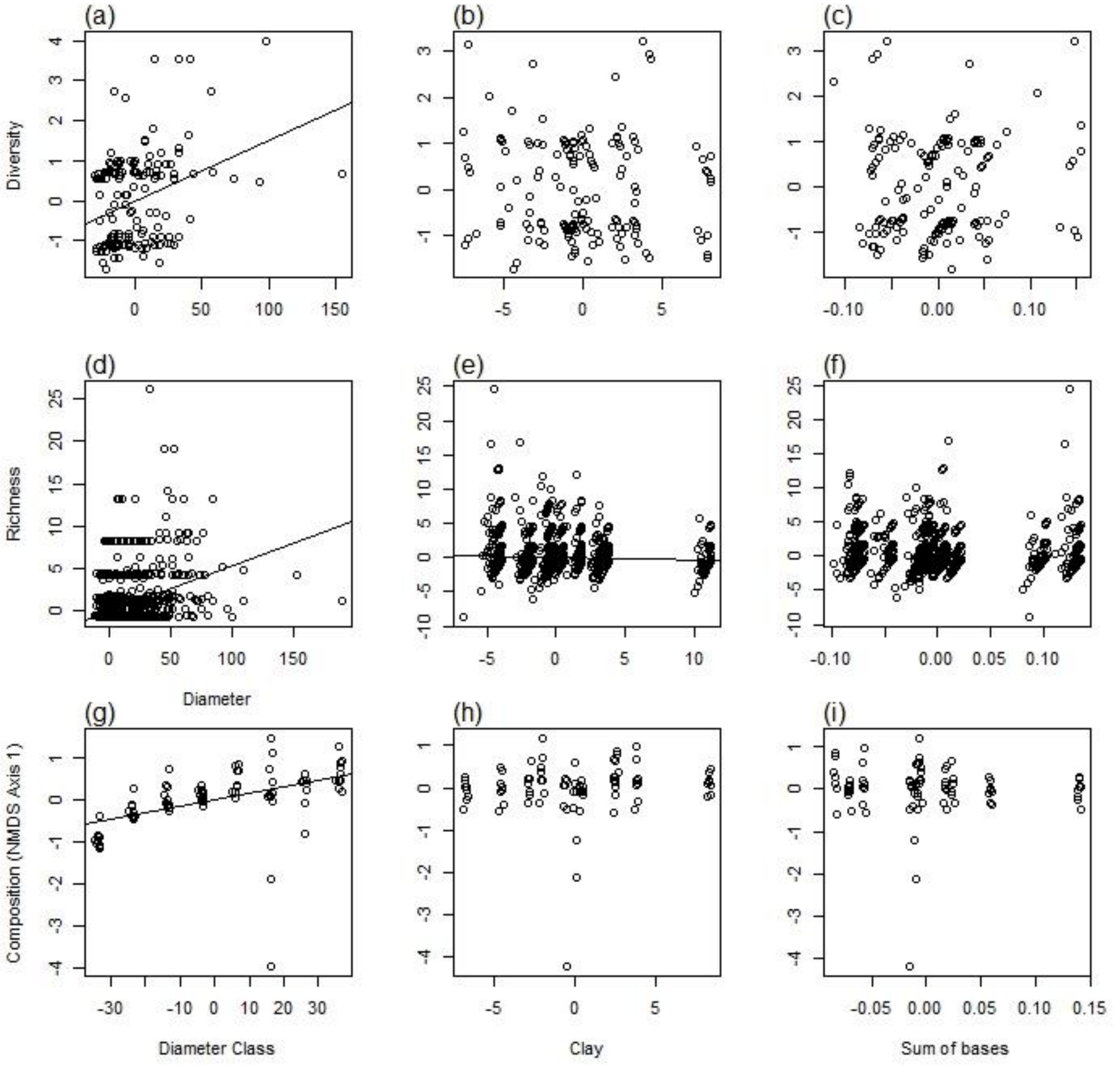


Appendix S2. Species accumulation curve of hemiepiphytes in Amapá National Forest

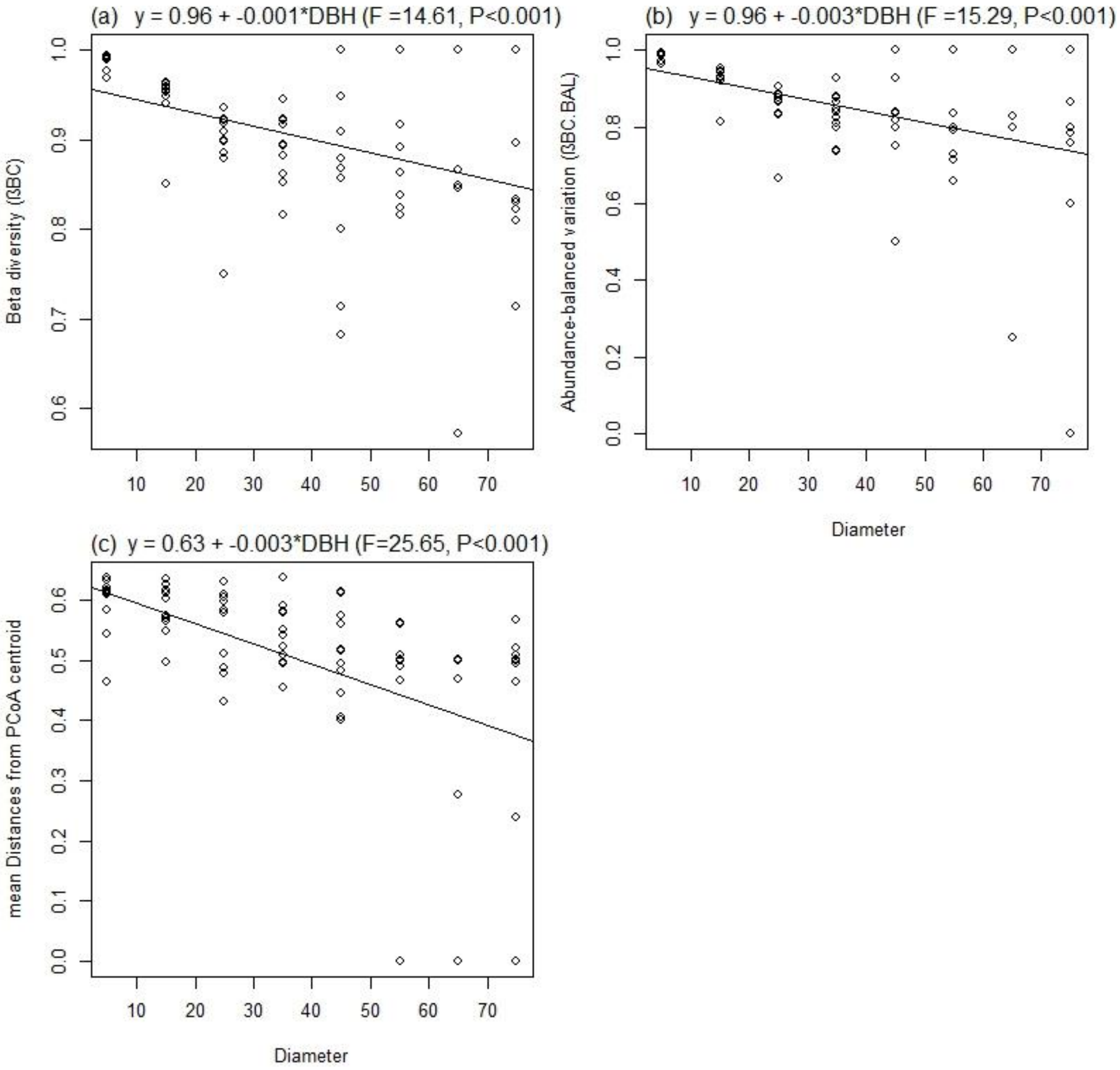
Appendix S3: Table of results of partial regressions testing the effects of host size (tree diameter), soil texture (clay) and fertility (sum of bases), on (upper) diversity} (Fisher´s Alpha), (center) richness (Chao Index), and composition.

	Partialcoefficients						
Dependentvariable	Intercept	Diameter	Clay	Sum of bases	F	R^2	P
Diversity	1.593**	0.015***	-0.023	1.697	8.73	0.148	<0.001
Richness	2.337***	0.053***	-0.033***	-0.378	222.7	0.165	<0.001
Composition (NMDS Axis 1)	-0.859	0.011**	0.021	-0.454	8.365	0.239	<0.001

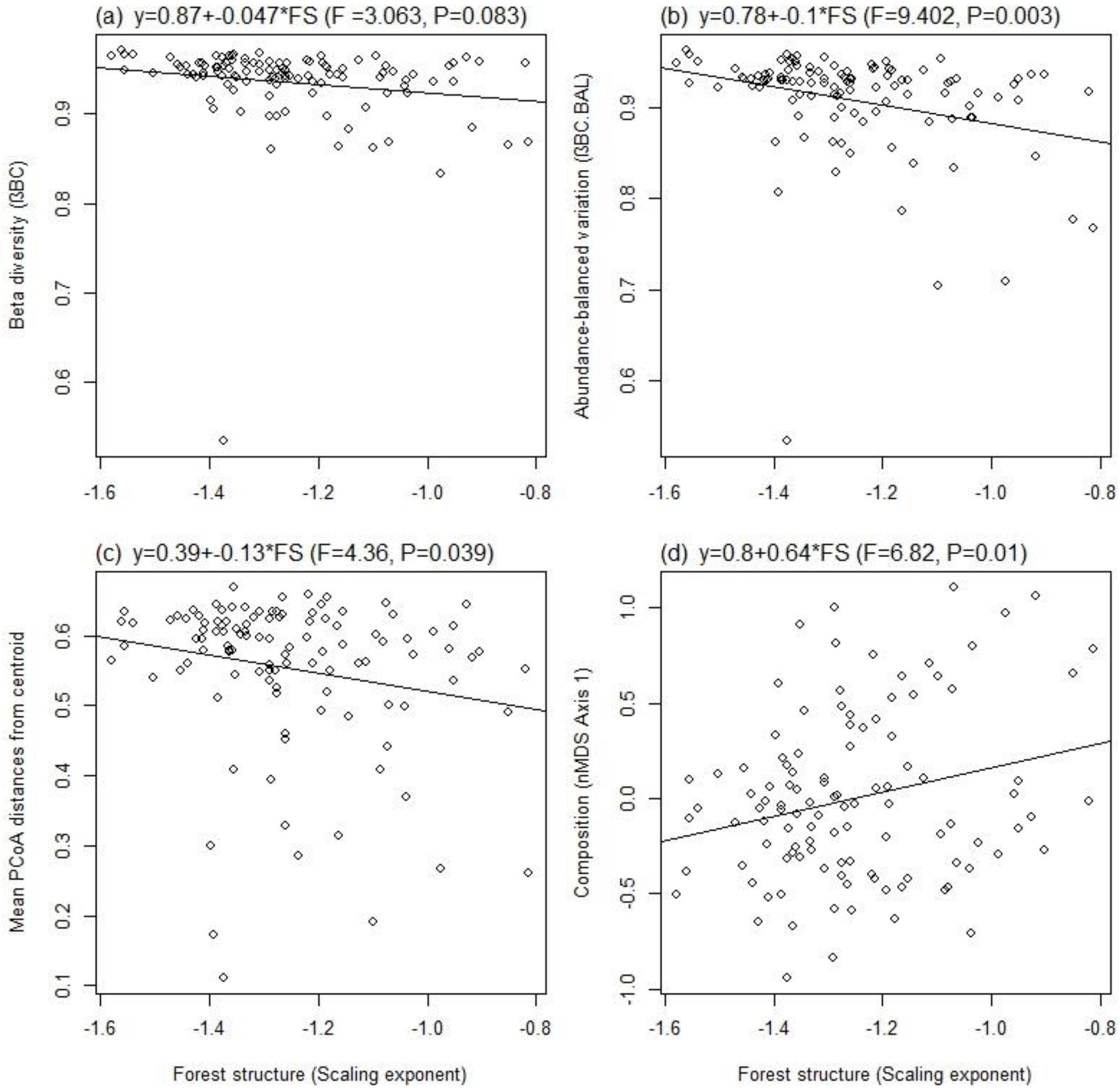
* P < 0.05, ** P < 0.01, *** P < 0.001



Appendix S4: Partial regressions testing the effects of host size (tree diameter), soil texture (clay) and fertility (sum of bases), on (upper) diversity (Fisher´s Alpha), (center) richness (Chao Index), and composition. Diversity and richness were analyzed at phorophyte level while composition was regressed at plot level. Lines denote significant partial regressions (see Appendix S3).



Appendix S5: Effects of host size (tree diameter) on (a) beta diversity (β_{BC}), (b) turnover of species as abundance balanced variation ($\beta_{BC.BAL}$) and (c) community heterogeneity represented by mean distances from PCoA centroid obtained based on abundance data at plot level.

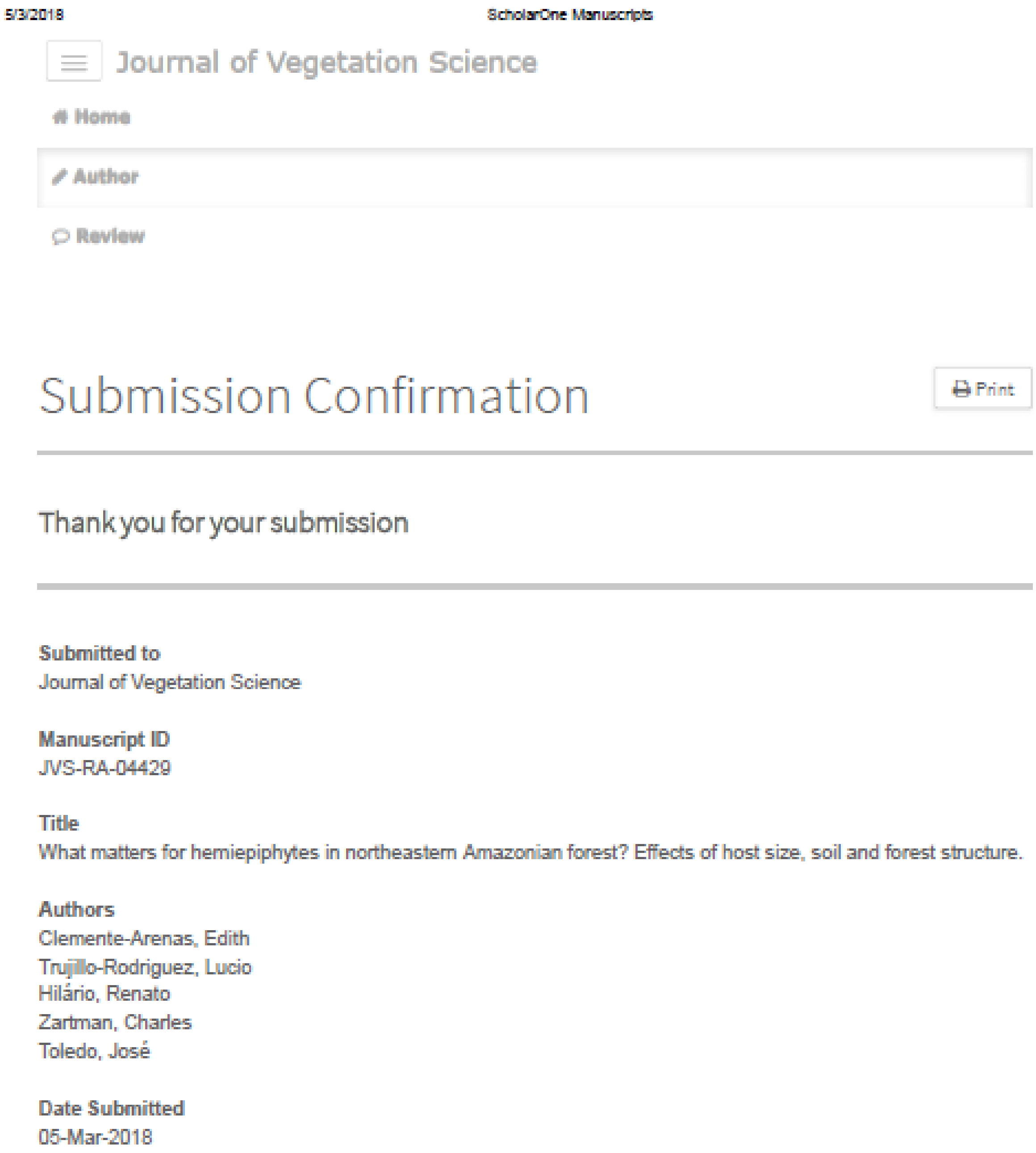


Appendix S6: Effects of forest structure represented by the scaling exponent of tree size-density distribution (FS) on (a) beta diversity (β_{BC}), (b) turnover of species as abundance balanced variation ($\beta_{BC.BAL}$), (c) community heterogeneity represented by mean distances from PCoA centroid and (d) composition obtained based on abundance data at plot level.

5. CONCLUSÕES

- O tamanho do hospedeiro e a estrutura da floresta foram preditores significativos das propriedades da comunidade de hemiepífitas.
- Uma alta diversidade alfa foi encontrada nos forófitos grandes provavelmente devido a uma maior disponibilidade de substrato e tempo para a colonização das hemiepífitas, enquanto a textura do solo foi umpreditor importante da composição de hemiepífitas, demostrando que o tipo de solo pode agir como um filtro, principalmente para lianas nômades as quais estão conectadas ao solo nos primeiros estádios do ciclo de vida.
- A diminuição da diversidade beta, substituição de espécies e heterogeneidade nas árvores grandes e manchas de floresta com alta proporção de árvores grandes sugere que a comunidade de hemiepífitas alcança um clímax com uma alta similaridade de espécies nas árvores maiores e manchas de florestas maduras.

6. ANEXO



5/3/2018 ScholarOne Manuscripts

Journal of Vegetation Science

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Thank you for your submission

Submitted to
Journal of Vegetation Science

Manuscript ID
JVS-RA-04429

Title
What matters for hemiepiphytes in northeastern Amazonian forest? Effects of host size, soil and forest structure.

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Date Submitted
05-Mar-2018