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ELINE TAINÁ GARCIA

DISTRIBUIÇÃO ESPACIAL DE BRIÓFITAS EM FLORESTAS OMBRÓFILAS NA AMAZÔNIA

Recife
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Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de Doutor(a) em Biologia Vegetal.

Área de Concentração: Ecologia e Conservação.

Orientadora: Profa. Dra. Kátia Cavalcanti Pôrto

Coorientadora: Profa. Dra. Sylvia Mota de Oliveira

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COMISSÃO EXAMINADORA

Profa. Dra. Kátia Cavalcanti Pôrto (Orientadora)
Universidade Federal de Pernambuco

Prof. Dr. Danilo Rafael Mesquita Neves (Titular Externo)
Universidade Federal de Minas Gerais

Profa. Dra. Adaíses Simone Maciel da Silva (Titular Externa)
Universidade Federal de Minas Gerais

Profa. Dra. Mércia Patrícia Pereira Silva (Titular Externa)
Universidade Federal de Pernambuco

Profa. Dra. Jarcilene Silva de Almeida Cortez (Titular Interna)
Universidade Federal de Pernambuco

Profa. Dra. Priscila Sanjuan de Medeiros Sarmento (Suplente Externa)
Instituto Tecnológico Vale

Prof. Dr. Antônio Fernando Morais de Oliveira (Suplente Interno)
Universidade Federal de Pernambuco

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que partiram este ano levando consigo um dos meus títulos
mais preciosos.
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quem sabe a vida
passeio urgente

quem sabe a vocação
sussurro do coração

quem sabe a coragem
vela para a viagem

(DAHMER, 2010)

RESUMO

A busca por explicações de padrões de distribuição, abundância e interações entre espécies, que resultam na distribuição espacial e na coexistência dos organismos, está no cerne dos estudos ecológicos. Este trabalho visou investigar como diferentes tipos de vegetação influenciam os atributos da comunidade (*i.e.* riqueza, diversidade, composição e proporção de espécies raras) e das espécies (*i.e.* gradiente vertical e guildas de tolerância à luminosidade) em assembleias de briófitas epífitas de três tipos de vegetação na Amazônia Oriental; e como esses atributos podem estar relacionados com os padrões de distribuição espacial das espécies em escala local. Nas vegetações de *Várzea*, de *Igapó* e de *Terra Firme* foram amostradas 24 árvores (oito por vegetação) e coletadas briófitas da base até a copa, em cinco zonas de altura. A composição, a riqueza, a diversidade, a distribuição de abundância e a proporção de espécies raras foram comparadas entre as vegetações e em relação à distribuição vertical ao longo dos forófitos arbóreos. Encontramos forte influência do tipo de vegetação e da zona de ocorrência no forófito na montagem de assembleias de briófitas promovendo variação, entre vegetações, de todos os atributos investigados. As florestas inundáveis diferem entre si em riqueza, diversidade, composição e gradiente vertical. *Igapó* apresentou a maior diversidade alfa e gradiente vertical mais evidente. *Terra Firme* representa um ambiente mais estável para o estabelecimento de briófitas que as florestas inundáveis. A *Várzea* apresentou composição de espécies mais homogênea e abundância semelhante à das outras duas vegetações, embora com menor riqueza e inexistência de gradiente vertical. Em escala local, as assembleias de briófitas epífitas são estruturadas principalmente em função do nicho das espécies. A riqueza, a diversidade e a similaridade foram maiores nas zonas extremas dos forófitos, enquanto que a distribuição das guildas explicou os principais padrões observados nas assembleias das vegetações. Na *Terra Firme* a maior diversidade foi encontrada no dossel externo; em *Várzea* e *Igapó* na base das árvores. Constatamos que além do nível de ocorrência (zona) no forófito o tipo de vegetação também regula a distribuição espacial de briófitas epífitas localmente, sendo as guildas de tolerância à luminosidade atributos importantes na explicação dos padrões de diversidade das espécies. Além disso, as características da vegetação afetam o gradiente vertical na composição de espécies, que pode ser inexistente mesmo em ambientes relativamente conservados, como na *Várzea*.

Palavras-chave: Diversidade alfa. Diversidade beta. Heterogeneidade Ambiental

ABSTRACT

The search for explanations of the patterns of distribution, abundance and interaction of species which rule their spatial distribution and coexistence is at the heart of ecological studies. This work aimed to investigate how different vegetation types influence the attributes of the community (richness, diversity, composition, and proportion of rare species) and of the species (vertical gradient and guilds of tolerance to light incidence) of epiphytic bryophyte assemblages in three vegetation types in the Eastern Amazon, and how such attributes may be related to the spatial distribution patterns of species on a local scale. Twenty-four trees were sampled *Várzea*, *Igapó* and *Terra Firme* vegetation (eight trees per vegetation type) and bryophytes were collected from the base to the top of the trees, in five zones. The composition, richness, diversity, abundance distribution, and proportion of rare species were compared between the vegetation type and along the vertical gradient in the hosts. We found strong influence of vegetation type and height zone in the host tree over the assemblage of bryophytes promoting variation of all attributes investigated across vegetation types. Flooded forests differed in richness, diversity, composition and vertical gradient. *Igapó* presented the highest alpha diversity and the most evident vertical gradient of bryophytes. In turn, *Terra Firme* represented a more stable environment for the establishment of bryophytes than the flooded forests. And *Várzea* presented a more homogeneous species composition and abundance similar to other vegetation types, although with lower richness and absence of vertical gradient. On a local scale, the epiphytic bryophyte assemblages were structured mainly according to the niche of the species. Richness, diversity and similarity were greatest between the extreme zones of the hosts, while the distribution of guilds explained the main patterns observed in the assemblages of the vegetation types. In *Terra Firme*, the greatest diversity was found in the outer canopy, while in *Várzea* and *Igapó*, it was found at the base of the trees. We observed that not only the zone of occurrence in the host tree, but also the vegetation type regulates the spatial distribution of epiphytic bryophytes at a local level, and the guilds of tolerance to light are important attributes in explaining important attributes in explaining the diversity patterns of the species. Furthermore, the characteristics of the vegetation types affect the vertical gradient in terms of species composition, which may be non-existent even in relatively conserved environments such as *Várzea*.

Keywords: Alpha diversity. Beta diversity. Environmental Heterogeneity.

LISTA DE FIGURAS

REVISÃO DE LITERATURA

HOW DOES EPIPHYTIC BRYOPHYTE DIVERSITY RESPOND TO DIFFERENCES IN THE VEGETATION OF EASTERN AMAZON?

VERTICAL GRADIENT OF EPIPHYTIC BRYOPHYTES IN THE AMAZON: THE RULE AND ITS EXCEPTION

LISTA DE TABELAS

HOW DOES EPIPHYTIC BRYOPHYTE DIVERSITY RESPOND TO DIFFERENCES IN THE VEGETATION OF EASTERN AMAZON?

VERTICAL GRADIENT OF EPYPHITIC BRYOPHYTES IN THE AMAZON: THE RULE AND ITS EXCEPTION

SUMÁRIO

1 INTRODUÇÃO

O que controla a diversidade alfa ou o número de espécies que podem coexistir em pequenas escalas espaciais é uma questão chave em ecologia. As florestas tropicais úmidas constituem os ambientes terrestres mais diversificados do globo abrigando inúmeras formas de crescimento vegetal que inclui ervas, arbustos, árvores, cipós, epífitas e plantas parasitas (RICHARDS, 1952). A composição e a variabilidade espacial da estrutura florestal alteram o microclima nesses ambientes (PARKER, 1995) e consequentemente a distribuição vertical de epífitas (ALLEE, 1926; CORNELISSEN; TER STEEGE, 1989; OLIVEIRA *et al.*, 2009).

Nesse contexto, as briófitas persistem ao longo do tempo devido a sua adaptação para ocupar uma gama de substratos que reflete na ampla distribuição biogeográfica do grupo (GRADSTEIN; CHURCHILL; SALAZAR-ALLEN, 2001). Essas plantas apresentam elevado potencial de dispersão e predominância de padrão determinístico baseado no nicho das espécies (OLIVEIRA *et al.*, 2009; SANTOS *et al.*, 2011), relacionado a restrições a condições ambientais que envolvem luminosidade, umidade e temperatura (RICHARDS, 1984). Esses fatores podem ser bastante limitantes em florestas tropicais a depender do microhabitat ocupado, como por exemplo, a menor luminosidade no subbosque (BRENES-ARGUEDAS *et al.*, 2011). Estudos apontam que ambientes heterogêneos tendem a abrigar uma elevada riqueza (ALLOUCHE *et al.*, 2012; STEIN; GERSTNER; KREFT, 2014), tanto pela complementaridade de nicho quanto pela exclusão competitiva, que favorecem a coocorrência de espécies (LEVINE; HILLERISLAMBERS, 2009; VELLEND, 2010; HILLERISLAMBERS *et al.*, 2012).

Diferentemente de outros grupos, estas plantas apresentam inúmeras estratégias que as permitem contornar o princípio da exclusão competitiva (SLACK, 1977, 1982; DURING, 1979; WATSON, 1980, 1981), a exemplo das espécies fugitivas (GLIME, 2017). Por essa razão, muitos trabalhos utilizam esse grupo como modelo para avaliar os efeitos de filtros ambientais sobre montagem de comunidades (SANTOS *et al.*, 2014; BATISTA; SANTOS, 2016; AMORIM *et al.*, 2017; PEÑALOZA-BOJACÁ *et al.*, 2018), uma vez que sua ocorrência reflete majoritariamente o nicho fundamental (SLACK, 1977) e o potencial de dispersão dos táxons (SANTOS *et al.*, 2014).

Estudos que possuem como objetivo entender regras de montagem de comunidades em florestas tropicais envolvem variações em condições ambientais nos habitats que influenciam padrões na distribuição das espécies. Na Amazônia ocorrem diversos gradientes como os de inundação e lençol freático (JUNK; PIEDADE, 2011; SCHIETTI *et al.*, 2014), ou ainda, variação em microescala, de luz e umidade relativa, do sub-bosque até o dossel da floresta (MAGALHÃES; MARENCO; CAMARGO, 2014) e outros (*e.g*. TUOMISTO *et al.*, 2002; TUOMISTO; ZUQUIM; CÁRDENAS, 2014; OLIVEIRA; TER STEEGE, 2015), que influenciam a diversidade de plantas em diferentes escalas. Apenas estudos pontuais compararam a riqueza e a composição de briófitas em diferentes habitats nessa região (BENAVIDES; IDARRAGA; ALVAREZ, 2004; BENAVIDES *et al.*, 2006; LOPES *et al.*, 2016; CERQUEIRA; ILKIU-BORGES; FERREIRA, 2017). Esses resultados contribuem para o conhecimento da brioflora, mas subestimam a diversidade que pode estar associada a variedade de ambientes que compõem o mosaico amazônico por serem restritos à brioflora do subbosque.

As vegetações de Terra Firme, Várzea e Igapó compõem a maior parte dos ecossistemas amazônicos (PIRES; PRANCE, 1985) e constituem um importante modelo de heterogeneidade a ser testado. As florestas de Terra Firme recobrem cerca de 90% da Amazônia, sobre terrenos, em geral, abaixo de 100 m, mas podendo se extender até mais de 200 m, vegetações densas ou abertas, com árvores altas, elevada riqueza de espécies por área, solo sombreado, rápida ciclagem de nutrientes e matéria orgânica, e sub-bosque com arbustos, lianas e uma cobertura vegetal no solo a depender da entrada de luz (PIRES; PRANCE, 1985). As vegetações inundáveis ocupam uma área de aproximadamente 20%, da Amazônia (JUNK *et al.,* 2011). As Várzeas caracterizam-se pela alta fertilidade dos solos que reflete a deposição de sedimentos por suas águas brancas ou barrentas (MELACK; HESS, 2010), enquanto a vegetação de Igapó é banhada por rios de água preta ou clara, com baixa carga de nutrientes, de pH ácido, que associados com a baixa fertilidade do solo caracterizam essa vegetação (JUNK *et al.*, 2012). A brioflora das planícies amazônicas é caracterizadas por baixo endemismo, predominância de espécies generalistas e de amplos padrões fitogeográficos (GRADSTEIN; CHURCHILL; SALAZAR-ALLEN, 2003). Estudos prévios em floresta de Terra Firme descreveram a brioflora epífita com um gradiente vertical na composição de espécies, que se mantém tanto em escala local quanto regional, com predomínio de táxons generalistas e maior riqueza de espécies raras (baixa frequência) (TAVARES, 2009; OLIVEIRA *et al.*, 2009; OLIVEIRA; TER STEEGE, 2015).

Devido à importância dos gradientes ambientais e das variações nas condições abióticas dos habitat nos quais as briófitas ocorrem na Amazônia vastamente documentada (ACEBEY; GRADSTEIN; KRÖMER, 2003; OLIVEIRA *et al.*, 2009; SPORN *et al.*, 2010; TAVARES-MARTINS; LISBOA; COSTA, 2014; OLIVEIRA; TER STEEGE, 2015) investigar como a heterogeneidade ambiental associada a diferentes tipos de vegetação atua sobre essas plantas pode nos ajudar a compreender o que as tem tornado raras em florestas de planície (OLIVEIRA; TER STEEGE, 2013).

Nesse contexto, essa tese foi norteada pela seguinte questão: Como diferentes tipos de vegetação influenciam a estrutura de assembleias de briófitas epífitas em escala local na Amazônia e qual a relevância dessa heterogeneidade para a distribuição espacial das espécies? Nossa principal hipótese de trabalho previa que as diferentes vegetações promoveriam heterogeneidade ambiental para as epífitas, modificando os atributos de comunidade e das espécies em função da preponderância das restrições de nicho sobre a distribuição das briófitas. Desse modo, os dados aqui apresentados visam preencher lacunas relacionadas aos aspectos da distribuição de briófitas epífitas em vegetações inundáveis, sobretudo da brioflora de dossel, comparando com padrões já observados em escalas local e regional em Terra Firme.

Assumindo que a brioflora epífita na região da bacia Amazônica constitui uma metacomunidade em vegetação de Terra Firme (OLIVEIRA; TER STEEGE, 2015), com a intenção de reduzir o efeito da limitação de dispersão definiu-se uma pequena escala geográfica (Local) para analisar, como a distribuição espacial das espécies está associada à diferentes habitats adjacentes (escala de paisagem) e influencia a raridade local das briófitas, com ênfase, na tolerância ambiental das espécies (BARBÉ; FENTON; BERGERON, 2016).

Os resultados encontrados estão apresentados nos itens 3.1 e 3.2 deste manuscrito organizados segundo as normas dos periódicos para os quais foram submetidos. No primeiro, investiga-se a influência da estrutura das vegetações nos atributos de comunidade (riqueza, diversidade, composição e proporção de espécies raras) comparando-os entre as vegetações. No segundo, analisa-se a influência das vegetações nos atributos de comunidade (riqueza, diversidade, composição) e das espécies (distribuição vertical e guildas de tolerância) comparando assembleias das zonas de altura dentro e entre vegetações. Os resultados poderão subsidiar não apenas estratégias de conservação de espécies mais suscetíveis ao desaparecimento, quanto predições sobre aquelas mais tolerantes às alterações nos habitats.

1.1 OBJETIVOS

1.1.1 Objetivo Geral

Investigar como diferentes tipos de vegetação influenciam os atributos da comunidade (*i.e.* riqueza, diversidade, composição e proporção de espécies raras) e das espécies (*i.e.* gradiente vertical e guildas de tolerância à luminosidade) em assembleias de briófitas epífitas de três tipos de vegetação na Amazônia Oriental; e como esses atributos podem estar relacionados com os padrões de distribuição espacial das espécies em escala local.

1.1.2 Objetivos Específicos

a) Analisar como a heterogeneidade ambiental, promovida por diferentes tipos de vegetação (Terra Firme, Igapó e Várzea), influencia os atributos de comunidade (riqueza, diversidade, composição e abundância) de briófitas epífitas na FLONA de Caxiuanã (Item 3.1).

b) Investigar como a mudança na paisagem (tipo de vegetação) e a zona de altura influenciam atributos de comunidade (riqueza, diversidade e composição) e das espécies (gradiente vertical e guildas de tolerância) na distribuição vertical de briófitas epífitas (Item 3.2).

2 REVISÃO DE LITERATURA

2.1 DISTRIBUIÇÃO ESPACIAL E MONTAGEM DE COMUNIDADES VEGETAIS

À ecologia de comunidades compete à busca por explicações dos padrões de distribuição, abundância e interações entre espécies (LEIBOLD *et al.*, 2004) sendo a distribuição e a coexistência dos organismos respostas à combinação de fatores históricos, ecológicos e evolutivos (WARREN *et al.*, 2014). Além destes fatores, as comunidades vegetais, têm a sua composição de espécies resultante da interação de filtros ambientais, limitação de dispersão e eventos estocásticos (OLIVEIRA; TER STEEGE, 2015).

Tradicionalmente, a montagem de comunidades está relacionada com processos determinísticos de nicho envolvendo filtragem abiótica ou competição interespecífica (CAVENDER-BARES *et al.*, 2009), sustentados pela diferenciação ecológica entre espécies, que fundamenta a Teoria de Nicho (HUTCHINSON, 1957). No entanto, com o advento da Teoria Neutra da Biodiversidade e Biogeografia (HUBBELL, 2001), processos estocásticos de dispersão, extinção e especiação ganharam espaço, principalmente como mecanismos alternativos que assumem equivalência ecológica entre indivíduos de diferentes espécies. O embate conceitual e prático entre essas teorias tem derivado os principais avanços no desenvolvimento de abordagens e inferências teóricas sobre a montagem de comunidades (CAVENDER-BARES *et al.*, 2009). Assim, a distribuição das espécies seria controlada por processos: 1) determinísticos, sendo desigual e delimitada por filtros ambientais (HUTCHINSON, 1957; TUOMISTO; RUOKOLAINEN; YLI-HALLA, 2003) e 2) estocásticos, onde a distribuição é aleatória embora, dependente espacialmente em consequência da limitação de dispersão (HUBBELL, 2001). No entanto, esses processos nas montagens de comunidades podem não ser totalmente excludentes (KEMBEL, 2009; LALIBERTÉ *et al.*, 2009).

Entre as quatro perspectivas de metacomunidade identificadas por Leibold *et al.* (2004), estão a perspectiva do modelo neutro, relacionado à teoria Neutra de Hubbell (2001) e a perspectiva de “arranjo de espécies” (“Sorting-Species”/SS), que está intimamente relacionada à teoria de nicho, a qual pressupõe a interação entre a heterogeneidade ambiental, as diferenças de nicho das espécies e as taxas de dispersão adequadas. Uma metacomunidade pode ser definida como um conjunto de comunidades locais conectadas pela dispersão de indivíduos de diferentes espécies, as quais interagem entre elas e o arcabouço teórico para seu estudo é fortemente influenciado por ideias sobre dinâmicas de metapopulações (LEIBOLD *et al.*, 2004; VELLEND, 2010). Um importante conceito que pode ser associado à dinâmica de metacomunidades é o de “*pool* regional de espécies” (*i.e.* conjunto) que compreende todas as espécies disponíveis para dispersar e colonizar um determinado local (CORNELL; HARRISON, 2014), embora em ecologia de comunidades, dinâmicas locais e regionais sejam interdependentes (LEIBOLD *et al.*, 2004). Nesse contexto, as comunidades biológicas seriam estruturadas tanto por colonização de espécies estrangeiras quanto por especiação, ambas podendo levar a padrões de distribuição não aleatórios de espécies em uma paisagem (WARREN *et al.*, 2014). Assim, a montagem de comunidades refere-se em síntese a qualquer processo que impõe restrições a um banco regional de táxons ("*pool*" de espécies), limitado por um conjunto de filtros (WEIHER *et al.*, 2011; HILLERISLAMBERS *et al.*, 2012) que determinam a coexistência de espécies formando as comunidades locais (WEIHER *et al.*, 2011; GÖTZENBERGER *et al.*, 2012; MENEZES; MARTINS; ARAÚJO, 2016).

Uma antiga lei em ecologia prevê que cada comunidade exibe muitas espécies raras e apenas algumas espécies comuns. A distribuição de abundância de espécies (SAD) descreve a abundância de cada espécie em uma comunidade e os diferentes tipos de SADs podem ser eficientes para descrever padrões de diversidade, relações com a heterogeneidade espacial (MCGILL *et al.*, 2007; HSIAO-PEI *et al.*, 2015) e como as espécies particionam recursos nos habitats (SUGIHARA *et al.*, 2003). Gradientes ambientais e habitats sob diferentes condições podem fornecer abordagens empíricas promissoras e uma base comparativa para SADs (MCGILL *et al.*, 2006; SILVA; CIANCIARUSO; BATALHA, 2010). Entre os vários modelos propostos para explicar distribuições de abundância em comunidades biológicas, estão o logseries e o lognomal, que fazem previsões distintas sobre a proporção de espécies raras (MCGILL *et al.*, 2007). O modelo lognormal está associado à conjuntos de espécies não perturbados e mais uniformes, com maior equidade na distribuição de abundâncias e por isso baixa proporção de espécies raras, enquanto o logseries descreve uma proporção maior, onde existem altas taxas de imigração e extinção local ou conjuntos sob efeito de perturbação (MAGURRAN; HENDERSON, 2003; MAGURRAN, 2004). É importante ressaltar que a semelhança no padrão não implica uma resposta a um mesmo mecanismo (MCGILL *et al.*, 2007). No entanto, dados empíricos para grandes conjuntos de diferentes linhas sustentam que comunidades mais abertas à imigração exibirão maior proporção de espécies raras (HUBBELL, 2001; MAGURRAN; HENDERSON, 2003; MAGURRAN, 2004; MCGILL *et al.*, 2007).

A elevada riqueza de espécies raras e/ou endêmicas é comum em ambiente tropical, o que as torna muito sensíveis às alterações nos habitats. Na Amazônia esse padrão é reportado para diversos grupos incluindo a comunidades de árvores (TER STEEGE *et al.*, 2013) e de briófitas epífitas em Terra Firme (OLIVEIRA; TER STEEGE, 2013). No entanto, há diferentes tipos de raridade de espécies de briófitas que variam de acordo com as escalas local e regional (core: regionalmente frequente e localmente abundante; rural: regionalmente frequente e localmente rara; urbana: regionalmente esparsa e localmente abundante; ou satélite: regionalmente esparsa e localmente rara) (SÖDERSTRÖM, 1989; SÖDERSTRÖM; DURING, 2005). Talvez por essa razão, espécies de florestas de planície que frequentemente exibem amplos padrões fitogeográficos (SCHUSTER, 1983; SANTOS; COSTA, 2010) possam ser raras nesses ambientes, uma vez que, a distribuição e a raridade de uma espécie estão intimamente ligadas a sua habilidade de dispersão (PÔRTO; SILVA, 2012). De acordo com Barbé, Fenton e Bergeron (2016), na dinâmica de metacomunidades de briófitas a tolerância ambiental das espécies durante o estabelecimento, aliada à capacidade de produzir grandes quantidades de esporos podem ser filtros mais importantes do que a distância de dispersão.

Informações derivadas da dinâmica de populações explicam padrões na dispersão de briófitas considerando que as abundâncias das populações variam com a distribuição espacial do habitat e as características das espécies (LÖBEL; SNÄLL; RYDIN, 2006; JOHST *et al.*, 2011). Em florestas de Terra Firme, estudos sobre dinâmicas de populações de briófitas concentraram-se em entender a influência de paisagens fragmentadas em assembleias de epífilas (*i.e.* estabelecem-se sobre folhas) em escala local, concluindo haver um declínio na diversidade de briófitas em pequenos fragmentos (<10-ha) (ZARTMAN; NASCIMENTO, 2006); baixa riqueza e diferenças na composição de espécies de fragmentos jovens (<25 anos) comparados à habitats contínuos (PHARO; LINDENMAYER; TAWS, 2004). Segundo Pharo e Zartman (2007), muitas briófitas provavelmente não se dispersam rotineiramente mais do que algumas dezenas de metros, e nesse contexto, a configuração espacial dos fragmentos e a qualidade da matriz, são fundamentais para a estrutura de comunidade e a dinâmica populacional. Quanto grupo biológico é importante ressaltar que as briófitas são cosmopolitas, no sentido de que ocorrem em todos os ambientes, exceto o marinho (GRADSTEIN; CHURCHILL; SALAZAR-ALLEN, 2001). Além disso, são plantas consideradas dispersoras superiores (TER STEEGE, 2010) por possuírem diversos mecanismos que permitem dispersão à curta e longas distâncias (TAN; PÓCS, 2000). Apesar dessas característisticas quando enfatizadas as espécies, percebe-se uma forte dependência de nicho determinando a presença destas nos microhabitats (OLIVEIRA; TER STEEGE, 2015).

A colonização de novos habitats por briófitas pode ser afetada por reduções no potencial de dispersão ou alterações na qualidade do substrato (PHARO; ZARTMAN, 2007). A tolerância ao microhabitat que caracteriza as guildas de tolerância (especialistas de sol, de sombra e generalistas) é determinada de acordo com a altura de ocorrência em um forófito arbóreo, considerando-se as variações microclimáticas (gradiente vertical) de umidade e temperatura (PÓCS, 1982; RICHARDS, 1984). Há indícios de que os táxons mais generalistas apresentam melhor efetividade de dispersão que os especialistas (VAN ZATEN; PÓCS, 1981; VAN ZATEN; GRADSTEIN, 1988). Os dados de Silva (2013) corroboram esta premissa, uma vez que todas as espécies abundantes, local e regionalmente, registradas em seu estudo, também eram generalistas quanto ao microhabitat. A predominância de generalistas foi documentada para epífitas com padrões que suportam a regulação da distribuição das espécies por meio de mecanismos determinísticos e estocásticos. Em escala local, as assembleias são reguladas pelo gradiente microclimático ao longo de forófitos arbóreos (OLIVEIRA *et al.*, 2009) e regionalmente, se observa também a influência da elevação e da temperatura (OLIVEIRA; TER STEEGE, 2015), embora, ao longo da bacia Amazônica a composição de espécies seja similar e, por isso, considerada uma metacomunidade (OLIVEIRA; TER STEEGE, 2013).

2.2 DIVERSIDADE BETA E HETEROGENEIDADE AMBIENTAL

A diversidade engloba dois componentes, a variedade e a abundância de espécies (MAGURRAM, 1988). Várias hipóteses, com diferentes mecanismos são utilizadas nas tentativas de explicar os padrões de diversidade no globo (*e.g.* área, fatores históricos, energia disponível, estabilidade ambiental, perturbação e interações ecológicas/biológicas) (WHITTAKER; WILLIS; FIELD, 2001). Entender os mecanismos que atuam nos processos gerando padrões de riqueza e diversidade dos organismos tem concentrado o esforço de muitos pesquisadores.

A diversidade beta corresponde a extensão da mudança na composição da comunidade, ou grau de diferenciação da comunidade, em relação a um gradiente ambiental complexo, ou um padrão de ambientes (WHITTAKER, 1960). Mais precisamente, ela quantifica o número de comunidades existentes em uma região (BASELGA, 2015) e pode refletir dois fenômenos, aninhamento e substituição ("*turnover*") espacial de espécies (HARRISON; ROSS; LAWTON, 1992; BASELGA; JIMÉNEZ-VALVERDE; NICCOLINI, 2007). O aninhamento ocorre quando biotas de locais com baixas riquezas são subconjuntos de biotas mais ricas de outro local (ULRICH; GOTELLI, 2007) refletindo um processo de perda de espécies, causado por um fator que promove a desagregação ordenada de assembleias. A substituição espacial implica na troca entre assembleias como consequência de seleção ambiental, ou restrições espaciais e históricas (BASELGA, 2010). Dessa forma, a diversidade beta pode não apenas nos informar sobre como a composição de espécies varia entre locais ou regiões em respostas a mudanças ambientais (TUOMISTO; RUOKOLAINEN, 2006), como também, fornecer inferências sobre quais espécies podem ser consideradas generalistas ou especialistas nos habitats e ainda, sobre semelhanças e diferenças de habilidades competitivas (PINEL-ALLOUL *et al.*, 2013).

A Heterogeneidade Ambiental (HA) favorece a diversidade garantindo coexistência e persistência de espécies pelo aumento da disponibilidade de nicho espacial ao longo de gradientes ambientais e diferentes tipos de habitats, que podem constituir refúgios diante de condições adversas e favorecer eventos de especiação, em resposta ao isolamento ou adaptação às condições ambientais distintas (STEIN; GERSTNER; KREFT, 2014). A HA, definida de uma maneira simplificada englobaria complexidade, diversidade, estrutura ou variabilidade nos ambientes, sendo considerada um preditor universal para riqueza de espécies (STEIN; KREFT, 2015).

2.3 GRADIENTES AMBIENTAIS E DIVERSIDADE DE BRIÓFITAS NA AMAZÔNIA

Nas florestas tropicais úmidas, as briófitas são principalmente epífitas (GRADSTEIN, 1992), e a elevada diversidade do grupo tem sido creditada à heterogeneidade ambiental (SHAW; SZÖVÉNYI; SHAW, 2011). Ao longo da Bacia na Amazônica ocorrem diferentes tipos de vegetação, desde abertas como as campinaranas e savanas, até densamente florestadas, como a floresta de Terra Firme e as vegetações inundáveis de Várzea e Igapó (PIRES; PRANCE, 1985). As florestas inundáveis possuem composição florística distinta devido à taxa de sedimentação e a disponibilidade de nutrientes (FERREIRA *et al.*, 2013) oriundos de diferentes origens geológicas (KEEL; PRANCE, 1979; FERREIRA; ALMEIDA; PAROLIN, 2010). As áreas ocupadas pelas vegetações inudáveis de Várzea e Igapó são repectivamente estimadas em, 300.000 km^2 e 180.000 km^2 (MELACK; HESS, 2010). Devido à extensão, representatividade e facilidade de acesso da vegetação de Terra Firme, os estudos sobre a diversidade de plantas na região têm se concentrado nesse ambiente, especialmente sobre a comunidade arbórea (TER STEEGE *et al.*, 2006, 2013). Nesta vegetação, um gradiente vertical na composição de briófitas epífitas tem sido frequentemente reportado em escalas locais e regionais, onde predominam táxons generalistas e há maior riqueza de táxons raros (baixa frequência) (OLIVEIRA *et al.*, 2009; OLIVEIRA; TER STEEGE, 2013; OLIVEIRA; TER STEEGE, 2015). Por outro lado, dados sobre a diversidade e a distribuição de briófitas epífitas em florestas inundáveis ainda são escassos e pontuais.

As briófitas são plantas avasculares que possuem a fase gametofítica como dominante no ciclo de vida e não apresentam cutícula epidérmica (SHAW, GOFFINET, 2000; GRADSTEIN; CHURCHILL; SALAZAR-ALLEN, 2001). Esses organismos são susceptíveis às flutuações e alterações ambientais, em função de suas particularidades morfofisiológicas e ocupam microhabitats e microclimas muito específicos (SCHOFIELD, 1985; GRADSTEIN *et al.*, 1996; HALLINGBÄCK; HODGETTS, 2000; GRADSTEIN; CHURCHILL; SALAZAR-ALLEN, 2001). Se comparadas às plantas de grande porte, a natureza poiquilohídrica das briófitas as torna eficientes no tocante a captação de água (PROCTOR, 2014) permitindo-lhes ocorrer em diferentes substratos e ambientes. Essas características explicam, em parte, os padrões não uniformes de distribuição da brioflora em florestas tropicais, onde há um incremento na biomassa e na diversidade com o aumento da altitude (PÓCS, 1982). Por sua vez, em áreas de planície, uma das hipóteses que explicaria a baixa cobertura de briófitas seria o efeito de temperaturas elevadas no balanço de carbono das espécies (WAGNER; ZOTZ; BADER, 2014).

Na Amazônia Oriental, estudos recentes reportaram padrões de riqueza e diversidade de briófitas contrastantes com os documentados para plantas vasculares ao longo da Bacia Amazônica. Um exemplo é o padrão de maior riqueza de espécies em Várzea que no Igapó (JUNK *et al.*, 2015), que não se manteve para briófitas, embora os estudos tenham reportado floras distintas entre elas (LOPES *et al.*, 2016; CERQUEIRA; ILKIU-BORGES; FERREIRA, 2017). Esses resultados contribuem para o conhecimento da brioflora, mas subestimam a diversidade que pode estar associada, por exemplo, ao dossel, tendo em vista que os estudos prévios foram baseados exclusivamente em dados de sub-bosque. O dossel tem sido responsável por abrigar parte considerável da riqueza de briófitas em habitats de Terra Firme (TAVARES, 2009; OLIVEIRA *et al.*, 2009; OLIVEIRA; TER STEEGE, 2015). Essas plantas possuem elevado potencial de dispersão e tem sua ocorrência fortemente influenciada pelo nicho das espécies (OLIVEIRA *et al.*, 2009; SANTOS *et al.*, 2011). Diferentemente de outros grupos, estas plantas apresentam inúmeras estratégias que as permitem contornar o princípio da exclusão competitiva (SLACK, 1977, 1982; DURING, 1979; WATSON, 1980, 1981). Por essa razão, podem ser bons modelos para avaliar como filtros ambientais atuam na montagem de comunidades, uma vez que sua ocorrência reflete majoritariamente o nicho fundamental (SLACK, 1977) e o potencial de dispersão dos táxons (SANTOS *et al.*, 2014).

2.4 PROCEDIMENTOS METODOLÓGICOS

As amostragens de material foram feitas para garantir que os objetivos dos trabalhos fossem alcançados, em duas escalas: a primeira delas utilizado o forófito como amostra considerando-se a distribuição entre vegetações (Item 3.1); a segunda avaliando diferentes estratos (zonas) do forófito (distribuição vertical), entre e dentro das vegetações (Item 3.2), sendo a amostra um conjunto de quatro plots de 10 cm² (40 cm²) (Figura 1).

As amostras botânicas foram coletadas em cinco zonas estabelecidas da base ao dossel, compreendendo: Zona 1 = da base até 1 m de altura; Zonas 2 e 3 = tronco inferior e superior; Zona 4 = base da copa; e Zona 5 = ramos e folhas do dossel expostos à luz solar (dossel externo). Em cada vegetação foi escolhida uma espécie arbórea, abundante, com casca de rugosidade intermediária e altura estimada em até 25 m. No total, 24 árvores foram amostradas, oito em cada vegetação.

Os forófitos foram identificados com uma fita de TNT e tiveram mensurados a altura do fuste e o DAP, enquanto a altura do dossel foi estimada visualmente. A primeira etapa das coletas consistiu na seleção e coletas de amostras (Zona 1-3) com auxílio de uma escada de 6m. Posteriormente, um método de acesso com cordas permitu a coleta de amostras das zonas mais altas, que incluíram os galhos das árvores expostos ao sol. Uma linha de nylon foi lançada por meio de estilingue e chumbada, para que atravessasse entre ramos que garantissem a sustentação do coletor, a linha foi substituída por um fio e em seguida pelas cordas. Na extremidade foi acoplada uma cadeira de base de madeira, sobre a qual o coletor se instalava munido de sacos de coleta, facão e equipamentos de segurança, os detalhes podem ser observados na Figura 2.

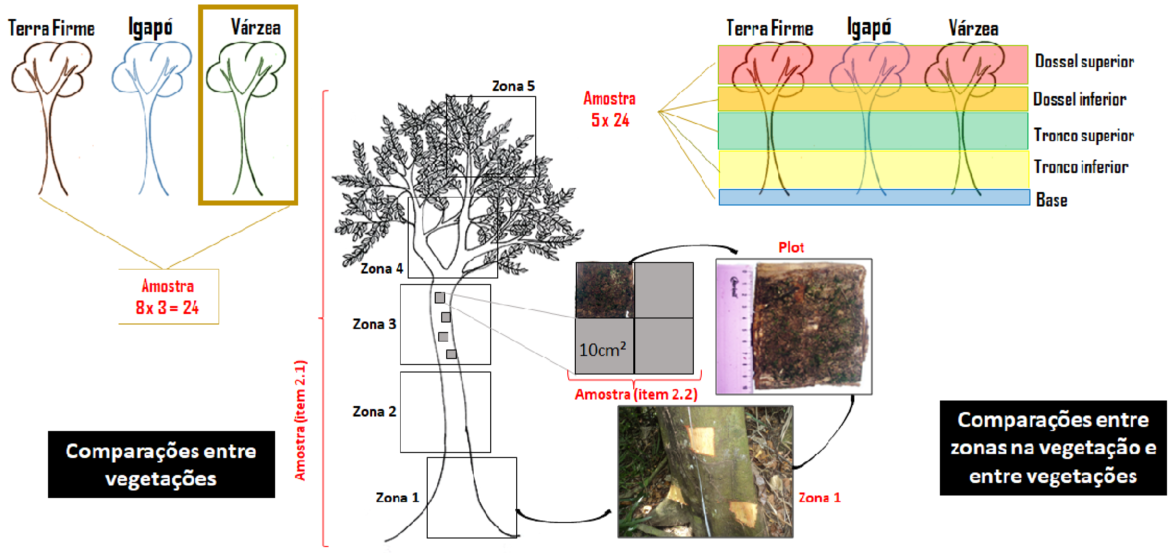

Figura 1. Esquema da amostragem e escala de análise para cada item dos resultados dessa tese (Itens 3.1 e 3.2).

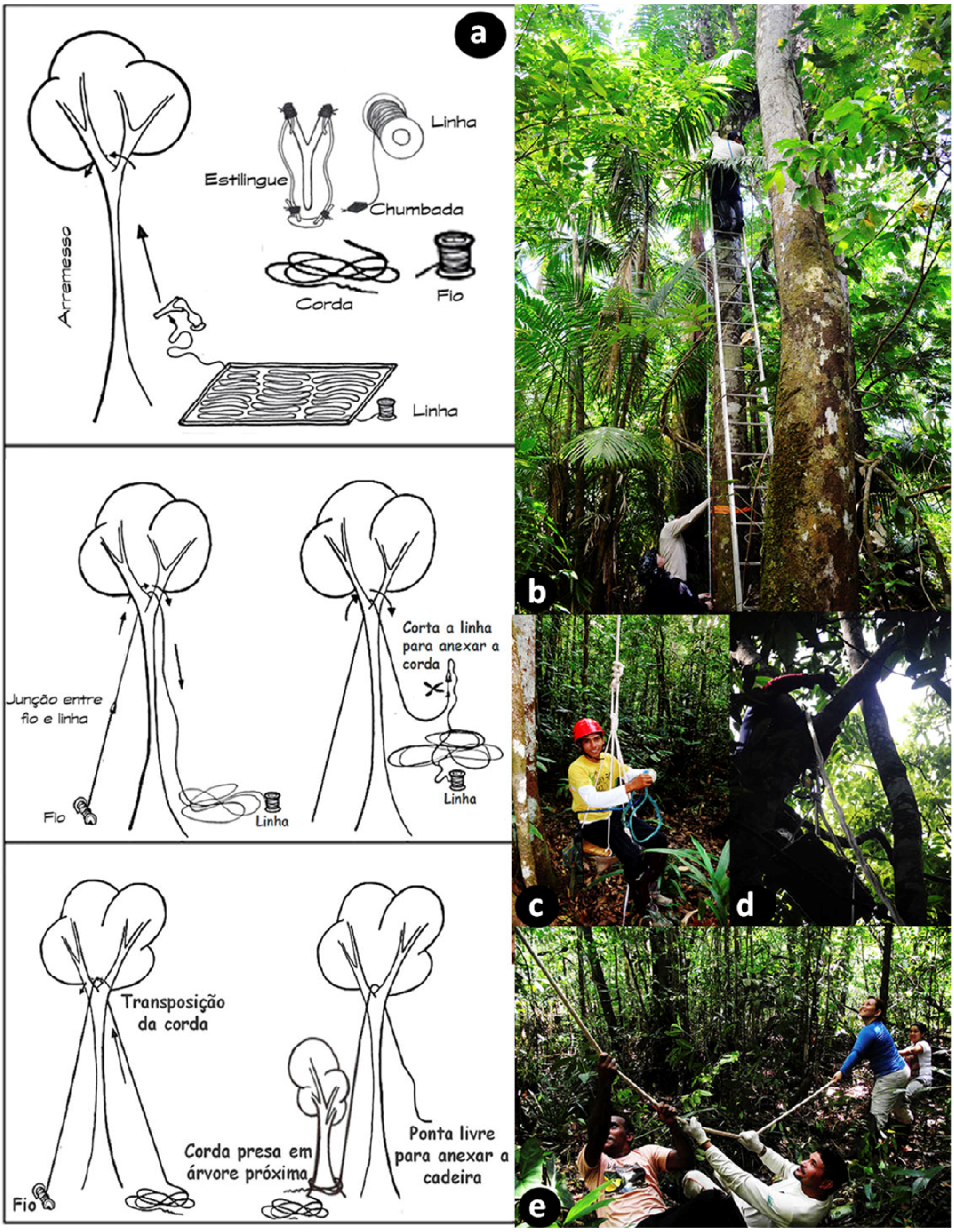

Figura 2. Ilustração dos métodos utilizados para amostragem, equipamentos e metodologia utilizada para as coletas de briófitas epífitas na FLONA de Caxiuanã.

2.5 CARACTERIZAÇÃO DAS ÁREAS DE ESTUDO

Este estudo foi realizado na Floresta Nacional de Caxiuanã (FLONA de Caxiuanã) que ocupa territórios dos municípios de Portel e Melgaço, no estado do Pará, entre os interflúvios dos rios Xingu e Tocantins. Essa área é uma das mais bem conhecidas quanto à brioflora na Amazônia, com inúmeros estudos documentando a diversidade de briófitas, sobretudo de caráter florístico (ver ILKIU-BORGES *et al.,* 2009, e ainda ILKIU-BORGES *et al.*, 2013; MORAES; LISBOA, 2009; LISBOA *et al.,* 2013; OLIVEIRA; TER STEEGE, 2013; CERQUEIRA *et al.,* 2016; 2017)

A vegetação predominante na FLONA de Caxiuanã é de floresta de Terra Firme embora ocorram também, vegetação savanoide, florestas inundáveis (Várzea e Igapó) e vegetação aquática. Na Amazônia as florestas inundáveis de Várzea e Igapó diferenciam-se entre si, em estrutura, diversidade e composição florística. Em razão dos regimes de inundação dessas vegetações as espécies tendem a apresentar adaptações para contornar os períodos de estresse à que são submetidas periodicamente (FURCH; JUNK, 1997; FERREIRA, 2000; PAROLIN, 2012).

As Várzeas apresentam alta fertilidade nos solos como reflexo da deposição de sedimentos dos rios de águas brancas e inundam periodicamente (MELACK; HESS, 2010). O Igapó, por sua vez, é inundado por rios de águas preta ou clara, pobres em nutrientes e de pH ácido e são caracterizados por solos de baixa fertilidade (JUNK *et al*., 2012). Na FLONA de Caxiuanã (Figura 3, a–e), as vegetações inundáveis são distintas, no que tange o grau de cobertura do dossel e a densidade de plantas no sub-bosque (MATOS *et al*., 2018), o Igapó possui um dossel mais fechado em relação ao da Várzea, assim como uma densidade de plantas maior no sub-bosque (FERREIRA *et al*., 2012).

No entorno de cada forófito foi estabelecida uma parcela de 10 m². Em cada vértice foi tomada uma foto hemisférica, a média das medidas de abertura do dossel foi calculada para cada parcela a qual foi utilizada como uma medida da abertura dossel ao redor do forófito (Fig. 3f).

Figura 3. Margem e interior das vegetações estudadas na FLONA de Caxiuanã. (a) Margem da vegetação de Várzea na baía de Caxiuanã; (b) Sub-bosque de vegetação de Várzea; Margem (c) e sub-bosque (d) da vegetação de Igapó; (e) Sub-bosque de Terra Firme; (f) Procedimento de tomada de fotografias hemisféricas no entorno de forófito para medida de abertura do dossel.

3 RESULTADOS

3.1 HOW DOES EPIPHYTIC BRYOPHYTE DIVERSITY RESPOND TO DIFFERENCES IN THE VEGETATION OF EASTERN AMAZON?

Highlights

- Igapó vegetation was the most richest and diverse habitat with many exclusive species.
- Differences in the vegetation types increase environmental heterogeneity for the bryophytes.
- Environmental filters influence the rarity of species in local assemblages.
- Epiphytic bryophytes assemblages of flooded vegetation types are very different from each other.

Abstract

In this study epiphytic bryophytes were collected from the base to the canopy of 24 host trees in Várzea, Igapó and Terra Firme vegetations. Measures of host trees and of canopy openness in their surroundings were used as proxies for vegetation structure and correlated with the composition of epiphytic bryophytes. Species richness, diversity and composition, and the proportion of rare species were compared among vegetation types. The floristic groups in each vegetation type were tested as to consistency and the dissimilarity between them was calculated. The alpha and beta diversity were analyzed for the total dataset. The richness, abundance, diversity and composition of species varied between vegetation types, mainly between the flooded forests, i.e. Várzea and Igapó. Igapó vegetation was the richest and most diverse, housing a large number of rare and exclusive species. Flooded forests contribute significantly to overall diversity and their species assemblages are not subsets of Terra Firme vegetation. The proportion of rare species was high in all vegetation types. The logseries model was the best-fit to describe the distribution of abundances in the flooded vegetation types, while the lognormal model described it better in Terra Firme vegetation. The environmental heterogeneity that results from the variation in vegetation types in the area promote a high diversity of epiphytic bryophytes and the rarity of these species seems to be a reflection of their requirements. Terra Firme vegetation constitutes a more stable environment for the establishment of bryophytes compared to flooded vegetations.

Keywords: alpha diversity; beta diversity; flooded forest; environmental heterogeneity; species composition.

Introduction

Larger areas are supposed to include higher environmental heterogeneity and, as consequence of it, higher number of species (Rosenzweig and Ziv, 1999). The staggering plant diversity of the Amazon, in this context, can be the result of a mosaic of environments shaped by, for instance, climatic and edaphic variability (Puig, 2007), flooding and water table gradients (Junk and Piedade, 2011; Schietti et al., 2014), hydrogeomorphological dynamics of migrating channels and evolving lakes (Wittmann et al., 2004) and microscale variation of light and relative humidity from the understory to the canopy of the forest (Magalhães et al., 2014). Still, most of the alpha and beta diversity patterns known for the region are related to a long history of studies in "terra firme" forests (*e.g.* Valencia et al., 1994, 2004; Pitman et al., 2001; ter Steege et al., 2003, 2006, 2013; Cintra et al., 2005; Montufar and Pintaud, 2006; Honorio-Coronado et al., 2009; Stropp et al., 2009; Guèze et al., 2012; Marra et al., 2014; Rodrigues et al., 2014; Tuomisto et al., 2014). This vegetation type is the most extensive in terms of total area as well as the most accessible to researchers. It is however expected that the change in community composition across vegetation types, *i.e.* beta diversity at a regional scale, adds to overall diversity (Whittaker, 1960).

In eastern Amazon, vegetation types such as "Várzea" and "Igapó" are flooded daily and annually by fluctuations in river levels of different origins and sediment loads. Besides, the floristic differences in tree species composition lead to variations in forest structure in relation to canopy openness and height, tree diameter (at breast height), vegetation composition in understory (Ferreira et al., 2012, 2013) and types of soil (Piccinin and Ruivo, 2012). The pattern of higher richness of white-water ("Várzea") in relation to black-water ("Igapó") floodplain forests (Junk et al., 2015) was not sustained in tree communities and in bryophytes at eastern Amazon, whereas a clear distinction between floristic compositions of trees and bryophyte in flooded forests was confirmed (Ferreira et al., 2005; Lopes et al., 2016; Cerqueira et al., 2017). Despite of the differentiated species composition and high bryophyte richness of the canopy recorded in the Amazon (Oliveira and ter Steege, 2013; Tavares-Martins et al., 2014), the surveys in the flooded forests did not include it up to present date.

In bryophytes, environmental heterogeneity is also put forward as the main driver of species diversity (Shaw et al., 2011), as these plants survive in a wide variety of habitats (Kürschner, 2004) and respond rapidly to variations in moisture, temperature, light and mineral deposition of substrates (Uniyal, 1999). The composition of Amazonian epiphytic bryophyte communities seems to be strongly influenced by the vertical microenvironmental gradient from the understory to the canopy of the forest as well as site elevation (Oliveira and ter Steege, 2015). It is suggested that other local and even regional gradients play a lesser role in structuring communities. Again, data used to study these patterns are focused on Terra Firme forests and knowledge of other vegetation types is scarce.

Similarities in alpha diversity patterns in epiphytic habitat were reported among bryophytes, ferns and lichens although beta diversity patterns have been different among them (Mandl et al., 2009). Studies with vascular plants in the Amazon have already observed some congruent patterns for diversity considering the different types of vegetation, e.g. the east-to-west gradient of increasing species diversity described for Terra Firme and Várzea (Wittmann et al., 2006).

Beta diversity refers to the degree of differentiation between communities (Whittaker, 1960) and may reflect two phenomena: spatial nesting or species turnover (Harrison et al., 1992; Baselga et al., 2007). Nesting occurs when biota from low richness sites correspond to subsets of richer biota from another site (Ulrich and Gotelli, 2007), reflecting a non-random process of loss of species driven by a factor that promotes orderly disaggregation of assemblages. Spatial substitution implies the exchange between assemblages as a consequence of environmental selection or spatial and historical constraints (Baselga, 2010). Analyzing how the different vegetation types contribute to the overall diversity and the patterns of beta diversity of epiphytic bryophytes is fundamental to understand what has been made them rare in Amazonia lowland tropical forests (Oliveira and ter Steege, 2013), where they have low endemism (Gradstein et al., 2001), predominance of generalist taxa (Oliveira et al., 2009; Tavares, 2009; Oliveira and ter Steege, 2015) and which often exhibit wide phytogeographic patterns (Schuster, 1983; Tavares-Martins et al., 2014).

Thus, our focus is to analyze the diversity of epiphytic bryophytes based on the distribution of species in the Caxiuanã National Forest (alpha diversity, local scale) and investigate to which extent different forest types contribute to epiphytic assemblage composition and structure (beta diversity, landscape scale). We hypothesize that species richness, composition, diversity and the proportion of rare species are different in the vegetation types and that Terra Firme forest exhibit a greater richness and proportion of rare species than flooded forests (Várzea and Igapó) (Oliveira and ter Steege, 2013). We expect that flooded forests contribute to overall diversity but showing significant lower diversity than Terra Firme forests, as the latter is dominant in the landscape and exhibits high similarity in the composition of epiphytic bryophytes on a regional scale (Oliveira and ter Steege, 2015).

Methods

Study area

The Caxiuanã National Forest (Caxiuanã FLONA) is located at the Eastern portion of the Brazilian Amazon, in the interfluve of Xingu and Tocantins rivers and occupies an area of 33,000 ha of tropical rain forest, on the west banks of the Caxiuanã bay, downstream Anapu river (Montag et al., 2008). According to Köppen classification, the region has characteristics of tropical monsoon climate (Am) (Alvares et al., 2014). The mean annual rainfall is between 2,000 and 2,500 mm, with a pronounced dry season between June and November (Costa et al., 2010), and the annual mean temperature is around 25.9 °C and air relative humidity around 82%, both with a small seasonal variation (Costa et al., 2013; Castro et al., 2013). The site elevation is 15 m above river level and a water table depth of 10 m has been observed in the wet season (Fisher et al., 1943). Terra Firme vegetation occupies 99% of the territory, while flooded vegetation approximately 0.2% (Ferreira et al., 2012). The annual flood pulse in this region presents smaller amplitude than in the Western Amazon, ranging from 1 to 1.5 m, under the influence of the seasonal precipitation regime and daily tidal movements that cause small variations of ca. 30 cm (Hida et al., 1999).

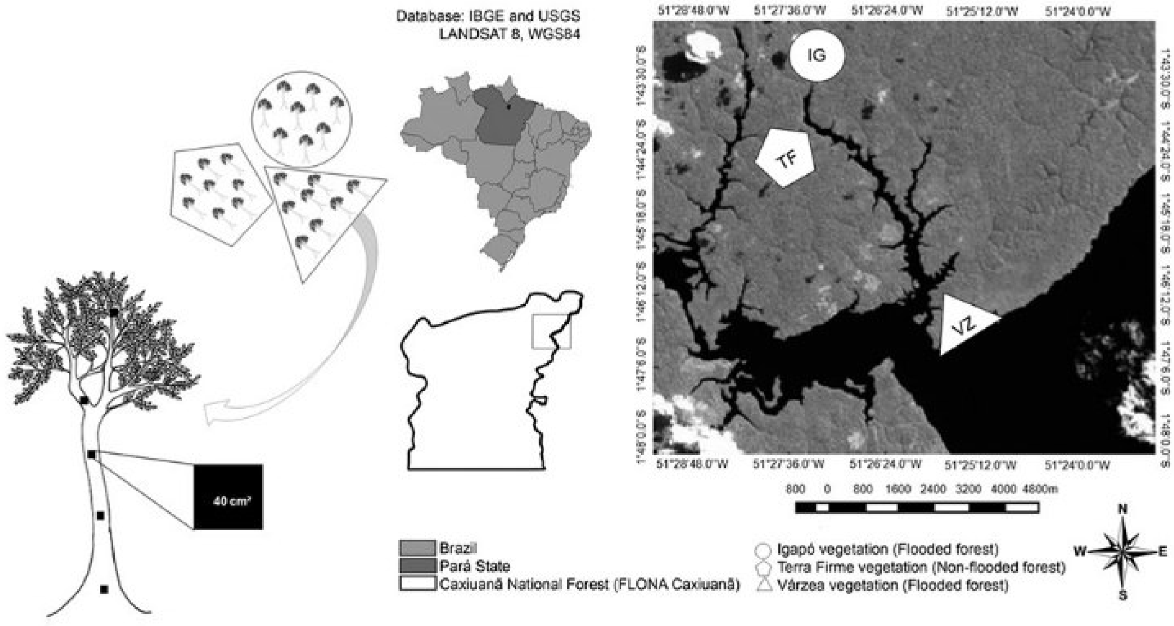

Figure 1. Sampling methods and study area.

Epiphytic bryophytes were collected in three forest habitats, recognized in the botanical literature as different Amazon vegetation types, namely, non-flooded "Terra Firme" vegetation, and flooded "Várzea" and "Igapó" vegetation. They have different nutrient levels and origins: Várzea vegetation has greater richness of nutrients and is under the influence of daily and annual fluctuations in the levels of great white-water rivers, while Igapó vegetation is associated to black-water and clear-water rivers (Junk et al., 2011). The floristic differences in tree species composition, understory vegetation composition (Ferreira et al., 2012, 2013) and soil types (Piccinin and Ruivo, 2012) are the main factors that lead to variations in the forest structure of these vegetation types, as for example different canopy openness and height and tree diameter at breast height (Ferreira et al., 2012). The main characteristics of the vegetation types analyzed in this study are described below.

1) "Várzea" vegetation (VZ): seasonally flooded by annual fluctuation of the Amazon drainage and daily fluctuations of tides. The canopy is relatively open and tree height varies from 20 to 30m, with an understory characterized by the presence of individuals of tree species at natural regeneration and absent herbaceous community, with exception of *Montrichardia arborescens* (L.) Schott (Araceae) (Ferreira et al., 2012, 2013). Soils are Plinthosols submitted to temporary effect of excess moisture and poor drainage (Piccinin and Ruivo, 2012).

2) "Igapó" vegetation (IG): seasonally flooded by annual fluctuation of black water rivers and streams and also by daily tidal fluctuations. The canopy is closed and tree height also varies from 20 to 30m and the understory is characterized by the presence of dense herbaceous vegetation (Ferreira et al., 2012). Soils are Gleysols submitted to permanent or periodic humidity, anaerobic environments, poor drainage and high fragility (Piccinin and Ruivo, 2012).

3) "Terra Firme" vegetation (TF): non-flooded forest on slightly higher elevations, covering most of the study area. The canopy is closed and tree height varies from 30 to 35m with emergent trees reaching up to 45m. The understory is clean and shaded, with ferns and herbaceous plants found in more humid places (Ferreira et al., 2012). Soils are yellow Oxisols with a thick stone⁄laterite layer at 3–4 m depth. Soil texture is composed of mixture of sand (75–83%), silt (6–10%) and clay (12–19%) (Ruivo and Cunha, 2003).

Collection, identification and organization of the dataset

Sampling was carried between September 2015 and July 2016. Samples of epiphytic bryophyte communities were taken from a total of twenty four host trees in Várzea and Igapó flooded vegetations and non-flooded Terra Firme vegetation. In each host tree, five botanical samples were collected from the base to the canopy (shaft, leaves and branches of canopy), to represent the total sampling of host tree. DBH and shaft height of each host tree were measured with the metric tape and canopy height was visually estimated. Using each host tree as the central point of a 10 m^2 plot, hemispheric photographs were taken with a digital camera (Nikon Coolpix 5400) and 8mm fisheye lens (Nikon FC-E9) at the corners of each plot. The average of values of canopy openness of the four photographs constituted a measure for this variable in the areas surrounding of host tree. A tripod was adjusted so as to place the camera at 1m above the ground and the pictures were taken always after 4 pm to avoid direct incidence of solar radiation. Images were analyzed using the Gap Light Analyzer software version 2.0 to estimate canopy openness (Frazer et al., 1999). The elevation of area was obtained with "Google Earth" using the points of geographic localization of host trees.

Bryophyte specimens present in the samples were identified to species level with aid of identification keys, illustrations and descriptions in specialized literature (Florschütz, 1964; Reese, 1993; Reiner-Drehwald, 2000; Reiner-Drehwald and Goda, 2000; Dauphin, 2003; Gradstein and Costa, 2003; Gradstein and Ilkiu-Borges, 2009; Moraes and Lisboa, 2009; Elena Reiner-Drehwald and Grolle, 2012; Bordin and Yano, 2013; Ilkiu-Borges, 2016). Materials were sent to taxonomists for confirmation and identification of species when necessary. The taxonomic classifications adopted were those of Goffinet et al., (2009) for Bryophyta and Crandall-Stotler et al., (2009) for Marchantiophyta. Vouchers were incorporated into the Geraldo Mariz (UFP) and João Murça Pires (MG) herbaria.

Data analysis

We compared the richness, diversity and composition of epiphytic bryophyte species to identify possible variations in these parameters between the different vegetation types. In order to compare the species richness of vegetation types, the variable "number of species" had its normality tested with the Shapiro–Wilks test and homogeneity of variances tested with the Levene's test of Car package (Fox and Weisberg, 2011). Mean species richness was therefore compared between vegetation types through One-way analysis of variance (ANOVA) at 5% level of significance. A sample unit corresponded to the whole host tree. Significant differences between groups were investigated through post hoc Tukey's honestly significant differences (HSD).

Floristic diversity was assessed by calculating Fisher's alpha (α) (Fisher et al., 1943) index using all individuals and species registered in each vegetation type. This index is little sensitive to sample size and can be considered a good measure of diversity (Magurran, 2004; Beck and Schwanghart, 2010). The multiplicative diversity partition method was used for the total dataset, being beta diversity (β) calculated as: ${}^{q}D_{\beta} = {}^{q}D_{\gamma}/{}^{q}D_{\alpha}$ (quotient of gamma diversity and mean alpha diversity (α)), using the entropart package (Marcon and Hérault, 2015). This measure can be interpreted as the 'effective number of completely distinct communities' (Jost, 2007), and can vary between 1 (when all communities are identical) and N (when all communities are completely different from each other). In this study, it varied from 1 to 3.

A Canonical Correspondence Analysis (CCA) was performed to evaluate the correspondence between species composition and variables of each sample variables, i.e. DBH, height of tree (shaft height + canopy height), elevation of and canopy openness. This method restricts the ordination of a species matrix through multiple linear regressions performed on the variables of a given environment (McCune and Grace, 2002a). This analysis was performed in the Fitopac 2.1 software (Shepherd, 2010).

A measure of dissimilarity the species composition in the vegetation types was calculated by Bray-Curtis index use the vegdist function of Vegan package (Oksanen et al., 2018). Multi-Response Permutation Procedure (MRPP) was used to evaluate the consistency of the floristic groups, according to the vegetation type where host trees occurred. MRRP evaluates whether similarity between groups is greater than expected by chance (McCune, and Grace, 2002b). The Nestedness metric based on Overlap and Decreasing Fill (NODF) was used to analyze the species composition among vegetation types, in the context of local metacommunity. This is a metric for nestedness based on overlap and decreasing fill in the analysis of a species composition matrix (Almeida-Neto et al., 2008). These analyses were carried out using NODF function of Vegan package in R (Oksanen et al., 2018).

The occurrence of few very abundant species and many rare species in natural systems is a common pattern (McGill et al., 2007). However, species shifts and adaptation to habitats may lead to changes in rarity patterns of species in different environments (Hanski, 1982). For this reason, we analyzed the rarity and regional distribution patterns of species.

The total number of records of the species was considered a measure of abundance in the vegetation types. To estimate the local rarity pattern of species, we used the rarity index (RI) = 1/n, where n is the number of host trees occupied by a given species. These RI values were square root transformed and normalized between 0 and 1 (Quinn and Keough, 2002). In each vegetation type, the RI values of the species were distributed in the 4th (upper) and 1st (lower) quartiles, to identify three classes of rarity (rare, frequent or common). Species in the first quartile (1st) were considered rare and in the fourth (4th), common; those in the intermediary quartiles were classified as frequent species (Appendix A). The number of vegetation types (Regional frequency), the rarity pattern and the number of host trees occupied (Local frequency) by a species were used to determine its distribution pattern (adapted from Söderström, 1989): Core - species occurring abundantly (1 to 8 hosts, common, frequent and/or rare, one vegetation type) in the majority of the available sites (2 to 3 vegetation types); Urban - species occurring abundantly (3 to 8 hosts, common or frequent) in few of the available sites (one vegetation type); Rural - species occurring in small populations (1 to 3 hosts, rare or common) in the majority of the available sites (2 to 3 vegetation types); and Satellite - species occurring in small populations (rare or common) in few of the available sites (1 to 3 hosts, one vegetation type).

In order to investigate the proportion of rare species and analyze whether species distribution and rarity patterns were associated with the different environments, species abundance distribution (SAD) models were compared and the occurrence of indicator species and the probability of taxa with more environmental plasticity in the vegetation types were tested. SAD describes the abundance of each species in a given community (McGill et al., 2007) being can also be useful to describe diversity patterns, relations with spatial heterogeneity (Hsiao-Pei et al., 2014) and shed light on how the partitioning of resources among species takes place (Sugihara et al., 2003). The Akaike's information criterion (AIC) method was used to compare SADs models logseries and lognormal (Burnham and Anderson, 2002), in the vegetation types. AIC is the most commonly used metric in SAD studies and provides an estimate of the loss of information when a certain model is used to represent a dataset (Matthews and Whittaker, 2014).

Species can be used as ecological indicators of community or habitat types, environmental conditions, or environmental changes (Cáceres et al., 2010). Indicator Species Analysis (ISA) was carried out to explore the preference of species in the vegetation types. The indicator value index is based exclusively on within-species abundance and occurrence comparisons, not being affected by the abundance of other species. The significance value for IndVal is obtained via randomizations (Legendre and Legendre, 1998).

Amazonian species may occur across wide geographical ranges, encompassing a number of vegetation types. We used the number of vegetation types in which a given species occur as a proxy for environmental plasticity. In order to test whether the bryoflora of each vegetation studied was formed by a set of species that showed similar levels of environmental plasticity, we used a permutation procedure based on the number of vegetation types in which each species was recorded in Brazil as well as in Caxiuanã FLONA. Data on the occurrence of species in other vegetation in Brazil were filtered from the site of the "Flora do Brasil 2020" (Flora do Brasil, 2020) while data on the occurrence of species in other vegetation types within Caxiuanã were obtained from studies in the area (Ilkiu-Borges and Lisboa, 2002; Moraes, 2006; Oliveira and ter Steege, 2013; Cerqueira et al., 2017 and this study). After the construction of the dataset, the species abundance distribution of our complete dataset, a total of 100 random communities were built, with the same number of species and individuals as the real communities. From the random communities, average and standard deviation of the number of vegetation types occupied by the different species were calculated and compared, by vegetation type, to the field data in order to test for significant deviations.

Results

A total of 1,056 specimens were recorded in the samples collected from the base to the top of 24 host trees in the three vegetation types. The specimens belonged to 13 families, 42 genera and 112 species (21 mosses and 91 liverworts) (Appendix A). The richness of epiphytic bryophytes varied between vegetation types and IG showed the highest total number of species and mean number of species per host tree, followed by TF and VZ (Tab. 1). A significantly different ($p > 0.05$) species richness was recorded only between the flooded forests (ANOVA, $F_{[2, 21]} = 4.863$, $p = 0.018$; HSD, $p = 0.014$), being IG the richest. The Fisher's alpha index indicated IG as the most diverse (Tab. 1). Total alpha diversity in the community was 62.33, and beta diversity was 1.79. In the analysis of the epiphytic bryophyte assemblages, no significant nested pattern was detected for the data, i.e. the bryophyte flora of different vegetation types were not restricted subsets of each other.

Host tree variables presented a variation in line with the literature for these vegetation types. Significant differences were found only for shaft height and DBH averages (Tab. 2); the first was significantly different between TF and the flooded forests ($F_{[2, 21]} = 5.594$, $p = 0.0013$; HSD, TF-VZ $p = 0.0401$, TF-IG, $p = 0.0141$), and the second, only between flooded forests ($F_{[2, 21}] = 8.563$, $p = 0.0019$; HSD, $p = 0.0013$). Average DBH, canopy height and canopy openness, were higher in VZ while TF had the highest average shaft height and total height of host trees.

The Bray-Curtis dissimilarity index indicated a higher floristic separation between flooded forests (VZ/IG= 0.732; IG/TF = 0.615; TF/VZ= 0.607). The MRPP applied to the dissimilarity matrix confirmed a significant distinction between the three floristic groups (A = 0.2718, $p = 0.001$ for vegetation). It was also possible to observe a significant separation of forest types in terms of species composition in the direct gradient analysis (CCA) (Fig. 2).

Table 1. Attributes of epiphytic bryophyte communities. Total and average richness of the species per host tree and Fisher's alpha (α) index of diversity per vegetation type. Comparison of Species Abundance Distribution (SAD) Log-series (ls) and Lognormal (ln) Models over best fits for the vegetation types using AIC.

Variables	Igapó			Terra Firme			Várzea		
Total and average richness per host tree	73; 27.87 ± 5.0			66; 24.25 ± 6.5			48; 19.25 ± 4.8		
Total frequency	380			347			329		
Fisher (α)	26.86			24.16			15.47		
	AIC	dAIC	df	AIC	dAIC	df	AIC	dAIC	df
Model SAD_ls	350	0.1	1	345	2.6	1	269	0.4	1
Model SAD_ln	370	19.4	2	342	0	2	279	9.7	2

Table 2. Average and standard deviation of host tree variables and canopy openness in each vegetation type. IG = Igapó vegetation; TF = Terra Firme vegetation; VZ = Várzea vegetation.

	Variables	IG	TF	VZ
Average and standard deviation	DBH	29.16 ± 5.8	36.21 ± 4.3	44.80 ± 10.8
	Shaft height	10.16 ± 2.5	13.96 ± 2.87	10.75 ± 1.83
	Canopy height	10.56 ± 3.3	9.62 ± 1.5	10.87 ± 2.1
	Total height	20.72 ± 2.2	23.58 ± 2.9	21.62 ± 2.4
	Canopy openness	12.50 ± 2.7	12.15 ± 1.8	12.89 ± 1.6

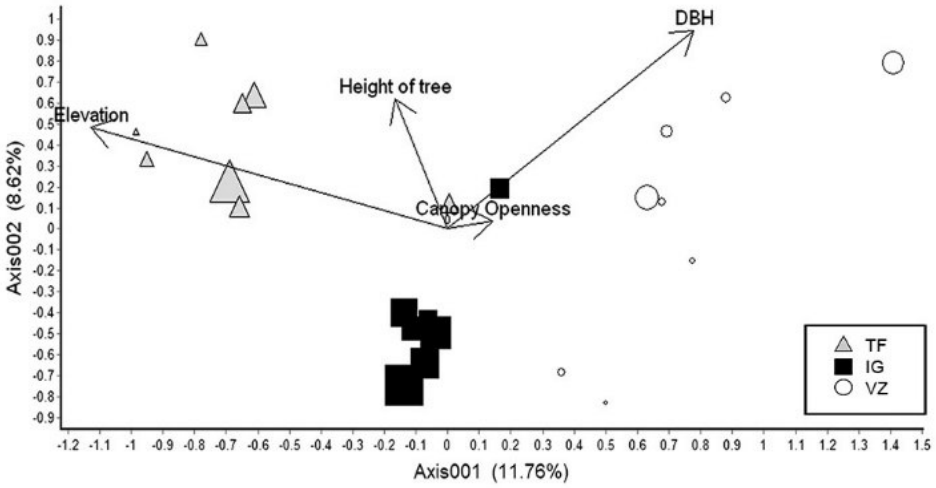

Figure 2. Canonical Correspondence Analysis (CCA) for vegetation samples (host trees). The size of the symbol indicates the species richness of the host tree, the shapes represent the vegetation types (TF = Terra Firme vegetation; IG = Igapó vegetation; VZ = Várzea vegetation).

Besides higher richness, IG also presented a larger number of occurrences of species and exclusive taxa (Fig. 3, Tab. 1), with highest proportion of satellites in this vegetation (Fig. 4a). Some of these species on the other hand were classified as urban because it was very abundant in this vegetation. Another highlight is the rural species, that although they occur also in other vegetations present low frequency of colonizing, in only of one to two host trees.

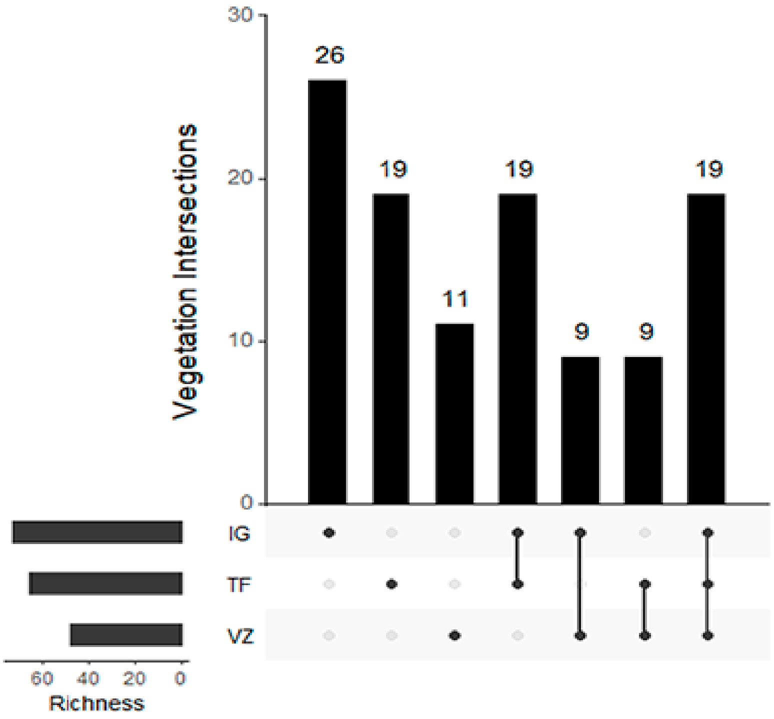

Figure 3. Overview of number of species and shared species per vegetation type. (a) - Horizontal bars represent the total richness per vegetation; Vertical bars represent number of species only found in one vegetation (points) and number of shared species between them (points connected by lines). (IG = Igapó vegetation; TF = Terra Firme vegetation; VZ = Várzea vegetation).

Core species predominated in terms of richness and abundance, and were present in all vegetation types (Fig. 4a, b) with the exception of *Rectolejeunea berteroana* which was classified as rural, due to its low frequency in the habitats. Considering the total number of species, although only ca. 21% were shared among all vegetation types, they accounted for more than 43% of the occurrences in this study. Another important point was the alternation in the abundance of species among the vegetation types, mainly of the moss species *Microcalpe subsimplex, Syrrhopodon ligulatus,* and *Mniomalia viridis* (Tab. 3). Although these species contributed to the richness of core species in the VZ (Fig. 4b), they were more abundant in the other vegetation types, especially in TF.

The total number of occurrences of epiphytes was very similar in the three vegetation types but the comparison of distribution models revealed difference in their best-fit models. Log-series distribution had the best AIC score in flooded forests, while lognormal distribution had the best score in non-flooded forest (Tab. 1).

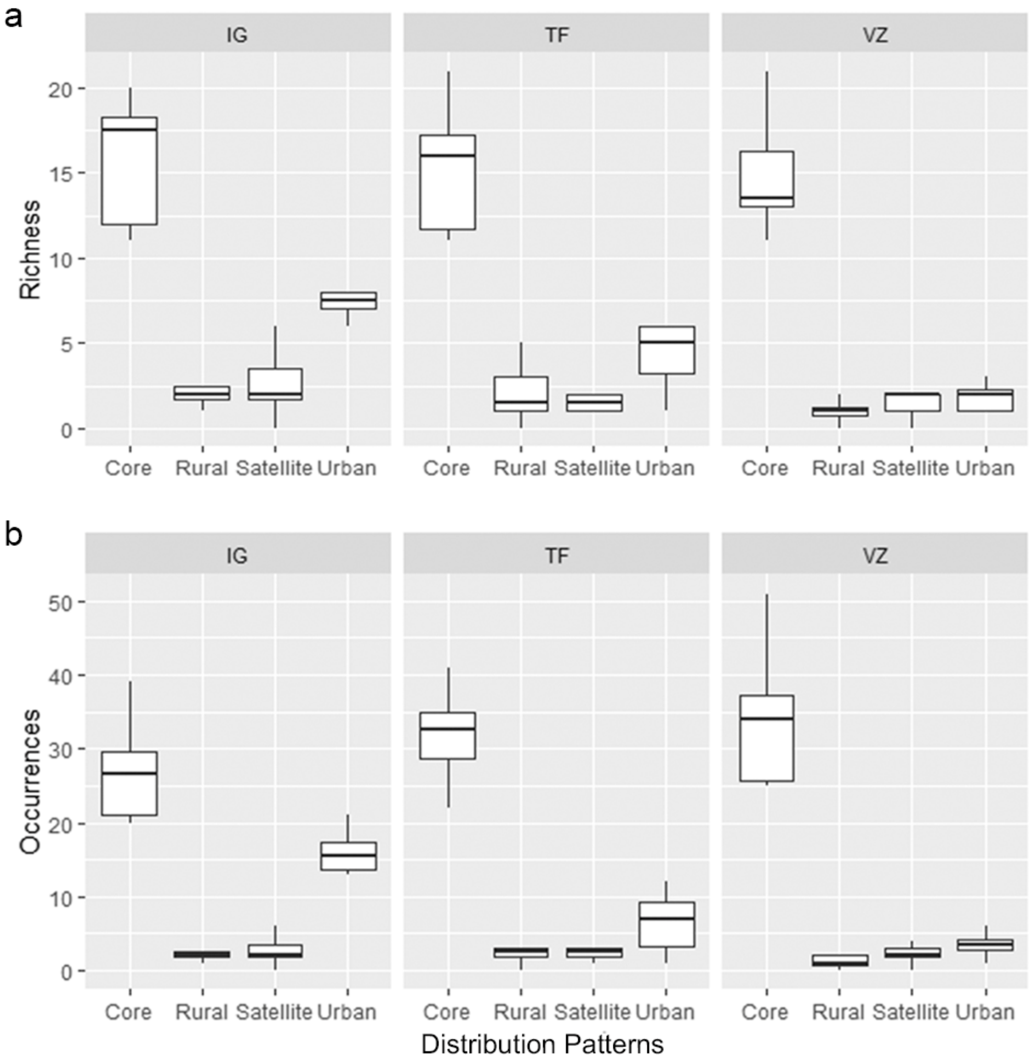

Figure 4. Overview of richness (a) and occurrences (b) of species in the spatial distribution categories per vegetation type: IG = Igapó vegetation; TF = Terra Firme vegetation; VZ = Várzea vegetation).

In the three vegetation types, a total of thirty species were pointed as indicators according to ISA (Tab. 3). Igapó vegetation showed the largest number of indicator species per vegetation type, most of them very frequent (Appendix A). Only three out of the 12 species assigned as indicators in IG were also recorded in other vegetation types, but two of them had a low frequency. Most indicator species in this vegetation were recorded in at least 30% of samples. *Calymperes platyloma* stood out in this vegetation type, occurring in 95% of the samples.

In Várzea vegetation, eight indicator species were identified, among them four of the most frequent. Only one species, *Acrolejeunea torulosa*, was exclusive of this vegetation type; all the indicator species were registered in at least 30% of the samples. The other indicator species that occurred also in TF and/or IG were uncommon in these vegetation types, occurring in less of 10% of the samples most of the time.

Table 3. Epiphytic bryophytes evaluated as indicators per vegetation types. Oc. = Number of occurrences; Indicator species per vegetation types its highlighted in grey. IG = Igapó vegetation; TF = Terra Firme vegetation; VZ = Várzea vegetation; IV = indicator value given by indicator species analysis; *p*val = p value reference (P < 0,005).

Family/Taxon	IndVal	val	IG	TF	VZ
Lejeuneaceae					
Acrolejeunea torulosa (Lehm. & Lindenb.) Schiffn.	0.9	0.001	.	.	22
Archilejeunea auberiana (Mont.) A.Evans	0.5	0.029	4	.	.
A. crispistipula (Spruce) Steph.	0.8	0.001	.	2	21
A. fuscescens (Hampe ex Lehm.) Fulford	0.6	0.006	.	8	.
A. parviflora (Nees) Schiffn.	0.5	0.014	.	15	4
Ceratolejeunea coarina (Gottsche) Steph.	0.7	0.002	1	4	16
C. cubensis (Mont.) Schiffn.	0.4	0.05	3	4	15
C. minuta Dauphin	0.5	0.033	25	28	6
Cheilolejeunea insecta Grolle & Gradst.	1	0.001	12	.	.
Cololejeunea subcardiocarpa Tixier	0.5	0.027	.	5	.
C. surinamensis Tixier	0.5	0.015	.	4	.
Haplolejeunea amazonica Ilkiu-Borges & Gradst.	0.6	0.004	.	7	.
Harpalejeunea tridens (Besch. & Spruce) Steph.	0.5	0.021	8	.	.
Lejeunea asperrima Spruce	0.8	0.001	8	.	.
L. boryana Mont.	0.8	0.001	10	.	.
L. cerina (Lehm. & Lindenb.) Gottsche	0.6	0.001	8	.	.
Mastigolejeunea auriculata (Wilson) Schiffn.	0.8	0.001	1	.	15
Neurolejeunea seminervis (Spruce) Schiffn.	1	0.001	29	1	.
Pictolejeunea picta (Gottsche ex Steph.) Grolle	0.6	0.003	.	9	.
Prionolejeunea scaberula (Spruce) Steph.	1	0.001	16	.	.
P. trachyodes (Spruce) Steph.	1	0.001	29	.	.
Pycnolejeunea contigua (Nees) Grolle	0.8	0.002	.	1	20
P. papillosa X.-L. He	0.7	0.002	1	5	23
Symbiezidium barbiflorum (Lindenb. & Gottsche) A.Evans	0.6	0.002	12	2	.
Calymperaceae					
Calymperes palisotii Schwägr.	0.4	0.041	5	.	12
Calymperes platyloma Mitt.	1	0.001	32	.	.
Syrrhopodon ligulatus Mont.	0.6	0.007	.	12	1
Syrrhopodon simmondsii Steere	0.5	0.011	.	10	.
Phyllodrepaniaceae					
Mniomalia viridis (Mitt.) Müll. Hal.	0.9	0.001	16	.	1
Sematophyllaceae					
Microcalpe subsimplex (Hedw.) W.R. Buck	0.7	0.001	.	12	1

As for TF, most of indicator species in this area were exclusive, but unlike most of indicators in other vegetation types, they were not so frequent. Six of the ten indicator species occurred in less than 10% of the samples of this vegetation type. *Ceratolejeunea minuta* stood out because, although occurring in other vegetation types, it was an indicator only in TF, and it was very abundant and present in all strata.

The bryophyte species found in the epiphyte flora of the Caxiuanã FLONA that occur in a greater number of vegetation types across Brazil had a probability above the average (4.61 ± 0.17) of occurring in VZ, whereas the opposite was observed for the species recorded in IG. Species of TF were close to the mean of the dataset (Fig. 5).

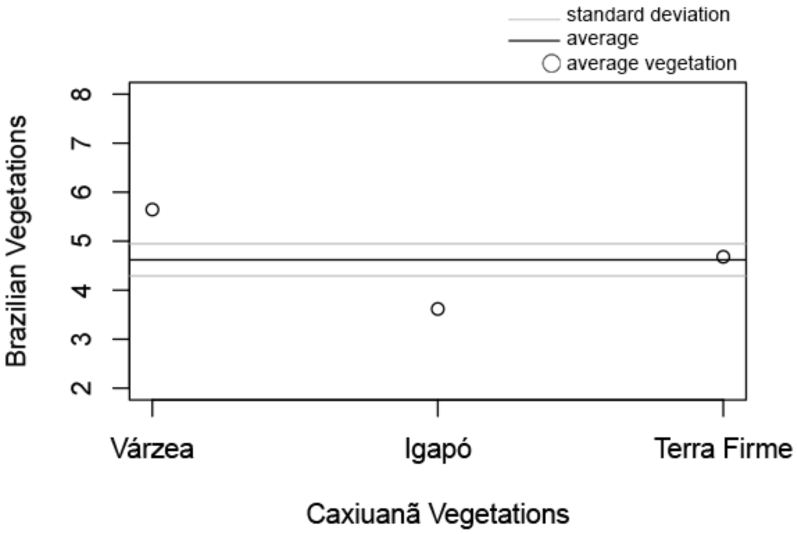

Figure 5. Permutation analysis considering the number of vegetations in which the species were recorded in Brazil and in Caxiuanã FLONA.

Discussion

The prediction that differences between the vegetation types drive changes in the attributes of epiphytic bryophyte communities was confirmed. Unexpectedly and contrary to our predictions, Igapó vegetation was the richest and most diverse habitat, housing a large number of exclusive species, contributing significantly to overall diversity.

We expected higher richness in TF which presents greater extension in the Amazon basin, this expectation was not confirmed in our data. Surprisingly, Igapó vegetation was very singular and showed the highest number of species, as well as the highest number of exclusive species and taxa little registered in the Amazon. Amazon basin is one of the most diverse areas where bryophytes occur in the Neotropics (Gradstein et al., 2001), and where epiphytes in TF operate as a meta-community (Oliveira and ter Steege, 2015). Thus, the rich bryophyte flora of IG may be a reflection of the geographical proximity to TF and possibly of a greater environmental heterogeneity, considering that diversity in local scale also depends on the regional diversity of species (Pärtel et al., 1996; Zobel et al., 1998; Brown et al., 2016). The relatively higher richness of epiphytic bryophytes in IG was also pointed out in two recent studies (Lopes et al., 2016; Cerqueira et al., 2017), but the lack of canopy sampling resulted in a slightly different conclusion in the same study area *i.e.* how the not significant differences in species richness between flooded vegetations. We attribute this to particularities of the sampling method, because the upper forest stratum, was included in our study, where many species were recorded mainly in IG and TF.

In general, the high epiphytic richness recorded is in agreement with the expectation for tropical environments (Gradstein, 1992; Gradstein et al., 2001; Gradstein and Costa, 2003) and represents about 45% (250 spp.) of the bryophytes of the Caxiuanã FLONA, one of the areas in the Amazon were bryophytes have been most studied (unpubl.). This variation in richness across vegetation types corroborates with the suggested in the literature that microclimatic alterations caused by fine-scale differences between habitats are precursors of bryophyte richness and composition (Benavides et al., 2004, 2006; Mandl et al., 2009; Santos et al., 2011; Batista and Santos, 2016).

The most diverse was Igapó vegetation according to the Fisher's alpha index. The bryophyte flora of flooded forests has been previously reported to be richer than swamps, non-flooded forests and white-sand areas in western Amazon (Benavides et al., 2004, 2006). These results were mainly attributed to the availability of substrates and to the variation of abiotic conditions in these vegetation types. We argue that the variations in abiotic conditions among vegetation types are the main drives of richness in eastern Amazon, because this pattern was maintained even analyzing only the arboreal substrate. Thus, we corroborate the suggestion of the literature that variation in structure and floristic composition of vegetation types promotes heterogeneity of abiotic conditions and favors the diversity of species (Richards, 1984; Gradstein and Pócs, 1989; Gradstein, 1992; Vanderpoorten and Engels, 2002; Márialigeti et al., 2009; Sanger and Kirkpatrick, 2015; Benítez et al., 2015; Valente et al., 2017).

We documented a high turnover of species in epiphytic bryophyte assemblages between vegetation types (beta diversity), similarly to what occurs with vascular plants, whose composition and diversity in the Amazon basin change at all spatial scales (Campbell, 1994). Although they exhibit similar patterns, we highlight that these groups of plants have important biological differences, implying also different mechanisms responsible for the observed patterns. The diversity of vascular plants in the Amazon has been credited to the existence of environmental gradients related mainly to climatic variation and soil and geological heterogeneity, together with an immense territorial extension (Willis, 1922;

Terborgh, 1973; Rosenzweig, 1995; Silman, 2011). Recently, the pre-Columbian anthropogenic contribution and the action of other organisms such as fungi have also been advocated as drivers of this diversity (Peay et al., 2013; Levis et al., 2017).

This study showed that species composition of epiphytic bryophytes in the Amazon is driven by environmental differences in vegetation types. Our initial expectations that dispersal ability and ecological plasticity of bryophytes would contribute to the structuring of highly similar epiphytic assemblages on a local scale were not confirmed. Environmental heterogeneity associated with different vegetation type's structures assemblies of epiphytic bryophytes with a remarkable degree of differentiation, mainly between the flooded forests (richness, diversity and composition). In addition, we found greater similarity between IG and TF, as did Lopes et al. (2016) who explained this similarity as a result of substrate availability in the understory. However, we believe that in our data, this similarity is primarily the result of proximity and the close microclimate. On the other hand, there is evidence that flood frequency and water level control the composition of bryophyte communities in flooded areas (Gillrich and Bowman, 2010). This could explain the greater dissimilarity between flooded vegetation types, also reported by Cerqueira et al. (2017). Environmental gradients represent variations in the abiotic conditions to which the bryophytes respond directly (Santos and Costa, 2010; Santos et al., 2014; Tavares-Martins et al., 2014; Oliveira and ter Steege, 2015; Oliveira and Oliveira, 2016). Thus, even at a local scale, variation in the structure and floristic composition of vascular plants favored the beta diversity of epiphytic bryophytes among vegetation types (Richards, 1984). The epiphytic bryophytes associated to Igapó vegetation seemed to be less tolerant to high temperatures and intense light incidence, as for example *Prionolejeunea* species, contrary to the *Ceratolejeunea* species, which were abundant in VZ. A clear change in floristic composition between bryophytes of distinct vegetation types was also documented in the western portion of the Amazon (Benavides et al., 2004, 2006) as well as in lowland vegetation in southeastern Brazil (Santos et al., 2011).

Species with low abundance (*i.e.* 1 - 5 occurrences) predominated in all vegetation types and only a few species were very frequent (Appendix A), which is predicted by one of the earliest principles in community ecology (McGill et al., 2007). A similar pattern has been reported for trees and epiphytic bryophytes in TF in the Amazon (Oliveira et al., 2009; Oliveira and ter Steege, 2013), although these results are counter intuitive taking into account that bryophytes of tropical lowland forests are considered to be generalists (*sensu* Richards, 1984) and of broad geographic distributions (Schuster, 1983; Santos and Costa, 2010; Santos et al., 2011). Our data suggest that this rarity among bryophytes is mainly a response to environmental filters, because changes in the abundance of some species between vegetation types were observed, although on a small scale. As a matter of fact, bryophyte species can be rare in various forms and at different scales (Söderström and During, 2005) which is supported in our data for the fact some species, registered with low frequency, change your frequency becoming more abundant in one or another vegetation types (Core or Rural). These changes in abundance and patterns of spatial distribution may be directly related to the demands of each species, as bryophytes depend on specific light, temperature and humidity conditions (Gradstein and Pócs, 1989). The availability of these conditions can vary between vegetation types (Evans et al., 2012) limiting the occurrence and the abundance of species like those that were registered in only one vegetation (satellite) and with low frequency, mainly in the Igapó vegetation.

In our data, the species abundance distribution in the two flooded forests differed from the non-flooded forest in terms of model fitting. A log-normal model better described the SAD of the TF, while log-series model better fitted the SADs of flooded vegetation types. The first is associated with undisturbed and more uniform assemblages and the second, with disturbed areas (Magurran, 2004). TF seems to present more stable conditions for the establishment of bryophytes, what may be related to habitat quality and structure and the history of the landscape. These are important factors for the probability of occurrence of species (Löbel et al., 2006). On the other hand, floodplains appear to be more dynamic, probably reflecting fluctuations in abiotic conditions related to daily and seasonal flooding of rivers and tides (Ferreira et al., 2012, 2013). These variations may even indirectly influence the abundance of species, which although have succeeded to get established, have not become abundant due to lack of optimal conditions. In the context of Amazonian vegetation, Benavides et al. (2006) consider that mosses depend more on moisture than liverworts, which in turn are mainly regulated by the availability of light. Perhaps for these reasons, in our dataset, mosses occurred only in the understory and with lower frequency, contrary to the liverworts, which were in general very abundant in these vegetation types (Benavides et al., 2006). Thus, the occurrence of exclusive taxa and very frequents (Urban) in Igapó, and the change in abundance of rare species between vegetation types may be related to the specific requirements of the species and to the process of environmental filtering of community assemblages.

A percentage of less than 30% of the surveyed species was found to be indicators. This finding was already expected because bryophytes of tropical lowland forests are usually considered generalists (Oliveira et al., 2009; Garcia et al., 2014; Pantoja et al., 2015) and of broad geographic distributions (Schuster, 1983; Gradstein and Costa, 2003; Santos et al., 2011). The species found in VZ also occur in a much larger range of vegetation in Brazil and belong mainly to genera considered generalists and sun specialists (Gradstein et al., 2001) these genera were very abundant in this vegetation type in the present study. On the other hand, indicator species in IG and TF occurred mainly in the understory and were restricted to one vegetation type. This suggests greater requirements for establishment, because specialists in this forest stratum are the first to disappear in of the case of disturbance (Acebey et al., 2003; Alvarenga et al., 2010; Tavares-Martins et al., 2014). These species also have a distribution restricted to a smaller number of vegetation types in Brazil (Flora do Brasil, 2020). Thus, we provide more evidence that the vegetation types investigated promote environmental heterogeneity, influencing the occurrence of species by determining environmental filters that play a preponderant role in the structuring of epiphyte bryophytes, even in a small local scale in the Amazon.

Conclusions

The varied vegetation types promoted remarkable environmental heterogeneity even at a small local scale, where abiotic conditions assembled epiphytic bryophyte communities with high diversity of species. Flooded vegetation types significantly contributed to the diversity of the local species pool, mainly the Igapó vegetation, due to the number of exclusive species. The distinction in the communities of flooded forests was more pronounced than expected, sheltering species of opposite extremes regarding tolerance to humidity, light incidence, and temperature variation. Thus, rarity in these assemblages appears to be influenced by environmental filters and TF constitutes a more stable environment for the establishment of bryophytes compared to flooded vegetations. Future research involving species attributes may clarify the mechanisms responsible for the patterns observed in tropical lowland forests.

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References

Acebey, A., Gradstein, S.R., Krömer, T., 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. J. Trop. Ecol. 19, 9–18. https://doi.org/10.1017/S026646740300302X

Almeida-Neto, M., Guimarães, P., Guimarães, P.R., Loyola, R.D., Ulrich, W., 2008. A consistent metric for nestedness analysis in ecological systems: Reconciling concept and measurement. Oikos. https://doi.org/10.1111/j.0030-1299.2008.16644.x

Alvarenga, L.D.P., Pôrto, K.C., de Oliveira, J.R. do P.M., 2010. Habitat loss effects on spatial distribution of non-vascular epiphytes in a Brazilian Atlantic forest. Biodivers. Conserv. 19, 619–635. https://doi.org/10.1007/s10531-009-9723-2

Alvares, C.A., Stape, J.L., Sentelhas, P.C., Gonçalves, J.L. de M., Sparovek, G., 2014. Köppen's climate classification map for Brazil. Meteorol. Zeitschrift 22, 711–728. https://doi.org/10.1127/0941-2948/2013/0507

Baselga, A., 2010. Multiplicative partition of true diversity yields independent alpha and beta components; additive partition does not. Ecology 91, 1974–1981. https://doi.org/10.1890/09-0320.1

Baselga, A., Jiménez-Valverde, A., Niccolini, G., 2007. A multiple-site similarity measure independent of richness. Biol. Lett. 3, 642–645. https://doi.org/10.1098/rsbl.2007.0449

Batista, W.V.S.M., Santos, N.D. dos, 2016. Can regional and local filters explain epiphytic bryophyte distributions in the Atlantic Forest of southeastern Brazil? Acta Bot. Brasilica 30, 462–472. https://doi.org/10.1590/0102-33062016abb0179

Beck, J., Schwanghart, W., 2010. Comparing measures of species diversity from incomplete inventories: an update. Methods Ecol. Evol. 1, 38–44. https://doi.org/10.1111/j.2041-210X.2009.00003.x

Benavides, J.C., Duque M., A.J., Duivenvoorden, J.F., Cleef, A.M., 2006. Species richness and distribution of understorey bryophytes in different forest types in Colombian Amazonia. J. Bryol. 28, 182–189. https://doi.org/10.1179/174328206X120040

Benavides, J.C., Idarraga, A., Alvarez, E., 2004. Padrões de Diversidade de Briófitas em Florestas FLOODED e Terra Firme na Região do Aconcágua, Amazônia Colombiana. Trop. Bryol. 25, 117–126.

Benítez, A., Prieto, M., Aragón, G., 2015. Large trees and dense canopies: Key factors for maintaining high epiphytic diversity on trunk bases (bryophytes and lichens) in tropical montane forests. Forestry 88, 521–527. https://doi.org/10.1093/forestry/cpv022

Bordin, J., Yano, O., 2013. Fissidentaceae (Bryophyta) do Brasil. Bol. do Inst. Bot. 22, 1–

168.

Brown, R.L., Reilly, L.A.J., Peet, R.K., 2016. Species Richness: Small Scale, in: ELS. John Wiley & Sons. John Wiley & Sons, Ltd, Chichester, UK, pp. 1–9. https://doi.org/10.1002/9780470015902.a0020488.pub2

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach, 2nd edn. Springer-Verlag, New York, New York Springer. https://doi.org/http://dx.doi.org/10.1016/j.biomaterials.2013.06.009

Cáceres, M. de, Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. Oikos 119, 1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x

Campbell, D.G., 1994. Scale and patterns of community structure in amazonian forests, in: Edwards, P.J., May, R.M., Webb, N.R. (Eds.), Large-Scale Ecology and Conservation Biology. Oxford, U.K: Blackwell Scientific, p. 384.

Castro, R.M. da S., Ruivo, M. de L.P., Costa, J.M.N., Costa, A.C.L. Da, 2013. Influência da sazonalidade na produção de serapilheira no experimento ESECAFLOR, na Floresta Nacional de Caxiuanã, in: Lisboa, P.L.B. (Ed.), Caxiuanã: Paraíso Ainda Preservado. Museu Paraense Emílio Goeldi, Belém, p. 856.

Cerqueira, G.R., Ilkiu-Borges, A.L., Ferreira, L. V., 2017. Species richness and composition of epiphytic bryophytes in flooded forests of Caxiuanã National Forest, Eastern Amazon, Brazil. Ann. Brazilian Acad. Sci. 88, 903–910. https://doi.org/http://dx.doi.org/10.1590/0001-3765201720160860

Cintra, R., Ximenes, A.C., Gondim, F.R., Kropf, M.S., 2005. Forest spatial heterogeneity and palm richness, abundance and community composition in Terra Firme forest, Central Amazon. Rev. Bras. Botânica 28, 75–84. https://doi.org/10.1590/S0100-84042005000100007

Costa, A.C.L. da, Galbraith, D., Almeida, S., Portela, B.T.T., Costa, M. da, Silva-Junior, J. de A., Braga, A.P., Gonçalves, P.H.L. de, Oliveira, A.A. de, Fisher, R., Phillips, O.L., Metcalfe, D.B., Levy, P., Meir, P., 2010. Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. New Phytol. 187, 579–591. https://doi.org/10.1111/j.1469-8137.2010.03309.x

Costa, A.C.L. Da, Oliveira, A.A.R. De, Neto, G.C., Costa, M.C. da, Silva-Júnior, J. de A., Portela, B.T.T., 2013. Caracterização metereológica da Floresta Nacional de Caxiuanã, in: Lisboa, P.L.B. (Ed.), Caxiuanã: Paraíso Ainda Preservado. Museu Paraense Emílio Goeldi, Belém, p. 656.

Crandall-Stotler, B., Stotler, R.E., Long, D.G., 2009. Phylogeny and classification of the Marchanthiophyta. Edinburgh J. Bot. 66, 155. https://doi.org/10.1017/S0960428609005393

Dauphin, G., 2003. Ceratolejeunea. Flora Neotrop. Monogr. 90, 1–86.

Elena Reiner-Drehwald, M., Grolle, R., 2012. Review of the genus Rectolejeunea (Lejeuneaceae, Marchantiophyta). Nov. Hedwigia 95, 451–482. https://doi.org/10.1127/0029-5035/2012/0063

Evans, S.A., Halpern, C.B., McKenzie, D., 2012. The contributions of forest structure and substrate to bryophyte diversity and abundance in mature coniferous forests of the Pacific Northwest. Bryologist 115, 278–294. https://doi.org/10.1639/0007-2745-115.2.278

Ferreira, L. V., Silva, A.S., Almeida, S.S., 2012. Os tipos de vegetação de Caxiuanã. Instituto Chico Mendes de Conservação da Biodiversidade.

Ferreira, L. V, Almeida, S.S., Amara, D.D., Parolin, P., 2005. Riqueza e composição de espécies da floresta de igapó e varzea da estação cientifica Ferreira Penna: Subsídios para o plano de manejo da Floresa Nacional de Caxiuanã. Pesqui. Botânica 56, 103–116. https://doi.org/10.1007/s12652-011-0069-8

Ferreira, L. V, Chaves, P.P., Cunha, D.D.A., Matos, D.C.L., Parolin, P., 2013. Variação da riqueza e composição de espécies da comunidade de plantas entre as florestas de igapos e várzeas na Estação Científica Ferreira Penna -Caxiuanã na Amazônia Oriental. Pesqui. Botânica 64, 175–195.

Fisher, R.A., Corbet, A.S., Williams, C.B., 1943. The Relation Between the Number of Species and the Number of Individuals in a Random Sample of an Animal Population. J. Anim. Ecol. 12, 42–58. https://doi.org/10.2307/1411

Flora do Brasil 2020 under construction. [WWW Document]. Jard. Botânico do Rio Janeiro. URL http://floradobrasil.jbrj.gov.br/ (accessed 12 August 2018).

Florschütz, P.A., 1964. The mosses of Suriname - Part I. Leiden.

Fox, J., Weisberg, S., 2011. An {R} Companion to Applied Regression, 2nd ed, Sage. Thousand Oaks CA.

Frazer, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser Univ. Inst. Ecosyst. Stud.

Garcia, E.T., Ilkiu-Borges, A.L., Tavares-Martins, A.C.C., 2014. Brioflora de duas florestas de terra firme na Área de Proteção Ambiental do Lago de Tucuruí, PA, Brasil. Hoehnea

41, 499–514. https://doi.org/10.1590/2236-8906-10/2013

Gillrich, J.J., Bowman, K.C., 2010. The Use of Bryophytes as Indicators of Hydric Soils and Wetland Hydrology during Wetland Delineations in the United States, Wetlands Regulatory Assistance Program.

Goffinet, B., Buck, W.R., Shaw, A.J., 2009. Morphology, anatomy, and classification of the Bryophyta, in: Shaw, A.J., Goffinet, B. (Eds.), Bryophyte Biology. Cambridge University Press, Cambrige, p. 580.

Gradstein, S.R., 1992. The vanishing tropical rainforest, in: Bates, J.W., Farmer, A.M. (Eds.), Bryophytes and Lichens in a Changing Environment. Clarendon Press, Oxford, p. 416.

Gradstein, S.R., Churchill, S.P., Salazar-Allen, N., 2001. Guide to the Bryophytes of Tropical America, Memoirs of the New York Botanical Garden. The New York Botunical Garden Press, New York.

Gradstein, S.R., Costa, D.P. da, 2003. The Hepaticae and Anthocerotae of Brazil, Memoirs of the New York Botanical Garden. The New York Botunical Garden Press, New York.

Gradstein, S.R., Ilkiu-Borges, A.L., 2009. Guide to the Plants of Central French Guiana. Part 4. Liverworts and Hornworts. Mem. N. Y. Bot. Gard. 76, 144.

Gradstein, S.R., Pócs, T., 1989. Bryophytes, in: Lieth, H., Werger, M.J.A. (Eds.), Tropical Rain Forest Ecosystems. Elsevier Science Publishers B.V., Amsterdam, p. 713.

Guèze, M., Paneque-Gálvez, J., Luz, A.C., Pino, J., Orta-Martínez, M., Reyes-García, V., Macía, M.J., 2012. Determinants of tree species turnover in a southern Amazonian rain forest. J. Veg. Sci. 24, 284–295. https://doi.org/10.1111/j.1654-1103.2012.01461.x

Hanski, I., 1982. Dynamics of Regional Distribution: The Core and Satellite Species Hypothesis. Oikos 38, 210. https://doi.org/10.2307/3544021

Harrison, S., Ross, S.J., Lawton, J.H., 1992. Beta Diversity on Geographic Gradients in Britain. J. Anim. Ecol. 61, 151. https://doi.org/10.2307/5518

Hida, N., Maia, J.G., Hiraoka, M., Shimmi, O., Mizutani, N., 1999. River water level changes of the Amazon Estuary: at Breves, Caxiuanã and Abaetetuba, in: Program, S. (Ed.), Manaus99. Hydrological and Geochemical Processes in Large Scale River Basins. Manaus, p. 85.

Honorio-Coronado, E.N., Baker, T.R., Phillips, O.L., Pitman, N.C.A., Pennington, R.T., Vásquez Martínez, R., Monteagudo, A., Mogollón, H., Dávila Cardozo, N., Ríos, M., García-Villacorta, R., Valderrama, E., Ahuite, M., Huamantupa, I., Neill, D.A., Laurance, W.F., Nascimento, H.E.M., Soares de Almeida, S., Killeen, T.J., Arroyo, L., Núñez, P., Freitas Alvarado, L., 2009. Multi-Scale Comparisons of Tree Composition in Amazonian

Terra Firme Forests. Biogeosciences 6, 2719–2731. https://doi.org/10.5194/bg-6-2719-2009

Hsiao-Pei, L., Yung-Chih, L., Shiao-Wei, H., Huang-Chi, C., Chih-hao, H., Hon-Tsen, Y., 2014. Spatial heterogeneity of gut microbiota reveals multiple bacterial communities with distinct characteristics. Sci. Rep. 4, 1–8. https://doi.org/10.1038/srep06185

Ilkiu-Borges, A.L., 2016. Prionolejeunea: Lejeuneaceae, Jungermanniopsida. Flora Neotrop. Monogr. 116, 1–131.

Ilkiu-Borges, A.L., Lisboa, R.C.L., 2002. Lejeuneaceae (Hepaticae), in: Lisboa, P.L.B. (Ed.), Caxiuanã. Populações, Meio Físico e Diversidade Biológica. Museu Paraense Emílio Goeldi, Belém, p. 734.

Jost, L., 2007. Partitioning diversity into independent alpha and beta components. Ecology. https://doi.org/10.1890/06-1736.1

Junk, W.J., Piedade, M.T.F., 2011. An Introduction to South American Wetland Forests: Distribution, Definitions and General Characterization, in: Junk, W.J., Piedade, M.T.F., Schöngart, J., Parolin, P. (Eds.), Amazonian Floodplain Forests. Ecological Studies (Analysis and Synthesis), Dordrecht, pp. 3–25.

Junk, W.J., Piedade, M.T.F., Schöngart, J., Cohn-Haft, M., Adeney, J.M., Wittmann, F., 2011. A Classification of Major Naturally-Occurring Amazonian Lowland Wetlands. Wetlands 31, 623–640. https://doi.org/10.1007/s13157-011-0190-7

Junk, W.J., Wittmann, F., Schöngart, J., Piedade, M.T.F., 2015. A classification of the major habitats of Amazonian black-water river floodplains and a comparison with their white-water counterparts. Wetl. Ecol. Manag. 23, 677–693. https://doi.org/10.1007/s11273-015-9412-8

Kürschner, H., 2004. Life strategies and adaptations in bryophytes from the near and Middle East. Turk. J. Botany 28, 73–84. https://doi.org/10.1016/0006-3207(92)90568-8

Legendre, P., Legendre, L., 1998. Numerical Ecology, 2nd ed. Elsevier Science B.V., Amsterdam.

Levis, C., Costa, F.R.C., Bongers, F., Peña-Claros, M., Clement, C.R., Junqueira, A.B., Neves, E.G., Tamanaha, E.K., Figueiredo, F.O.G., Salomão, R.P., Castilho, C. V., Magnusson, W.E., Phillips, O.L., Guevara, J.E., Sabatier, D., Molino, J.-F., Cardenas Lopez, D., Mendonza, A.M., Pitman, N.C.A., ter Steege, H., 2017. Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. Science (80-.). 355, 925–931. https://doi.org/10.1126/science.aal0157

Löbel, S., Dengler, J., Hobohm, C., 2006. Species richness of vascular plants, bryophytes and lichens in dry grasslands: The effects of environment, landscape structure and competition. Folia Geobot. 41, 377–393. https://doi.org/10.1007/BF02806555

Lopes, M.O., Pietrobom, M.R., Carmo, D.M. do, Peralta, D.F., 2016. Estudo comparativo de comunidades de briófitas sujeitas a diferentes graus de inundação no município de São Domingos do Capim , PA , Brasil 43, 159–171.

Magalhães, N. dos S., Marenco, R.A., Camargo, M.A.B., 2014. Do soil fertilization and forest canopy foliage affect the growth and photosynthesis of Amazonian saplings? Sci. Agric. 71, 58–65. https://doi.org/10.1590/S0103-90162014000100008

Magurran, A.E., 2004. Measuring of Biological Diversity, Blackwell science. https://doi.org/10.2989/16085910409503825

Mandl, N.A., Kessler, M., Robbert Gradstein, S., 2009. Effects of environmental heterogeneity on species diversity and composition of terrestrial bryophyte assemblages in tropical montane forests of southern Ecuador. Plant Ecol. Divers. 2, 313–321. https://doi.org/10.1080/17550870903341877

Marcon, E., Hérault, B., 2015. entropart : An R Package to Measure and Partition Diversity. J. Stat. Softw. 67, 1–26. https://doi.org/10.18637/jss.v067.i08

Márialigeti, S., Németh, B., Tinya, F., Ódor, P., 2009. The effects of stand structure on ground-floor bryophyte assemblages in temperate mixed forests. Biodivers. Conserv. 18, 2223–2241. https://doi.org/10.1007/s10531-009-9586-6

Marra, D.M., Chambers, J.Q., Higuchi, N., Trumbore, S.E., Ribeiro, G.H.P.M., Dos Santos, J., Negrón-Juárez, R.I., Reu, B., Wirth, C., 2014. Large-scale wind disturbances promote tree diversity in a Central Amazon forest. PLoS One 9. https://doi.org/10.1371/journal.pone.0103711

Matthews, T.J., Whittaker, R.J., 2014. Fitting and comparing competing models of the species abundance distribution: assessment and prospect. Front. Biogeogr. 6, 67–82. https://doi.org/10.21425/f56220607

McCune, B and Grace, J., 2002. MRPP (Multi-response Permutation Procedures) and related techniques. Analysis of Ecological Communities. Cap. 24. p. 128.

McCune, B., Grace, J.B., 2002. Canonical Correspondence Analysis. Analysis of Ecological Communities. cap. 21. p. 164.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., Dornelas, M., Enquist, B.J., Green, J.L., He, F., Hurlbert, A.H., Magurran, A.E., Marquet, P.A., Maurer, B.A., Ostling, A., Soykan, C.U., Ugland, K.I., White, E.P., 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecol. Lett. 10, 995–1015. https://doi.org/10.1111/j.1461-0248.2007.01094.x

Montag, L.F. a, Freitas, T.M.S., Wosiacki, W.B., Barthem, R.B., 2008. Os peixes da Floresta Nacional de Caxiuanã (municípios de Melgaço e Portel , Pará - Brasil). Bol. Mus. Para. Emílio Goeldi, Ciências Nat. 3, 11–34.

Montufar, R., Pintaud, J.-C., 2006. Variation in species composition, abundance and microhabitat preferences among western Amazonian terra firme palm communities. Bot. J. Linn. Soc. 151, 127–140. https://doi.org/10.1111/j.1095-8339.2006.00528.x

Moraes, E. de N.R., 2006. Diversidade, Aspectos Florísticos e Ecológicos dos Musgos (Bryophyta) da Estação Científica Ferreira Penna, Flona de Caxiuanã, Pará, Brasil. Universidade Federal Rural da Amazônia/Museu Paraense Emílio Goeldi.

Moraes, E. de N.R., Lisboa, R.C.L., 2009. Diversidade, taxonomia e distribuição por estados brasileiros das famílias Bartramiaceae, Brachytheciaceae, Bryaceae, Calymperaceae, Fissidentaceae, Hypnaceae e Leucobryaceae (Bryophyta) da Estação Científica Ferreira Penna, Caxiuanã, Pará, Brasil. Acta Amaz. 39, 773–792. https://doi.org/10.1590/S0044-59672009000400006

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018. vegan: Community Ecology Package. R package version 2.5-2 [WWW Document]. CRAN R. https://doi.org/ISBN 0-387-95457-0

Oliveira, H.C. de, Oliveira, S.M. de, 2016. Vertical distribution of epiphytic bryophytes in Atlantic Forest fragments in northeastern Brazil. Acta Bot. Brasilica 30, 609–617. https://doi.org/10.1590/0102-33062016abb0303

Oliveira, S.M. de, ter Steege, H., 2015. Bryophyte communities in the Amazon forest are regulated by height on the host tree and site elevation. J. Ecol. 103, 441–450. https://doi.org/10.1111/1365-2745.12359

Oliveira, S.M. de, ter Steege, H., 2013. Floristic overview of the epiphytic bryophytes of terra firme forests across the Amazon basin. Acta Bot. Brasilica 27, 347–363. https://doi.org/10.1590/S0102-33062013000200010

Oliveira, S.M. de, ter Steege, H., Cornelissen, J.H.C., Robbert Gradstein, S., 2009. Niche assembly of epiphytic bryophyte communities in the Guianas: a regional approach. J. Biogeogr. 36, 2076–2084. https://doi.org/10.1111/j.1365-2699.2009.02144.x

Pantoja, A., Ilkiu-Borges, A., Tavares-Martins, A., Garcia, E., 2015. Bryophytes in fragments of Terra Firme forest on the great curve of the Xingu River, Pará state, Brazil 1 Part of

Master's Dissertation of the first author. Brazilian J. Biol. 75, 238–249. https://doi.org/10.1590/1519-6984.02814BM

Pärtel, M., Zobel, M., Zobel, K., van der Maarel, E., 1996. The Species Pool and Its Relation to Species Richness: Evidence from Estonian Plant Communities. Oikos 75, 111–117. https://doi.org/10.2307/3546327

Peay, K.G., Baraloto, C., Fine, P.V.A., 2013. Strong coupling of plant and fungal community structure across western Amazonian rainforests. ISME J. 7, 1852–1861. https://doi.org/10.1038/ismej.2013.66

Piccinin, J.L., Ruivo, M.L.P., 2012. Caracterização Unidades Pedológicas, Plano de Manejo da Floresta Nacional de Caxiuanã. Instituto Chico Mendes de Conservação da Biodiversidade.

Pitman, N.C.A., Terborgh, J.W., Silman, M.R., NúÑez Vargas, P., Neill, D.A., Cerón, C.E., Palacios, W. a, Aulestia, M., 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. Ecology 82, 2101–2117.

Puig, H., 2007. A Floresta Tropical Úmida. UNESP, São Paulo.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists, Cambridge University Press. Cambridge University Press, New York.

Reese, W.D., 1993. Calymperaceae. Flora Neotrop. Monogr. 58, 102.

Reiner-Drehwald, M.E., 2000. Las Lejeuneaceae (Hepaticae) de Misiones, Argentina VI. Lejeunea y Taxilejeunea. Trop. Bryol. 19, 81–131. https://doi.org/http://dx.doi.org/10.11646/bde.19.1.14

Reiner-Drehwald, M.E., Goda, A., 2000. Revision of the genus Crossotelejeunea (Lejeuneaceae, Hepaticae). J. Hattori Bot. Lab. 89, 1–54.

Richards, P.W., 1984. The Ecology of tropical forest bryophytes, in: Schuster, R.M. (Ed.), New Manual of Bryology. The Hattori Botanical Laboratory, Nichinan, Japan.

Rodrigues, L.F., Cintra, R., Castilho, C.V., De Sousa Pereira, O., Pimentel, T.P., 2014. Influences of forest structure and landscape features on spatial variation in species composition in a palm community in central Amazonia. J. Trop. Ecol. 30, 565–578. https://doi.org/10.1017/S0266467414000431

Rosenzweig, L.M., Ziv, Y., 1999. The echo pattern of species diversity : pattern and processes. Ecography (Cop.). 22, 614–628.

Rosenzweig, M.L., 1995. Species diversity in space and time. The press syndicate of the university of Cambridge, Cambridge.

Ruivo, M.L.P., Cunha, E.S., 2003. Mineral and organic components in archaeological black earth and yellow latosol in Caxiuana, Amazon, Brazil, in: Tiezzi, E., Brebbia, C.A., Uso, J.L. (Eds.), Ecosystems and Sustainable Development IV. WIT Press, UK, p. 10.

Sanger, J.C., Kirkpatrick, J.B., 2015. Moss and vascular epiphyte distributions over host tree and elevation gradients in Australian subtropical rainforest. Aust. J. Bot. 63, 696. https://doi.org/10.1071/BT15169

Santos, N.D. Dos, Costa, D.P. Da, 2010. Phytogeography of the liverwort flora of the Atlantic Forest of southeastern Brazil. J. Bryol. 32, 9–22. https://doi.org/10.1179/037366810X12578498135634

Santos, N.D. Dos, Costa, D.P. Da, Kinoshita, L.S., Shepherd, G.J., 2011. Bryophytic and phytogeographical aspects of two types of forest of the Serra do Mar State Park, Ubatuba/SP, Brazil. Biota Neotrop. 11, 425–438. https://doi.org/10.1590/S1676-06032011000200040

Santos, N.D. Dos, Costa, D.P. Da, Kinoshita, L.S., Shepherd, G.J., 2014. Windborne: Can liverworts be used as indicators of altitudinal gradient in the Brazilian Atlantic Forest? Ecol. Indic. 36, 431–440. https://doi.org/10.1016/j.ecolind.2013.08.020

Schietti, J., Emilio, T., Rennó, C.D., Drucker, D.P., Costa, F.R.C., Nogueira, A., Baccaro, F.B., Figueiredo, F., Castilho, C. V., Kinupp, V., Guillaumet, J.L., Garcia, A.R.M., Lima, A.P., Magnusson, W.E., 2014. Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. Plant Ecol. Divers. 7, 241–253. https://doi.org/10.1080/17550874.2013.783642

Schuster, R.M., 1983. Phytogeography of bryophytes, in: Schuster, R.M. (Ed.), New Manual of Bryophytes. Hattori Botanical Laboratory, Nichinan, Japan.

Shaw, A.J., Szövényi, P., Shaw, B., 2011. Bryophyte diversity and evolution: Windows into the early evolution of land plants. Am. J. Bot. 98, 352–369. https://doi.org/10.3732/ajb.1000316

Shepherd, G.J., 2010. Fitopac 2.1. Universidade Estadual de Campinas.

Silman, M.R., 2011. Tropical Rainforest Responses to Climatic Change, in: Bush, M.B., Flenley, J.R., Gosling, W. (Eds.), Tropical Rainforest Responses to Climatic Change. Springer Berlin Heidelberg, Berlin, Heidelberg, p. 428. https://doi.org/10.1007/978-3-540-48842-2

Söderström, L., 1989. Regional Distribution Patterns of Bryophyte Species on Spruce Logs in Northern Sweden. Bryologist 92, 349. https://doi.org/10.2307/3243403

Söderström, L., During, H.J., 2005. Bryophyte rarity viewed from the perspectives of life history strategy and metapopulation dynamics. J. Bryol. 27, 261–268.

https://doi.org/10.1179/174328205X70010

Stropp, J., ter Steege, H., Malhi, Y., ATDN, RAINFOR, 2009. Disentangling regional and local tree diversity in the Amazon. Ecography (Cop.). 32, 46–54. https://doi.org/10.1111/j.1600-0587.2009.05811.x

Sugihara, G., Bersier, L.-F., Southwood, T.R.E., Pimm, S.L., May, R.M., 2003. Predicted correspondence between species abundances and dendrograms of niche similarities. Proc. Natl. Acad. Sci. 100, 5246–5251. https://doi.org/10.1073/pnas.0831096100

Tavares, A.C.C., 2009. Florística e Ecologia das Comunidades de Briófitas em Florestas de Terra Firme no Estado do Pará, Amazônia. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro/Escola Nacional de Botânica Tropical.

Tavares-Martins, A.C.C., Lisboa, R.C.L., Costa, D.P. da, 2014. Bryophyte flora in upland forests at different successional stages and in the various strata of host trees in northeastern Pará, Brazil. Acta Bot. Brasilica 28, 46–58. https://doi.org/10.1590/S0102-33062014000100005

ter Steege, H., Pitman, N., Sabatier, D., Castellanos, H., van Der Hout, P., Daly, D.C., Silveria, M., Phillips, O., Vasquez, R., van Andel, T., Duivenvoorden, J., Adalardo De Olivier, A., Ek, R., Lilwah, R., Thomas, R., van Essen, J., Baider, C., Maas, P., Mori, S., Terborgh, J., Vargas, P.N., Mogollon, H., Morawetz, W., 2003. A spatial model of tree α-diversity and -density for the Amazon. Biodivers. Conserv. 12, 2255–2277. https://doi.org/10.1023/a:1024593414624

ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J.-F., Prévost, M.-F., Spichiger, R., Castellanos, H., Von Hildebrand, P., Vásquez, R., 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. Nature 443, 444–447.

ter Steege, H., Pitman, N.C. A, Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., Phillips, O.L., Castilho, C. V, Magnusson, W.E., Molino, J.-F., et al., 2013. Hyperdominance in the Amazonian tree flora. Science 342, 1243092. https://doi.org/10.1126/science.1243092

Terborgh, J., 1973. On the Notion of Favorableness in Plant Ecology. Am. Nat. 107, 481–501. https://doi.org/10.1086/282852

Tuomisto, H., Zuquim, G., Cárdenas, G., 2014. Species richness and diversity along edaphic and climatic gradients in Amazonia. Ecography (Cop.). 37, 1034–1046. https://doi.org/10.1111/ecog.00770

Ulrich, W., Gotelli, N.J., 2007. Null model analysis of species nestedness patterns. Ecology

88, 1824–1831. https://doi.org/10.1890/06-1208.1

Uniyal, P.L., 1999. Role of bryophytes in conservation of ecosystems and biodiversity. Botanica 49, 101–115.

Valencia, R., Balslev, H., Paz Y Miño C, G., 1994. High tree alpha-diversity in Amazonian Ecuador. Biodivers. Conserv. 3, 21–28. https://doi.org/10.1007/BF00115330

Valencia, R., Foster, R.B., Villa, G., Condit, R., Svenning, J., Hernández, C., Romoleroux, K., Losos, E., Magard, E., Balslev, H., 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. J. Ecol. 92, 214–229. https://doi.org/10.1111/j.0022-0477.2004.00876.x

Valente, E. de B., Pôrto, K.C., Bastos, C.J.P., 2017. Habitat heterogeneity and diversity of bryophytes in campos rupestres. Acta Bot. Brasilica 31, 241–249. https://doi.org/10.1590/0102-33062016abb0450

Vanderpoorten, A., Engels, P., 2002. The effects of environmental variation on bryophytes at a regional scale. Ecography (Cop.). 25, 513–522. https://doi.org/10.1034/j.1600-0587.2002.250501.x

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30, 279–338. https://doi.org/https://doi.org/10.2307/1943563

Willis, J.C., 1922. Age and area: a study in geographical distribution and origin of species. Cambridge University Press, Cambrige.

Wittmann, F., Junk, W.J., Piedade, M.T.F., 2004. The várzea forests in Amazonia: Flooding and the highly dynamic geomorphology interact with natural forest succession. For. Ecol. Manage. 196, 199–212. https://doi.org/10.1016/j.foreco.2004.02.060

Wittmann, F., Schongart, J., Montero, J.C., Motzer, T., Junk, W.J., Piedade, M.T.F., Queiroz, H.L., Worbes, M., 2006. Tree species composition and diversity gradients in white-water forests across the Amazon Basin. J. Biogeogr. 33, 1334–1347. https://doi.org/10.1111/j.1365-2699.2006.01495.x

Zobel, M., van der Maarel, E., Dupré, C., 1998. Species pool: the concept, its determination and significance for community restoration. Appl. Veg. Sci. 1, 55–66. https://doi.org/10.2307/1479085

Appendix A. Bryophytes epiphytes and distribution patterns of species of the vegetations in the Caxiuanã National Forest, Pará state, Brazil. VZ = Várzea vegetation; IG = Igapó vegetation; TF = Terra Firme vegetation. C = common; F = frequent; R = Rare. The distribution patterns (local and regional) are suitable only for this dataset.

Division/Family/Taxon	Distribution patterns				Nº of occurrences	Nº of vegetations	Nº of trees	Testimony (Host Tree)
	Local			Regional				
	VZ	IG	TF					
Bryophyta								
Calymperaceae								
Calymperes erosum Müll. Hal.	F	R	F	Core	14	3	8	IG1; TF1; VZ1
Calymperes locnchophyllum Schwägr.	.	C	F	Core	18	2	9	IG4; TF1
Calymperes palisotii Schwägr.	C	F	.	Core	17	2	8	IG3; VZ7
Calymperes platyloma Mitt.	.	C	.	Urban	32	1	8	IG4
Octoblepharum albidum Hedw.	F	F	C	Core	23	3	11	IG5; TF1; VZ1
Octoblepharum pulvinatum (Dozy & Molk.) Mitt.	.	.	F	Satellite	3	1	2	TF2
Syrrhopodon cymbifolius Müll. Hal.	.	R	C	Core	10	2	5	IG7; TF7
Syrrhopodon gaudichaudii Mont.	.	.	R	Satellite	1	1	1	TF7
Syrrhopodon incompletus Schwägr.	R	F	F	Core	12	3	6	IG5; TF2; VZ3
Syrrhopodon ligulatus Mont.	R	.	C	Core	13	2	6	TF2; VZ4
Syrrhopodon simmondsii Steere	.	.	C	Core	10	1	4	TF4
Fissidentaceae								
Fissidens guinanensis Mont.	.	C	C	Core	14	2	10	IG1; TF1
Fissidens pellucidus Hornsch.	R	F	F	Core	7	3	5	IG8; TF6; VZ7
Leucobryaceae								
Leucobryum martianum (Hornsch.) Hampe ex Müll. Hal.	.	R	.	Satellite	1	1	1	IG6
Leucomiaceae								
Leucomium strumosum (Hornsch.) Mitt.	.	R	R	Rural	2	2	2	IG6; TF8
Phyllodrepaniaceae								
Mniomalia viridis (Mitt.) Müll. Hal.	R	C	.	Core	17	2	9	IG5; VZ3
Pylaisiadelphaceae								
Isopterygium tenerum (Sw.) Mitt.	F	.	.	Satellite	2	1	2	VZ1
Sematophyllaceae								
Microcalpe subsimplex (Hedw.) W.R. Buck	R	.	C	Core	13	2	7	TF5; VZ6

Division/Family/Taxon	Distribution patterns				Nº of occurrences	Nº of vegetations	Nº of trees	Testimony (Host Tree)
	Local			Regional				
	VZ	IG	TF					
Trichosteleum papillosum (Hornsch.) Jaeg.	R	R	.	Rural	2	2	2	IG2; VZ5
Trichosteleum subdemissum (Hornsch.) A.Jaeger.	R	F	.	Rural	3	2	3	IG6; VZ7
Stereophyllaceae								
Pilosium chlorophyllum (Hornsch.) Müll. Hal.	.	.	F	Urban	3	1	3	TF6
Marchantiophyta								
Frullaniaceae								
Frullania caulisequa (Nees) Nees	.	R	R	Rural	1	2	2	IG2; TF2
Frullania gibbosa Nees, Ann	R	.	.	Satellite	1	1	1	VZ2
Frullania sp1.	.	F	.	Satellite	2	1	2	IG1
Frullania sp2.	.	R	.	Satellite	1	1	1	IG6
Lejeuneaceae								
Acrolejeunea emergens (Mitt.) Steph.	R	.	.	Satellite	1	1	1	VZ8
Acrolejeunea torulosa (Lehm. & Lindenb.) Schiffn.	C	.	.	Urban	22	1	7	VZ1
Archilejeunea auberiana (Mont.) A.Evans	.	F	.	Urban	4	1	4	IG5
Archilejeunea badia (Spruce) Steph.	.	.	R	Satellite	1	1	1	TF2
Archilejeunea crispistipula (Spruce) Steph.	C	.	F	Core	23	2	9	TF2; VZ6
Archilejeunea fuscescens (Hampe ex Lehm.) Fulford	.	.	C	Urban	8	1	5	TF2
Archilejeunea parviflora (Nees) Schiffn.	F	.	C	Core	19	2	8	TF7; VZ6
Caudalejeunea lehmanniana (Gottsche) A.Evans	.	.	F	Satellite	2	1	2	TF1
Ceratolejeunea coarina (Gottsche) Steph.	C	R	F	Core	21	3	11	IG4; TF2; VZ4
Ceratolejeunea confusa R.M.Schust.	F	.	R	Rural	3	2	3	TF2; VZ1
Ceratolejeunea cornuta (Lindenb.) Schiffn.	C	C	C	Core	47	3	21	IG5; TF1; VZ1
Ceratolejeunea cubensis (Mont.) Schiffn.	C	F	F	Core	22	3	9	IG6; TF1; VZ3
Ceratolejeunea guianensis (Nees & Mont.) Steph.	R	.	.	Satellite	3	1	1	VZ3
Ceratolejeunea minuta Dauphin	F	C	C	Core	59	3	20	IG2; TF2; VZ3
Cheilolejeunea adnata (Kunze) Grolle	C	R	C	Core	17	3	11	IG4; TF2; VZ2
Cheilolejeunea aneogyna (Spruce) A.Evans	C	R	C	Core	19	3	10	IG4; TF3; VZ2
Cheilolejeunea clausa (Nees & Mont.) R.M.Schust.	.	.	R	Satellite	1	1	1	TF6

Division/Family/Taxon	Distribution patterns				Nº of occurrences	Nº of vegetations	Nº of trees	Testimony (Host Tree)
	Local			Regional				
	VZ	IG	TF					
Cheilolejeunea comans (Spruce) R.M.Schust.	R	.	.	Satellite	1	1	1	VZ4
Cheilolejeunea holostipa (Spruce) Grolle & R.-L.Zhu.	F	R	C	Core	12	3	8	IG4; TF1; VZ1
Cheilolejeunea insecta Grolle & Gradst.	.	C	.	Urban	12	1	8	IG1
Cheilolejeunea neblinensis Ilkiu-Borges & Gradst.	.	.	F	Satellite	4	1	2	TF5
Cheilolejeunea oncophylla (Aongström) Grolle & E.Reiner	C	C	C	Core	72	3	22	IG5; TF2; VZ1
Cheilolejeunea rigidula (Mont.) R.M.Schust.	F	C	C	Core	18	3	14	IG5; TF2; VZ1
Cololejeunea camillii (Lehm.) A.Evans	R	.	R	Rural	2	2	2	TF2; VZ5
Cololejeunea cardiocarpa (Mont.) A.Evans	.	.	R	Satellite	1	1	1	TF2;
Cololejeunea contractiloba A.Evans	R	.	F	Rural	3	2	3	TF3; VZ5
Cololejeunea minutissima (Sm.) Schiffn.	F	.	.	Satellite	4	1	2	VZ7
Cololejeunea sp1.	.	R	.	Satellite	1	1	1	IG1
Cololejeunea sp2.	.	R	.	Satellite	1	1	1	IG6
Cololejeunea subcardiocarpa Tixier	.	.	C	Urban	5	1	4	TF1
Cololejeunea surinamensis Tixier	.	.	C	Urban	4	1	4	TF1
Cyclolejeunea convexistipa (Lehm. & Lindenb.) A.Evans	.	R	R	Rural	2	2	2	IG3; TF5
Diplasiolejeunea brunnea Steph.	.	F	F	Core	5	2	5	IG1; TF2
Diplasiolejeunea cobrensis Gottshe ex Steph.	.	F	.	Satellite	2	1	2	IG1
Diplasiolejeunea rudolphiana Steph.	.	F	R	Rural	3	2	3	IG5; TF3
Drepanolejeunea fragilis Bischl.	.	F	F	Core	7	2	6	IG4; TF1
Haplolejeunea amazonica Ilkiu-Borges & Gradst.	.	.	C	Urban	7	1	5	TF5
Harpalejeunea stricta (Lindenb. & Gottshe) Steph.	R	F	.	Rural	4	2	4	IG2; VZ7
Harpalejeunea tridens (Besch. & Spruce) Steph.	.	F	.	Urban	8	1	4	IG8
Lejeunea adpressa Nees	F	.	.	Urban	3	1	3	VZ2
Lejeunea asperrima Spruce	.	C	.	Urban	8	1	6	IG3
Lejeunea boryana Mont.	.	C	.	Urban	10	1	6	IG2
Lejeunea cerina (Lehm. & Lindenb.) Gottsche	.	C	.	Urban	8	1	5	IG1
Lejeunea controversa Gottsche	.	F	F	Core	7	2	5	IG6; TF8
Lejeunea flava Nees	R	.	F	Rural	3	2	3	TF3; VZ5

Division/Family/Taxon	Distribution patterns				Nº of occurrences	Nº of vegetations	Nº of trees	Testimony (Host Tree)
	Local			Regional				
	VZ	IG	TF					
Lejeunea grossitexta (Steph.) E.Reiner & Goda	.	.	R	Satellite	2	1	1	TF6
Lejeunea immersa Spruce	.	R	.	Satellite	1	1	1	IG5
Lejeunea laetevirens Nees	F	F	.	Core	5	2	5	IG7; VZ1
Lejeunea sp1.	.	R	.	Satellite	1	1	1	IG4
Lejeunea sp2.	.	R	.	Satellite	1	1	1	IG4
Lejeunea sp3.	.	R	F	Rural	2	2	3	IG6; TF8
Lejeunea sp4.	.	F	.	Satellite	2	1	2	IG8
Lejeunea tapajosensis Spruce	.	.	R	Satellite	1	1	1	TF2
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	.	C	F	Core	7	2	7	IG1; TF1
Lopholejeunea subfusca (Nees) Schiffn.	C	C	F	Core	25	3	13	IG2; TF6; VZ3
Mastigolejeunea auriculata (Wilson) Schiffn.	C	R	.	Core	16	2	8	IG3; VZ1
Mastigolejeunea innovans (Spruce) Steph.	.	R	.	Satellite	1	1	1	IG1
Mastigolejeunea plicatiflora (Spruce) Steph.	F	R	F	Core	11	3	6	IG1; TF1; VZ3
Metalejeunea cucullata (Reinw. Et al.) Grolle	.	R	.	Satellite	1	1	1	IG3
Microlejeunea bullata (Taylor) Steph.	.	R	.	Satellite	1	1	1	IG6
Microlejeunea epiphylla Bischl.	C	C	C	Core	31	3	21	IG2; TF2; VZ3
Neurolejeunea seminervis (Spruce) Schiffn.	.	C	R	Core	30	2	9	IG4; TF6
Pictolejeunea picta (Gottsche ex Steph.) Grolle	.	.	C	Urban	9	1	5	TF4
Prionolejeunea aemula (Gottsche) A.Evans	.	R	.	Satellite	1	1	1	IG1
Prionolejeunea denticulata (Weber) Schiffn.	.	C	F	Core	14	2	9	IG5; TF6
Prionolejeunea muricato-serrulata (Spruce) Steph.	.	F	F	Core	8	2	5	IG5; TF1
Prionolejeunea scaberula (Spruce) Steph.	.	C	.	Urban	16	1	8	IG3
Prionolejeunea trachyodes (Spruce) Steph.	.	C	.	Urban	29	1	8	IG2;
Pycnolejeunea contigua (Nees) Grolle	C	.	R	Core	21	2	8	TF1; VZ1
Pycnolejeunea gradsteinii Ilk.-Borg.	.	.	F	Satellite	2	1	2	TF2
Pycnolejeunea papilosa X.-L. He	C	R	F	Core	29	3	11	IG1; TF3; VZ1
Pycnolejeunea sp.	F	F	.	Core	8	2	7	IG1; VZ5
Rectolejeunea berteroana (Gottsche ex Steph.) A.Evans	F	R	R	Rural	4	3	4	IG3; TF4; VZ4
Rectolejeunea flagelliformis A.Evans	F	C	F	Core	16	3	12	IG4; TF2; VZ3

Division/Family/Taxon	Distribution patterns				Nº of occurrences	Nº of vegetations	Nº of trees	Testimony (Host Tree)
	Local			Regional				
	VZ	IG	TF					
Symbiezidium barbiflorum (Lindenb. & Gottsche) A.Evans	.	C	F	Core	14	2	8	IG1; TF6
Symbiezidium transversale (Sw.) Trevis	F	.	.	Urban	3	1	3	VZ5
Thysananthus amazonicus (Spruce) Schiffn.	.	R	.	Satellite	1	1	1	IG3
Vitalianthus sp1.	.	.	F	Satellite	2	1	2	TF1
Vitalianthus sp2.	.	.	F	Urban	5	1	3	TF7
Xylolejeunea crenata (Nees & Mont) X.-L. He & Grolle	.	R	F	Rural	4	2	4	IG2; TF3
Lepidoziaceae								
Zoopsidella integrifolia (Spruce) R.M.Schust.	.	R	.	Satellite	1	1	1	IG6
Plagiochilaceae								
Plagiochila aerea Taylor	.	R	R	Rural	3	2	2	IG8; TF1
Plagiochila montagnei Nees	F	.	.	Satellite	2	1	2	VZ2
Plagiochila raddiana Lindenb.	F	.	.	Satellite	3	1	2	VZ8
Plagiochila subplana Lindenb.	.	R	R	Rural	2	2	2	IG7; TF8
Radulaceae								
Radula javanica Gottsche	R	F	.	Rural	4	2	3	IG6; VZ3
Radula stenocalyx Mont.	.	F	.	Satellite	2	1	2	IG1

3.2 VERTICAL GRADIENT OF EPIPHYTIC BRYOPHYTES IN THE AMAZON: THE RULE AND ITS EXCEPTION

Abstract

In Amazonian *Terra Firme* vegetation, epiphytic bryophytes present a deterministic distribution along height zones in host trees, at both local and regional scale. Recent findings about the influence of vegetation structure variation on epiphytic bryophyte assemblages suggest that the vertical gradient may also change among adjacent vegetation types. In order to analyze this influence, bryophytes were sampled in five zones from the base to the top of 24 host trees in *Várzea* and *Igapó* (flooded) and *Terra Firme* (non-flooded) vegetation. The species richness and diversity, distribution of guilds of tolerance to light incidence, floristic similarity, and turnover of species composition were evaluated within and between vegetation types. The vertical gradient was observed only in *Igapó* and *Terra Firme.* Species richness and diversity were higher at the base in flooded forests, and at the outer canopy in non-flooded forests. These zones also showed higher floristic similarities among vegetation types. The distribution of guilds explained the main patterns observed in assemblages. The spatial distribution of epiphytes in the studied forests is regulated by the interaction between the height zone and vegetation type, and light tolerance is one of the most important attributes explaining the distribution patterns of epiphytes in the Amazon.

Keywords: Amazonia**.** Canopy. Community assembly, *Igapó* vegetation. Beta diversity. Environmental Heterogeneity. Conservation Units.

Introduction

Plant communities in the Amazon respond to different environmental gradients, both locally and regionally (Tuomisto & Poulsen, 2000; Tuomisto *et al.,* 2002; Wittmann *et al.,* 2006; Oliveira & ter Steege, 2015; Quaresma *et al.,* 2017). In this context, the assembly of epiphytic bryophytes is strongly influenced by local environmental filters, involving vertical zoning, successional stages and variation in vegetation types (Acebey *et al.,* 2003; Oliveira *et al.,* 2009; Tavares-Martins *et al.,* 2014; Oliveira & ter Steege, 2015; Cerqueira *et al.,* 2017).

The vertical distribution of epiphytes in tropical forests is mainly determined by variations in environmental conditions that occur from the understory to the canopy (Allee, 1926; Cornelissen & ter Steege, 1989). This gradient is one of the most consistently observed in bryophytes and reflects the environmental filtering associated to changes in the availability of light, water and temperature (Pócs, 1982; Richards, 1984; Acebey *et al.,* 2003), however, without taking into account the interactions between species (Kraft *et al.,* 2015).

The vertical distribution of bryophytes in tropical forests has been mainly addressed in the context of effects of habitat loss and fragmentation in the natural environments of these plants (Alvarenga *et al.,* 2010; Sporn *et al.,* 2010; Silva & Pôrto, 2010; 2013). Particularly in the Amazon, studies on the vertical gradient of epiphytic bryophytes have been concentrated in *Terra Firme* vegetation (Oliveira *et al.,* 2009; Tavares-Martins *et al.,* 2014; Oliveira & ter Steege, 2015), while information about floodplains such as *Várzea* and *Igapó* is still missing. Among other characteristics, these forest types differ from each other by their arboreal vegetation structure and floristic composition as well as the periodic and seasonal flood flows ruled by regimes of adjacent rivers (Junk *et al.,* 2011). In the eastern Amazon, the richness and composition of epiphytic bryophytes has been observed to vary among these vegetation types on a local scale (Cerqueira *et al.,* 2017), where *Igapó* forests are richer and more diverse than those of *Várzea*, in agreement with the patterns found for vascular plants in the region (Ferreira *et al.,* 2013).

In *Terra Firme* vegetation of the Amazon basin, the vertical gradient of bryophytes has been observed both at local and regional scale: height zone is a significant element in these assemblages (Oliveira & ter Steege, 2015) while species composition per zone is relatively homogeneous across large distances (Oliveira & ter Steege, 2013). The pattern was attributed to the combination of strong niche assembly with high dispersal potential of bryophytes. In view of these patterns and the responses of bryophyte assemblages to changes in host tree structure and composition recently reported in the understory of flooded forested areas (Cerqueira *et al*., 2017), it is possible that the vertical distribution of bryophytes also changes on a local scale even between preserved habitats.

Thus, we hypothesized that: (1) the vertical gradient is present in the non-flooded (*Terra Firme*) and flooded (*Igapó* and *Várzea*) vegetation types, but weaker in the latter due to differences in landscape structure and the existence of flood dynamics in the understory; (2) the proportion of generalist taxa is greater in the flooded forests in response to their more intense dynamics, which filter species with wider niches; (3) the species richness and diversity, as well as the similarity between communities are higher at the base and outer canopy of host trees within and between vegetation types because these zones represent the two extremes of the microenvironmental gradient.

Methods

The study was conducted in the Caxiuanã National Forest (Caxiuanã FLONA), located in the eastern portion of the Amazon (01°42' 30” S and 51°31' 45” W, 62m altitude) (Montag *et al.,* 2008). The climate of the region is tropical according to Köppen's classification (Köppen & Geiger, 1928; Alvares *et al.,* 2014). The average annual precipitation varies between 2000 and 2500 mm, with a pronounced dry season from June to November (Costa *et al.,* 2010), the annual average temperature is 25.9°C and the relative humidity of the air varies around 82% (Castro *et al.,* 2013).

Sampling and taxonomic identification

Samples were collected in *Terra Firme* (TF, non-flooded), *Igapó* (IG, flooded) and *Várzea* (VZ, flooded) vegetation. Fieldwork was carried out between September 2015 and July 2016. Eight 20-25 meter-tall host trees, with diameter at breast height (DBH) ≥ 20 cm, and bark presenting intermediate roughness were selected in each vegetation type, totaling 24 trees. The minimum distance between sampled trees was 20 m, and their canopies were not in contact with each other. To facilitate climbing, we selected trees with branches that could resist the weight of an adult person and upper branches that were visible from the ground (Gradstein *et al.,* 1996).

Bryophytes were collected in five height zones, namely: zone 1 = from the base up to 1 m; zones 2 and 3 = lower and upper trunk, respectively; zone 4 = base of crown; and zone 5 = outer sun-lit twigs/leaves (outer canopy). A set of four 10 cm^2 plots were collected in each height zone and pooled into a single sample (40 cm^2) (Oliveira *et al*., 2009; Oliveira & ter Steege, 2013), thus totaling five samples per host tree (Fig. 1). DBH and shaft height of each host tree were measured with a metric tape and canopy height was visually estimated. Each host tree served as the central point of a 10 m² plot, and hemispheric photographs were taken with a digital camera (Nikon Coolpix 5400) and 8mm fisheye lens (Nikon FC-E9) at the corners of each plot. The canopy openness of the areas surrounding each host tree corresponded to the average of the four photographs. The mean values and standard deviations (SD) of the samples in each vegetation type are listed in Table 1.

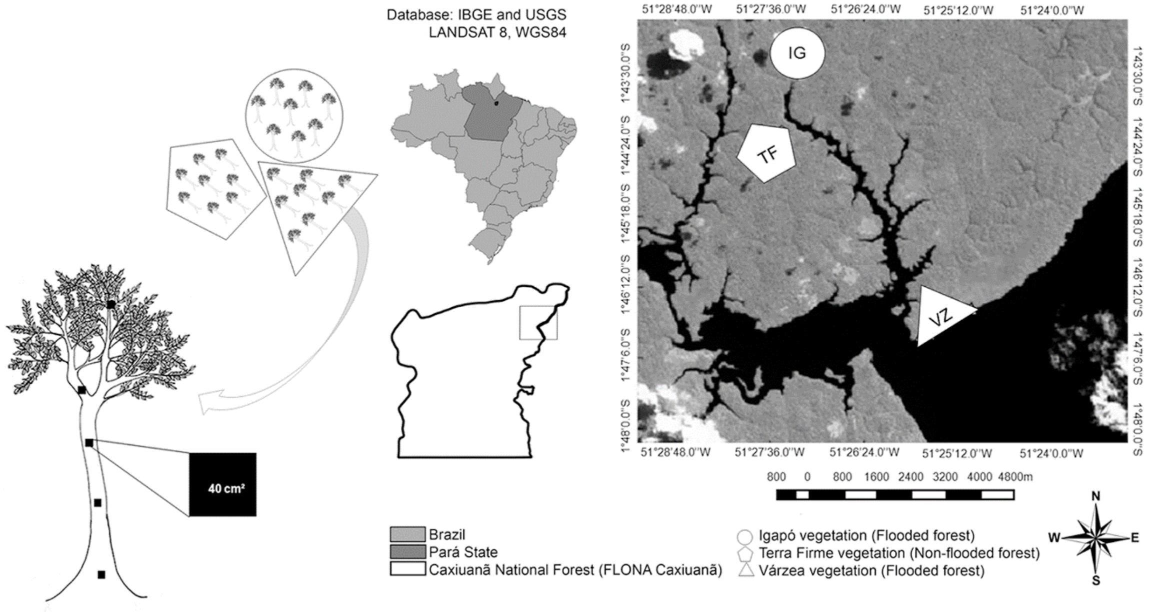

Figure 1. Sampling methods and study area.

Table 1. Mean and standard deviation (SD) of host tree variables and canopy openness per vegetation type. IG = *Igapó*; TF = *Terra Firme*; VZ = *Várzea*.

Variables	Vegetation Type		
	IG	TF	VZ
DBH	29.16 ± 5.8	36.21 ± 4.3	44.80 ± 10.8
Height of the shaft	10.16 ± 2.5	13.96 ± 2.8	10.75 ± 1.8
Height of the canopy	10.56 ± 3.3	9.62 ± 1.5	10.87 ± 2.1
Total height	20.72 ± 2.2	23.58 ± 2.9	21.62 ± 2.4
Canopy openness	12.50 ± 2.7	12.15 ± 1.8	12.89 ± 1.6

Bryophytes were identified with the aid of specialized bibliography and specimens of difficult determination were sent to taxonomists for confirmation and taxonomic identification. The most used works were Florschütz (1964), Reese (1993), Reiner-Drehwald (2000), Reiner-Drehwald & Goda (2000), Dauphin (2003), Gradstein & Costa (2003), Gradstein & Ilkiu-Borges (2009), Moraes & Lisboa (2009), Reiner-Drehwald & Grolle

(2012), Bordin & Yano (2013) and Ilkiu-Borges (2016). The classifications of Goffinet *et al.* (2009) for Bryophyta and Crandall-Stotler *et al.* (2009) for Marchantiophyta were adopted in this study. Taxonomic updates of some species were made based on recently published literature for the genera *Microcalpe*, *Archilejeunea, Cheilolejeunea* and *Myriocoleopsis* (YU *et al*., 2014; SHI *et al.,* 2015; Bastos *et al.,* 2017; Carvalho *et al.,* 2017), the “World checklist of hornworts and liverworts” (Söderström et al., 2016), and Flora do Brasil 2020 database (Flora do Brasil, 2020). Vouchers were deposited in the collections of the Geraldo Mariz (UFP) and João Murça Pires (MG) herbaria. In this study, we use the following definition of guild “group of species that exploit the same class of environmental resources in a similar way” (Root, 1967; Blondel, 2003). Also, the term guild was used as a synonymous of the synusia defined by Richards (1984). The considered resources for bryophytes were light and moisture.

Data analysis

Bryophyte assemblages were analyzed to evaluate the variation of richness, diversity, proportion of guilds of tolerance to light incidence, and species composition along height zones within and between vegetation types, as well as to check the existence of a vertical gradient in the assemblages of each vegetation type. All analyses were performed using R (R Core Team, 2019).

Richness corresponded to the number of species recorded in each height zone or forest type. Species richness was compared between height zones in each vegetation type, and between each height zone in different vegetation types. These comparisons were tested by one-way analysis of variance (ANOVA) at 5% level of significance, whenever assumptions were met. Species richness data were checked for normality using the Shapiro-Wilk test, and the homogeneity of the variances was tested with the Levene's test of the Car package (Fox & Weisberg, 2011). The Tukey Honestly Difference Test (HSD) was applied *a posteriori* to verify the existence of significant differences between groups.

The Fisher's alpha (α) was calculated to determine the species diversity per height zone in each vegetation type, as this index ($S=a*\ln(1+n/a)$ where S is number of taxa, n is number of individuals and a is the Fisher's alpha) is considered a robust measure, not so sensitive to sample size (Fisher *et al.,* 1943; Magurran, 2004; Beck & Schwanghart, 2010). For this calculation, we considered the abundance and richness of species recorded per height zone in each vegetation type. Because of the impossibility of dissociating bryophyte individuals present in the samples, the incidence of each species in the plot was used to define its abundance, which could vary along the different zones of the same host tree (1-5) and between host trees of the same vegetation type (1-8).

The floristic composition of height zones within and between forest types was compared using the Sørensen's similarity index, which attributes double weight to double presences (Legendre & Legendre, 1998), and the Bray-Curtis dissimilarity index (Bray & Curtis, 1957). Two matrices with presence-absence and abundance data per height zone of each vegetation type were created. The Sørensen and Bray-Curtis indexes were calculated by the betadiver function of the vegan package (Oksanen *et al.,* 2018).

The non-metric multidimensional scaling (NMDS) method was used to evaluate the variation of species composition between vegetation types and between height zones. For this purpose, a presence/absence matrix was created using samples from each height zone of the 24 host trees. One of the samples had to be excluded due to low number of species. The metaMDS function of the vegan package was used to perform the NMDS (Oksanen *et al.,* 2018). This ordination (resizing) tries to represent objects by reducing them to a few dimensions and at the same time preserving the respective distance between them (Legendre & Legendre, 1998).

A multivariate analysis by permutation - PERMANOVA ('Adonis' function) was used to test the existence of statistically significant differences in species composition between the three vegetation types in relation to the five height zones, whose groups were defined *a priori*. Changes in the composition of species with respect to the guilds of tolerance to light incidence (*sensu* Richards, 1984) were evaluated in the three vegetation types, correlating them with the height zones of occurrence. To this end, the species were classified according to the works of Richards (1984), Cornelissen & ter Steege (1989), Gradstein (1992a), Gradstein *et al.* (2001), Oliveira *et al.* (2009), and Tavares-Martins *et al.* (2014). The following literature-based classification was used: shade specialist epiphytes - Sha, present in the understory microhabitat; sun specialist epiphytes - Sun, present in the canopy; and generalist epiphytes - Gen, occurring in both microhabitats (Richards, 1984).

The correlation between the occurrence of guilds in the height zones was checked with the chi-square test, analyzing the degree of association between categorical variables (height zone x guild). In this analysis, we used matrices of guild abundance per height zone in each forest type. The chi-square (X^2) test assumes the null hypothesis that the observed frequencies are not different from those generated by chance, and there is therefore no difference between them due to the absence of association between the variables (Gotelli & Ellison, 2011).

Results

A total of 112 species of epiphytic bryophytes, among 21 mosses and 91 liverworts, were recorded in *Igapó* (73 spp.), *Terra Firme* (66 spp.) and *Várzea* (48 spp.) (S1). The mean species richness per height zone increased in the outer canopy in *Igapó* and in *Terra Firme*, while the opposite occurred in *Várzea* (Fig. 2). The mean richness varied between zones in all forest types, but this variation was statistically significant only in *Igapó* ($F_{[4, 35]} = 6.48$, $p = 0.0005$) where the richest zones (base and outer canopy) differed from the upper trunk and the inner canopy (Fig. 2, lowercase letters).

The base of the trunks was the richest zone in the flooded forests (Z1), while the outer canopy had the highest number of species in *Terra Firme* (Z5) (Fig. 3A-C). The mean species richness of height zones compared across the different vegetation types showed significant differences only in the case of the extreme zones, *i.e.* base and outer canopy ($F_{[2, 24]} = 3.113$, $p = 0.065$); this differences were slight between the base of *Igapó* and *Terra Firme* and consistent between the outer canopy of *Igapó* and *Várzea* (Fig. 2, uppercase letters).

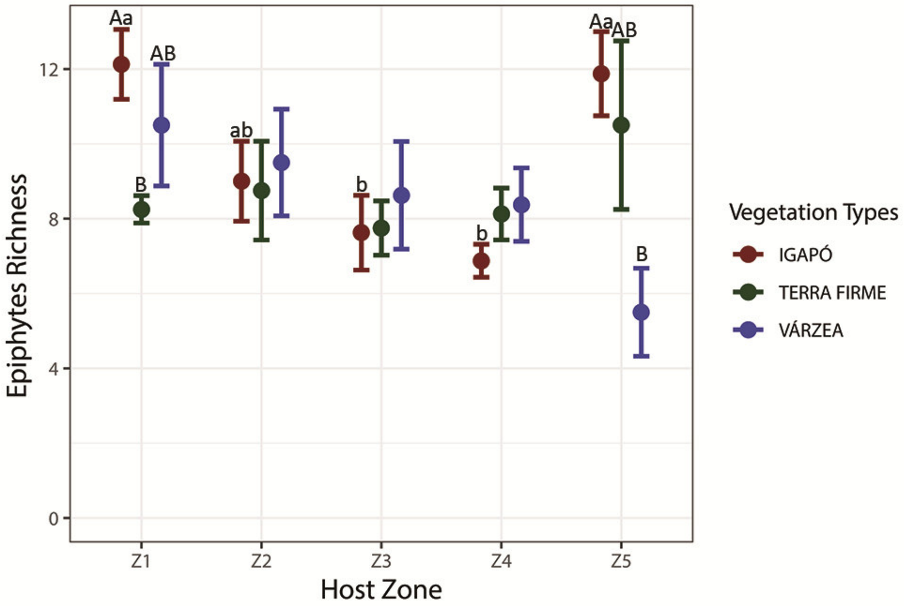

Figure 2. Mean and standard error of the richness of epiphytic bryophytes in the height zones per vegetation type. Lowercase letters are used to indicate differences between height zones and uppercase letters to indicate differences between height zones compared in the different vegetation types in *Igapó*.

The base and the outer canopy were the zones with the greater number of exclusive species in the forests. In *Igapó* and *Terra Firme*, species that occurred exclusively in the outer canopy stood out (Fig. 3A, B), while in *Várzea*, 25% of the species were restricted to the trunks and more than 50% of them occurred in all zones (Fig. 3C).

The diversity of species followed the patterns observed for richness in the vegetation types. In *Várzea*, the recorded diversity was greatest at the base of the trunks and decreased towards the canopy; in *Terra Firme*, there was an increase towards the outer canopy, where the greatest diversity of all zones and vegetation types was observed (α 33.4); and in *Igapó*, although the base had the greatest diversity as in *Várzea*, both extremities concentrated a high diversity. The base was one of the least rich and diverse height zones in *Terra Firme* (Tab. 2).

The composition of epiphytes between the intermediate height zones within each vegetation type was highly similar, always sharing more than 30% of the species (Tab. 2, Sørensen index). The extremities (base and outer canopy) of the host trees were more similar to the corresponding zones in *Igapó* and *Terra Firme* (base/Z1, 0.52; outer canopy/Z5 0.47, Sørensen index). The composition of bryophytes in the outer canopy (Z5) of *Terra Firme* also closely resembled that of the base (Z1) of *Várzea* (0.49). The floristic composition was less similar between the flooded forests (Fig. 4, Tab. 2), which was distant from that of *Terra Firme*, mainly in relation to the outer canopy and the understory (*Igapó/Z5* - *Terra Firme*/Z1, 0.90, *Várzea/Z5* - *Terra Firme/*Z1, 0.94, *Terra Firme*/Z5 - *Igapó*/Z1, 0.88, Bray-Curtis index).

In addition, the structure of the floristic composition in the ordination evidenced the influence of two factors shaping the assemblages (Fig. 4). The first one is related to the vegetation type (1st axis, colors) and the second to the height zone in the host tree (2nd axis, symbols). These factors (vegetation type and height zone) were tested and found to be consistent (Tab. 3). A turnover in the composition of species along height zones was observed in *Terra Firme* and *Igapó*, which characterized the vertical gradient of bryophytes. This pattern was not observed in *Várzea*, where species composition was very similar between zones (Fig. 4).

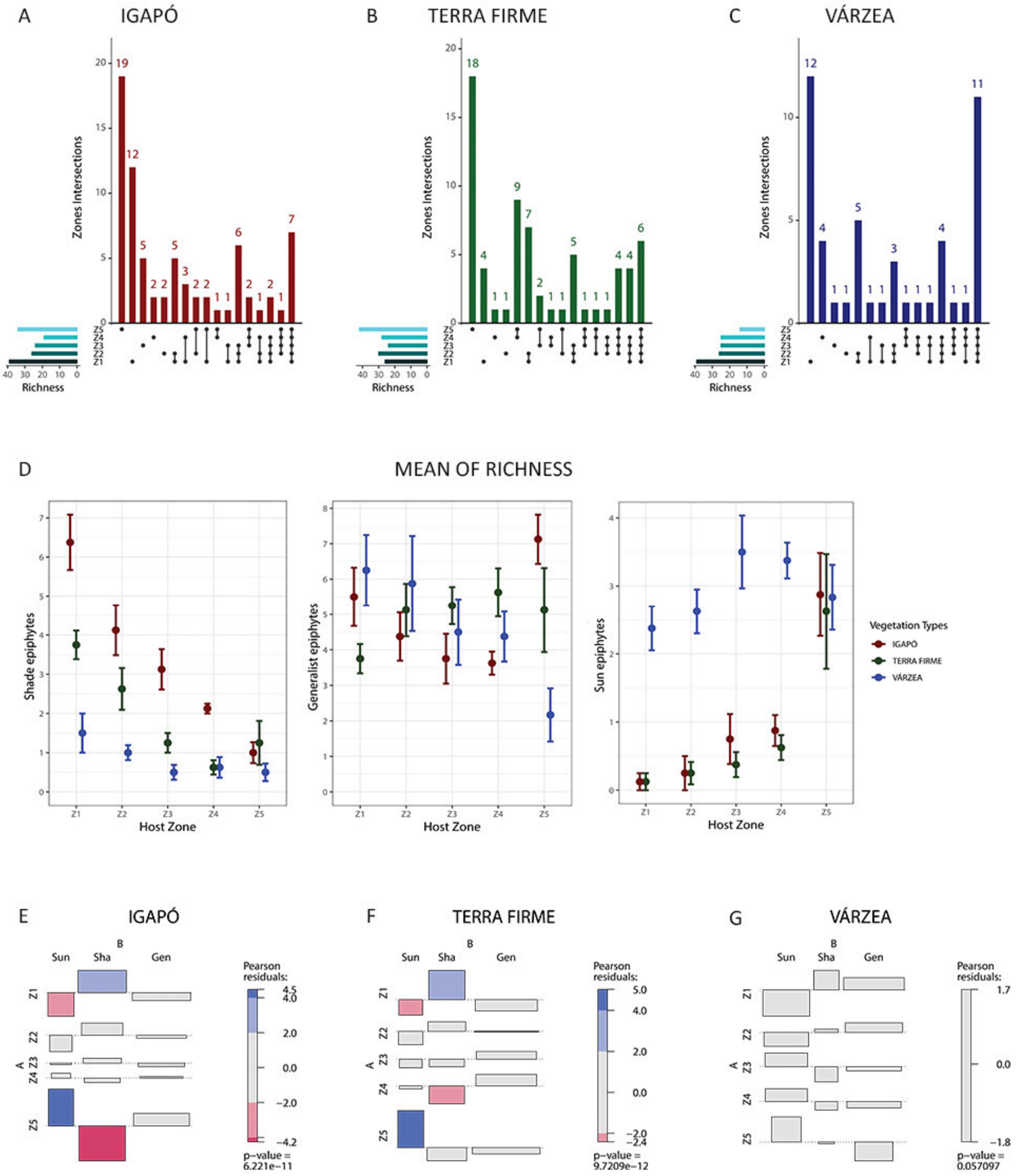

Figure 3. A-C: Overview of the number of species and shared species per vegetation type. Horizontal bars represent the total richness per zone; vertical bars represent the number of species found per each zone (points) and the number of species shared between zones (points connected by lines). D: Mean and standard error of species richness per guild in the zones. E-F: Association between zones and guilds based on the absolute frequency of taxa. Sun = Sun specialist epiphytes; Sha = Shade specialist epiphytes, Gen = Generalist epiphytes; Z = Zone.

Table 2. Similarity (Sørensen) and dissimilarity (Bray-Curtis) indices between height zones and vegetation types. Species richness and diversity per height zone are highlighted in gray.

Sørensen

Bray-Curtis

	VZ1	VZ2	VZ3	VZ4	VZ5	IG1	IG2	IG3	IG4	IG5	TF1	TF2	TF3	TF4	TF5
VZ1	39/28.2	0.36	0.41	0.46	0.64	0.81	0.85	0.86	0.8	0.82	0.79	0.65	0.6	0.6	0.65
VZ2	0.71	26/13.9	0.24	0.33	0.47	0.82	0.82	0.84	0.76	0.75	0.82	0.7	0.64	0.57	0.66
VZ3	0.66	0.78	25/14.0	0.24	0.39	0.86	0.87	0.85	0.69	0.76	0.84	0.71	0.74	0.64	0.66
VZ4	0.56	0.67	0.8	25/14.4	0.36	0.87	0.87	0.84	0.7	0.77	0.91	0.78	0.75	0.67	0.67
VZ5	0.45	0.6	0.72	0.72	14/9.1	0.92	0.9	0.87	0.73	0.84	0.94	0.84	0.87	0.76	0.74
IG1	0.36	0.34	0.28	0.28	0.19	39/24.2	0.42	0.54	0.67	0.82	0.63	0.65	0.76	0.83	0.88
IG2	0.28	0.31	0.2	0.24	0.2	0.65	26/14.6	0.32	0.46	0.71	0.81	0.73	0.76	0.77	0.83
IG3	0.29	0.32	0.33	0.37	0.32	0.51	0.64	24/14.5	0.38	0.69	0.83	0.77	0.77	0.78	0.82
IG4	0.31	0.36	0.41	0.36	0.36	0.45	0.49	0.56	19/10.2	0.63	0.87	0.78	0.78	0.72	0.76
IG5	0.25	0.33	0.31	0.27	0.21	0.25	0.33	0.34	0.42	34/18.9	0.9	0.81	0.73	0.7	0.62
TF1	0.31	0.27	0.27	0.2	0.15	0.52	0.35	0.28	0.27	0.17	26/15.8	0.32	0.58	0.76	0.88
TF2	0.43	0.36	0.36	0.29	0.23	0.46	0.36	0.3	0.29	0.22	0.79	30/19.8	0.36	0.53	0.71
TF3	0.41	0.36	0.33	0.24	0.16	0.35	0.28	0.29	0.28	0.28	0.6	0.74	24/14.3	0.32	0.67
TF4	0.42	0.44	0.45	0.34	0.33	0.3	0.26	0.31	0.38	0.35	0.37	0.55	0.65	28/18.6	0.5
TF5	0.49	0.38	0.42	0.39	0.36	0.22	0.24	0.27	0.3	0.47	0.18	0.33	0.39	0.6	42/33.4

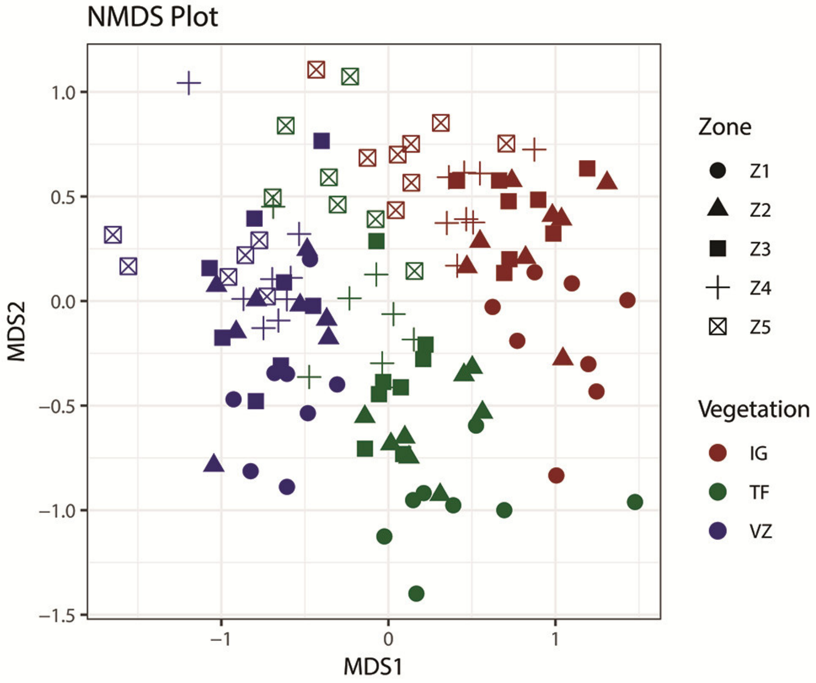

Figure 4. Non-metric multidimensional scaling (NMDS) plot of samples per zone in the vegetation types (stress = 0.1942709) using Sørensen distance. (Z1 = base to 1 m, Z2 = lower trunk, Z3 = upper trunk, Z4 = inner canopy, Z5 = outer sun-lit twigs/leaves (outer canopy)).

Table 3. PERMANOVA results for the different groups (height zones and vegetation types) of epiphytic bryophytes in the Caxiuanã FLONA.

	Df	Sums Sqs	Mean Sqs	F. Model	R2	Pr (> F)	
Vegetation type	2	11.622	5.8109	23.471	0.28987	0.001	***
Residuals	115	28.471	0.2476	0.71013			
Total	117	40.093	1				
Heigth zone	4	4.063	1.01563	3.1852	0.10133	0.001	***
Residuals	113	36.031	0.31885	0.89867			
Total	117	40.093	1				

The distribution of specialist species varied between zones (Fig. 3D) and there was a reduction in the proportion of shade specialists and a concomitant increase of sun specialists and generalists towards the canopy. Specialist taxa were correlated with the height zones in the Igapó and Terra Firme vegetation (*Igapó*, $X^2 = 64.4$, df = 8, $p < 0.001$; *Terra Firme*, $X^2 = 68.5$, df = 8, $p < 0.001$) (Fig. 3E-F). . The exception of this pattern was seen in *Várzea*, where generalist and sun specialist taxa predominated in all height zones, and there was no association between the distribution of guilds and height zones ($X^2 = 15.1$, df = 8, $p = 0.057$) (Fig.3G).

Discussion

Vertical gradient and turnover of epiphytic bryophytes in different Amazonian vegetation types

The expectation that the composition of species would present a vertical gradient in the host trees was supported in *Igapó* and *Terra Firme* vegetation. On the other hand, the composition was more homogeneous along the height zones in *Várzea*. These data show that the turnover of species (vertical gradient) is consistent at local scale in *Terra Firme*, as previously reported (Oliveira *et al.,* 2009), as well as in *Igapó*, and it is also regulated by the type of vegetation, since this pattern was observed in these vegetation types but not in *Várzea*. In *Igapó* and *Terra Firme*, the similarity in the composition of bryophytes found in the extreme height zones (base and outer canopy) of trees across vegetation types was higher than that among zones of host trees within the same vegetation type. This ratifies the relation between the height of occurrence and distribution of species, as previously observed in *Terra Firme* in the Amazon (Oliveira & ter Steege, 2015). Thus, the sharing of exclusive taxa of the understory (e.g*., Prionolejeunea denticulata* and *P. muricatosserrulata*) and the canopy (e.g., *Diplasiolejeunea brunnea* and *D. rudolphiana*) supports the fact that, regardless of the vegetation type, these species have typical niches adapted to these microhabitats. These results are in line with the literature, since bryophytes have been reported to have their occurrence strongly regulated by niche (Slack, 1990; Oliveira *et al.,* 2009), responding efficiently to fluctuations in light incidence, humidity and temperature (Schofield, 1985; Gradstein *et al.,* 1996; Hallingbäck & Hodgetts, 2000; Gradstein *et al.,* 2001). These abiotic factors vary greatly from the base to the canopy in humid tropical forests (Allee, 1926; Cornelissen & ter Steege, 1989), establishing the well documented vertical gradient of bryophyte species (Pócs, 1982; Oliveira *et al.,* 2009; Sporn *et al.,* 2010; Oliveira & ter Steege, 2015), although not observed in the *Várzea* forest in the present study. The floristic similarity between *Terra Firme* and *Igapó* has already been highlighted in previous studies (Lopes *et al.,* 2016). In the present work, we further found that such similarity is associated with the extreme zones (base and outer canopy) of the host trees, thus not reflecting only the geographic proximity but also, and mainly, the niche of the species. Despite of correlation between the floristic composition of the samples and the spatial distance observed when considered the samples of all vegetation types, this effect disappears if analyzed specifically each vegetation types (Mantel tests performed additionally, supports independence of host trees). Thus, both spatial distance and species niche appear to determine the occurrence of species. At the local scale, similarity between height zones is well supported in the literature, although the available data almost always consist of comparisons between zones of the same vegetation type (Cornelissen & ter Steege, 1989; Oliveira *et al.,* 2009; Oliveira & ter Steege, 2015).

The weaker turnover across the height zones in *Várzea* can be a response to the more extreme conditions to which the species are subjected in this environment, which may be associated with greater canopy openness in this vegetation (Matos *et al.,* 2019). According Richards (1984) differences in forest structure may cause changes in the internal microclimate, which in turn regulate the distribution of epiphytes (Cornellissen & ter Steege 1989; Oliveira *et al.,* 2009). The reduction of canopy cover has shown to negatively affect the composition and diversity of epiphytic bryophytes (Benítez *et al.,* 2015). In our results, if greater canopy openness is taken as an indication of a less dense canopy, the absence of vertical gradient in *Várzea* may be related to the loss and/or shift of species with low tolerance to high levels of light incidence. Similarly, a homogenous floristic composition in the vertical distribution and predominance of sun specialists and generalists have been reported in the literature, almost always attributed to the state of conservation and the history of fragmentation of the area (Alvarenga *et al*., 2010; Silva & Pôrto, 2013; Oliveira & Oliveira, 2016).

The difference in the species composition of flooded vegetation types has been previously reported in other studies (Cerqueira *et al.,* 2017), and our data indicates that it can be partly explained by the vertical distribution of species. According to Slack (1990), bryophytes do not disappear from the habitats due to competitive exclusion, but migrate to more favorable environments, thus being considered fugitive species. This would explain the greater similarity between species found in *Várzea* and those of the extreme zones of the canopy (outer canopy) in *Igapó* and *Terra Firme*, where more desiccation tolerant (Pardow *et al.,* 2012) and light demanding taxa occur. In this case, the different vegetation types would act as reservoirs of species with distinct characteristics that occur in habitats better suited to their niche requirements.

Our results suggest that variations in abiotic factors occur in the studied environment in relation to both height in the host tree and type of vegetation, causing a differentiation in the assemblages. The moisture content of the air, temperature and daily variation of UV radiation, as well as the structure of the substrates are ecological factors that determine local patterns in the composition of bryophytes in tropical forests (Richards, 1984; Wolf, 1993; Bader *et al.,* 2013; Wagner *et al.,* 2014). In this way, both can represent surrogates of abiotic filters that determine high beta diversity even on a small local scale.

Species composition: representation of guilds in the vegetation types

The distribution of guilds in the different vegetation types confirmed the vertical gradient in terms of taxonomic composition of species in *Terra Firme* and *Igapó*, and explained the non-existence of such gradient in *Várzea*. Guilds are established according to their responses to microclimatic variations over the vertical gradient in the host trees (Pócs, 1982; Richards, 1984). The patterns observed in our data followed the expectation for tropical forests, with a clear variation in the proportion of specialists (reduction of Shade specialist and increase of Sun specialist) from the base to the canopy of hosts in the forests (Cornelissen & ter Steege, 1989).

In *Várzea* vegetation, generalist and sun specialist species prevailed in all zones, becoming gradually less represented towards the canopy. Taxa with these characteristics are common in open habitats such as rocky outcrops, fragmented areas, and secondary forests (Silva & Germano, 2013; Tavares-Martins *et al.,* 2014; Pantoja *et al.,* 2015). On the other hand, the displacement of sun specialists towards the understory, as well as the loss of shade specialists in this stratum is observed in areas with poor canopy coverage (Richards, 1984; Gradstein *et al.,* 2001; Benítez *et al.,* 2015). Because habitat quality affects practically all species and is relevant to the survival and reproduction of species (Kawecki, 2008) the change in the abundance of species among vegetation types is maybe a response to the strong restrictions imposed by habitats on the taxa. This was evident, for instance, in the occurrence of *Pycnolejeuna papilosa* Xiao L.He (Sunesp) (23 spp. in *Várzea*, 5 in *Terra Firme*, and 1 in *Igapó*), which was present and frequent in all zones in *Várzea*, but little frequent in the other vegetation types. Another example is *Syrrhopodon ligulatus* Mont. and *S. incompletus* Schwägr. (Shaesp), rare in *Várzea* but very common in *Igapó* and *Terra Firme*. On the other hand, of the 30 shade tolerant epiphytes recorded in this study, 10 occurred exclusively in *Igapó* vegetation, where taxa such as *Prionolejeunea scaberula* (Spruce) Steph. and *P. trachyoides* (Spruce) Steph. were very frequent and restricted to the understory. In spite of the lower richness found in *Várzea*, the number of occurrences of bryophytes was not much different between the vegetation types, being common or rare species frequently abundant in other vegetation types. These data indicate that rarity of bryophytes in the studied environments may be partially a result of the ecological restrictions imposed by availability of light and humidity. Therefore, guilds can be taken as an informative and robust measure of the ecological range of taxa that explain, at least in part, the abundance distribution of the species.

Species richness along the vertical gradient in host trees in the eastern Amazon

In the flooded forests, the base of the trees (Z1) was richer and more diverse than the outer canopy. The outer canopy, in turn, stood out in *Terra Firme*. The diversity of species in this zone was also greater in relation to the zones of the other vegetation types. The canopy is commonly reported as the richest microhabitat for epiphytes in tropical forests (Gradstein, 1992b), which is likely associated with the filtering of species at the extremes where establishment is more limited (Oliveira & ter Steege, 2015). It is important to highlight that the outer canopy (Z5) included canopy leaf and branch samples, but only in *Terra Firme* the leaves were colonized by bryophytes. Epiphyll species were mainly sun specialists and were also eventually found in other height zones of other vegetation types (e.g. *Caudalejeunea lehmanniana, Cololejeunea cardiocarpa, C. subcardiocarpa, C. surinamensis, Pycnolejeunea gradsteinii* and *Vitalianthus* sp.). Coverage of epiphylls in tropical forests can be considered a proxy for relative humidity because pronounced fluctuations have the potential to constrain the growth and occurrence of these species (Sonnleitner *et al.,* 2009). The greater connectivity between the crown of the trees in *Terra Firme* may have contributed to minimize the effects of the increase of air temperature and decrease of humidity that takes place from the base towards the canopy, promoting better conditions for the establishment of epiphylls. Moreover, richness can be increased by means of colonization by foreign species to the community as well as by speciation (Warren *et al.,* 2014) and may be more evident on a local scale (Oliveira & ter Steege, 2015). High canopy richness has been reported in previous studies carried out in the Amazon (Oliveira *et al.,* 2009; Tavares-Martins *et al.,* 2014) and in the Brazilian Atlantic Forest (Costa, 1999).

Although our expectations were confirmed, the greater diversity in the extreme zones in the forests reveals still other aspects yet to be analyzed, such as the fact that the base of the host trees was the zone with lower richness in *Terra Firme*, while it presented a major importance in the other vegetation types. Bryophytes are poiquilohidric and therefore unable to regulate the loss or storage of water (Vanderpoorten & Goffinet, 2009). For this reason, they are more susceptible to adjacent environmental fluctuations (Schofield, 1985; Gradstein *et al.,* 1996; Hallingbäck & Hodgetts, 2000; Gradstein *et al.,* 2001). Unlike in *Terra Firme* vegetation, the availability of substrates in *Várzea* and *Igapó* may be lower due to periodic flooding, making the base of the trees more suitable for the establishment of species.

The high richness and diversity of bryophytes (Oliveira & ter Steege, 2015) and vascular epiphytes (Pos & Sleegers, 2010) in the vertical gradient had already been reported for *Terra Firme* vegetation in the study area of the present work. Here, we also highlight the representativeness of these attributes in *Igapó* vegetation. Thus, variations in abiotic conditions along the hosts explain not only the diversity at the extremes of the gradient, but also the greater alpha diversity in this forest when compared to the others (Garcia et al., unpublished). Thus, the spatial distribution of epiphytic bryophytes in the zones reflected the assembly of species according to the distribution of guilds, because the differentiation of composition over the height zones (beta diversity) was shaped by the niche of the species.

The vertical gradient in the composition of the epiphytic bryophytes along trees is consistent, but varies depending on the type of vegetation, and the local spatial distribution of the species is a combination of niche (height zone) and characteristics of the vegetation type. Species guilds are important attributes that indicate the processes that shape the epiphytic assemblages and regulate the vertical gradient, which may not exist even in forests with good conservation status. Due to changes in community and species attributes from one vegetation type to the other, we highlight the importance of investigations of the diversity patterns of epiphytes in the Amazon to include different habitats. In view of the responses of guilds to the environmental gradients, we emphasize the need for studies focused on traits of the species related to their environmental tolerance and also reproductive aspects, since the latter also regulate the distribution of the taxa.

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S1. Bryophytes epiphytes and distribution in the zones per vegetations in the Caxiuanã National Forest, Pará state, Brazil. Floristic Group, M = Moss; L = Liverworts; Guild, Sun = Sun specialist epiphytes; Sha = Shade specialist epiphytes, Gen = Generalist epiphytes; Zones = 1 – 5.

		Igapó						***Terra Firme***						***Várzea***					
Species Name/Guild	**Group**	**Occ.**	**1**	**2**	**3**	**4**	**5**	**Occ.**	**1**	**2**	**3**	**4**	**5**	**Occ.**	**1**	**2**	**3**	**4**	**5**
Shade specialist epiphytes																			
Archilejeunea crispistipula (Spruce) Steph.	L							2		x			x	21	x	x	x	x	x
Calymperes platyloma Mitt.	M	32	x	x	x	x	x												
Cololejeunea camillii (Lehm.) A. Evans	L							1					x	1	x				
Cololejeunea contractiloba A. Evans	L							2					x	1	x				
Cololejeunea surinamensis Tixier	L							4					x						
Cyclolejeunea convexistipa (Lehm. & Lindenb.) A.Evans	L	1					x	1					x						
Fissidens guianensis Mont.	M	6	x			x		8	x	x	x	x							
Fissidens pellucidus Hornsch.	M	3	x	x				3	x	x				1	x				
Haplolejeunea amazonica Ilkiu-Borges & Gradst.	L							7	x	x									
Harpalejeunea tridens (Besch. & Spruce) Steph.	L	8	x	x	x	x													
Lejeunea asperrima Spruce	L	8	x	x	x														
Lejeunea controversa Gottsche	L	4	x	x				3	x	x									
Leucobryum martianum (Hornsch.) Hampe ex Müll. Hal.	M	1	x																
Leucomium strumosum (Hornsch.) Mitt.	M	1		x				1	x										
Metalejeunea cucullata (Reinw., Blume et Nees) Grolle	L	1					x												
Pictolejeunea picta (Steph.) Grolle	L							9	x	x									
Plagiochila aerea Taylor	L	1	x					2	x	x									
Plagiochila montagnei Nees	L													2	x				
Plagiochila raddiana Lindenb.	L													3	x	x	x		
Plagiochila subplana Lindenb.	L	1	x					1	x										
Prionolejeunea aemula (Gottsche) A.Evans	L	1	x																
Prionolejeunea denticulata (F.Weber) Schiffn.	L	8	x	x	x			6	x	x	x								
Prionolejeunea muricatoserrulata (Spruce) Steph.	L	3	x		x			5	x	x									

		Igapó						*Terra Firme*						*Várzea*					
Species Name/Guild	**Group**	**Occ.**	**1**	**2**	**3**	**4**	**5**	**Occ.**	**1**	**2**	**3**	**4**	**5**	**Occ.**	**1**	**2**	**3**	**4**	**5**
Prionolejeunea scaberula (Spruce) Steph.	L	16	x	x	x														
Prionolejeunea trachyodes (Spruce) Steph.	L	29	x	x	x	x	x												
Radula stenocalyx Mont.	L	2	x																
Syrrhopodon incompletus Schwägr.	M	5	x	x	x			6	x	x	x			1				x	
Syrrhopodon ligulatus Mont.	M							12		x	x	x	x	1	x				
Trichosteleum subdemissum (Besch.) A.Jaeger	M	2	x											1	x				
Xylolejeunea crenata (Nees et Mont.) Xiao L.He et Grolle	L	1	x					3	x										
Generalist epiphytes																			
Archilejeunea fuscescens (Hampe ex Lehm.) Fulford	L							8		x	x	x	x						
Calymperes erosum Müll. Hal.	M	1			x			7	x	x	x	x		6	x	x			
Calymperes lonchophyllum Schwägr.	M	8	x	x				10	x	x	x	x	x						
Calymperes palisotii Schwägr.	M	5	x	x		x								12	x	x	x	x	x
Ceratolejeunea coarina (Gottsche) Schiffn.	L	1	x					4				x	x	16	x	x	x	x	x
Ceratolejeunea confusa R.M.Schust.	L							1					x	2	x			x	
Ceratolejeunea cornuta (Lindenb.) Steph.	L	11	x	x	x	x	x	17	x	x	x	x	x	19	x	x	x	x	x
Ceratolejeunea cubensis (Mont.) Schiffn.	L	3	x				x	4	x	x	x			15	x	x	x	x	
Ceratolejeunea guianensis (Nees et Mont.) Steph.	L													3			x	x	x
Ceratolejeunea minuta G.Dauphin	L	25	x	x	x	x	x	28	x	x	x	x	x	6	x	x	x		
Cheilolejeunea adnata (Kunze ex Lehm.) Grolle	L	1	x					8		x	x	x	x	8	x	x	x	x	
Cheilolejeunea aneogyna (Spruce) A.Evans	L	2	x			x		6	x	x				11	x	x	x	x	x
Cheilolejeunea clausa (Nees et Mont.) R.M.Schust.	L							1				x							
Cheilolejeunea comans (Spruce) R.M.Schust	L													1				x	
Cheilolejeunea holostipa (Spruce) Grolle & R.-L.Zhu	L	1					x	6				x	x	5		x	x	x	x
Cheilolejeunea oncophylla (Ångstr.) Grolle & M.E. Reiner	L	13	x	x	x	x	x	28	x	x	x	x	x	31	x	x	x	x	x
Cheilolejeunea rigidula (Nees ex Mont.) R.M.Schust.	L	5		x			x	8		x	x	x	x	5	x	x			
Cololejeunea cardiocarpa (Mont.) A.Evans	L							1					x						
Dibrachiella parviflora (Nees) X.Q.Shi, R.L.Zhu & Gradst.	L							15	x	x	x	x	x	4	x		x		

Species Name/Guild	Group	*Igapó*						*Terra Firme*						*Várzea*					
		Occ.	**1**	**2**	**3**	**4**	**5**	**Occ.**	**1**	**2**	**3**	**4**	**5**	**Occ.**	**1**	**2**	**3**	**4**	**5**
Drepanolejeunea fragilis Bischl.ex L.Söderstr.,A.Hagborg et von Konrat	L	4					x	3				x	x						
Harpalejeunea stricta (Lindenb. et Gottsche) Steph.	L	3		x			x							1		x			
Isopterygium tenerum (Sw.) Mitt.	M													2	x				
Lejeunea adpressa Nees	L													3	x	x			
Lejeunea boryana Mont.	L	10	x	x	x														
Lejeunea cerina (Lehm. et Lindenb.) Lehm. et Lindenb.	L	8	x	x	x														
Lejeunea flava (Sw.) Nees	L							2			x		x	1	x				
Lejeunea grossitexta (Steph.) E.Reiner et Goda	L							2			x	x							
Lejeunea immersa Spruce	L	1	x																
Lejeunea laetevirens Nees et Mont.	L	2	x	x										3	x	x			
Leptolejeunea elliptica (Lehm. et Lindenb.) Besch.	L	5					x	2					x						
Microcalpe subsimplex (Hedw.) W.R. Buck	M							12	x	x	x			1	x				
Microlejeunea bullata (Taylor) Steph.	L	1					x												
Microlejeunea epiphylla Bischl.	L	10			x	x	x	9			x	x	x	12	x	x	x	x	x
Mniomalia viridis (Mitt.) Müll. Hal.	M	16	x	x	x	x								1				x	
Neurolejeunea seminervis (Spruce) Schiffn.	L	29	x	x	x	x	x	1					x						
Octoblepharum albidum Hedw.	M	4	x			x		14	x	x	x	x		5	x	x	x		
Octoblepharum pulvinatum (Dozy & Molk.) Mitt.	M							4		x	x	x							
Pilosium chlorophyllum (Hornsch.) Müll. Hal.	M							3	x										
Rectolejeunea berteroana (Gottsche ex Steph.) A.Evans.	L	1					x	1					x	2	x				
Rectolejeunea flagelliformis A.Evans	L	7				x	x	4				x	x	5	x	x	x	x	
Symbiezidium barbiflorum (Lindenb. & Gottsche) A. Evans	L	12	x	x	x	x	x	2				x	x						
Syrrhopodon gaudichaudii Mont.	M							1		x									
Syrrhopodon simmondsii Steere	M							10	x	x	x	x							
Trichosteleum papillosum (Hornsch.) Jaeg.	M	1	x											1	x				
Zoopsidella integrifolia (Spruce) R.M.Schuster	L	1	x																

Species Name/Guild	Group	*Igapó*						*Terra Firme*						*Várzea*					
		Occ.	1	2	3	4	5	Occ.	1	2	3	4	5	Occ.	1	2	3	4	5
Sun specialist epiphytes																			
Acrolejeunea emergens (Mitt.) Steph.	L													1				x	
Acrolejeunea torulosa (Lehm. et Lindenb.) Schiffn.	L													22	x	x	x	x	x
Archilejeunea badia (Spruce) Steph.	L							1					x						
Caudalejeunea lehmanniana (Gottsche) A.Evans	L							2					x						
Cheilolejeunea cyrtolejeuneoides C.J. Bastos & Schäf.-Verw.	L	12			x	x	x												
Cheilolejeunea neblinensis Ilk-Borg. et Gradst.	L							4	x	x	x								
Cololejeunea subcardiocarpa Tixier	L							5				x	x						
Dibrachiella auberiana (Mont.) X.Q.Shi, R.L.Zhu & Gradst.	L	4					x												
Diplasiolejeunea brunnea Steph.	L	2					x	3					x						
Diplasiolejeunea cobrensis Steph.	L	2					x												
Diplasiolejeunea rudolphiana Steph.	L	2					x	1					x						
Frullania caulisequa (Nees) Mont.	L	1					x	2			x		x						
Frullania gibbosa Nees, Ann	L													1			x		
Lejeunea tapajosensis Spruce	L							1					x						
Lopholejeunea subfusca (Nees) Schiffn.	L	9		x	x	x	x	3		x		x	x	13	x		x	x	x
Mastigolejeunea auriculata (Wilson et Hook.) Steph.	L	1			x									15	x	x	x	x	
Mastigolejeunea innovans (Spruce) Steph.	L	1					x												
Mastigolejeunea plicatiflora (Spruce) Steph.	L	1			x			2					x	8	x	x	x	x	x
Myriocoleopsis minutissima (Sm.) R.L.Zhu, Y.Yu et Pócs	L													4	x		x	x	
Pycnolejeunea contigua (Nees) Grolle	L							1					x	20	x	x	x	x	x
Pycnolejeunea gradsteinii Ilk.-Borg.	L							2					x						
Pycnolejeunea papillosa Xiao L.He	L	1			x			5				x	x	23	x	x	x	x	x
Radula javanica Gottsche	L	2	x	x										2	x	x			
Symbiezidium transversale (Sw.) Trevis.	L													3	x				
Thysananthus amazonicus (Spruce) Schiffn.	L	1			x														

		Igapó						*Terra Firme*						*Várzea*					
Species Name/Guild	**Group**	**Occ.**	**1**	**2**	**3**	**4**	**5**	**Occ.**	**1**	**2**	**3**	**4**	**5**	**Occ.**	**1**	**2**	**3**	**4**	**5**
Unclassified																			
Cololejeunea sp.	L	1					x												
Cololejeunea sp3	L	1					x												
Frullania exilis Taylor	L	1				x													
Frullania sp.	L	2					x												
Lejeunea sp1	L	1					x												
Lejeunea sp2	L	1					x												
Lejeunea sp3	L	1				x		2					x						
Lejeunea sp4	L	2		x															
Pycnolejeunea sp.	L	4					x							4		x	x	x	
Syrrhopodon cymbifolius Müll. Hal.	M	2	x				x	8	x	x	x	x	x						
Vitalianthus sp1.	L							2				x	x						
Vitalianthus sp2	L							5				x	x						
		380						347						329					

References

ACEBEY A., GRADSTEIN S.R. & KRÖMER T. 2003 — Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *Journal of Tropical Ecology* 19: 9–18. https://doi.org/10.1017/S026646740300302X

ALLEE W.C. 1926 — Measurement of Environmental Factors in the Tropical Rain-Forest of Panama. *Ecology* 7: 273–302.

ALVARENGA L.D.P. PÔRTO K.C. & DE OLIVEIRA J.R.DOP.M. 2010 — Habitat loss effects on spatial distribution of non-vascular epiphytes in a Brazilian Atlantic forest. *Biodiversity and Conservation* 19: 619–635. https://doi.org/10.1007/s10531-009-9723-2

ALVARES C.A., STAPE J.L., SENTELHAS P.C., GONÇALVES J.L.DEM. & SPAROVEK G. 2014 — Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22: 711–728. https://doi.org/10.1127/0941-2948/2013/0507

BADER M.Y., REICH T., WAGNER S., GONZÁLEZ-GONZÁLEZ A.S. & ZOTZ G., 2013 — Differences in desiccation tolerance do not explain altitudinal distribution patterns of tropical bryophytes. *Journal of Bryology* 35: 47–56. https://doi.org/10.1179/1743282012Y.0000000033

BASTOS C.J.P. 2017 — O gênero *Cheilolejeunea* (Spruce) Steph. (Lejeuneaceae, Marchantiophyta) nas Américas. *Pesquisas. Botânica* 70: 5–78.

BECK J. & SCHWANGHART W. 2010 — Comparing measures of species diversity from incomplete inventories: an update. *Methods in Ecology and Evolution* 1: 38–44. https://doi.org/10.1111/j.2041210X.2009.00003.x

BENÍTEZ A., PRIETO M. & ARAGÓN G. 2015 — Large trees and dense canopies: Key factors for maintaining high epiphytic diversity on trunk bases (bryophytes and lichens) in tropical montane forests. *Forestry* 88: 521–527. https://doi.org/10.1093/forestry/cpv022

BLONDEL J. 2003 — Guilds or functional groups: does it matter? *Oikos* 100: 223–231.

BORDIN J. & YANO O. 2013 — Fissidentaceae (Bryophyta) do Brasil. *Boletim do Instituto de Botanica* 22*:* 1–168.

BRAY J.R. & CURTIS J.T. 1957 — An Ordination of Upland Forest Communities of Southern Wisconsin. *Ecological Monographs* 27: 325–349. http://dx.doi.org/10.2307/1942268

CARVALHO-SILVA M., STECH M., SOARES-SILVA L.H., BUCK W.R., WICKETT N.J., LIU Y. & CÂMARA P.E.A.S. 2017 — A molecular phylogeny of the Sematophyllaceae sl (Hypnales) based on plastid, mitochondrial and nuclear markers, and its taxonomic implications. *Taxon* 66: 811–831. https://doi.org/10.12705/664.2

CASTRO R.M.DAS., RUIVO M.DE.L.P., COSTA J.M.N. & COSTA A.C.L.DA. 2013 — Influência da sazonalidade na produção de serapilheira no experimento ESECAFLOR, na Floresta Nacional de Caxiuanã. *In*: Lisboa P.L.B.(ed.), *Caxiuanã: paraíso ainda preservado* Museu Paraense Emílio Goeldi, Belém, 856 p.

CERQUEIRA G.R., ILKIU-BORGES A.L. & FERREIRA L.V. 2017 — Species richness and composition of epiphytic bryophytes in flooded forests of Caxiuanã National Forest, Eastern Amazon, Brazil. *Anais da Academia Brasileira de Ciências 89*: 2371–2382. https://doi.org/http://dx.doi.org/10.1590/0001-3765201720160860

CORNELISSEN J.H.C. & TER STEEGE H. 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *Journal of Tropical Ecology* 5: 131–150.

COSTA A.C.L.DA, GALBRAITH D., ALMEIDA S., PORTELA B.T.T., COSTA M.DA, SILVA-JUNIOR J.DEA.,…MEIR P. 2010 — Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytologist* 187: 579–591. https://doi.org/10.1111/j.1469-8137.2010.03309.x

COSTA D.P.DA. 1999 — Epiphytic Bryophyte Diversity in Primary and Secondary Lowland Rainforests in Southeastern Brazil. *The Bryologist* 102: 320. https://doi.org/10.2307/3244372

CRANDALL-STOTLER B., STOTLER R.E., LONG D.G. 2009 — Phylogeny and Classification of the Marchantiophyta. *Edinburgh Journal of Botany* 66: 155–198. https://doi.org/10.1017/S0960428609005393

DAUPHIN G. 2003 — *Ceratolejeunea*. *Flora Neotropica Monograph* 90: 1–86.

FERREIRA L.V, CHAVES P.P., CUNHA D.D.A., MATOS D.C.L. & PAROLIN P. 2013 — Variação da riqueza e composição de espécies da comunidade de plantas entre as florestas de igapos e várzeas na Estação Científica Ferreira Penna - Caxiuanã na Amazônia Oriental. *Pesquisas, Botânica* 64: 175–195.

FISHER R.A., CORBET A.S. & WILLIAMS C.B. 1943 — The Relation Between the Number of Species and the Number of Individuals in a Random Sample of an Animal Population. *Journal of Animal Ecology* 12: 42–58. https://doi.org/10.2307/1411

FLORA DO BRASIL. 2020 — Flora do Brasil 2020 under construction. Retrieved from http://floradobrasil.jbrj.gov.br/

FLORSCHÜTZ P.A. 1964 — *The mosses of Suriname - Part I*. Brill E.J. (ed.). Leiden. 271 p.

FOX J. & WEISBERG S. 2011 — *An {R} Companion to Applied Regression*. *Sage* (2nd ed.). Thousand Oaks CA. Retrieved from http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

GOFFINET B., BUCK W.R. & SHAW A.J. 2009 — Morphology, anatomy, and classification of the Bryophyta. *in:* Shaw AJ. & Goffinet B. (eds.), *Bryophyte Biology* (2nd ed.). Cambrige: Cambridge University Press, pp. 55–138.

GOTELLI N.J. & ELLISON A.M., 2011 — *Princípios de estatística em ecologia*. Landeiro VL. (ed.). J. - Artmed, Porto Alegre, 510 p.

GRADSTEIN S.R., 1992a — The vanishing tropical rainforest. *in:* Bates JW. & Farmer AM (eds.), *Bryophytes and Lichens in a Changing Environment* Clarendon Press, Oxford. pp. 234–256.

GRADSTEIN S.R. 1992b — Threatened bryophytes of the neotropical rain forest: a status report. *Tropical Bryology* 6: 83–93.

GRADSTEIN S.R., HIETZ P., LÜCKING R., LÜCKING A., SIPMAN H.J.M., VESTER H.F.M.,…GARDETTE E. 1996 — How to sample the epiphytic diversity of tropical rain forest. *Ecotropica* 2: 59–72.

HALLINGBÄCK T. & HODGETTS N. 2000 — *Mosses, Liverworts, and Hornworts. Status Survey and Conservation Action Plan for Bryophytes*. Oxford.

GRADSTEIN S.R., CHURCHILL S.P. & SALAZAR-ALLEN N. 2001 — *Guide to the Bryophytes of Tropical America*. Memoirs of the New York Botanical Garden (Vol. 86). The New York Botunical Garden Press, New York, 577 p.

GRADSTEIN S.R. & COSTA D.P.DA. 2003 — *The Hepaticae and Anthocerotae of Brazil*. Memoirs of the New York Botanical Garden (Vol. 87). The New York Botunical Garden Press, New York, 673 p.

GRADSTEIN S.R. & ILKIU-BORGES A.L. 2009 — *Guide to the Plants of Central French Guiana. Part 4. Liverworts and Hornworts*. (Vol. 76). Memoirs of the New York Botanical Garden, New York, 140 p.

ILKIU-BORGES A.L. 2016 — *Prionolejeunea*: Lejeuneaceae, Jungermanniopsida. *Flora Neotropica Monograph* 116: 1–131.

JUNK W.J., PIEDADE M.T.F., SCHÖNGART J., COHN-HAFT M., ADENEY J.M. & WITTMANN F. 2011 — A Classification of Major Naturally-Occurring Amazonian Lowland Wetlands. *Wetlands* 31: 623–640.

KAWECKI T.J. 2008 — Adaptation to Marginal Habitats. *Annual Review of Ecology, Evolution, and Systematics* 39: 321–342.

KÖPPEN W., & GEIGER R. 1928 — Klimate der Erde. Gotha: Verlag Justus Perthes. Wall-map 150cmx200cm.

KRAFT N.J.B., ADLER P.B., GODOY O., JAMES E.C., FULLER S. & LEVINE J.M. 2015 — Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* 29: 592–599.

LEGENDRE P. & LEGENDRE L. 1998 — *Numerical Ecology* (2nd ed.). Elsevier Science B.V., Amsterdam: 852 p.

LOPES M.O., PIETROBOM M.R., CARMO D.M.DO & PERALTA D.F. 2016 — Comparative study of communities of bryophytes in different degrees of flooding in the municipality of São Domingos do Capim, Pará State, Brazil. *Hoehnea* 43: 159–171. https://doi.org/10.1590/2236-8906-54/2015

MAGURRAN A.E. 2004 — *Measuring of Biological Diversity*. Blackwell science. 264 p.

MATOS D.C.L., FERREIRA L.V. & Marcos Bergmann CARLUCCI, M.B. 2018 — Estratégias funcionais de *Macrolobium angustifolium* (Benth.) R.S.Cowan para coexistir em florestas inundadas na Amazônia oriental. *Revista Espacios.* 39: 1–16.

MONTAG L.F.A, FREITAS T.M.S., WOSIACKI W.B. & BARTHEM R.B. 2008 — Os peixes da Floresta Nacional de Caxiuanã (municípios de Melgaço e Portel, Pará - Brasil). *Boletim do Museu Paraense. Emílio Goeldi, Ciências Naturais* 3: 11–34.

MORAES E.DEN.R. & LISBOA R.C.L. 2009 — Diversidade, taxonomia e distribuição por estados brasileiros das famílias Bartramiaceae, Brachytheciaceae, Bryaceae, Calymperaceae, Fissidentaceae, Hypnaceae e Leucobryaceae (Bryophyta) da Estação Científica Ferreira Penna, Caxiuanã, Pará, Brasil. *Acta Amazonica* 39: 773–791. https://doi.org/10.1590/S0044596720090004000006

OKSANEN J., BLANCHET F.G., FRIENDLY M., KINDT R., LEGENDRE P., MCGLINN D.,…WAGNER H. 2018 — vegan: Community Ecology Package. R package version 2.5-2. https://doi.org/ISBN 0-387-95457-0

OLIVEIRA H.C.DE & OLIVEIRA S.M.DE. 2016 — Vertical distribution of epiphytic bryophytes in Atlantic Forest fragments in northeastern Brazil. *Acta Botanica Brasilica* 30: 609–617. https://doi.org/10.1590/0102-33062016abb0303

OLIVEIRA S.M.DE & TER STEEGE H. 2013 — Floristic overview of the epiphytic bryophytes of terra firme forests across the Amazon basin. *Acta Botanica Brasilica* 27: 347–363. https://doi.org/10.1590/S0102-33062013000200010

OLIVEIRA S.M.DE & TER STEEGE H. 2015 — Bryophyte communities in the Amazon forest are regulated by height on the host tree and site elevation. *Journal of Ecology* 103:

441–450. https://doi.org/10.1111/1365-2745.12359

OLIVEIRA S.M.DE, TER STEEGE H., CORNELISSEN J.H.C. & GRADSTEIN R.S. 2009 — Niche assembly of epiphytic bryophyte communities in the Guianas: a regional approach. *Journal of Biogeography* 36: 2076–2084. https://doi.org/10.1111/j.1365-2699.2009.02144.x

PANTOJA A.C.C., ILKIU-BORGES A.L., TAVARES-MARTINS A.C.C. & GARCIA E.T. 2015 — Bryophytes in fragments of Terra Firme forest on the great curve of the Xingu River, Pará state, Brazil. *Brazilian Journal of Biology* 75*:* 238–249. https://doi.org/10.1590/1519-6984.02814BM

PARDOW A., GEHRIG-DOWNIE C., GRADSTEIN R.S. & LAKATOS M. 2012 — Functional diversity of epiphytes in two tropical lowland rainforests, French Guiana: using bryophyte life-forms to detect areas of high biodiversity. *Biodiversity and Conservation* 21: 3637–3655. https://doi.org/10.1007/s10531-012-0386-z

PÓCS T. 1982 — Tropical Forest Bryophytes. *in*: Smith A.J.E. (ed.) *Bryophyte Ecology*. Dordrecht: Springer Netherlands, pp. 59–104.

POS E.T. & SLEEGERS A.D.M. 2010 — Vertical distribution and ecology of vascular epiphytes in a lowland tropical rain forest of Brazil. *Boletim Do Museu Paraense Emílio Goeldi. Ciências Naturais* 5: 335–344.

QUARESMA A.C., PIEDADE M.T.F., FEITOSA Y.O., WITTMANN F. & TER STEEGE H. 2017 — Composition, diversity and structure of vascular epiphytes in two contrasting Central Amazonian floodplain ecosystems. *Acta Botanica Brasilica* 31: 686–697. https://doi.org/10.1590/0102-33062017abb0156

R Core Team 2019 — R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

REESE W.D. 1993 — Calymperaceae. *Flora Neotropica Monograph* 58: 1-102.

REINER-DREHWALD M.E. 2000 — Las Lejeuneaceae (Hepaticae) de Misiones, Argentina VI. Lejeunea y Taxilejeunea. *Tropical Bryology* 19: 81–131. https://doi.org/http://dx.doi.org/10.11646/bde.19.1.14

REINER-DREHWALD M.E. & GODA A. 2000 — Revision of the genus *Crossotelejeunea* (Lejeuneaceae, Hepaticae). *The Journal of the Hattori Botanical Laboratory* 89: 1–54.

REINER-DREHWALD M.E. & GROLLE R. 2012 — Review of the genus *Rectolejeunea* (Lejeuneaceae, Marchantiophyta). *Nova Hedwigia* 95: 451–482. https://doi.org/10.1127/0029-5035/2012/0063

RICHARDS P.W. 1984 — The Ecology of tropical forest bryophytes. *in:* SCHUSTER R.M.

(ed.), *New Manual of Bryology*. The Hattori Botanical Laboratory, Japan, Nichinan. pp. 1233–1270.

ROOT R.B. 1967 — The Niche Exploitation Pattern of the Blue-Gray Gnatcatcher. *Ecological Monographs* 37: 317–350. https://doi:10.2307/1942327

SCHOFIELD W.B. 1985 — *Introduction to Bryology*. The Blackburn Press New York, 431 p.

SHI X.-Q., GRADSTEIN S.R. & ZHU, R.-L. 2015 — Phylogeny and taxonomy of *Archilejeunea* (Marchantiophyta: Lejeuneaceae) based on molecular markers and morphology. *Taxon* 64: 881–892. https://doi.org/10.12705/645.1

SILVA J.B. & GERMANO S.R. 2013 — Bryophytes on rocky outcrops in the caatinga biome: a conservationist perspective. *Acta Botanica Brasilica* 27: 827–835. https://doi.org/10.1590/S0102-33062013000400023

SILVA M.P.P. & PÔRTO K.C. 2010 — Spatial structure of bryophyte communities along an edge-interior gradient in an Atlantic Forest remnant in Northeast Brazil. *Journal of Bryology* 32: 101–112. https://doi.org/10.1179/037366810X12578498136110

SILVA M.P.P. & PÔRTO K.C. 2013 — Bryophyte communities along horizontal and vertical gradients in a human-modified Atlantic Forest remnant. *Botany* 91: 155–166. https://doi.org/10.1139/cjb-2012-0194

SLACK N.G. 1990 — Bryophytes and ecological niche theory. *Botanical Journal of the Linnean Society* 104: 187–213.

SÖDERSTRÖM L, HAGBORG A, VON KONRAT M, BARTHOLOMEW-BEGAN S, BELL D, BRISCOE L, BROWN E,…, ZHU R-L. 2016. World checklist of hornworts and liverworts. *PhytoKeys* 59: 1-821. https://doi.org/10.3897/phytokeys.59.6261

SONNLEITNER M., DULLINGER S., WANEK W. & ZECHMEISTER H. 2009 — Microclimatic patterns correlate with the distribution of epiphyllous bryophytes in a tropical lowland rain forest in Costa Rica. *Journal of Tropical Ecology* 25: 321–330. https://doi.org/10.1017/S0266467409006002

SPORN S.G., BOS M.M., KESSLER M. & GRADSTEIN S.R. 2010 — Vertical distribution of epiphytic bryophytes in an Indonesian rainforest. *Biodiversity and Conservation* 19: 745–760. https://doi.org/10.1007/s10531-009-9731-2

TAVARES-MARTINS A.C.C., LISBOA R.C.L. & COSTA D.P.DA. 2014 — Bryophyte flora in upland forests at different successional stages and in the various strata of host trees in northeastern Pará, Brazil. *Acta Botanica Brasilica* 28: 46–58. http://dx.doi.org/10.1590/S0102-33062014000100005

TER STEEGE,H. 2010 — How Neutral is Ecology? *Biotropica* 42: 631–633. https://doi.org/10.1111/j.1744-7429.2010.00701.x

TUOMISTO H. & POULSEN A.D. 2000 — Pteridophyte diversity and species composition in four Amazonian rain forests. *Journal of Vegetation Science* 11: 383–396. https://doi.org/10.2307/3236631

TUOMISTO H., RUOKOLAINEN K., POULSEN A.D., MORAN R.C., QUINTANA C., CANAS G. & CELI J. 2002 — Distribution and Diversity of Pteridophytes and Melastomataceae along Edaphic Gradients in Yasuni National Park, Ecuadorian Amazonia1. *Biotropica* 34: 516–533. https://doi.org/10.1111/j.1744-7429.2002.tb00571.x

VANDERPOORTEN A. & GOFFINET B. 2009 — *Introduction to Bryophytes* (Vol. 91). Cambridge University Press, 329 p.

WAGNER S., BADER M.Y. & ZOTZ G. 2014 — Physiological Ecology of Tropical Bryophytes. *In:* Hanson D.T. & Rice S.K. (eds.) *Photosynthesis in Bryophytes and Early Land Plants* (Vol. 37). Dordrecht: Springer Netherlands, pp. 269–289.

WARREN D.L., CARDILLO M., ROSAUER D.F. & BOLNICK D.I. 2014 — Mistaking geography for biology: inferring processes from species distributions. *Trends in Ecology & Evolution* 29: 572–580. https://doi.org/10.1016/j.tree.2014.08.003

WITTMANN F. SCHONGART J., MONTERO J.C., MOTZER T., JUNK W.J., PIEDADE M.T.F.,…WORBES M. 2006 — Tree species composition and diversity gradients in white-water forests across the Amazon Basin. *Journal of Biogeography* 33: 1334–1347. https://doi.org/10.1111/j.1365-2699.2006.01495.x

WOLF J.H.D. 1993 — Diversity Patterns and Biomass of Epiphytic Bryophytes and Lichens Along an Altitudinal Gradient in the Northern Andes. *Annals of the Missouri Botanical Garden* 80: 928–960.

YU Y., PÓCS T., ZHU R.-L. 2014 — Notes on Early Land Plants Today. 62. A synopsis of *Myriocoleopsis* (Lejeuneaceae, Marchantiophyta) with special reference to transfer of *Cololejeunea minutissima* to *Myriocoleopsis*. *Phytotaxa* 183: 293-297. http://dx.doi.org/10.11646/phytotaxa.183.4.11

4 CONCLUSÃO

Essa tese evidenciou que diferentes tipos de vegetação na Amazônia Oriental promovem heterogeneidade ambiental, que influencia briófitas epífitas determinando variações nos atributos das assembleias entre as vegetações. A distribuição espacial em escala local é determinística, sendo regulada pelo nível de ocorrência no forófito (zona) e pelo tipo de vegetação que podem ser considerados substitutos para os filtros ambientais que moldam a composição de espécies.

Os resultados ampliam o conhecimento sobre a diversidade de briófitas epífitas, sobretudo para habitats pouco estudados, como Igapó e Várzea que parecem ser menos estáveis para as espécies que a Terra Firme. As vegetações inundáveis constituem reservatórios de táxons com nichos distintos em relação às demandas por umidade, luminosidade e/ou tolerâncias à variação de temperatura, que explicam, pelo menos em parte, a raridade local e incrementam a diversidade do banco regional de espécies.

O tipo de vegetação influenciou os atributos de comunidade e das espécies, como o gradiente vertical observado na Terra Firme e no Igapó e também, a homogeneidade da composição entre zonas na Várzea, ambos confirmados pela distribuição das guildas. Assim, as guildas de tolerância à luminosidade são atributos importantes no entendimento dos padrões de diversidade de briófitas epífitas.

Em função da diversidade e do número de espécies exclusivas registradas no Igapó ressalta-se a importância desse ambiente em particular e de se representar a variedade de ambientes amazônicos em estudos sobre padrões diversidade e de distribuição espacial de espécies. Considerando as respostas das briófitas aos filtros ambientais sugere-se que estudos futuros enfoquem caracteres morfofisiológicos das espécies associados à tolerância nas variações de condições, além de aspectos reprodutivos que permitam mensurar a influência da limitação de dispersão na estruturação das assembleias locais.

REFERÊNCIAS

ACEBEY, A.; GRADSTEIN, S. R.; KRÖMER, T. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. **Journal of Tropical Ecology**, v. 19, n. 1, p. 9–18, 2003.

ALLEE, W. C. Measurement of Environmental Factors in the Tropical Rain-Forest of Panama. **Ecology**, v. 7, n. 3, p. 273–302, 1926.

ALLOUCHE, O. *et al.* Area-heterogeneity tradeoff and the diversity of ecological communities. **Proceedings of the National Academy of Sciences**, v. 109, n. 43, p. 17495–17500, 2012.

ALMEIDA-NETO, M. *et al.* A consistent metric for nestedness analysis in ecological systems: Reconciling concept and measurement. **Oikos**, 2008.

ALVARENGA, L. D. P.; PÔRTO, K. C.; OLIVEIRA, J. R. DO P. M. DE. Habitat loss effects on spatial distribution of non-vascular epiphytes in a Brazilian Atlantic forest. **Biodiversity and Conservation**, v. 19, n. 3, p. 619–635, 2010.

ALVARES, C. A. *et al.* Köppen's climate classification map for Brazil. **Meteorologische Zeitschrift**, v. 22, n. 6, p. 711–728, 2014.

AMORIM, E. T. DE *et al.* Distribution of Bryophytes in South-Eastern Brazil: An Approach on Floristic Similarity and Environmental Filtering. **Cryptogamie, Bryologie**, v. 38, n. 1, p. 3–17, 2017.

BADER, M. Y. *et al.* Differences in desiccation tolerance do not explain altitudinal distribution patterns of tropical bryophytes. **Journal of Bryology**, v. 35, n. 1, p. 47–56, 2013.

BARBÉ, M.; FENTON, N. J.; BERGERON, Y. So close and yet so far away: long-distance dispersal events govern bryophyte metacommunity reassembly. **Journal of Ecology**, v. 104, n. 6, p. 1707–1719, 2016.

BASELGA, A. Partitioning the turnover and nestedness components of beta diversity. **Global Ecology and Biogeography**, v. 19, n. 1, p. 134–143, 2010a.

BASELGA, A. Multiplicative partition of true diversity yields independent alpha and beta components; additive partition does not. **Ecology**, v. 91, n. 7, p. 1974–1981, 2010b.

BASELGA A. **What is Beta Diversity?** Disponível em: <https://methodsblog.wordpress.com/2015 /05/27/beta_diversity/>. Acesso em: 7 set. 2016.

BASELGA, A.; JIMÉNEZ-VALVERDE, A.; NICCOLINI, G. A multiple-site similarity measure independent of richness. **Biology Letters**, v. 3, n. 6, p. 642–645, 2007.

BASTOS C. J. P. O gênero *Cheilolejeunea* (Spruce) Steph. (Lejeuneaceae, Marchantiophyta) nas Américas. **Pesquisas. Botânica,** v. 70, p. 5–78, 2017.

BATISTA, W. V. S. M.; SANTOS, N. D. DOS. Can regional and local filters explain epiphytic bryophyte distributions in the Atlantic Forest of southeastern Brazil? **Acta Botanica Brasilica**, v. 30, n. 3, p. 462–472, 2016.

BECK, J.; SCHWANGHART, W. Comparing measures of species diversity from incomplete inventories: an update. **Methods in Ecology and Evolution**, v. 1, n. 1, p. 38–44, 2010.

BENAVIDES, J. C. *et al.* Species richness and distribution of understorey bryophytes in different forest types in Colombian Amazonia. **Journal of Bryology**, v. 28, n. 3, p. 182–189, 2006.

BENAVIDES, J. C.; IDARRAGA, A.; ALVAREZ, E. Padrões de Diversidade de Briófitas em Florestas FLOODED e Terra Firme na Região do Aconcágua, Amazônia Colombiana. **Tropical Bryology**, v. 25, n. 1, p. 117–126, 2004.

BENÍTEZ, A.; PRIETO, M.; ARAGÓN, G. Large trees and dense canopies: Key factors for maintaining high epiphytic diversity on trunk bases (bryophytes and lichens) in tropical montane forests. **Forestry**, v. 88, n. 5, p. 521–527, 2015.

BLONDEL J. 2003 — Guilds of functional groups: does it matter? **Oikos** v. 100, n. 2, 223–231.

BORDIN, J.; YANO, O. Fissidentaceae (Bryophyta) do Brasil. **Boletim do Instituto de Botanica**, v. 22, p. 1–168, 2013.

BRAY J. R.; CURTIS J. T. An Ordination of Upland Forest Communities of Southern Wisconsin. **Ecological Monographs,** v. 27, 325–349. 1957.

BRENES-ARGUEDAS, T. *et al.* Do differences in understory light contribute to species distributions along a tropical rainfall gradient? **Oecologia,** v. 166, n. 2, p. 443–456, 2011.

BROWN, R. L.; REILLY, L. A. J.; PEET, R. K. Species Richness: Small Scale. *In*: **eLS. John Wiley & Sons**. Chichester, UK: John Wiley & Sons, Ltd, 2016. p. 1–9.

CÁCERES, M. DE; LEGENDRE, P.; MORETTI, M. Improving indicator species analysis by combining groups of sites. **Oikos**, v. 119, n. 10, p. 1674–1684, 2010.

CAMPBELL, D. G. Scale and patterns of community structure in amazonian forests. *In*: EDWARDS, P. J.; MAY, R. M.; WEBB, N. R. (Eds.). **Large-scale Ecology and Conservation Biology**. [s.l.] Oxford, U.K: Blackwell Scientific, 1994. p. 179–194.

CARVALHO-SILVA, M.; STECH, M.; SOARES-SILVA, L. H.; BUCK, W. R., WICKETT, N. J.; LIU, Y.; CÂMARA, P. E. A. S. A molecular phylogeny of the Sematophyllaceae sl (Hypnales) based on plastid, mitochondrial and nuclear markers, and its taxonomic implications. **Taxon**, v. 66, p. 811–831, 2017.

CASTRO, R. M. DA S. *et al.* Influência da sazonalidade na produção de serapilheira no experimento ESECAFLOR, na Floresta Nacional de Caxiuanã. *In*: LISBOA, P. L. B. (Ed.). . **Caxiuanã: paraíso ainda preservado**. Belém: Museu Paraense Emílio Goeldi, 2013. p. 856.

CAVENDER-BARES, J. *et al.* The merging of community ecology and phylogenetic biology.

Ecology Letters, v. 12, n. 7, p. 693–715, 2009.

CERQUEIRA, G.R. **Riqueza, composição e expressão sexual da comunidade de briófitas epífitas em florestas inundadas na Floresta Nacional de Caxiuanã, Amazônia Oriental**. Universidade Federal Rural da Amazônia: Museu Paraense Emílio Goeldi, 2013.

CERQUEIRA, G. R., ILKIU-BORGES, A. L., FERREIRA, L. V. Seasonality of reproduction of epiphytic bryophytes in flooded forests from the Caxiuanã National Forest, Eastern Amazon. **Anais da Academia Brasileira de Ciências** v. 88 1–8, 2016.

CERQUEIRA, G. R.; ILKIU-BORGES, A. L.; FERREIRA, L. V. Species richness and composition of epiphytic bryophytes in flooded forests of Caxiuanã National Forest, Eastern Amazon, Brazil. **Anais da Academia Brasileira de Ciências**, v. 89, p. 2371–2382, 2017.

CINTRA, R. *et al.* Forest spatial heterogeneity and palm richness, abundance and community composition in Terra Firme forest, Central Amazon. **Revista Brasileira de Botânica**, v. 28, n. 1, p. 75–84, 2005.

CORNELISSEN, J. H. C.; TER STEEGE, H. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. **Journal of Tropical Ecology**, v. 5, n. 02, p. 131–150, 1989.

CORNELL, H. V.; HARRISON, S. P. What Are Species Pools and When Are They Important? **Annual Review of Ecology, Evolution, and Systematics**, v. 45, n. 1, p. 45–67, 2014.

COSTA, A. C. L. DA *et al.* Caracterização metereológica da Floresta Nacional de Caxiuanã. *In*: LISBOA, P. L. B. (Ed.). **Caxiuanã: paraíso ainda preservado**. Belém: Museu Paraense Emílio Goeldi, 2013. p. 656.

COSTA, A. C. L. DA *et al.* Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. **New Phytologist**, v. 187, n. 3, p. 579–591, 2010.

COSTA, D. P. DA. Epiphytic Bryophyte Diversity in Primary and Secondary Lowland Rainforests in Southeastern Brazil. **The Bryologist**, v. 102, n. 2, p. 320, 1999.

CRANDALL-STOTLER, B.; STOTLER, R. E.; LONG, D. G. PHYLOGENY AND CLASSIFICATION OF THE MARCHANTIOPHYTA. **Edinburgh Journal of Botany**, v. 66, n. 01, p. 155, 2009.

DAUPHIN, G. Ceratolejeunea. **Flora Neotropica Monograph**, v. 90, n. 27, p. 1–86, 2003.

DURING, H. J. Life Strategies of Bryophytes: A Preliminary Review. **Oikos**, v. 5, n. 1, p. 2–18, 1979.

EVANS, S. A.; HALPERN, C. B.; MCKENZIE, D. The contributions of forest structure and substrate to bryophyte diversity and abundance in mature coniferous forests of the Pacific Northwest. **The Bryologist**, v. 115, n. 2, p. 278–294, 2012.

FERREIRA, L. V. Effect of flooding duration on species richness, floristic composition and forest structure in river margin habitats in Amazonian blackwater floodplain forests: Implications for future Design of protected areas. **Biodiversity and Conservation**, v. 9, p. 1–14, 2000.

FERREIRA, L. V.; ALMEIDA, S. S. DE; PAROLIN, P. Amazonian white-and blackwater floodplain forests in Brazil: Large differences on a small scale. **Ecotropica**, v. 16, n. 1, p. 31–41, 2010.

FERREIRA, L. V.; SILVA, A. S.; ALMEIDA, S. S. **Os tipos de vegetação de Caxiuanã**. [s.l.] Instituto Chico Mendes de Conservação da Biodiversidade, 2012. Disponível em: <http://www.icmbio.gov.br/portal/unidadesdeconservacao/biomas-brasileiros/amazonia/unidades-de-conservacao-amazonia/1928-flona-de-caxiuana>.

FERREIRA, L. V. *et al.* Riqueza e composição de espécies da floresta de igapó e varzea da estação cientifica Ferreira Penna: Subsídios para o plano de manejo da Floresa Nacional de Caxiuanã. **Pesquisas, Botânica**, v. 56, p. 103–116, 2005.

FERREIRA, L. V. *et al.* Variação da riqueza e composição de espécies da comunidade de plantas entre as florestas de igapos e várzeas na Estação Científica Ferreira Penna -Caxiuanã na Amazônia Oriental. **Pesquisas, Botânica**, v. 64, p. 175–195, 2013.

FISHER, R. A.; CORBET, A. S.; WILLIAMS, C. B. The Relation Between the Number of Species and the Number of Individuals in a Random Sample of an Animal Population. **Journal of Animal Ecology**, v. 12, n. 1, p. 42–58, 1943.

FLORA DO BRASIL. **Flora do Brasil 2020 under construction.** Disponível em: <http://floradobrasil.jbrj.gov.br/>. Accesso em: 12 ago. 2018.

FLORSCHÜTZ, P. A. **The mosses of Suriname - Part I**. Leiden: [s.n.].

FOX, J.; WEISBERG, S. **An {R} Companion to Applied Regression**. 2. ed. Thousand Oaks CA: [s.n.].

FRAZER, G. W.; CANHAM, C. D.; LERTZMAN, K. P. **Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentationSimon Fraser University, Institute of Ecosystem Studies**Burnaby, British Columbia, and Millbrook, New YorkSimon Fraser University and the Institute of Ecosystem Studies, , 1999. Disponível em: <http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Gap+Light+Analyzer+(+GLA+):+Users+manual+and+program+documentation,+version+2.0#5%5Cnhttp://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Gap+light+analyzer+(GLA).+Users+manual+and+pro>

FURCH, K.; JUNK, W. J. Physico-chemical conditions in floodplains lakes. *In*: JUNK, W. J. (Org.). **The Central Amazon Floodplain: Ecology of a Pulsing System.** 1 ed. Berlin: Springer Verlag. p. 69-108, 1997.

GARCIA, E. T.; ILKIU-BORGES, A. L.; TAVARES-MARTINS, A. C. C. Brioflora de duas florestas de terra firme na Área de Proteção Ambiental do Lago de Tucuruí, PA, Brasil. **Hoehnea**, v. 41, n. 4, p. 499–514, 2014.

GILLRICH, J. J.; BOWMAN, K. C. **The Use of Bryophytes as Indicators of Hydric Soils and Wetland Hydrology during Wetland Delineations in the United StatesWetlands Regulatory Assistance Program**. [s.l: s.n.]. Disponível em: <http://hdl.handle.net/11681/5531>.

GLIME, J. M. Adaptive Strategies: Life Cycles. Chapt. 4-6. *In*: GLIME, J. M. **Bryophyte Ecology**. Volume 1. Physiological 4-6-1 Ecology Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Last updated 6 March 2017 and available at <http://digitalcommons.mtu.edu/bryophyte-ecology/>.

GOFFINET, B.; BUCK, W. R.; SHAW, A. J. Morphology, anatomy, and classification of the Bryophyta. *In*: SHAW, A. J.; GOFFINET, B. (Eds.). . **Bryophyte Biology**. 2. ed. Cambrige: Cambridge University Press, 2009. p. 580.

GOTELLI, N. J.; ELLISON, A. M. **Princípios de estatística em ecologia**. Porto Alegre: J. - Artmed, 2011.

GÖTZENBERGER, L. *et al.* Ecological assembly rules in plant communities-approaches, patterns and prospects. **Biological Reviews**, v. 87, n. 1, p. 111–127, 2012.

GRADSTEIN, S. R. The vanishing tropical rainforest. *In*: BATES, J. W.; FARMER, A. M. (Eds.). **Bryophytes and Lichens in a Changing Environment**. Oxford: Clarendon Press, 1992a. p. 416.

GRADSTEIN, S. R. Threatened bryophytes of the neotropical rain forest: a status report. **Tropical Bryology**, v. 6, p. 83–93, 1992b.

GRADSTEIN, S. R.; COSTA, D. P. DA. **The Hepaticae and Anthocerotae of Brazil**. v. 87. New York: The New York Botanical Garden Press, 2003. p. 673.

GRADSTEIN, S. R.; ILKIU-BORGES, A. L. Guide to the Plants of Central French Guiana. Part 4. Liverworts and Hornworts. **Memoirs of the New York Botanical Garden** v. 76. 2009. p. 140.

GRADSTEIN, S. R.; PÓCS, T. Bryophytes. *In*: LIETH, H.; WERGER, M. J. A. (Eds.). **Tropical Rain Forest Ecosystems**. Amsterdam: Elsevier Science Publishers B.V., 1989. p. 713.

GRADSTEIN, S. R.; CHURCHILL, S. P.; SALAZAR-ALLEN, N. **Guide to the Bryophytes of Tropical America**. v. 86. New York: The New York Botanical Garden Press, 2001. p. 577.

GRADSTEIN, S. R. *et al.* How to sample the epiphytic diversity of tropical rain forest. **Ecotropica**, v. 2, p. 59–72, 1996.

GUÈZE, M. *et al.* Determinants of tree species turnover in a southern Amazonian rain forest. **Journal of Vegetation Science**, v. 24, n. 2, p. 284–295, 2012.

HALLINGBÄCK, T.; HODGETTS, N. **Mosses, Liverworts, and Hornworts:** Status Survey and Conservation Action Plan for Bryophytes. IUCN/SSC Bryophyte Specialist Group. Gland: Switzerland and Cambridge: Information Press, Oxford, UK, 2000. p. 106.

HANSKI, I. Dynamics of Regional Distribution: The Core and Satellite Species Hypothesis. **Oikos**, v. 38, n. 2, p. 210-221, 1982.

HARRISON, S.; ROSS, S. J.; LAWTON, J. H. Beta Diversity on Geographic Gradients in Britain. **The Journal of Animal Ecology**, v. 61, n. 1, p. 151, 1992.

HIDA, N. *et al.* **River water level changes of the Amazon Estuary: at Breves, Caxiuanã and Abaetetuba** (S. Program, Ed.)Manaus99. Hydrological and Geochemical Processes in Large Scale River Basins. **Anais** [...] Manaus: 1999. Disponível em: http://horizon.documentation.ird.fr/exl-doc/pleins_textes/divers16-12/010059695.pdf

HILLERISLAMBERS, J. *et al.* Rethinking Community Assembly through the Lens of Coexistence Theory. **Annual Review of Ecology, Evolution, and Systematics**, v. 43, n. 1, p. 227–248, 2012.

HONORIO-CORONADO, E. N. *et al.* Multi-Scale Comparisons of Tree Composition in Amazonian Terra Firme Forests. **Biogeosciences**, v. 6, n. 11, p. 2719–2731, 2009.

HSIAO-PEI, L. *et al.* Spatial heterogeneity of gut microbiota reveals multiple bacterial communities with distinct characteristics. **Scientific Reports**, v. 4, n. 1, p. 6185, 2015.

HUBBELL, S. P. **The unified neutra of biodiversity and biogeography**. [s.l.] Princeton University Press, 2001.

HUTCHINSON, G. E. Concluding Remarks. **Cold Spring Harbor Symposia on Quantitative Biology**, v. 22, p. 415–427, 1957.

ILKIU-BORGES, A. L. *Prionolejeunea*: Lejeuneaceae, Jungermanniopsida. **Flora Neotropica Monograph**, v. 116, p. 1–131, 2016.

ILKIU-BORGES, A. L.; LISBOA, R. C. L. Lejeuneaceae (Hepaticae). *In*: LISBOA, P. L. B. (Ed.). **Caxiuanã:** Populações, Meio Físico e Diversidade Biológica. Belém: Museu Paraense Emílio Goeldi. 2002. p. 399-419.

ILKIU-BORGES, A. L. MORAES, E. N. R; LISBOA, R. C. L. Avanços no conhecimento da brioflora. *In*: Pedro Luiz Braga Lisboa. (Org.). **Caxiuanã:** Desafios para a conservação de uma Floresta Nacional na Amazônia. Belém: Museu Paraense Emílio Goeldi. 2009. p. 313-330.

ILKIU-BORGES, A. L. *et al.* Briófitas em Caxiuanã: Resultados do Levantamento em duas parcelas da Grade do PPBIO. *In*: Lisboa P.L.B. (org.) **Caxiuanã:** Paraíso Preservado. Belém: Museu Paraense Emílio Goeldi. 2013. p. 287-295.

JOHST, K. *et al.* Biodiversity conservation in dynamic landscapes: trade-offs between number, connectivity and turnover of habitat patches. **Journal of Applied Ecology**, v. 48, n. 5, p. 1227–1235, 2011.

JOST, L. Partitioning diversity into independent alpha and beta components. **Ecology**, v. 88, n. 10, p. 2427-2439, 2007.

JUNK W. J. *et al.* A classification of major natural habitats of Amazonian whitewater river floodplains (várzeas). **Wetlands Ecology and Management,** 20, 461-475, 2012.

JUNK, W. J. *et al.* A classification of the major habitats of Amazonian black-water river floodplains and a comparison with their white-water counterparts. **Wetlands Ecology and Management**, v. 23, n. 4, p. 677–693, 2015.

JUNK, W. J.; PIEDADE, M. T. F. An Introduction to South American Wetland Forests: Distribution, Definitions and General Characterization. *In*: JUNK, W. J. *et al.* (Eds.). . **Amazonian Floodplain Forests**. Dordrecht: Ecological Studies (Analysis and Synthesis), 2011. p. 3–25.

JUNK, W. J. *et al.* A Classification of Major Naturally-Occurring Amazonian Lowland Wetlands. **Wetlands**, v. 31, n. 4, p. 623–640, 2011.

KAWECKI, T. J. Adaptation to Marginal Habitats. **Annual Review of Ecology, Evolution, and Systematics**, v. 39, n. 1, p. 321–342, 2008.

KEEL, S. H. K.; PRANCE, G. T. Studies of the vegetation of a white-sand black-water igapó (Rio Negro, Brazil). **Acta Amazonica**, v. 9, p. 645–655, 1979.

KEMBEL, S. W. Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. **Ecology Letters**, v. 12, n. 9, p. 949–960, 2009.

KÖPPEN W.; GEIGER R. Klimate der Erde. Gotha: Verlag Justus Perthes. Wall-map 150 cm x 200 cm. 1928.

KRAFT, N. J. B. *et al.* Community assembly, coexistence and the environmental filtering metaphor. **Functional Ecology**, v. 29, n. 5, p. 592–599, 2015.

KÜRSCHNER, H. Life strategies and adaptations in bryophytes from the near and Middle East. **Turkish Journal of Botany**, v. 28, n. 1–2, p. 73–84, 2004.

LALIBERTÉ, E. *et al.* Assessing the scale-specific importance of niches and other spatial processes on beta diversity: a case study from a temperate forest. **Oecologia**, v. 159, n. 2, p. 377–388, 2009.

LEGENDRE, P.; LEGENDRE, L. **Numerical Ecology**. 2. ed. Amsterdam: Elsevier Science B.V., 1998.

LEIBOLD, M. A. *et al.* The metacommunity concept: a framework for multi-scale community ecology. **Ecology Letters**, v. 7, n. 7, p. 601–613, 2004.

LEVINE, J. M.; HILLERISLAMBERS, J. The importance of niches for the maintenance of species diversity. **Nature**, v. 461, n. 7261, p. 254–257, 2009.

LEVIS, C. *et al.* Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. **Science**, v. 355, n. 6328, p. 925–931, 2017.

LISBOA, P. L. B; BEZERRA, M. G. F; CARDOSO, A. L. R. **Caxiuanã:** História natural e ecologia de uma floresta nacional da Amazônia. Belém: Museu Paraense Emílio Goeldi. 2013. p. 299.

LÖBEL, S.; DENGLER, J.; HOBOHM, C. Species richness of vascular plants, bryophytes and lichens in dry grasslands: The effects of environment, landscape structure and competition. **Folia Geobotanica**, v. 41, n. 4, p. 377–393, 2006.

LÖBEL, S.; SNÄLL, T.; RYDIN, H. Metapopulation processes in epiphytes inferred from patterns of regional distribution and local abundance in fragmented forest landscapes. **Journal of Ecology**, v. 94, n. 4, p. 856–868, 2006.

LOPES, M. O. *et al.* Estudo comparativo de comunidades de briófitas sujeitas a diferentes graus de inundação no município de São Domingos do Capim, PA, Brasil. **Hoehnea**, v. 43, n. 2, p. 159–171, 2016.

MAGALHÃES, N. DOS S.; MARENCO, R. A.; CAMARGO, M. A. B. Do soil fertilization and forest canopy foliage affect the growth and photosynthesis of Amazonian saplings? **Scientia Agricola**, v. 71, n. 1, p. 58–65, 2014.

MAGURRAN. A. E. **Ecological Diversity and its Measurement**. Princeton, U.S.A: Princeton University Press, 1988. p. 179.

MAGURRAN, A. E. **Measuring of Biological Diversity**. Inglaterra: Blackwell Science, 2004. p. 264.

MAGURRAN, A. E.; HENDERSON, P. A. Explaining the excess of rare species in natural species abundance distributions. **Nature**, v. 422, n. 6933, p. 714–716, 2003.

MANDL, N. A.; KESSLER, M.; GRADSTEIN, S. R. Effects of environmental heterogeneity on species diversity and composition of terrestrial bryophyte assemblages in tropical montane forests of southern Ecuador. **Plant Ecology & Diversity**, v. 2, n. 3, p. 313–321, 2009.

MARCON, E.; HÉRAULT, B. entropart : An R Package to Measure and Partition Diversity. **Journal of Statistical Software**, v. 67, n. 8, p. 1–26, 2015.

MÁRIALIGETI, S. *et al.* The effects of stand structure on ground-floor bryophyte assemblages in temperate mixed forests. **Biodiversity and Conservation**, v. 18, n. 8, p. 2223–2241, 2009.

MARRA, D. M. *et al.* Large-scale wind disturbances promote tree diversity in a Central Amazon forest. **PLoS ONE**, v. 9, n. 8, 2014.

MATOS, D. C. L.; FERREIRA, L. V.; CARLUCCI, M. B. Estratégias funcionais de *Macrolobium angustifolium* (Benth.) R.S. Cowan para coexistir em florestas inundadas na Amazônia oriental. **Revista Espacios**, v. 39, n. 39, p. 1-16, 2018.

MATTHEWS, T. J.; WHITTAKER, R. J. Fitting and comparing competing models of the species abundance distribution: assessment and prospect. **Frontiers of Biogeography**, v. 6, n. 2, p. 67–82, 2014.

MCCUNE, B.; GRACE, J. M. R. P. P. (Multi-response Permutation Procedures) and related techniques. *In:* MCCUNE, B.; GRACE (Eds.) **Analysis of Ecological Communities**, 2002a. Cap, 24, p. 188197.

MCCUNE, B.; GRACE, J. M. R. P. P. Canonical Correspondence Analysis. *In:* MCCUNE, B.; GRACE (Eds.) **Analysis of Ecological Communities**, 2002b. Cap. 21, p. 164–177.

MCGILL, B. J. *et al.* Rebuilding community ecology from functional traits. **Trends in Ecology and Evolution**, v. 21, n. 4, p. 178–185, 2006.

MCGILL, B. J. *et al.* Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. **Ecology Letters**, v. 10, n. 10, p. 995–1015, 2007.

MELACK, J. M.; HESS, L. L. **Remote Sensing of the Distribution and Extent of Wetlands in the Amazon Basin**. *In:* JUNK, W.; PIEDADE, M.; WITTMANN, F.; SCHÖNGART, J.; PAROLIN, P. (Eds) Amazonian Floodplain Forests. Ecological Studies (Analysis and Synthesis), vol 210. Dordrecht: Springer Netherlands, 2010. p. 43–59.

MENEZES, B. S.; MARTINS, F. R.; ARAÚJO, F. S. COMMUNITY ASSEMBLY: CONCEPTS, DOMAIN AND THEORETICAL STRUCTURE. **Oecologia Australis**, v. 20, n. 01, p. 1–17, 2016.

MONTAG, L. F. A *et al.* Os peixes da Floresta Nacional de Caxiuanã (municípios de Melgaço e Portel, Pará - Brasil). **Bol. Mus. Para. Emílio Goeldi, Ciências Naturais**, v. 3, n. 1, p. 11–34, 2008.

MONTUFAR, R.; PINTAUD, J.-C. Variation in species composition, abundance and microhabitat preferences among western Amazonian terra firme palm communities. **Botanical Journal of the Linnean Society**, v. 151, p. 127–140, 2006.

MORAES, E. DE N. R. **Diversidade, Aspectos Florísticos e Ecológicos dos Musgos (Bryophyta) da Estação Científica Ferreira Penna, Flona de Caxiuanã, Pará, Brasil**. 2006. 163f. Dissertação de Mestrado Universidade Federal Rural da Amazônia/Museu Paraense Emílio Goeldi, Belém, 2006.

MORAES, E. DE N. R.; LISBOA, R. C. L. Diversidade, taxonomia e distribuição por estados brasileiros das famílias Bartramiaceae, Brachytheciaceae, Bryaceae, Calymperaceae, Fissidentaceae, Hypnaceae e Leucobryaceae (Bryophyta) da Estação Científica Ferreira Penna, Caxiuanã, Pará, Brasil. **Acta Amazonica**, v. 39, n. 4, p. 773–792, 2009.

OKSANEN, J. *et al.* **vegan: Community Ecology Package. R package version 2.5-2**.

OLIVEIRA, H. C. DE; OLIVEIRA, S. M. DE. Vertical distribution of epiphytic bryophytes in Atlantic Forest fragments in northeastern Brazil. **Acta Botanica Brasilica**, v. 30, n. 4, p. 609–617, 2016.

OLIVEIRA, S. M. DE *et al.* Niche assembly of epiphytic bryophyte communities in the Guianas: a regional approach. **Journal of Biogeography**, v. 36, n. 11, p. 2076–2084, 2009.

OLIVEIRA, S. M. DE; TER STEEGE, H. Floristic overview of the epiphytic bryophytes of terra firme forests across the Amazon basin. **Acta Botanica Brasilica**, v. 27, n. 2, p. 347–363, 2013.

OLIVEIRA, S. M. DE; TER STEEGE, H. Bryophyte communities in the Amazon forest are regulated by height on the host tree and site elevation. **Journal of Ecology**, v. 103, n. 2, p. 441–450, 2015.

PANTOJA, A. *et al.* Bryophytes in fragments of Terra Firme forest on the great curve of the Xingu River, Pará state, Brazil 1 Part of Master's Dissertation of the first author. **Brazilian Journal of Biology**, v. 75, p. 238–249, 2015.

PARDOW, A. *et al.* Functional diversity of epiphytes in two tropical lowland rainforests, French Guiana: using bryophyte life-forms to detect areas of high biodiversity. **Biodiversity and Conservation**, v. 21, n. 14, p. 3637–3655, 2012.

PARKER, G. G. Structure and Microclimate of Forest Canopies. *In*: LOWMAN, M. D.; NADKARNI, N. M. (Eds.). **Forest Canopies**. 1. ed. New York: Academic Press, 1995. p. 322.

PAROLIN, P. Diversity of Adaptations to flooding in trees of Amazonian floodplains. **Pesquisas, Botânica,** n. 63, p. 7–28. 2012

PÄRTEL, M. *et al.* The Species Pool and Its Relation to Species Richness: Evidence from Estonian Plant Communities. **Oikos**, v. 75, n. 1, p. 111–117, 1996.

PEAY, K. G.; BARALOTO, C.; FINE, P. V. A. Strong coupling of plant and fungal community structure across western Amazonian rainforests. **The ISME Journal**, v. 7, n. 9, p. 1852–1861, 2013.

PEÑALOZA-BOJACÁ, G. F. *et al.* Bryophytes on Brazilian ironstone outcrops: Diversity, environmental filtering, and conservation implications. **Flora**, v. 238, p. 162–174, 2018.

PHARO, E. J.; LINDENMAYER, D. B.; TAWS, N. The effects of large-scale fragmentation on bryophytes in temperate forests. **Journal of Applied Ecology**, v. 41, n. 5, p. 910–921, 2004.

PHARO, E. J.; ZARTMAN, C. E. Bryophytes in a changing landscape: The hierarchical effects of habitat fragmentation on ecological and evolutionary processes. **Biological Conservation**, v. 135, n. 3, p. 315–325, 2007.

PICCININ, J. L.; RUIVO, M. L. P. **Caracterização Unidades Pedológicas Plano de Manejo da Floresta Nacional de Caxiuanã**. [s.l.] Instituto Chico Mendes de Conservação da Biodiversidade, 2012. Disponível em: <http://www.icmbio.gov.br/portal/unidadesdeconservacao/biomas-brasileiros/amazonia/unidades-de-conservacao-amazonia/1928-flona-de-caxiuana>.

PINEL-ALLOUL, B. *et al.* Large-scale geographic patterns of diversity and community structure of pelagic crustacean zooplankton in Canadian lakes. **Global Ecology and Biogeography**, v. 22, n. 7, p. 784–795, 2013.

PIRES, J. M.; PRANCE, G. T. The vegetation types of the Brazilian Amazon. *In*: PRANCE, G. T.; LOVEJOY, T. E. (Eds.). **Key environments: Amazonia**. First ed. [s.l.] Pergamon Press, 1985. p. 109-145.

PITMAN, N. C. A. *et al.* Dominance and distribution of tree species in upper Amazonian terra firme forests. **Ecology**, v. 82, n. 8, p. 2101–2117, 2001.

PÓCS, T. Tropical Forest Bryophytes. *In*: **Bryophyte Ecology**. Dordrecht: Springer Netherlands, 1982. p. 59–104.

PÔRTO, K. C.; SILVA, M. P. P. A frequência de reprodução sexuada afeta a distribuição de briófitas? Uma abordagem regional para a Floresta Atlântica Nordestina. *In*: 63º Congresso Nacional de Botânica. **Anais** [...]. Joinville: Sociedade Botânica do Brasil, 2012. p. 12-20.

POS, E. T.; SLEEGERS, A. D. M. Vertical distribution and ecology of vascular epiphytes in a lowland tropical rain forest of Brazil. **Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais**, v. 5, n. 3, p. 335–344, 2010.

PROCTOR, M. C. F. The diversification of bryophytes and vascular plants in evolving terrestrial environments. *In*: HANSON, D. T.; RICE, S. K. (Eds.). **Photosynthesis in Bryophytes and Early Land Plants**. Springer Netherlands, 2014. v. 37. p. 59-77.

PUIG, H. **A Floresta Tropical Úmida**. São Paulo: UNESP, 2007. p. 496.

QUARESMA, A. C. *et al.* Composition, diversity and structure of vascular epiphytes in two contrasting Central Amazonian floodplain ecosystems. **Acta Botanica Brasilica**, v. 31, n. 4, p. 686–697, 2017.

QUINN, G. P.; KEOUGH, M. J. **Experimental Design and Data Analysis for Biologists**. New York: Cambridge University Press, 2002.

R CORE TEAM. **R: A language and environment for statistical computing**. R Foundation for Statistical Computing, Vienna, Austria. 2019. <URL https://www.R-project.org/>

REESE, W. D. Calymperaceae. **Flora Neotropica Monograph**, v. 58, 1993. p. 102.

REINER-DREHWALD, M. E. Las Lejeuneaceae (Hepaticae) de Misiones, Argentina VI. Lejeunea y Taxilejeunea. **Tropical Bryology**, v. 19, p. 81–131, 2000.

REINER-DREHWALD, M. E.; GODA, A. Revision of the genus Crossotelejeunea (Lejeuneaceae, Hepaticae). **The Journal of the Hattori Botanical Laboratory**, v. 89, p. 1–54, 2000.

REINER-DREHWALD, M. E.; GROLLE, R. Review of the genus *Rectolejeunea* (Lejeuneaceae, Marchantiophyta). **Nova Hedwigia**, v. 95, n. 3–4, p. 451–482, 2012.

RICHARDS, P. W. **The Tropical Rain Forest: An ecological study**. New York:Cambridge University Press, 1952. p. 450.

RICHARDS, P. W. The Ecology of tropical forest bryophytes. *In*: SCHUSTER, R. M. (Ed.). **New Manual of Bryology**. Nichinan, Japan: The Hattori Botanical Laboratory, 1984. p. 1233-1270.

RODRIGUES, L. F. *et al.* Influences of forest structure and landscape features on spatial variation in species composition in a palm community in central Amazonia. **Journal of Tropical Ecology**, v. 30, n. 6, p. 565–578, 2014.

ROOT, R. B. The Niche Exploitation Pattern of the Blue-Gray Gnatcatcher. **Ecological Monographs**, v. 37, n. 4, p. 317–350. 1967.

ROSENZWEIG, M. L. **Species diversity in space and time**. Cambridge: The press syndicate of the University of Cambridge, 1995.

ROSENZWEIG, M. L.; ZIV, Y. The echo pattern of species diversity: pattern and processes. **Ecography**, v. 22, n. 6, p. 614–628, 1999.

RUIVO, M. L. P.; CUNHA, E. S. Mineral and organic components in archaeological black earth and yellow latosol in Caxiuana, Amazon, Brazil (E. Tiezzi, C. A. Brebbia, & J. L. Uso, Eds.)Ecosystems and Sustainable Development IV. **Anais [**...]. UK: WIT Press, 2003.

SANGER, J. C.; KIRKPATRICK, J. B. Moss and vascular epiphyte distributions over host tree and elevation gradients in Australian subtropical rainforest. **Australian Journal of Botany**, v. 63, n. 8, p. 696, 2015.

SANTOS, N. D. DOS *et al.* Bryophytic and phytogeographical aspects of two types of forest of the Serra do Mar State Park, Ubatuba/SP, Brazil. **Biota Neotropica**, v. 11, n. 2, p. 425–438, 2011.

SANTOS, N. D. DOS *et al.* Windborne: Can liverworts be used as indicators of altitudinal gradient in the Brazilian Atlantic Forest? **Ecological Indicators**, v. 36, p. 431–440, 2014.

SANTOS, N. D. DOS; COSTA, D. P. DA. Phytogeography of the liverwort flora of the Atlantic Forest of southeastern Brazil. **Journal of Bryology**, v. 32, n. 1, p. 9–22, 2010.

SCHIETTI, J. *et al.* Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. **Plant Ecology and Diversity**, v. 7, n. 1–2, p. 241–253, 2014.

SCHOFIELD, W. B. **Introdution to Bryology**. New York: MacMillan Publishing, 1985. p. 431.

SCHUSTER, R. M. Phytogeography of bryophytes. *In*: SCHUSTER, R. M. (Ed.). **New Manual of Bryophytes**. Nichinan, Japan: Hattori Botanical Laboratory, 1983. p. 463-626.

SHAW, A. J.; GOFFINET, B. **Bryophyte biology**. 1. ed. Cambridge: Cambridge University Press, 2000. p. 476.

SHAW, A. J.; SZÖVÉNYI, P.; SHAW, B. Bryophyte diversity and evolution: Windows into the early evolution of land plants. **American Journal of Botany**, v. 98, n. 3, p. 352–369, 2011.

SHI, X. -Q.; GRADSTEIN, S. R.; ZHU, R. -L. Phylogeny and taxonomy of *Archilejeunea* (Marchantiophyta: Lejeuneaceae) based on molecular markers and morphology. **Taxon,** v. 64, n. 5, p. 881–892, 2015.

SILMAN, M. R. Tropical Rainforest Responses to Climatic Change. *In*: BUSH, M. B.; FLENLEY, J. R.; GOSLING, W. (Eds.). . **Tropical Rainforest Responses to Climatic Change**. Berlin, Heidelberg: Springer Berlin Heidelberg, 2011. p. 428.

SILVA, I. A.; CIANCIARUSO, M. V.; BATALHA, M. A. Abundance distribution of common and rare plant species of Brazilian savannas along a seasonality gradient. **Acta Botanica Brasilica**, v. 24, n. 2, p. 407–413, 2010.

SILVA, J. B.; GERMANO, S. R. Bryophytes on rocky outcrops in the caatinga biome: a conservationist perspective. **Acta Botanica Brasilica**, 27, n. 4, p. 827–835, dez. 2013.

SILVA, M. P. P. **Padrões de Distribuição de Briófitas na Floresta Atlântica do Nordeste do Brasil: Relações Ambientais, Biogeográficas e Conservação.** 2013. 208f. Tese de Doutorado, Universidade Federal de Pernambuco, Recife. 2013.

SILVA, M. P. P.; PÔRTO, K. C. Spatial structure of bryophyte communities along an edge-interior gradient in an Atlantic Forest remnant in Northeast Brazil. **Journal of Bryology**, v. 32, n. 2, p. 101–112, 2010.

SILVA, M. P. P.; PÔRTO, K. C. Bryophyte communities along horizontal and vertical gradients in a human-modified Atlantic Forest remnant. **Botany**, v. 91, n. 3, p. 155–166, 2013.

SLACK, N. G. Species diversity and community structure in bryophytes: New York State studies. **TS Museum Bulletin**, v. 428, p. 1–70, 1977.

SLACK, N. G. Bryophytes in relation to ecological niche theory. **Journal of the Hattori Botanical hboralory**, v. 52, p. 199–217, 1982.

SLACK, N. G. Bryophytes and ecological niche theory. **Botanical Journal of the Linnean Society**, v. 104, n. 1–3, p. 187–213, 1990.

SÖDERSTRÖM, L. Regional Distribution Patterns of Bryophyte Species on Spruce Logs in Northern Sweden. **The Bryologist**, v. 92, n. 3, p. 349, 1989.

SÖDERSTRÖM, L. *et al.* World checklist of hornworts and liverworts. **PhytoKeys** v. 59: p. 1-821. 2016.

SÖDERSTRÖM, L.; DURING, H. J. Bryophyte rarity viewed from the perspectives of life history strategy and metapopulation dynamics. **Journal of Bryology**, v. 27, p. 261–268, mar 2005.

SONNLEITNER, M. *et al.* Microclimatic patterns correlate with the distribution of epiphyllous bryophytes in a tropical lowland rain forest in Costa Rica. **Journal of Tropical Ecology**, v. 25, n. 3, p. 321–330, 2009.

SPORN, S. G. *et al.* Vertical distribution of epiphytic bryophytes in an Indonesian rainforest. **Biodiversity and Conservation**, v. 19, n. 3, p. 745–760, 2010.

STEIN, A.; GERSTNER, K.; KREFT, H. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. **Ecology Letters**, v. 17, n. 7, p. 866–880, 2014.

STEIN, A.; KREFT, H. Terminology and quantification of environmental heterogeneity in species-richness research. **Biological Reviews**, v. 90, n. 3, p. 815–836, 2015.

STROPP, J. *et al.* Disentangling regional and local tree diversity in the Amazon. **Ecography**, v. 32, n. 1, p. 46–54, 2009.

SUGIHARA, G. *et al.* Predicted correspondence between species abundances and dendrograms of niche similarities. **Proceedings of the National Academy of Sciences**, v. 100, n. 9, p. 5246–5251, 2003.

TAN, B. C.; PÓCS, T. Biogeography and conservation of bryophytes. *In*: SHAW, A. J.; GOFFINET, B. (Eds.). **Bryophyte biology**. 1. ed. Cambridge: Cambridge University Press, 2000. p. 403–448.

TAVARES, A. C. C. **Florística e Ecologia das Comunidades de Briófitas em Florestas de Terra Firme no Estado do Pará, Amazônia**. 2009. 132f. Tese de Doutorado - Instituto de Pesquisas Jardim Botânico do Rio de Janeiro/Escola Nacional de Botânica Tropical, Rio de Janeiro. 2009.

TAVARES-MARTINS, A. C. C.; LISBOA, R. C. L.; COSTA, D. P. DA. Bryophyte flora in upland forests at different successional stages and in the various strata of host trees in northeastern Pará, Brazil. **Acta Botanica Brasilica**, v. 28, n. 1, p. 46–58, 2014.

TER STEEGE, H. How Neutral is Ecology? **Biotropica**, v. 42, n. 6, p. 631–633, 2010.

TER STEEGE, H. *et al.* A spatial model of tree α-diversity and -density for the Amazon. **Biodiversity and Conservation**, v. 12, p. 2255–2277, 2003.

TER STEEGE, H. *et al.* Continental-scale patterns of canopy tree composition and function across Amazonia. **Nature**, v. 443, n. 7110, p. 444–447, 2006.

TER STEEGE, H. *et al.* Hyperdominance in the Amazonian tree flora. **Science (New York, N.Y.)**, v. 342, n. 6156, p. 1243092, 2013.

TERBORGH, J. On the Notion of Favorableness in Plant Ecology. **The American Naturalist**, v. 107, n. 956, p. 481–501, 1973.

TUOMISTO, H.; POULSEN, A. D. Pteridophyte diversity and species composition in four Amazonian rain forests. **Journal of Vegetation Science**, v. 11, n. 3, p. 383–396, 2000.

TUOMISTO, H.; RUOKOLAINEN, K. Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. **Ecology**, v. 87, n. 11, p. 2697–2708, 2006.

TUOMISTO, H.; RUOKOLAINEN, K.; YLI-HALLA, M. Dispersal, Environment, and Floristic Variation of Western Amazonian Forests. **Science**, v. 299, n. 5604, p. 241–244, 2003.

TUOMISTO, H.; ZUQUIM, G.; CÁRDENAS, G. Species richness and diversity along edaphic and climatic gradients in Amazonia. **Ecography**, v. 37, p. 1034–1046, jul. 2014.

TUOMISTO, H. *et al.* Distribution and Diversity of Pteridophytes and Melastomataceae along Edaphic Gradients in Yasuni National Park, Ecuadorian Amazonia1. **Biotropica**, v. 34, n. 4, p. 516–533, 2002.

ULRICH, W.; GOTELLI, N. J. Null model analysis of species nestedness patterns. **Ecology**, v. 88, n. 7, p. 1824–1831, jul. 2007.

UNIYAL, P. L. Role of bryophytes in conservation of ecosystems and biodiversity. **Botanica**, v. 49, p. 101–115, 1999.

VALENCIA, R. *et al.* High tree alpha-diversity in Amazonian Ecuador. **Biodiversity and Conservation**, v. 3, n. 1, p. 21–28, 1994.

VALENCIA, R. *et al.* Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. **Journal of Ecology**, v. 92, p. 214–229, 2004.

VALENTE, E. DE B.; PÔRTO, K. C.; BASTOS, C. J. P. Habitat heterogeneity and diversity of bryophytes in campos rupestres. **Acta Botanica Brasilica**, v. 31, n. 2, p. 241–249, 2017.

VAN ZATEN, B. O.; GRADSTEIN, S. R. Experimental dispersal geography of neotropical liverworts. **Beiheft zur Nova Hedwigia**, v. 90, p. 41–94, 1988.

VAN ZATEN, B. O.; PÓCS, T. Distribution and dispersal of Bryophytes. *In*: SCHULTZE-MOTEL, W. (Ed.). **Advances in Bryology 1**. [s.l.] Cramer, Vaduz, 1981. p. 315.

VANDERPOORTEN, A.; ENGELS, P. The effects of environmental variation on bryophytes at a regional scale. **Ecography**, v. 25, n. 5, p. 513–522, 2002.

VANDERPOORTEN, A.; GOFFINET, B. **Introduction to Bryophytes**. v. 91 New York: Cambridge University Press, 2009.

VELLEND, M. Conceptual Synthesis in Community Ecology. **The Quarterly Review of Biology**, v. 85, n. 2, p. 183–206, 2010.

WAGNER, S.; BADER, M. Y.; ZOTZ, G. Physiological Ecology of Tropical Bryophytes. *In*: HANSON, D. T.; RICE, S. K. (Eds.). **Photosynthesis in Bryophytes and Early Land Plants**. Advances in Photosynthesis and Respiration. Dordrecht: Springer Netherlands, 2014. v. 37. p. 269–289.

WAGNER, S.; ZOTZ, G.; BADER, M. Y. The temperature acclimation potential of tropical bryophytes. **Plant Biology**, v. 16, n. 1, p. 117–124, 2014.

WARREN, D. L. *et al.* Mistaking geography for biology: inferring processes from species distributions. **Trends in Ecology & Evolution**, v. 29, n. 10, p. 572–580, 2014.

WATSON, M. A. Shifts in Patterns of Microhabitat Occupation by Six Closely Related Species of Mosses Along Along a Complex Altitudinal Gradient. **Oecologia**, v. 47, p. 46–55, 1980.

WATSON, M. A. Patterns of Microhabitat Occupation of Six Closely Related Species of Mosses Along a Complex Altitudinal Gradient. **Ecology**, v. 62, n. 4, p. 1067–1078, 1981.

WEIHER, E. *et al.* Advances, challenges and a developing synthesis of ecological community assembly theory. **Philosophical Transactions of the Royal Society B: Biological Sciences**, v. 366, n. 1576, p. 2403–2413, 2011.

WHITTAKER, R. J. Vegetation of the Siskiyou Mountains, Oregon and California. **Ecological Monographs**, v. 30, p. 280–338, 1960.

WHITTAKER, R. J.; WILLIS, K. J.; FIELD, R. Scale and species richness : towards a general, theory of species diversity hierarchical. **Diversity**, v. 28, n. 4, p. 453–470, 2001.

WILLIS, J. C. **Age and area: a study in geographical distribution and origin of species**. Cambrige: Cambridge University Press, 1922. p. 284.

WITTMANN, F.; JUNK, W. J.; PIEDADE, M. T. F. The várzea forests in Amazonia: Flooding and the highly dynamic geomorphology interact with natural forest succession. **Forest Ecology and Management**, v. 196, n. 2–3, p. 199–212, 2004.

WITTMANN, F. *et al.* Tree species composition and diversity gradients in white-water forests across the Amazon Basin. **Journal of Biogeography**, v. 33, n. 8, p. 1334–1347, 2006.

WOLF, J. H. D. Diversity Patterns and Biomass of Epiphytic Bryophytes and Lichens Along an Altitudinal Gradient in the Northern Andes. **Annals of the Missouri Botanical Garden**, v. 80, n. 4, p. 928-960, 1993.

YU, Y.; PÓCS, T.; ZHU, R.-L. Notes on Early Land Plants Today. 62. A synopsis of *Myriocoleopsis* (Lejeuneaceae, Marchantiophyta) with special reference to transfer of *Cololejeunea minutissima* to *Myriocoleopsis*. **Phytotaxa,** v. 183, n. 4, 293-297, 2014.

ZARTMAN, C. E.; NASCIMENTO, H. E. M. Are habitat-tracking metacommunities dispersal limited? Inferences from abundance-occupancy patterns of epiphylls in Amazonian forest fragments. **Biological Conservation**, v. 127, n. 1, p. 46–54, 2006.

ZOBEL, M.;, VAN DER MAAREL, E.; DUPRÉ, C. Species pool: the concept, its determination and significance for community restoration. **Applied Vegetation Science**, v. 1, n. 1, p. 55–66, 1998.