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DISTRIBUIÇÃO ESPACIAL DE TRAÇOS FUNCIONAIS DE BRIÓFITAS AO LONGO DE GRADIENTES AMBIENTAIS NA FLORESTA ATLÂNTICA

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Dissertação apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Pernambuco como requisito para obtenção do título de mestre em Biologia Vegetal

Área de concentração: Ecologia e Conservação

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A minha mãe (Francilene Silva), avos (Francisco e Antônia Silva), e as minhas orientadoras (Kátia e Mércia) que sempre me apoiaram e acreditaram em mim,

Dedico

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RESUMO

A Floresta Atlântica atualmente corresponde a mínimos 15% de sua cobertura original, distante do que foi há 500 anos atrás, antes do início da colonização, uso da terra e exploração de recursos naturais. O elevado grau de perturbação de seus remanescentes dificulta a compreensão dos processos ecológicos de diversos grupos biológicos, incluindo as briófitas, plantas sensíveis a alterações ambientais. Neste estudo, visamos verificar como a distribuição espacial de traços funcionais de briófitas está configurada em uma paisagem tropical fragmentada. As questões norteadoras desta pesquisa foram: A distribuição espacial de briófitas relaciona-se à diversidade funcional ao longo dos gradientes vertical (base-dossel) e horizontal (borda-núcleo)? Os traços funcionais variam qualitativamente e quantitativamente ao longo dos gradientes? Para este estudo, foi analisada uma comunidade de briófitas distribuída espacialmente ao longo de gradientes ambientais, vertical e horizontal do maior fragmento florestal da Estação Ecológica de Murici (ESEC Murici), Alagoas, Brasil. Seis traços funcionais das briófitas relacionados à manutenção hídrica e à proteção a intensidade luminosa foram utilizados para verificar como determinadas funções distribuem-se espacialmente ao longo dos gradientes ambientais. A diversidade funcional pouco explicou a distribuição espacial das briófitas, no entanto a composição funcional, juntamente com a variação morfológica do lóbulo foram altamente correlacionadas com os gradientes ambientais. Os traços lóbulo, pigmento escuro e papila, apresentaram elevada correlação com os gradientes, principalmente o vertical, onde foram os principais promotores de variação. As formas de vida também explicaram a distribuição espacial no gradiente vertical, a ocorrência das mais resistentes à elevada luminosidade e desidratação no dossel. Finalmente, constatamos que o lóbulo nas hepáticas folhosas ampliou sua área da base ao dossel, e apresentou maiores dimensões significativamente da base ao dossel, e na borda do fragmento. Assim, sugere-se que essa estrutura contribui funcionalmente na estocagem e na manutenção hídrica, estando associado ao tipo de microhabitat ocupado pelas espécies. As implicações de nossos achados confirmam a existência de filtros ambientais modeladores da distribuição espacial de traços funcionais de briófitas na Floresta Atlântica.

Palavras-chave: Diversidade e composição funcional. Filtros ambientais. Gradiente vertical. Gradiente horizontal. Antropização.

ABSTRACT

The Atlantic Forest currently accounts for 15% of its original coverage, far from what it was 500 years ago, prior to the start of colonization, land use and exploitation of natural resources. The unbound disturbance of its remnants makes it difficult to understand the ecological processes of various biological groups including bryophytes, plants susceptible to environmental changes. This paper aims to show how the spatial distribution of functional features of bryophytes is configured in a fragmented tropical landscape. The guiding questions of this research were: Does the spatial distribution of bryophytes relate to functional diversity along vertical (base - canopy) and horizontal (edge-interior) gradients? Do the functional traits vary qualitatively and quantitatively along the gradients? For this study we analyzed a community of bryophytes spatially distributed along environmental, vertical and horizontal gradients of the largest forest fragment of the Murici Ecological Station (ESEC Murici), Alagoas, Brazil. Six functional traits of bryophytes related to water maintenance and protection from light intensity were used to verify how certain functions were spatially distribute along environmental gradients. The functional diversity alone failed to explain the spatial distribution of bryophytes, however the functional composition, along with the morphological variations of the lobule, were highly correlated with the environmental gradients. The traits lobule, dark pigment and papillae presented a high correlation with the gradients, mainly vertical, in which they were the main ingredients of variation. The life forms also explained the spatial distribution in the vertical gradient. Among them, the occurrence of forms with higher resistance to high luminosity and dehydration predominated in the canopy. Finally, we observed that the lobule in the leafy liverworts expanded its area as we moved from the understory to the canopy. It's dimensions also expanded significantly in the same direction, as well as on the edge of the fragment. Thus, it is suggested that this structure contributes functionally to storage and water maintenance, being associated to the type of microhabitat occupied by the species. The implications of our findings confirm the existence of environmental filters that shape the spatial distribution of functional bryophyte traits in the Atlantic Forest.

Key words: Functional diversity and composition. Environmental filters. Vertical gradient. Horizontal gradient. Anthropisation.

SUMÁRIO

1 INTRODUÇÃO

As paisagens naturais em todo planeta estão submetidas a algum tipo de pressão antrópica, seja ela relacionada à exploração de recursos ou à expansão urbana, que acarretam na perda de vegetação primária e, muitas vezes, as transforma em mosaicos de fragmentos florestais (HAUTIER et al., 2015). Consequentemente, com a perda da cobertura vegetal ocorre drástica mudança dos fatores abióticos, tais como luz, temperatura e umidade, que por sua vez funcionam como filtros ambientais, os quais moldam as comunidades biológicas segundo suas características adaptativas (KRAFT et al., 2015). Assim, levando a perda de espécies sensíveis e a proliferação de táxons resistentes e bem adaptados à perturbação (PONCE-REYES et al., 2013).

Em ambientes fragmentados tais filtros ocorrem em escala microclimática, comumente conhecido como efeito de borda (FAHRIG, 2003), efeito este, que seleciona espécies resistentes a condições ambientais extremas nas proximidades da borda e servem de barreira, impedindo o fluxo genético de populações, levando à perda de diversidade e extinção de diversos táxons (WILLI et al., 2007, MACHADO-FILHO et al., 2015). Esses efeitos deletérios são reportados em todo o domínio fitogeográfico da Floresta Atlântica, tendo em vista que atualmente o mesmo possui cerca de 15,2% de sua cobertura vegetal original, compondo um mosaico de vegetação fragmentada, florestas secundárias e plantações (RIBEIRO et al., 2009, SOS MATA ATLÂNTICA & INPE, 2018). Contudo, este domínio ainda comporta elevada diversidade vegetal e é considerado um *hotspot* de biodiversidade, assim sendo área prioritária para conservação (MYERS et al., 2000, TABARELLI et al., 2010, MITTERMEIER et al., 2011). A sua total conservação ainda está longe de ser alcançada, tendo em vista que de seus remanescentes, apenas 9% estão em áreas protegidas (RIBEIRO et al., 2009).

Para o desenvolvimento de medidas de conservação úteis para áreas extremamente deterioradas como a Floresta Atlântica, há a necessidade de extensivos estudos ecológicos, principalmente relacionados a sua vegetação, uma vez que controla uma gama de processos ecossistêmicos. Estudos neste domínio foram e estão sendo desenvolvidos a fim de se entender de forma mais clara o papel dos organismos nos ecossistemas e como maneja-los para elaboração de medidas de conservação eficientes (TABARELLI et al., 2010). No entanto, a grande maioria dos trabalhos utiliza somente a métrica de diversidade taxonômica para analisar os processos ecológicos, tais como riqueza e composição de espécies, e estas vêm se mostrando insuficientes, sendo necessárias métricas complementares, como a utilização da ecologia funcional (GIRÃO et al., 2007, LOPES et al., 2009).

A métrica funcional utiliza traços associados a estratégias ecológicas dos organismos relacionados à persistência, uso dos recursos (traços respostas) e manutenção dos ecossistemas (traços efeito) (LAVOREL; GARNIER, 2002, DÍAZ et al., 2007, CIANCIARUSO et al., 2009). Conhecendo estes traços, pode-se verificar a diversidade funcional das comunidades nos ambientes, e detectar qual o papel dos organismos na manutenção dos ecossistemas (VIOLLE et al., 2007, SLADE et al., 2007). Está métrica é atualmente bastante utilizada para determinar de forma eficiente os efeitos deletérios das alterações ambientais (DEYN et al., 2008).

Traços funcionais das briófitas podem espelhar os já descritos em plantas com semente, mas outros representam alternativas ecológicas únicas (TAO; ZHANG, 2012), tais como lóbulos, papilas, lamelas e etc., e essas plantas desempenham importantes papeis ecológicos, tornando-se essenciais na compreensão da dinâmica dos ecossistemas (DEANE-COE; STANTON, 2017). Assim, para compreender os efeitos da fragmentação sobre a distribuição espacial das briófitas, é viável utilizar a métrica funcional, tendo em vista a sua sensibilidade e a plasticidade fenotípica destas plantas em relação a flutuações de fatores ambientais.

Considerando o estado de conhecimento sobre a distribuição espacial de briófitas na Floresta Atlântica, esta pesquisa visou verificar como a diversidade funcional deste grupo está relacionado aos gradientes ambientais de uma paisagem fragmentada, e como os traços variam em termos de composição e plasticidade na comunidade de briófitas.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 EFEITO DAS ATIVIDADES ANTRÓPICAS E DA FRAGMENTAÇÃO NA FLORESTA ATLÂNTICA

Atividades antrópicas vêm modificando paisagens naturais em toda biota do planeta, sendo as principais causas de alterações a exploração excessiva de recursos naturais e expansão urbana (CHAPIN, 2003, HAUTIER et al., 2015). Neste contexto, áreas de vegetação primária são perdidas, modificadas e/ou convertem-se em fragmentos de diversos tamanhos e formas (FOLEY et al., 2005). Acarretando em drástica flutuação dos fatores físicos do ambiente, tais como temperatura, luminosidade e umidade (HENDERSON-SELLER et al., 1993, PONCE-REYES et al., 2013). Esses fatores abióticos funcionam como filtros ambientais, que influenciam diretamente na dinâmica de comunidades da fauna e flora, e podem levar a perda de espécies e substituição por táxons tolerantes à perturbação (WALTHER et al., 2002, OLIVEIRA FILHO et al., 2007).

Efeitos das atividades antrópicas afetam fortemente as espécies vegetais, sobretudo aquelas que possuem baixas taxas de crescimento e altas taxas de mortalidade, o que as torna mais sensíveis a permanecer em habitats modificados (MANDUJANO et al., 2007). Em contraposição, espécies vegetais que possuem mais ampla plasticidade estrutural e resistência frente às alterações abióticas se beneficiam de eventos de perturbação, destacando as espécies invasoras e ruderais (DIAS-FILHO, 2006, AMORIM; JÚNIOR, 2016). Os aspectos que atribuem resistência a essas espécies são suas características fisiológicas, morfológicas e ecológicas, que contribuem na colonização em ambientes perturbados (BATAGIN et al., 2009). Assim, acarretando na proliferação de populações resistentes a estresse ambiental, e por sua vez, reestruturação e homogeneização da biota (MACHADO-FILHO et al., 2015).

Em processos de fragmentação florestal são criadas “ilhas” de vegetação remanescentes com composição biológica variável nos seus diferentes gradientes existentes entre borda-interior (OLIVEIRA; GRILLO; TABARELLI, 2004; RIBEIRO et al., 2009). Tal variação biológica é consequência dos filtros ambientais existentes entre borda-interior de um fragmento, impulsionada por variações abiótica e biótica comumente conhecidas como efeito de borda (ESSEEN; RENHORN 1998, CHEN et al., 1999, HARPER et al., 2005). O efeito de borda muitas vezes acarreta homogeneização e perda de espécies nas proximidades da borda, enquanto o interior abriga maior número de espécies (YOUNG et al., 1996, WILLI et al., 2007, MACHADO-FILHO et al., 2015).

A Floresta Atlântica é considerada um dos 35 *hotspots* de biodiversidade prioritários para conservação, e corresponde a segunda maior área florestal do neotrópico, representando uma das regiões ecológicas mais ricas em termos de biodiversidade do planeta (MITTERMEIER et al., 2011). Para sua flora vascular como um todo sugerem-se 40% de táxons endêmicos (TABARELLI et al., 2010). Em relação as angiospermas estimam-se que este domínio possua cerca de 20.000 espécies, correspondendo a 36% do total esperado para o território brasileiro, já para samambaias e licófitas cerca de 950 espécies (73% do estimado para o Brasil e 8% para o mundo) (CAMPANILI; SCHÄFFER, 2010). Para a brioflora (musgos, hepáticas e antóceros), encontram-se neste domínio 1350 espécies (86,1% do estimado para o Brasil) (FLORA DO BRASIL 2020 EM CONSTRUÇÃO, 2018), e em termos de endemismo estima-se o dobro da região amazônica, com 12 famílias exclusivas (GRADSTEIN; COSTA, 2003).

A biodiversidade encontrada neste domínio fitogeográfico sofre pressões antrópicas documentadas desde o início do período de colonização do Brasil, há mais de cinco séculos, estando principalmente associado à exploração excessiva dos recursos naturais, sobretudo aqueles relacionados, a extração madeireira, expansão demográfica, e uso de largas áreas para culturas agrícolas (LIMA; GARCIA, 2018). A cobertura vegetal remanescente está majoritariamente incorporada em mosaicos de vegetação, incluindo, fragmentos florestais de diversos tamanhos e formas, florestas secundárias recentes e tardias e monoculturas de espécies exóticas (TABARELLI et al., 2010). Por consequência, a fragmentação tornou-se uma das principais causas de perda de biodiversidade (TABARELLI et al., 2010). Atualmente a Floresta Atlântica encontra-se reduzida a 15,2% de sua cobertura original no Brasil (SOS MATA ATLÂNTICA & INPE, 2018). A maioria dos remanescentes (80%) possui menos de 50 ha e apenas 9% encontram-se em áreas protegidas, contemplando ao todo 1% do bioma original (RIBEIRO et al., 2009). Os mais significativamente preservados inseridos em Unidades de Conservação, Restingas, Áreas Indígenas e Mangues (ZAÚ, 1998), e esses ainda se mostram ineficientes na conservação (TABARELLI et al., 2010).

As prolongadas perturbações, crônicas e agudas, acarretam em mudanças nas paisagens naturais da Floresta Atlântica, dificultam a compreensão do funcionamento de seus ecossistemas. Sendo assim, para elucidar processos relacionados às perturbações ambientais, há a necessidade de extensivos estudos ecológicos direcionados para o funcionamento ecossistêmico e o papel das espécies na manutenção dos mesmos, os quais possibilitem, a elaboração de medidas de conservação específicas e eficientes.

2.2 DISTRIBUIÇÃO ESPACIAL DE BRIÓFITAS

As briófitas constituem um grupo de três filos distintos que reúnem as hepáticas (Marchantiophyta), os antóceros (Anthocerotophyta) e os musgos (Bryophyta) (GOFFINET; SHAW, 2008). São plantas de pequeno porte, com ausência de sistema vascular lignificado e cutícula epidérmica (GRADSTEIN et al., 2001) com metabolismo intrinsecamente dependente dos fatores abióticos do meio, principalmente relacionados à umidade e à luminosidade (GOFFINET; SHAW, 2008).

As briófitas são conhecidas como bioindicadoras de mudanças ambientais (HALLINGBACK; HODGETTS 2000). Características morfológicas, fisiológicas, reprodutivas das briófitas, assim como taxas relativamente rápidas de extinção e de colonização, alta especificidade de substrato, condição haploide dominante e pequeno tamanho, as tornam extremamente sensíveis às variações ambientais, sendo comumente utilizadas como modelo biológico para se detectar distúrbios ambientais a curto e longo prazo (HALLINGBACK; HODGETTS 2000, ZARTMAN, 2003). Tendo em vistas estas características, diversos trabalhos vêm sendo desenvolvidos analisando a composição, riqueza, diversidade de briófitas em ambientes antropizados, os quais demonstram uma clara modificação desses parâmetros em relação aos distúrbios, evidenciando-as boas preditoras de qualidade ambiental (COSTA, 1999, BRITO; ILKIU-BORGES, 2013, PANTOJA et al., 2015).

O grupo atinge seu pico de diversidade e biomassa nas florestas tropicais (GRADSTEIN et al., 2001, GRADSTEIN; COSTA, 2003). Isto devido à ampla variedade de habitats e microhabitats existentes (FRAHM, 1990, WERNER et al., 2012, AH-PENG et al., 2017). A elevada amplitude de microhabitats disponíveis para as briófitas neste ambiente é bem documentada, onde táxons se estabelecem em uma ampla gama de substratos, possuindo diversos hábitos, como principalmente os epífitos, rupícolas, terrícolas, epíxilas entre outros (RICHARDS, 1984, ALVARENGA; LISBOA, 2009, BATISTA et al., 2018). Entre esses hábitos, destacam-se os epifíticos, que se distribuem verticalmente nos forófitos arbóreos ao longo de um gradiente microclimático vertical (ACEBEY et al., 2003, MOTA-DE-OLIVEIRA et al., 2009, MOTA-DE-OLIVEIRA; TER STEEGE, 2015).

Para as briófitas epífitas em ambientes tropicais como a Floresta Amazônica, o gradiente mais e preditor para a complexidade do grupo é o gradiente vertical, que se mantem em diferentes escalas espaciais, tanto locais quanto regionais (MOTA-DE-OLIVEIRA; TER STEEGE, 2015). Este gradiente é influenciado por variações físicas de microhabitats, p. ex.: estrutura das cascas dos forófitos, e microclimáticas p. ex.: luz, temperatura, umidade e velocidade do vento, ao longo do sub-bosque ao dossel (CORNELISSEN; TER STEEGE, 1989, HOLZ et al., 2002, SPORN et al., 2010).

O padrão de distribuição ao longo do gradiente vertical é bem documentado para a Floresta Amazônica (ACEBEY et al., 2003, MOTA-DE-OLIVEIRA et al., 2009, MOTA-DE-OLIVEIRA; TER STEEGE, 2015). Padrão este, aparentemente ausente na Floresta Atlântica, onde estudos foram desenvolvidos e não foi detectada variação entre zonas de altura ao longo do gradiente (ALVARENGA et al. 2009, OLIVEIRA et al. 2011, SILVA; PÔRTO 2010, 2013). Na Floresta Atlântica Nordestina SILVA; PÔRTO (2013) não observaram a presença do gradiente vertical em termos de diversidade e riqueza de espécies, no entanto, verificaram variação na composição, bem como mudanças das guildas de tolerância a luminosidade (especialistas de sombra e sol e generalistas). Posteriormente, OLIVEIRA; OLIVEIRA (2016), obtiveram resultados semelhantes para a mesma porção do domínio fitogeográfico, com distinção na composição de espécies e de alguns traços funcionais, entre as zonas da base dos forófitos e dossel superior.

Os diversos trabalhos que tentaram verificar este gradiente nas florestas tropicais assumem esta variação biológica por distintas condições de microhabitas e microclimas, que são os principais filtros para as briófitas epífitas (CORNELISSEN; TER STEEGE, 1989). No entanto, o gradiente vertical encontrado nos padrões de distribuição das briófitas pode não ser associável para todas as florestas, tendo em vista que a complexidade microclimática pode variar em diferentes vegetações e em relação ao seu estado de perturbação. Assim sendo, a perda da complexidade microclimática no gradiente vertical na Floresta Atlântica causada por distúrbios antrópicos pode ser o fator que impossibilita uma nítida diferenciação biológica.

Frente a processos de fragmentação, as briófitas são utilizadas como grupo biológico eficiente no que se diz respeito a prever perda de biodiversidade e qualidade ambiental a curto e longo prazo (ZARTMAN, 2003, ZARTMAN; SHAW, 2006, ZARTMAN; NASCIMENTO, 2006, ALVARENGA; PÔRTO, 2007). ZARTMAN (2003), ao estudar briófitas epifilas em fragmentos de diferentes tamanhos na Amazônia Central, verificou que pequenos fragmentos (1-10ha) apresentam baixos valores de riqueza e abundância de espécies comparadas a florestas contínuas. Posteriormente, ZARTMAN; NASCIMENTO (2006), também com o mesmo grupo e área de estudo, evidenciaram que a limitação de dispersão em pequenos fragmentos explica melhor a perda de espécies do que a qualidade de habitat submetida ao efeito de borda.

Em relação aos ambientes fragmentados na Floresta Atlântica, ALVARENGA; PÔRTO (2007), verificaram que a diversidade de briófitas é negativamente afetada pelo tamanho e isolamento de fragmentos. Em relação ao efeito de borda sobre a diversidade do grupo, vários estudos têm evidenciado, no entanto, não haver modificação expressiva na riqueza e na composição taxonômica (ALVARENGA et al., 2009, OLIVEIRA et al., 2011, SILVA; PÔRTO, 2009, 2010, 2013). Sendo assim, é incerta a relação das briófitas frente aos processos de fragmentação, principalmente relacionados ao efeito de borda, necessitando de novas analises em relação a outros parâmetros de diversidade, tais como diversidade funcional e ou filogenética.

A distribuição espacial de briófitas em ambientes tropicais como a Floresta Amazônica é bem marcada, vertical e horizontalmente (MOTA-DE-OLIVEIRA et al., 2009, ZARTMAN; NASCIMENTO, 2006, TAVARES-MARTINS et al., 2014), gradientes estes não expressivos na Floresta Atlântica (SILVA; PÔRTO, 2009, 2010, 2013). Possivelmente, a distribuição espacial de briófitas em ambientes altamente modificados, pode não estar somente associada a diversidade taxonômica, mas também, a traços funcionais relacionados a adaptações a condições estressantes, como já verificado para espécies arbóreas (MAGNAGO et al., 2014). Isto, pelo fato que processos altamente deletérios como os encontrados no domínio fitogeográfico em questão, tornam muitos fragmentos compostos majoritariamente por ambientes de bordas (SILVA; PÔRTO, 2010). Sendo assim, traços funcionais podem ser preditores mais sensíveis para se detectar variação na estratificação (horizontal e vertical) de briófitas frente a processos de fragmentação, pois as mesmas respondem a pequenas variações ambientais em escalas microclimáticas (HALLINGBACK; HODGETTS, 2000).

Traços funcionais das briófitas são resultado da história evolutiva, as quais possuem traços funcionais únicos, muitos dos quais são relacionados à reprodução, tolerância à luminosidade e à regulação hídrica (GLIME, 2017a, b). Esses traços podem ser usados simultaneamente para elucidar como os fatores bióticos e abióticos atuam sobre as comunidades e as funções ecossistêmicas (MAGNAGO et al., 2014) de tal maneira que, se torna viável utilizar a métrica funcional para detectar de forma mais clara distúrbios ocasionados pela fragmentação sobre a distribuição espacial das briófitas.

2.3 DIVERSIDADE FUNCIONAL E TRAÇOS FUNCIONAIS EM BRIÓFITAS

A grande parte dos estudos que busca compreender as consequências das alterações ambientais sobre a diversidade vegetal utiliza a métrica clássica taxonômica para elucidar processos ecológicos, tais como composição e riqueza (RICOTTA, 2005). Entretanto, esta métrica tornou-se insuficiente para o entendimento do papel dos organismos nos ecossistemas (RICOTTA, 2000). Nesse sentido, as métricas de diversidade filogenética e funcional tornaram-se alternativas viáveis para compreender de maneira completa a função de cada espécie no seu ambiente.

Para entender a diversidade funcional, deve-se, primeiramente, compreender qual a unidade de estudo, as quais são, características e/ou traços funcionais existentes nos organismos, que atribuem alguma estratégia ecológica em relação ao ambiente (DÍAZ et al., 2007). Estas características podem ser morfológicas, fisiológicas ou fenológicas mensuráveis, que representem alguma funcionalidade ao ambiente (CIANCIARUSO et al., 2009) e podem proporcionar informações fundamentais para se entender questões ecológicas desde o nível de espécie (como uso e requerimento de habitat) até ecossistemas (como ciclagem de nutrientes e carbono) (SLADE et al., 2007, VIOLLE et al., 2007).

TILMAN (2001) conceitua a diversidade funcional como “o valor e variação das espécies e de suas características que influenciam no funcionamento das comunidades”. A maneira de medir a diversidade funcional é classificar e ou mensurar os caracteres funcionais, que são componentes dos fenótipos dos organismos que influenciam nos processos da comunidade (CIANCIARUSO et al., 2009). O conjunto de métricas e índices de diversidade funcional tem se mostrado sensível para detectar respostas das comunidades às mudanças ambientais (traços resposta), complementando as métricas clássicas de diversidade (LAVOREL; GARNIER 2002, RICOTTA 2005), e a partir destas métricas também é possível verificar como os organismos influenciam na manutenção dos ecossistemas (traços efeito) (LAVOREL; GARNIER 2002).

Nos últimos anos, diversos trabalhos vêm utilizando a métrica funcional para complementar os estudos de diversidade biológica, assim revelando informações mais precisas da funcionalidade dos organismos nos ecossistemas (CARRIÉ et al., 2016, MAGURA, 2017). Destes, muitos abordam as características funcionais das plantas, principalmente os relacionados às alterações ambientais, uma vez que elas controlam uma variedade de processos dos ecossistemas terrestres, tal como o armazenamento de carbono, ciclagem de nutrientes e requerimento de recursos (DEYN et al., 2008). Grande parte dos estudos está direcionada a plantas com sementes (GIRÃO et al., 2007, LOPES et al., 2009), ao passo que trabalhos que abordam diversidade funcional de briófitas são escassos, e estão apenas começando a serem desenvolvidos (TAO; ZHANG, 2012, HENRIQUES et al., 2017, SILVA et al., 2017). E tendo em vista a importância das briófitas em termos de diversidade, biomassa, ciclagem de nutrientes e fixação de carbono (HALLINGBACK; HODGETTS, 2000), as mesmas pode revelar importantes aspectos sobre funcionamento dos ecossistemas.

OLIVEIRA (2018) para briófitas da família Lejeuneaceae, constatou que a presença de pigmentos escuros e filídios côncavos possuem influencia na ocorrência das espécies ao longo do gradiente vertical na Floresta Amazônica, contribuindo para presença de espécies no dossel e/ou dificultando a permanecias das mesmas no sub-bosque. Já Floresta Atlântica OLIVEIRA; OLIVEIRA (2016) verificaram mudança na composição de traços funcionais ao longo do gradiente vertical, sendo os principais promotores de variação os traços: filídios côncavos e células hialinas. SILVA at al. (2017), em afloramentos rochosos na Caatinga testaram a relação de traços funcionais com a sazonalidade (precipitação e temperatura), no entanto não verificam relação positiva com esses parâmetros, mas sim, diferentes arranjos funcionais para lidar com as restrições ambientais de cada comunidade dos afloramentos rochosos.

Uma das dificuldades em trabalhar com diversidade funcional de briófitas em ambientes tropicais deve-se à falta de consenso sobre a real função dos traços, ausência de testes empíricos sobre suas funcionalidades e de uma listagem consistente de traços funcionais que possam ser uteis para analises de diversidade funcional. Sendo assim, revisamos e copilamos algumas características do grupo que pudessem revelar funções e estratégias ecológicas relacionadas à regulação e necessidade hídrica e proteção à intensidade luminosa e literatura pertinente (Tabela 1) (Figuras 1 -15).

Tabela 1 - Traços funcionais de briófitas relacionados à regulação hídrica e a proteção à intensidade luminosa para espécies.

Traços vegetativos	**Funções**	**Estratégias**	**Referências**	**Figura**
Forma de Crescimento				
Pleurocárpico	Otimizar transporte de água e amenizar danos da radiação solar	Evitar dessecação e danos da radiação solar	(ØKLAND, 2000)	Figura 1 - A
Acrocárpico	Captar/Absorver água atmosférica	Rápido fluxo hídrico	(ØKLAND, 2000)	Figura 1 - B
Morfologia do filídio				
Lóbulo	Armazenar água extracelular	Evitar dessecação	(KRAICHAK, 2012, RENNER et al., 2013, RENNER, 2015)	Figura 2
Costa	Rápida absorção e transporte de água	Evitar dessecação	(FRAHM, 1985, PROCTOR, 1979)	Figura 3
Pelo hialino	Reflexão de luz solar e otimizar a capitação de água	Evitar dessecação e danos da radiação solar	(TAO; ZHANG, 2012)	Figura 4
Lamela	Reflexão de luz solar e otimizar a capitação de água	Evitar dessecação e danos da radiação solar	(KÜRSCHNER, 2003, 2004)	Figura 5
Forma do filídio				
Áspero, ondulado, imbricado, côncavo, dobrado, torcido e etc.	Captar e transportar água	Evitar dessecação	(KÜRSCHNER, 2003, 2004)	
Margem do filídio				
Involuto e revoluto	Captar e transportar água	Evitar dessecação	(KÜRSCHNER, 2003, 2004)	Figura 6
Células				
Célula hialina	Acumular água intracelular e transporte	Evitar dessecação	(TAO; ZHANG, 2012)	Figura 7

Papila	Otimizar a capitação de água e regulação osmótica	Evitar ou facilitar a dessecação	(PROCTOR, 1979, KÜRSCHNER, 2004)	Figura 8
Teníola	Otimizar a capitação e condução de água	Evitar dessecação	(REESE, 1993)	Figura 9
Oleocorpo	Contribuir quimicamente para resistência a dessecação	Evitar dessecação	(PRESSEL et al., 2010)	Figura 10
Forma de vida				
Dendroide, flabelado, pendente, talosa, tapete, trama, tufo e etc.	Diferentes relações com regulação hídrica e resistência a intensidade luminosa	Evitar dessecação e tolerância à intensa radiação	(KÜRSCHNER, 2003, 2004)	Figura 11, 12
Cor do gametófito				
Pigmento escuro	Amenizar danos da radiação solar	Tolerância à intensa radiação	(MELICK; SEPPEL 1994, DELTORO et al., 1998)	Figura 13
Traços reprodutivos Estratégia reprodutiva	**Funções**	**Estratégias**	**REFERÊNCIAS**	
Sexuada	Aumentar a necessidade de água para produção e transporte de propágulos	Uso de água, facilitando a dessecação	(NEWTON; MISHLER, 1994)	Figura 14
Assexuada	Diminuir uso de água para produção e transporte de propágulos	Evitar dessecação	(MOGENSEN, 1981, NEWTON; MISHLER, 1994)	Figura 15

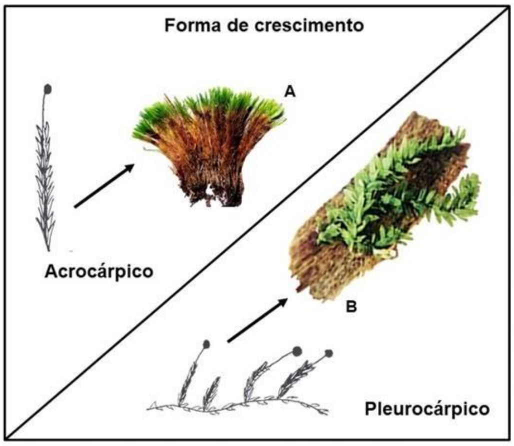


Figura 1 – Formas de crescimento; A – Acrocarpico, B – Pleurocárpico.

Fonte: A – Google imagens, B – (BATISTA et al., 2018).

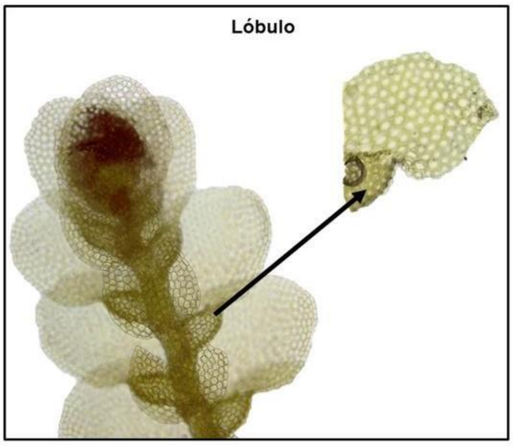


Figura 2 – Lóbulo; Porção do filídio em forma de saco para armazenamento de água.

Fonte: Arquivo pessoal.

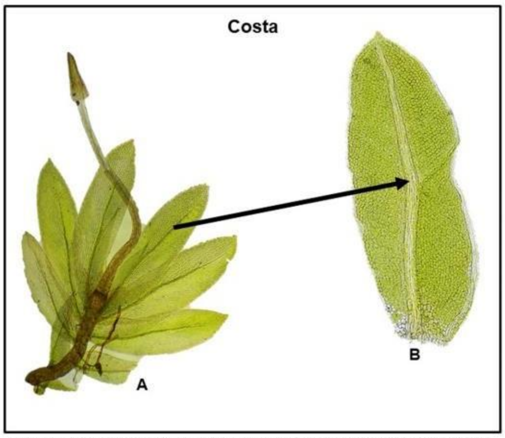


Figura 3 – Costa; A costa é a estrutura de apoio para muitos musgos, associada ao transporte de água (FRAHM 1985). A – Fissidens, B – Filídio com costa

Fonte: A –Wagner Santos, B – Glime 2018.

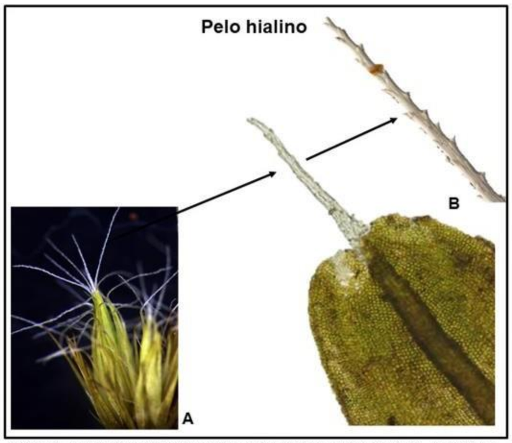


Figura 4 – Pelo hialino; Prolongamento de células hialinas no ápice do filídio, associadas a absorção de água, e reflexão de luz. A – Filídios com pelos hialinos, B – Pelo hialino.

Fonte: A –Google imagens, B – Glime 2018.

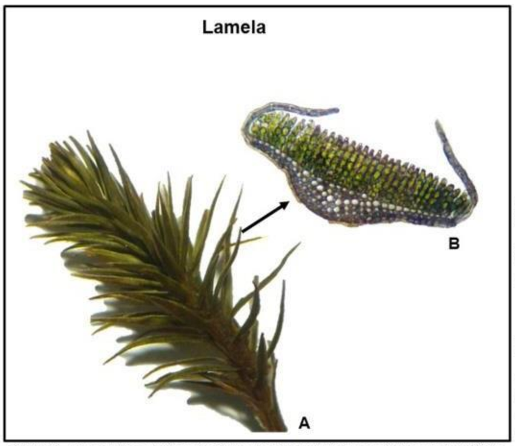


Figura 5 – Lamela; Pilhas verticais de células que formam fileiras, associadas a reduzução de perda de água. A – Gametofito **Polytrichaceae**, B – Corte transversal. .

Fonte: A –Google imagens, B – Glime 2018.

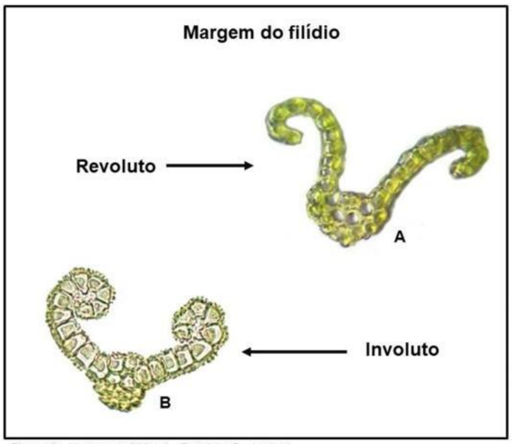
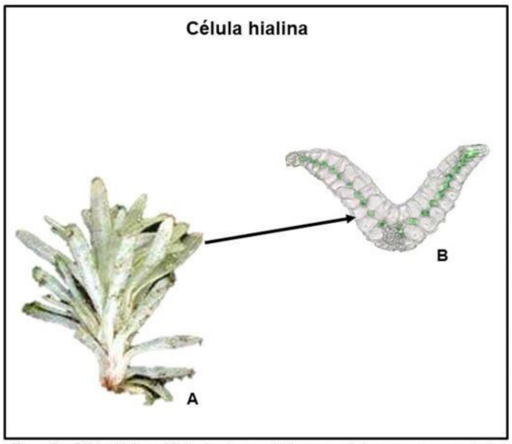


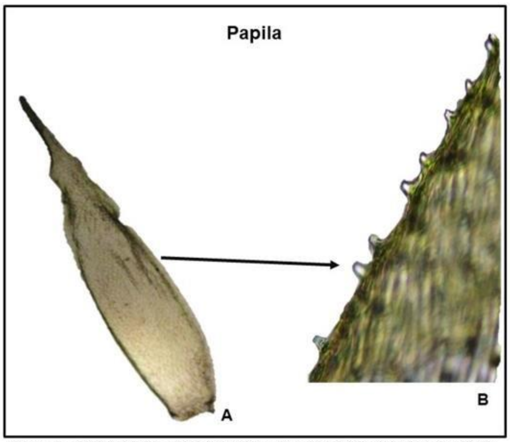
Figura 6 – Margem do filídio; A - Revoluto, B – Involuto.

Fonte: A, B – Glime 2018.



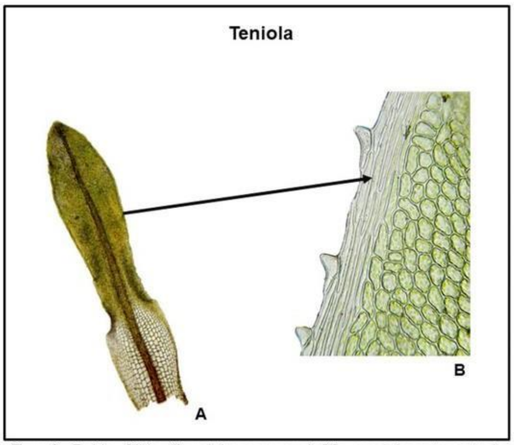
Fonte: A –Google imagens, B – Glime 2018.

Figura 7 – Células hialinas, Células incolores ou hialinas, associadas ao armazenamento de água. A – Gametofito **Octoblepharum**, B – Corte transversal.



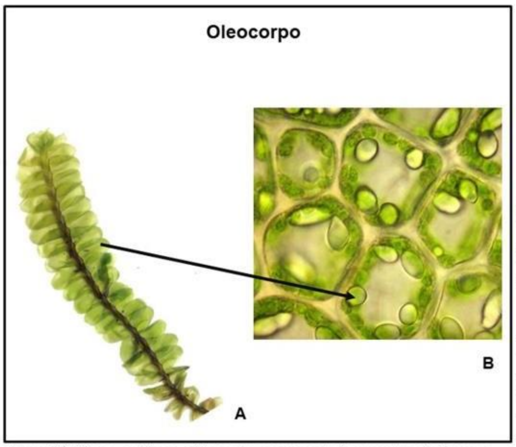
Fonte: A –Google imagens, B – Glime 2018.

Figura 8 – Papilas; papilas são protuberâncias celulares solidas, associadas a regulação hídrica. A – Gametofito **Taxithelium**, B – Papila.



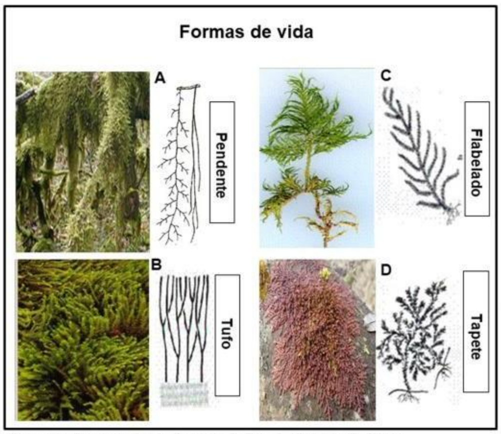
Fonte: A –Google imagens, B – Glime 2018.

Figura 9 – Teniolas; Células diferenciadas na margem do filífio, associadas ao transporte de água. A – Gametofito **Syrrhopodon**, B – Teniola.



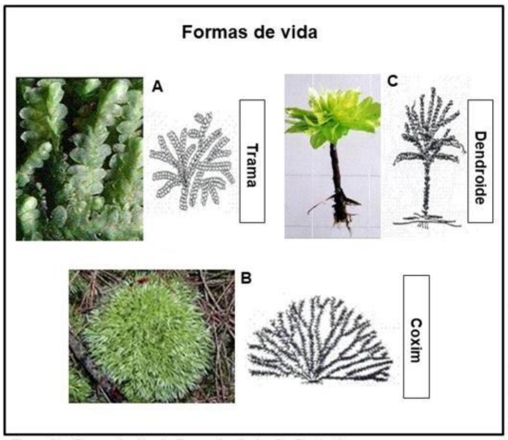
Fonte: A –Google imagens, B – Glime 2018.

Figura 10 –Oleocorpo; Corpos celulares de armazenamento de compostos oleaginosos. A – Gametofito, B – Oleocorpo.



Fonte: Arquivo pessoal.

Figura 11 – Formas de vida; A - Pendente, B - Tufo, C – Flabelado, D - Tapete.



Fonte: Arquivo pessoal.

Figura 12 – Formas de vida; A - Trama, C – Coxim, B – Dendroide.

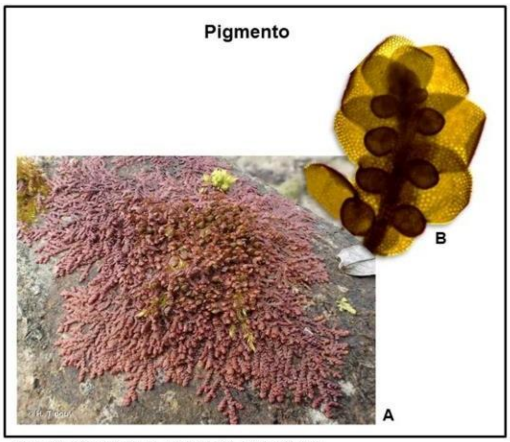


Figura 13 – Pigmentação; A – **Frullania**, B – **Ceratolejeunea**.

Fonte: A –Google imagens, B – Arquivo pessoal.

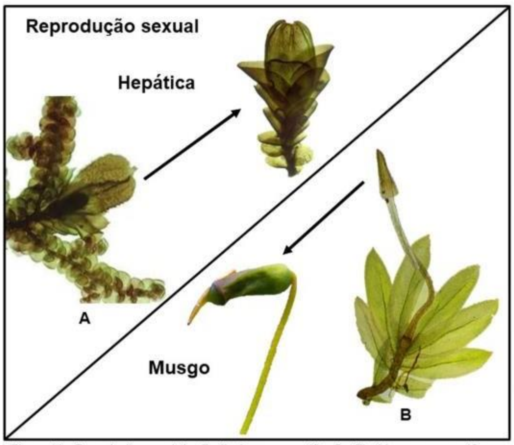


Figura 14 – Reprodução sexual; A – **Frullania** com esporófito, B – **Fissidens** com esporófito.

Fonte: A –Google imagens, B – Wagner Santos.

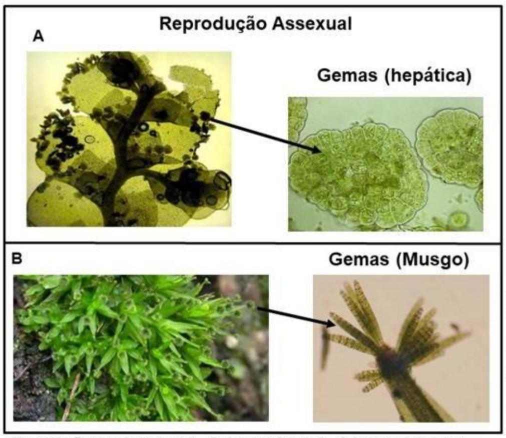


Figura 15 – Reprodução assexual; A – **Radula** com Gemas, B – **Calymperes** com gemas.

Fonte: A, B – Glime 2018.

3 SPATIAL DISTRIBUTION OF FUNCTIONAL TRAITS OF BRYOPHYTES THROUGH ENVIRONMENTAL GRADIENTS IN THE ATLANTIC FOREST

Manuscrito submetido no periódico **Plant Ecology & Diversity**

SPATIAL DISTRIBUTION OF FUNCTIONAL TRAITS OF BRYOPHYTES THROUGH ENVIRONMENTAL GRADIENTS IN A NORTHEASTERN ATLANTIC FOREST REMNANT

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Background: Functional trait-based approaches may reveal patterns of species diversity and composition related to environmental changes, especially in bryophytes, which participate in important ecosystem functions and are rapidly affected by perturbations at different spatial scales.

Aim: To verify the response of the functional diversity and composition of bryophytes to vertical (height zones in the host tree) and horizontal (edge distance classes) gradients in an Atlantic Forest remnant, in the state of Alagoas, Brazil.

Methods: Six functional traits related to water management and light tolerance were selected. One of the traits, the leaf lobule of liverworts, was elected for morphometric measurements and was analyzed to investigate its variability along the gradients. Functional diversity and composition metrics of bryophytes were tested along gradients.

Results: A substitution of traits in the functional composition along the vertical and horizontal gradients was observed, particularly in the traits lobule and dark pigments, as well as a significant structural variation in the leaf lobules, which presented an increased proportional area in relation to the lobe.

Conclusions: The spatial distribution of functional traits is related to both gradients and there are morphological variations along specific microhabitats as well as greater niche breadth in the understory and core area of the forest.

Keywords: Functional diversity and composition; Environmental filters; Vertical gradient; Horizontal gradient; Anthropization.

INTRODUCTION

Tropical rainforests provide a wide variety of microhabitats and microclimates that explain the high diversity and productivity of epiphytic biomass (Frahm 1990; Werner et al., 2012; Ah-Peng et al., 2017). In these environments, bryophytes (liverworts, mosses and hornworts) reach the greatest number of species and exuberance in the planet (Gradstein et al. 2001; Gradstein & Costa 2003). Bryophyte diversity and distribution patterns are influenced by microclimatic fluctuations along phorophytes (arboreal substrate), which generally determine a vertical stratification of species from the understory to the canopy (Cornelissen & ter Steege 1989; Holtz et al., 2002; Sporn et al., 2010).

In the Amazon, the vertical stratification of bryophytes has been confirmed both at local and regional scales (Acebey et al., 2003; Mota-de-Oliveira et al. 2009; Tavares-Martins et al. 2014; Mota-de-Oliveira & ter Steege 2015). However, a similar clear stratification has not been observed in surveys carried out in the Northeastern Atlantic Forest (Alvarenga et al. 2010; Oliveira et al. 2011; Silva & Pôrto 2010, 2013), with the exception of Oliveira & Oliveira (2016) who observed a subtle difference in species composition between the understory and upper canopy.

The absence of vertical gradation in the composition of bryophyte communities in the Northeastern Atlantic Forest has been attributed mainly to the effects of historical and recurrent disturbance (Alvarenga et al. 2010; Oliveira et al. 2011; Silva & Pôrto 2010, 2013), first by indigenous people, with effective use and management of forest systems (Posey 1985), and then aggravated in chronic and acute disorders with the colonization of Brazil more than five centuries ago, especially with exploitation of wood and mineral resources and rapid expansion of agricultural crops and urban centers (Lima & Garcia 2018). As a consequence of these anthropogenic activities, only ca. 15.2% of the original coverage of the Atlantic Forest in Brazil, and only 17.5% of the Northeastern portion exists today (SOS Mata Atlântica & INPE 2018).

Currently, the remnants of Atlantic Forest are inserted in a highly fragmented landscape, have different shapes and sizes, and are unsustainable for the maintenance of biological diversity (Tabarelli et al. 2010). This situation has been reported for bryophytes in several studies surveying the taxonomic diversity of the group carried out in this region (Alvarenga et al. 2010; Oliveira et al. 2011; Silva & Pôrto 2010, 2013).

Despite of this, gaps remain to be investigated, as for example the extent to which the functional traits of bryophytes reflect and/or respond to stressful conditions of environmental gradients in fragmented habitats. Some studies have already investigated the relation of functional traits of bryophytes with environmental gradients in Atlantic Forest (Silva & Pôrto 2013; Oliveira & Oliveira 2016). Silva & Pôrto (2013) analyzed the spatial distribution of bryophytes along environmental gradients in a forest fragment and showed evidence of the importance of studying community functionality; they found that the richness of shade tolerant species significantly decreased with edge proximity and with conditions inside the canopy.

Analyses of functionality of organisms use functional diversity metrics based on morphological, physiological or phenological traits, which respond to environmental variations (Díaz et al. 2007; Violle et al. 2007; Cianciaruso et al. 2009). Currently, the use of these metrics complements studies of biological diversity, contributing to more in-depth information about the functionality of organisms in ecosystems (Carrié et al. 2016; Magura 2017). Several studies have focused on the functional characteristics of plants because they are responsible for controlling a range of ecosystem processes (Díaz et al. 2001; Deyn et al. 2008; Kuebbing et al. 2018). However, most of these studies are directed to spermatophytes (Díaz et al. 2001; Laliberté 2017; Bardgett 2018). The functionality of bryophytes has only recently started to be explored, but the findings of the few studies conducted indicate a promising theme yet to be explored (Tao & Zhang 2012; Silva et al. 2017; Henriques et al. 2017).

Functional traits related to reproduction, light tolerance and water regulation in bryophytes (Glime 2017a, b) may respond simultaneously to biotic and abiotic factors and serve as useful indicators of their effects on communities (Deane-Coe & Stanton 2017). For example, these traits may be related to different functions and filtered by distinct microhabitats along environmental gradients in a forest fragment, in view of the antagonistic conditions imposed from the understory to the canopy (Cornelissen & ter Steege 1989), and from the edge to the core of the forest (Harper et al. 2005). In this sense, the lobe of leafy liverworts stands out for its role in the water storage and maintenance, and may vary morphologically as a function of the microhabitats (Cornelissen & Steege 1989; Daniels 1998; Michel 2001; Glime 2017b). However, this morphofunctional variation of the lobule still remains speculative and observational and require empirical tests for confirmation.

In this study, it is assumed that the understory and the core areas of the forest offer more favorable conditions for most of bryophytes in terms of less exposure to sun light and greater availability of water and microhabitats (Gradstein et al. 2001; Silva & Porto 2013), which may result in a greater number of associated functions. On the other hand, the canopy and the edge of the fragment are expected to select fewer functions, although more specifically related to stress tolerance. Our goal was to investigate whether the functional diversity and composition of bryophytes follow the microenvironmental gradient from the base to the canopy of phorophytes and from the edge to the core areas of an Atlantic Forest fragment. The work sought to answer the following questions:

(1) Is the spatial distribution of bryophytes along environmental gradients related to functional diversity?

(2) Does the composition of functional traits vary qualitatively (type of trait) and quantitatively (morphological variation of a given trait - lobule of leafy liverworts) along the gradients?

MATERIALS AND METHODS

Study site and sampling

The bryophyte samples used in this study came from the largest forest fragment of the Murici Ecological Station (ESEC Murici) (2628.00 ha) (9º11’05” – 9º16’48” S; 35º45’20” - 35º55’12” W), located in the Municipalities of Murici and Messias, state of Alagoas, Brazil, collected by Silva & Pôrto (2013) and deposited in the Geraldo Mariz UFP/UFPE Herbarium.

The sampling method adopted by Silva & Pôrto (2013) consisted in collecting bryophytes in three host trees per each one of five distance classes from the edge to the core of the fragment to express the horizontal gradient (C1: 0-200 m; C2: 201-400 m; C3: 401-600 m; C4: 601-800 m; C5: 801-1100 m), totaling 15 trees (average height of 25 m). Each host tree was subdivided into five height zones to express the vertical gradient: base (0-2 m); trunk (2-8 m); first ramification; second ramification; and final ramification. The base and trunk correspond to the understory; the first and second ramification to the inner canopy; and the final ramification to the outer canopy. A sample of all bryophyte species present in each height zone was collected, and this was considered the sampling unit.

The biological material was re-analyzed for confirmation of the taxonomic identity of the specimens. Taxonomic and nomenclatural updates were made following the Flora do Brasil 2020 (2018). The revised floristic list consists of 80 species distributed in 53 liverworts (Marchantiophyta) and 27 mosses (Bryophyta), with a total of 359 occurrences (Supplementary material 1).

Six functional traits related to water acquisition and retention and protection from light were selected for analyses (Table 1). The occurrence of traits in each species present in each sample was noted. Considering the role of the lobule of liverworts in water maintenance (Kraichak 2012; Renner et al. 2013; Renner 2015) and the large representation of liverworts (66.5%) in the set of bryophytes recorded, this trait was chosen for morphometric analysis to investigate whether morphological variations relate to environmental gradients. Thus, the leaf lobule was analyzed as binary variable for functional diversity and composition, and a continuous variable in the morphometric approach.

Table 1 - Traits related to water regulation and protection from light used in the analyses of functional diversity and composition of bryophytes, with respective values and associated functions.

Taxonomic group/traits	Trait type	Values	Associated functions	References
Liverworts				
Lobules	Binary	0 - Absent, 1 - Present	Storage of extracellular water	(Kraichak 2012; Renner et al. 2013; Renner 2015)
Mosses				
Costa	Binary	0 - Absent, 1 - Present	Rapid water absorption and transport	(Frahm 1985; Proctor 1979)
Mosses and liverworts				
Hyaline cells	Binary	0 - Absent, 1 - Present	Water accumulation and transport	(Tao & Zhang 2012)
Papillae	Binary	0 - Absent, 1 - Present	Optimization of osmotic water intake and regulation	(Proctor 1979; Kürschner 2004)
Dark pigments	Binary	0 - Absent, 1 - Present	Mitigation of damages caused by solar radiation (protection of chlorophyll and DNA) and transpiration	(Melick & Seppel 1994; Deltoro et al.1998)
Life forms	Categorical	Dendroid, flabellate, pendant, talose, mat, weft and tuft	Different capabilities of water maintenance and protection from light incidence	(Kürschner 2003, 2004)

Data analysis

The functional diversity along environmental gradients was evaluated using three indices to describe the distance and the distribution of the species in the multidimensional niche space (Mason et al. 2005; Villéger et al. 2008). The indices and the aspects they describe are as follows: Functional richness (FRic) - volume of the functional space occupied by the community; Functional evenness (FEve) - equity of distribution of traits in the functional space; and Functional divergence (FDiv) - distance of the species abundances from the center of the functional space. These indices were applied to the whole group of bryophytes (mosses and liverworts) and then to mosses and liverworts separately. After checking the assumptions, one-way ANOVAs and the post-hoc Tukey test were conducted to see if there were overall significant differences between height zones and distance classes.

Community-level weighted means (CWM) of trait values were generated and a Principal Component Analysis (PCA) was performed with all samples included individually (sampling unit) and then with the sum of samples in each height zone and distance class in order to investigate whether functional composition is related to spatial gradients. Diversity and composition were analyzed considering the whole bryophyte community, and then liverworts and mosses separately. CWM describes the composition of communities with respect to species-specific characteristics and indicates the average functional value of a given species in the community. This index is very sensitive to environmental variation and has been correlated with ecosystem properties in various habitats (Peres-Neto et al. 2016).

Non-metric multidimensional scaling (NMDS) was used for graphical representation of the functional composition area (functional area) in both environmental gradients, using the CWM matrix for the individual sampling units. NMDS is an interactive method that seeks to find the best geometric position, with the lowest stress; in ecological community data, stress values below 0.15 are considered low and values close to 0.2 are worrisome (McCune & Grace 2002). The distance matrix was constructed using Sorensen's metrics with 999 randomizations.

Morphometric data included the total area of the leaf lobules (LA) and the proportional leaf lobule area in relation to the lobe area (LL). In the morphometric study, we first selected the liverwort species; each species in each sample was considered a sampling individual. In each individual, 10-15 mature branches were selected, and in each of these branches, two (2) leaves were measured, totaling 20-30 leaves measured per individual. Individuals with less than ten (10) branches per sample were disregarded. Subsequently, the average LA and LL of samples and sampling individuals were calculated to be used in the analyses. The leaves were photographed with a digital camera and the images were processed in the ImageJ Software (Schneider et al. 2012). One-way ANOVAs and the post-hoc Tukey test were performed to verify if there were significant differences between height zones and distance classes.

The functional diversity, functional composition and ordination (NMDS) were computed in the R version 3.4.0 (R Core Development Team 2014) using the vegan and FD packages. ANOVAs and the Tukey test were performed in the PAST software (Hammer et al. 2001) and PCA and similarity analyses were performed in the FITOPAC 2.1 software (Shepherd 2010).

RESULTS

Functional diversity

Functional diversity differed significantly along the vertical gradient in terms of functional evenness, in the whole group of bryophytes and in the liverworts (Table 2). In the case of the bryophytes altogether, the canopy was significantly different from the others zones, and in the liverworts, the tree base was significantly distinct from the canopy. As for the horizontal gradient, the functional divergence of the whole group of bryophytes was significantly different; the core of the fragment (801-1100m) was significantly distinct from the edge, up to 600 m towards the core. The comparison of other distance classes was not significant.

Table 2 - Mean values ± SD of the variances of indices (FRic, FEve and FDiv) in the vertical and horizontal gradients and results of the one-way ANOVA. Values followed by the same lower case letter indicate no statistical difference (Tukey's test, *P* ≤ 0.05). NA = not available.

	Vertical gradient								
	Indexes	Base	Trunk	1st Ramification	2nd Ramification	Canopy	*P*	*F*	*df*
All bryophytes	FRic	0.58 ± 0.31	0.55 ± 0.28	0.57 ± 0.28	0.26 ± 0.15	0.34 ± 0.26	0.22	1.54	4
	FEve	0.52 ± 0.13	0.53 ± 0.11	0.50 ± 0.11	0.53 ± 0.10	0.30 ± 0.14	**0.03**	3.17	4
	FDiv	0.76 ± 0.05	0.80 ± 0.05	0.84 ± 0.09	0.75 ± 0.05	0.83 ± 0.06	0.15	1.85	4
Mosses	FRic	0.33 ± 0.14	0.26 ± 0.18	0.29 ± 0.33	0.11 ± 0.07	0.13 ± 0.08	0.45	0.96	4
	FEve	0.68 ± 0.18	0.73 ± 0.12	0.62 ± 025	0.66 ± 0.09	0.62 ± 0.26	0.93	0.20	4
	FDiv	0.80 ± 0.05	0.74 ± 0.06	0.76 ± 0.06	0.77 ± 0.05	0.74 ± 0.08	0.61	0.68	4
Liverworts	FRic	0.49 ± 0.42	0.41 ± 0.22	0.25 ± 0.09	0.33 ± 0.44	0.43 ± 0.03	0.81	0.38	4
	FEve	0.36 ± 0.08^{a}	0.31 ± 0.08^{ab}	0.24 ± 0.07^{ab}	0.26 ± 0.10^{ab}	0.16 ± 0.02^{b}	**0.05**	3.06	4
	FDiv	0.75 ± 0.15	0.79 ± 0.11	0.85 ± 0.06	0.86 ± 0.006	0.89 ± 0.03	0.36	1.18	4
	Horizontal gradient								
	Indexes	0-200 m	201-400 m	401-600 m	601-800 m	801-1100 m	*P*	*F*	*df*
All bryophytes	FRic	0.38 ± 0.26	0.48 ± 0.17	0.11 ± 0.17	0.23 ± 0.35	0.04 ± 0.03	0.17	1.94	4
	FEve	0.37 ± 0.05	0.46 ± 0.09	0.40 ± 0.14	0.42 ± 0.16	0.45 ± 0.06	0.83	0.34	4
	FDiv	0.86 ± 0.02^{a}	0.88 ± 0.02^{a}	0.86 ± 0.04^{a}	0.81 ± 0.03^{ab}	0.72 ± 0.06^{b}	**0.004**	7.54	4
Mosses	FRic	0.20 ± 0.19	0.42 ± 0.12	0.02 ± 0.02	0.25 ± 0.06	0.11 ± 0.15	0.15	2.35	4
	FEve	0.47 ± 0.24	0.80 ± 0.19	0.49 ± 0.22	0.67 ± 0.02	0.68 ± 0.20	0.44	1.04	4
	FDiv	0.81 ± 0.15	0.83 ± 0.05	0.74 ± 0.007	0.83 ± 0.002	0.79 ± 0.11	0.89	0.26	4
Liverworts	FRic	0.44 ± 0.15	0.80 ± 0.14	0.24 ± 0.30	0.52 ± 0.11	NA	0.06	4.18	3
	FEve	0.20 ± 0.02	0.28 ± 0.09	0.25 ±0.001	0.28 ± 0.15	NA	0.66	0.54	3
	FDiv	0.88 ± 0.06	0.87 ± 0.04	0.63 ± 0.20	0.86 ± 0.05	NA	0.10	3.25	3

Functional composition

The cumulative variance in the first two PCA axes using all samples separately was 52.5% (Figure 1a). When the samples were grouped per height zone and edge distance class, the cumulative variance in the first two axes was 84% (Figure 1b) and 86% (Figure 1a), respectively. The lobule and costa were the traits that presented the highest correlation (≤ 0.9) with the first PCA axis in the analysis with all the samples separately (Table 3). As for the vertical gradient (Figure 1b), the traits lobule, costa, dark pigments and mat life form presented the highest correlation, whereas in the horizontal gradient (Figure 1c), the lobule, dark pigments, hyalocysts and mat life form were more explanatory.

Table 3 - Pearson correlation between traits and the first two PCA axes, explanatory variance of each of the axes, and eigenvalues. Correlations with values ≤ 0.9 are presented in bold.

Traits	All samples		G. vertical		G. horizontal	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Lobule	**0.90**	0.06	**-0.90**	0.41	**0.98**	0.01
Costa	**-0.91**	0.06	**-0.90**	0.42	-0.83	-0.28
Papilla	-0.65	0.35	**0.95**	0.28	-0.84	-0.01
Dark pigments	0.38	0.49	**-0.98**	0.09	**0.94**	-0.27
Hyaline cells	-0.87	-0.36	0.70	-0.70	**-0.94**	0.07
Pendant	-0.16	0.43	0.74	0.20	0.56	-0.74
Flabellate	0.09	0.70	0.58	0.78	0.75	0.33
Tuft	-0.83	-0.25	0.89	-0.42	**-0.98**	0.13
Talose	0.01	0.17	-0.40	-0.70	0.16	**-0.94**
Mat	0.76	-0.53	**-0.98**	-0.14	0.33	0.88
Weft	0.01	0.24	0.24	-0.05	0.60	0.60
Dendroid	-0.15	0.56	0.71	0.60	0.16	**-0.94**
Explanatory variance (%)	36.2	16.3	61.8	22.1	54.5	31.5
Eigenvalues	4.3	1.9	7.4	2.6	6.5	3.7

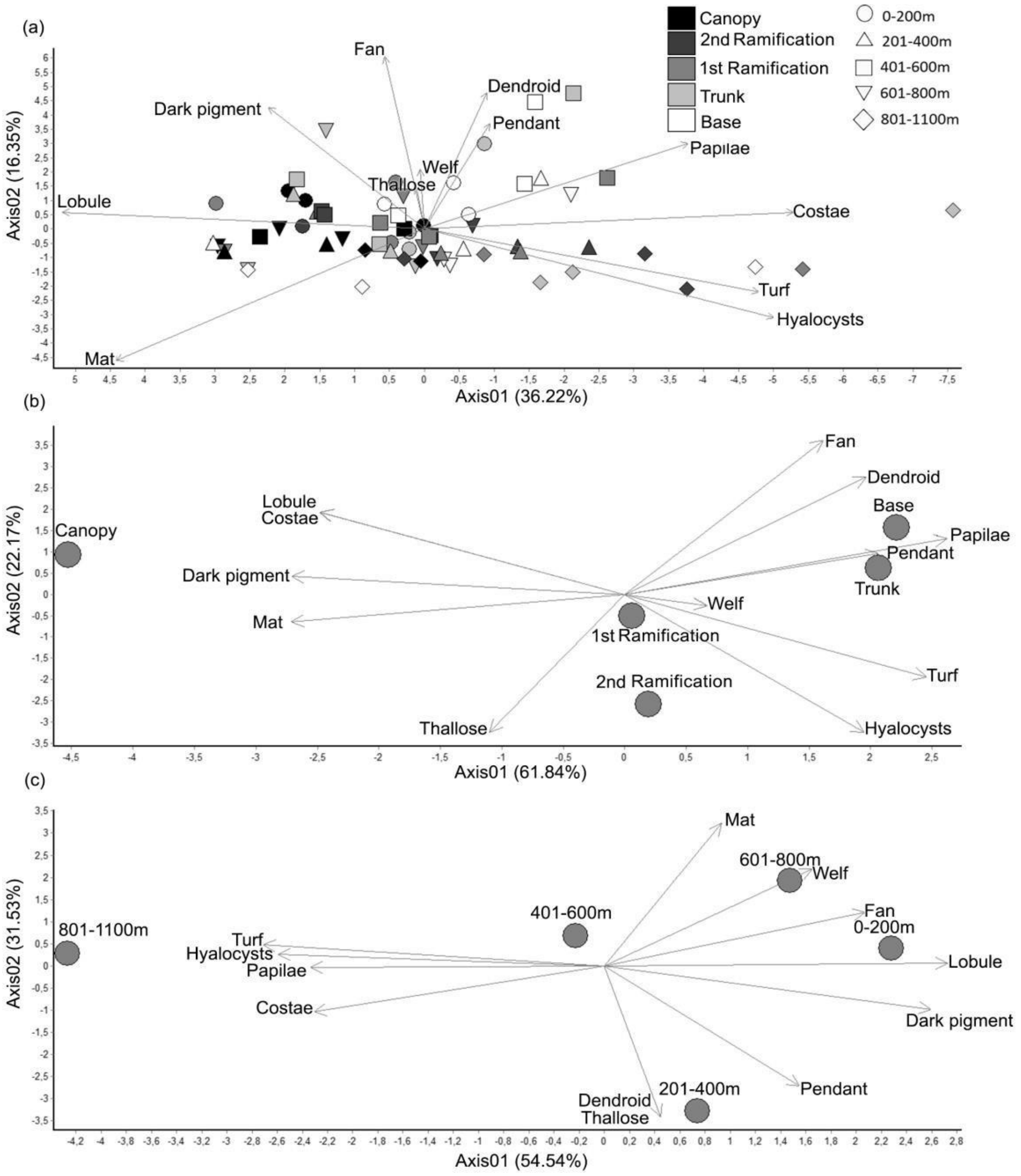

Figure 1 - Ordination diagrams of the first two Principal Component Analysis (PCA) axes of the CWM matrices by Traits. (a) CWM matrix of individual samples – the gray scale denotes height classes and the symbols represent edge distance classes. (b) CWM matrix of the sum of all samples per height zone. (c) CWM matrix of the sum of all samples per edge distance class.

The NMDS showed no differentiation between height zones (Figure 2a). On the other hand, it was observed that the functional area of all the zones overlapped, and there was a gradual reduction of functional area in the direction of the outer canopy, with the larger areas found in the understory (Base and Trunk) (Figure 2i and k) and smaller areas in the outer canopy (Figure 2c). In the horizontal gradient, there was s separation of functional areas only between the edge and core of the forest (Figure 2b), while intermediate classes overlapped (Figures 2f, h and j). The edge had clearly smaller functional area (Figure 2l), while the core had a larger functional area and was less overlapped with the other classes (Figure 2d).

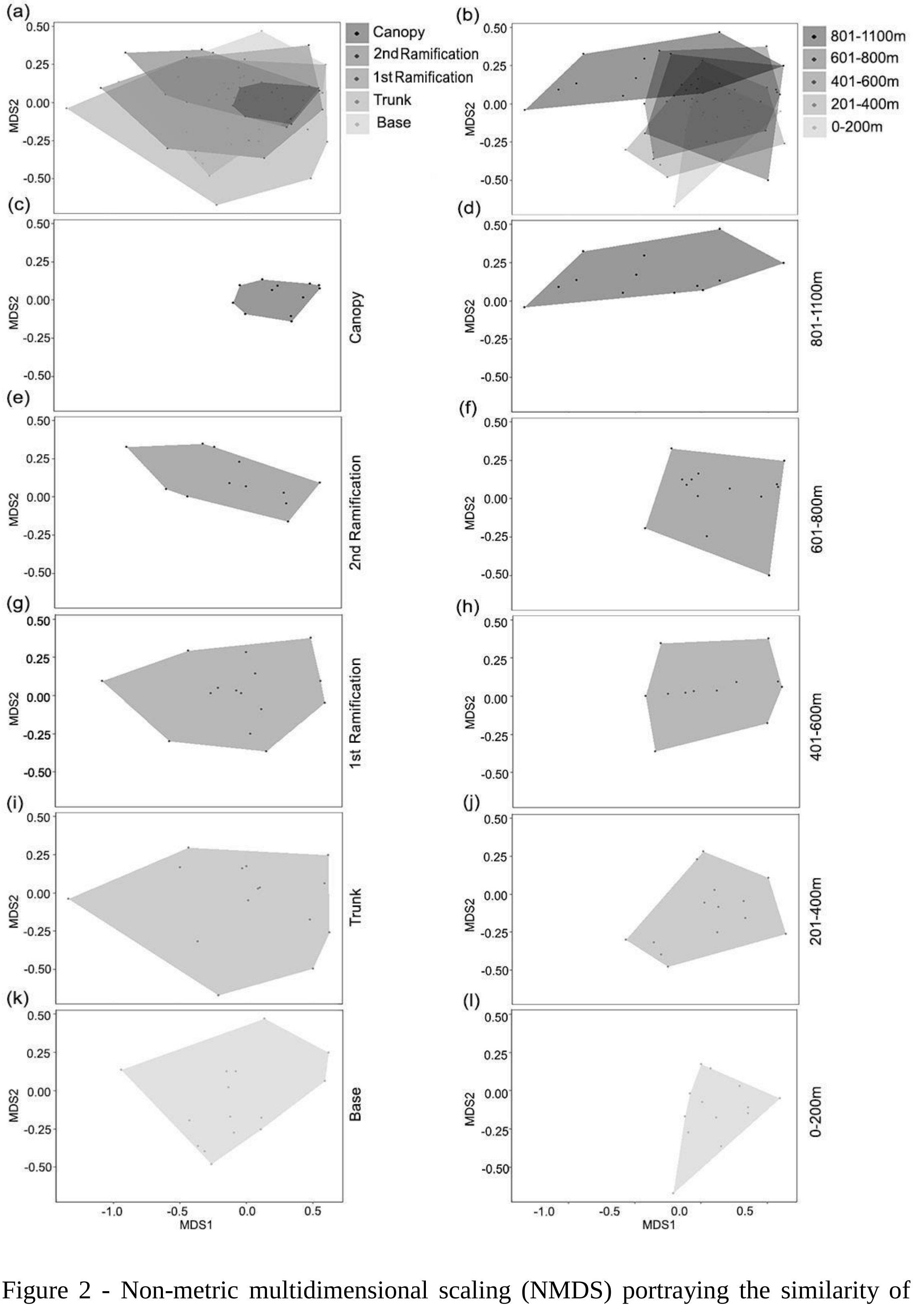

Figure 2 - Non-metric multidimensional scaling (NMDS) portraying the similarity of functional composition along the vertical (a, c, e, g, i and k) and horizontal (b, d, f, h, j and l) gradients. Stress: 0.1331091.

Lobule morphometry

The ANOVAs showed a significant difference in LA (F = 12.35; df = 4; *P* = 0.001) and LL (F = 7.73; gl = 4; *P* = 0.001) in the vertical gradient (Figure 3a and c). In the case of LA, only the outer canopy was significantly different from the other groups (*P* = 0.01), and in LL, there was a gradual variation between the height zones, where the outer canopy showed to be different from the base, trunk and first ramification (*P* < 0.05), and the second ramification was distinct from the base (*P* = 0.02). Lobule area presented significant differences along the horizontal gradient (F = 6.30; df = 4; *P* = 0.001) (Figure 3b); the edge differed significantly from the other distance classes (*P* < 0.01). In turn, LL showed no variation along the gradient (F = 2.05, df = 4; *P* > 0.05) (Figure 3d).

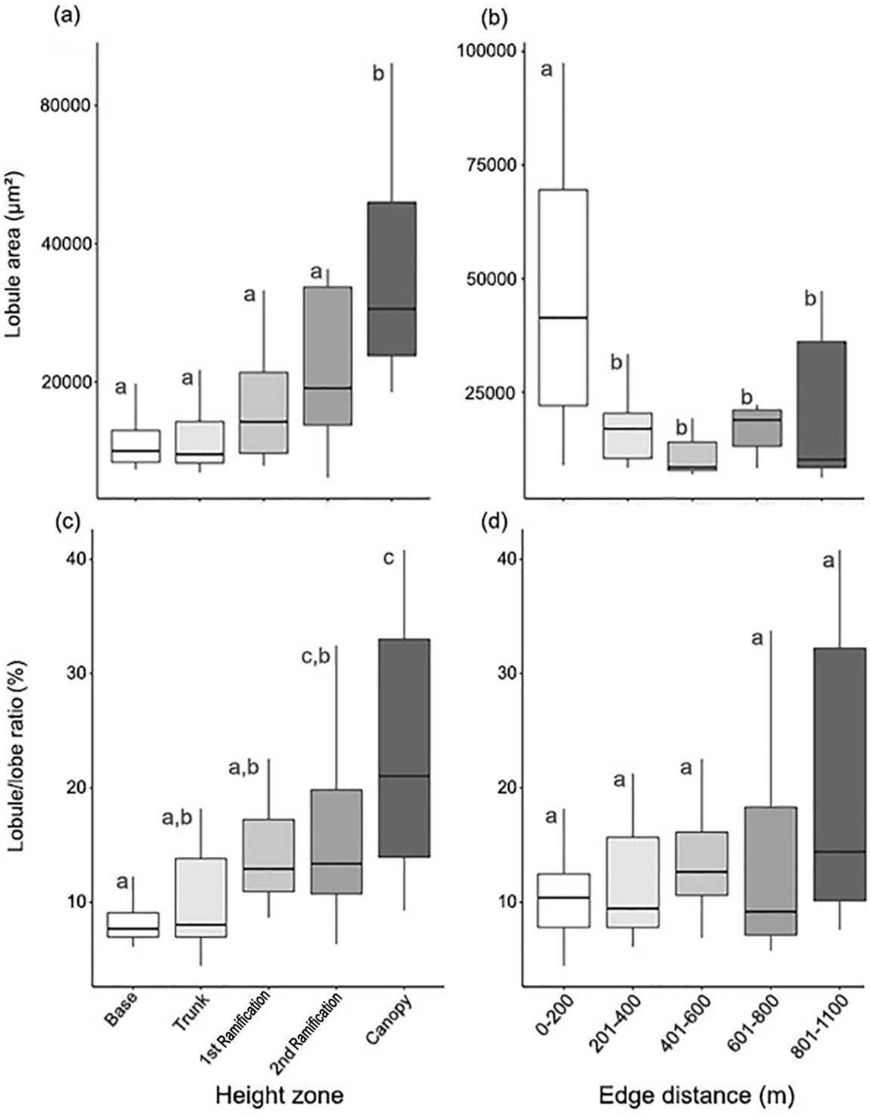

Figure 3 - Boxplot of the total lobule area (LA) and lobule/lobe ratio (LL) along the vertical (a and c) and horizontal (b and d) gradients. Values followed by the same lower case letter indicate no statistical difference (Tukey's test, $P \leq 0.05$).

DISCUSSION

Is the spatial distribution of bryophytes along environmental gradients related to functional diversity?

The functional diversity along the gradients explained little of the spatial distribution of bryophytes in the Atlantic Forest fragment studied in the ESEC Murici. However, the functional evenness had a significant variation along the vertical gradient in the analyses with all the bryophytes and with the group of liverworts alone. In these two analyses, the outer canopy presented low functional evenness either in relation to all the other height zones (all bryophytes) or in relation to the base (liverworts alone), indicating an irregular distribution of abundance of traits in the outer canopy. Functional evenness is maximized when the abundance of the species has a homogeneous distribution in the functional space, and decreases when some parts of the functional space are not filled while others are overrepresented (Mouchet et al. 2010). This was confirmed in our study by the fact that there was a high abundance of species with few functional characteristics in the outer canopy (e.g., lobules and dark pigments), which is related to environmental filtering and high abiotic stress imposed in this microhabitat.

The studied fragment presents a high and diffuse pattern of disturbance resulting from random perturbation throughout its extension, mainly due to chronic extraction of plant resources such as the felling of large trees and consequent opening of clearings (Silva & Pôrto 2009, 2010, 2013). This situation also seems to influence the taxonomic and functional diversity of bryophytes in the horizontal gradient. The abovementioned studies did not detect a linear effect from the edge to the core on the taxonomic diversity of bryophytes. In the present study, the first three distance classes had greater functional divergence in relation to the core, which can be attributed to the effects of chronic anthropic disturbances in the central areas of the forest (Silva & Pôrto 2013) that lead them to become functionally distinct from the other distance classes. Considering that the functional traits of bryophytes are related to environmental filtering (Vieira et al. 2012; Deane-Coe & Stanton 2017), the environmental homogeneity caused by anthropic disturbances may compromise the functional dynamics along the fragment, preventing variations in taxonomic and functional diversity.

Functional richness showed no relation to the vertical or horizontal gradient. With respect to functional richness and edge effect, Magnago et al. (2014) suggested that tree communities are not affected in this sense, indicating that the number of functions provided is similar and non-related to proximity to the edge. A similar process may take place in the spatial distribution of bryophytes in this community.

Does the composition of functional traits vary qualitatively (type of trait) and quantitatively (morphological variation of a given trait - lobule of leafy liverworts) along the gradients?

Functional composition showed to be qualitatively distinct along the height zones, with a change of functional dominance of traits typical of the understory from the base to the canopy. In height zones corresponding to the understory, life forms that are less desiccation tolerant and more adapted to low light incidence such as pendant, flabellate and dendroid predominated (Kürschner 2003). On the other hand, there was a greater functional dominance of traits directly related to rapid water uptake and regulation and protection from solar radiation such as lobule, dark pigments and mat life form, in the outer canopy. For example, most of the more frequent liverwort species (≥ 6 occurrences) in the outer canopy, namely, *Ceratolejeunea cornuta* (Lindenb.) Schiffn., *Frullania apiculata* (Reinw. et al.) Nees and *Symbiezidium barbiflorum* (Lindenb. & Gottsche) A. Evans, are characterized by the simultaneous presence of these traits. In parallel, the functional area overlapped along the height zones, indicating the co-occurrence of most of the traits throughout the zones, despite the varied abundances. Height zones corresponding to the understory presented a larger functional area, which decreased towards the canopy. This change seen from the understory to the canopy is probably due to the reduction of niche breadth and more specific stress-related traits.

Papillae presented a high correlation with the first PCA axis in the vertical gradient, directing the functional dominance towards the understory. The function of papillae in the cells of bryophytes is a contradictory subject because these structures seem to work for both water absorption (Kürschner 2004) and loss (Pressel et al. 2010). However, there is consensus about their role in osmotic regulation and rapid cellular water movement (Proctor 1979; Kürschner 2004; Pressel et al. 2010). It is, therefore, possible that the rapid movement of water promoted by the papillae is unfavorable to canopy species in view of their exposure to intense sunlight incidence and consequent greater water loss.

The relation between life forms and the vertical gradient is clear. Bryophyte life forms reflect strategies to maximize light capture for photosynthesis and minimize water loss according to microclimatic conditions (Richards 1984; Ah-Peng et al. 2014). Filtering of different life forms from the understory to the outer canopy has been well documented (Leerdam 1990; Pardow et al. 2012), even in the Southeastern Atlantic Forest (Costa 1999). Pardow et al. (2012) also described the change of life forms and emphasized that there are fewer forms in the canopy of tropical lowland rainforests in the Guianas. They described mat as a generalist life form that indicates drier and more exposed microclimatic conditions, in line with our present observations in the canopy bryophytes. Life forms represent a variable trait that predicts the vertical gradient. The importance of this functional group in the vertical zonation of bryophytes is, therefore, endorsed.

In the fragment studied, the vertical gradient was not directly related to functional diversity, as described earlier, but rather to trait substitution. The substitution of adaptive morphological traits in bryophytes along environmental gradients is well reported in the literature (Frahm 2003; Kürschner 2003; Vieira et al. 2012). Henriques et al. (2017) confirmed that the functional composition related to the trais leaf width, ornamentation and incurved margins was negatively affected along the altitudinal gradient (0-1000 m) in the Azorean archipelago. Oliveira & Oliveira (2016) observed that concave leaves, hyaline cells and mat and weft life forms were associated with different microhabitats in the vertical gradient of Atlantic Forest fragments. On the other hand, Oliveira (2018) found that in addition to concave leaves, dark pigments influence the occurrence of species along the vertical gradient in the Amazon, contributing positively to the presence of species in the canopy. Rigal et al. (2018) proved that trait composition strongly shifted across land uses in Azores and the indigenous and the exotic arthropod species were functionally distinct in all land uses. The latter authors also pointed out that anthropic processes can act in the filtering and in the selection of functional traits, as well as we reported for bryophytes in the present study.

Regarding the functional composition in the horizontal gradient, the functional dominance changed from the core to the other distance classes, with greater difference between the core and the edge. In relation to the size of the functional area of the distance classes, it is notable that the edge and the core were little associated, while the intermediate classes were overlapped and did not express a homogeneous gradient. It is noteworthy the edge was better related to attributes of desiccation tolerance and high light exposure, such as lobules and dark pigments. These results indicate that the edge and the core of the fragment have distinct functional composition. Furthermore, in functional terms, the edge extends up to about 800 m within the fragment studied. Moreover, the edge presented a more restricted functional area than the other distance classes, probably due to the smaller niche breadth associated with stress-related traits.

The morphometry of lobules corroborated the pattern of trait selection along gradients. In the vertical gradient, this attribute varied significantly both in terms of lobule area and in the lobule/lobe ratio. For example, *Ceratolejeunea cornuta* (Lindenb.) Schiffn. and *C. cubensis* (Mont.) Schiffn. had the largest ranges of variation LA and LL, presenting reduced lobules in the understory to utricles (widely developed lobules, with relatively large area in relation to the leaf lobe, see Dauphin 2003) in the outer canopy. In the horizontal gradient, lobule area differed between the edge and other distance classes. These results point to the abiotic stress that the canopy and the edge of the fragment impose on bryophyte communities, including lower humidity and greater exposure to light, causing a greater investment in larger and varied lobules for water storage and retention.

It was evident that the lobule contributes functionally in the community of leafy liverworts, displaying an association with the type of microhabitat where the species lives. The present study is pioneer in the empirical evaluation of the morphological function of lobules along gradients and stressful conditions. Here we present data that suggest that lobules play an important role in water regulation in leafy liverworts, but further in-depth analysis are required on the functionality and variation of this trait, as well as of papillae and dark pigments along environmental gradients, particularly in tropical environments whose bryophyte communities hold the greatest abundance worldwide (Gradstein et al. 2001).

CONCLUSION

Functional diversity showed little correlation with the spatial distribution of bryophytes in the studied fragmented Atlantic Forest landscape. However, functional composition played an explanatory role on the vertical gradient, pointing to the filtering of specific traits in the microhabitats present from the understory to the canopy, such as reduction of the functional area towards the canopy and edge of the fragment. As for the functional traits distinctly related to the spatial distribution, the lobule of leafy liverworts stood out. The different microhabitats along the studied gradients impose environmental filters that select intrinsic characteristics of the species and their morphological variations, particularly those related to water storage and protection from light incidence, as adaptive strategies.

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REFERENCES

Acebey A, Gradstein SR, 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.

Ah-Peng C, Cardoso AW, Flores O, West A, Wilding N, Strasberg D, Hedderson TA. 2017. The role of epiphytic bryophytes in interception, storage, and the regulated release of atmospheric moisture in a tropical montane cloud forest. Journal of Hydrology 548: 665-673.

Ah-Peng C, Flores O, Wilding N, Bardat J, Marline L, Hedderson TA, Strasberg D. 2014. Functional diversity of subalpine bryophyte communities in an oceanic island (La Réunion). Arctic, Antarctic, and Alpine Research 46: 841-851.

Alvarenga LDP, Pôrto KC, Oliveira JRPM. 2010. Habitat loss effects on spatial distribution of non-vascular epiphytes in a Brazilian Atlantic forest. Biodiversity and Conservation 19: 619-635.

Bardgett RD. 2018. Plant trait-based approaches for interrogating belowground function. In Biology and Environment: Proceedings of the Royal Irish Academy. Royal Irish Academy. 117B: 1-13.

Carrié R, Andrieu E, Cunningham SA, Lentini PE, Loreau M, Ouin A. 2016. Relationships among ecological traits of wild bee communities along gradients of habitat amount and fragmentation. Ecography 40: 85-97.

Cianciaruso MV, Silva IA, Batalha MA. 2009. Diversidades filogenética e funcional: novas abordagens para a Ecologia de comunidades. Biota Neotropica 9: 93–103.

Cornelissen JHC, ter Steege H. 1989. Distribuition and ecology of epiphytic bryophytes and lichens in dry evergreen Forest of Guyana. Tropical Ecology 5: 131-150.

Costa DP. 1999. Epiphytic Bryophyte Diversity in Primary and Secondary Lowland Rainforests in Southeastern Brazil. The Bryologist 102: 320–326.

Daniels AED. 1998. Ecological adaptations of some bryophytes of the Western Ghats. Journal of Ecobiology 10: 261-270.

Dauphin G. 2003. Ceratolejeunea. Flora Neotropica. monograph 90: 1-86.

Deane-coe KK, Stanton D. 2017. Functional ecology of cryptogams: scaling from bryophyte, lichen, and soil crust traits to ecosystem processes. New Phytologist 213: 993–995.

Deltoro VI, Calatayud A, Gimeno C, Abadía A, Barreno E. 1998. Changes in chlorophyll a fluorescence, photosynthetic CO2 assimilation and xanthophyll cycle interconversions during dehydration in desiccation-tolerant and intolerant liverworts. Planta 207: 224–228.

Deyn GB, Cornelissen JHC, Bardgett RD. 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecology Letters 11: 516–531.

Díaz S, Cabido M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16: 646-655.

Díaz S, Lavorel S, Bello F, Quétier F, Grigulis K, Robson TM. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of the National Academy of Sciences of the United States of America 104: 20684-20689.

FLORA DO BRASIL 2020 EM CONSTRUÇÃO. Jardim Botânico do Rio de Janeiro. [accessed 2018 May 16]. http://floradobrasil.jbrj.gov.br/.

Frahm JP. 1985. The ecological significance of the costal anatomy in the genus Campylopus. Abstracta Botanica 2: 159-169.

Frahm JP. 1990. Bryophyte phytomass in tropical ecosystems. Botanical Journal of the Linnean Society 104: 23-33.

Frahm, JP, Pócs T, O'shea B, Koponen T, Piipo S, Enroth J, Rao P, Fang Y. 2003. Manual of tropical bryology. Tropical bryology.

Glime JM. 2017a. Water Relations: Plant Strategies. Chapt. 7-3. In: Glime JM. Bryophyte Ecology. Volume 1. Physiological 7-3-1 Ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Last updated 7 March 2017 and available at. [accessed 2018 May 18]. http://digitalcomoons.mtu.edu/bryophyte-ecolog/.

Glime JM. 2017b. Water Relations: Leaf Strategies – Structural. Chapt. 7-4a. In: Glime JM. Bryophyte Ecology. Volume 1. Physiological Ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Last updated 9 March 2017 and available at. [accessed 2018 May 18]. http://digitalcomoons.mtu.edu/bryophyte-ecolog/.

Gradstein SR. 1995. Bryophyte diversity of the tropical rainforest. Arch. Siences Genève. Société de physique et d'histoire naturelle de Genève. 48: 91–96.

Gradstein SR, Churchill SP, Salazar-Allen N, Reiner-Drehwald ME. 2001. Guide to the bryophytes of tropical America. Bronx, NY: New York Botanical Garden Press.

Gradstein SR, Costa DP. 2003. The hepaticae and anthocerotae of Brazil. Memoirs-New York Botanical Garden.

Harper KA, Macdonald SE, Burton PJ, Chen J, Brosofske KD, Saunders SC, Euskirchen ES, Roberts D, Jaiteh MS, Esseen P-A. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology 19: 768-782.

Henderson SA, Dickinson RE, Durbidge TB, Kennedy PJ, McGuffie K. Pitman AJ. 1993. Tropical Deforestation: Modeling Local- to Regional-Scale Climate Change. Journal of Geophysical 98: 7289–7315.

Henriques DS, Rigal F, Borges PA, Ah-Peng C, Gabriel R. 2017. Functional diversity and composition of bryophyte water-related traits in Azorean native vegetation. Plant Ecology & Diversity 10: 127-137.

Holz I, Gradstein SR, Heinrichs J, Kappelle M. 2002. Bryophyte diversity, microhabitat differentiation, and distribution of life forms in Costa Rican upper montane Quercus forest. The Bryologist 105: 334-348.

Hammer O, Harper DAT, Ryan PD. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica 4:9.

Kraichak E. 2012. Asexual propagules as an adaptive trait for epiphylly in tropical leafy liverworts (Lejeuneaceae). American Journal of Botany 99: 1436–1444.

Kuebbing SE, Maynard DS, Bradford MA. 2018. Linking functional diversity and ecosystem processes: A framework for using functional diversity metrics to predict the ecosystem impact of functionally unique species. Journal of Ecology 106: 687-698.

Kürschner H. 2003. Epiphytic bryophyte communities of southwestern Arabia-phytosociology, ecology and life strategies. Nova Hedwigia 77: 55-71.

Kürschner H. 2004. Life strategies and adaptations in bryophytes from the near and Middle East. Turkish Journal of Botany 28: 73-84.

Leerdam A, Zagt RJ, Veneklaas EJ. 1990. The distribution of epiphyte growth-forms in the canopy of a Colombian cloud-forest. Vegetatio 87: 59-71.

Laliberté E. 2017. Below‐ground frontiers in trait‐based plant ecology. New Phytologist, 213: 1597-1603.

Lima CMG, Garcia RA. 2018. Dinâmica da Mata Atlântica 510 anos após o descobrimento: Tendências e drivers atuais. Cadernos do LESTE 10: 17-34.

Magnago LFS, Edwards DP, Edwards FA, Magrach A, Martins SV, Laurance WF. 2014. Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. Journal of Ecology 102: 475-485.

Mason NW, Mouillot D, Lee WG, Wilson JB. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111: 112-118.

McCune B, Grace JB. 2002. Analysis of ecological communities. Gleneden Beach, Oregon: MjM Software Design.

Melick DR, Seppel RD. 1994. Seasonal Investigations of Soluble Carbohydrates and Pigment Levels in Antarctic Bryophytes and Lichens. American Bryological and Lichenological Society 97: 13–19.

Michel EL. 2001. Hepáticas epifíticas sobre o pinheirobrasileiro no Rio Grande do Sul. Editora da Universidade Federal do Rio Grande do Sul, Porto Alegre 191p.

Mota-de-Oliveira S, Ter Steege H, Cornelissen JH, Robbert Gradstein S. 2009. Niche assembly of epiphytic bryophyte communities in the Guianas: a regional approach. Journal of Biogeography 36: 2076-2084.

Mota-de-Oliveira S, 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.

Mouchet MA, Villéger S, Mason NW, Mouillot D. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology, 24: 867-876.

Oliveira JRPM, Pôrto KC, Silva, MPP. 2011. Richness preservation in a fragmented landscape: a study of epiphytic bryophytes in an Atlantic forest remnant in Northeast Brazil. Journal of Bryology 33: 279-291.

Oliveira HCD, Oliveira SMD. 2016. Vertical distribution of epiphytic bryophytes in Atlantic Forest fragments in northeastern Brazil. Acta Botanica Brasilica 30: 609-617.

Oliveira SM. 2018. The double role of pigmentation and convolute leaves in community assemblage of Amazonian epiphytic Lejeuneaceae. PeerJ, 6: e5921.

Pardow A, Gehrig-Downie C, Gradstein R, 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.

Peres‐Neto PR, Dray S, ter Braak CJ. 2017. Linking trait variation to the environment: critical issues with community‐weighted mean correlation resolved by the fourth‐corner approach. Ecography 40: 806-816.

Posey DA. 1985. Indigenous management of tropical forest ecosystems: the case of the Kayapo Indians of the Brazilian Amazon. Agroforestry systems 3: 139-158.

Pressel S, P’ng KMY, Duckett JG. 2010. A cryoscanning electron microscope study of the water relations of the remarkable cell wall in the moss Rhacocarpus purpurascens (Rhacocarpaceae, Bryophyta). Nova Hedwigia 91: 289-299.

Proctor MCF. 1979. Surface wax on the leaves of some mosses. Journal of Bryology 10: 531-538

R Core Development Team. 2014. R: A language and environmentfor statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Renner MAM, Devos N, Brown EA, von Konrat MJ. 2013. Three modes of heterochrony explain lobule diversity in *Radula* subgenus Cladoradula (porellales: Jungermanniopsida), a small lineage of early land plants today. Botanical Journal of the Linnean Society 173: 153–175.

Renner MAM. 2015. Lobule shape evolution in *Radula* (Jungermanniopsida): One rate fits all? Botanical Journal of the Linnean Society 178: 222–242.

Richards PW. 1984. The ecology of tropical forest bryophytes. Pp. 1233-1270 in: Schuster R. M. (ed.) New Manual of Bryology. The Hattori Botanical Laboratory, Miyazaki.

Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9: 671.

Silva JB, Sfair JC, Santos ND, Pôrto KC. 2017. Different trait arrangements can blur the significance of ecological drivers of community assembly of mosses from rocky outcrops. Flora 51073.

Silva MPP, Pôrto KC**. 2009. Effect of fragmentation on the Community structure of epixylic bryophytes in Atlantic Forest remnants in the northeast of Brazil. Biodiversity Conservation 18:317–337.**

Silva MPP, Pôrto KC**. 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.

Silva MPP, Pôrto KC**.** 2013. Bryophyte communities along horizontal and vertical gradients in a human-modified atlantic forest remnant. Botany 91: 155-166.

Shepherd GJ. 2010. Fitopac 2.1. Campinas: Departamento de Botânica, Universidade Estadual de Campinas.

SOS Mata Atlântica & INPE. 2018. Atlas dos remanescentes florestais da Mata Atlântica, Período 2016-2017. Fundação SOS Mata Atlântica & INPE, São Paulo: Fundação SOS Mata Atlântica/INPE.

Sporn SG, Bos MM, Kessler M, Gradstein SR. 2010. Vertical distribution of epiphytic bryophytes in an Indonesian rainforest. Biodiversity and Conservation 19(3): 745-760.

Tabarelli M, Aguiar AV, Ribeiro, MC, Metzger JP, Peres CA. 2010. Prospects for biodiversity conservation in the Atlantic Forest: Lessons from aging human-modified landscapes. Biological Conservation 143: 2328–2340.

Tao Y, Zhang YM. 2012. Effects of leaf hair points of a desert moss on water retention and dew formation: Implications for desiccation tolerance. Journal of Plant Research 125: 351–360.

Tavares-Martins ACC, Lisboa RCL, Costa DP. 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.

Vieira C, Séneca A, Sérgio C, Ferreira MT. 2012. Bryophyte taxonomic and functional groups as indicators of fine scale ecological gradients in mountain streams. Ecological Indicators 18: 98-107.

Villéger S, Mason H, Mouillot D. 2008. New Multidimensional Functional Diversity Indices for a Multifaceted Framework. Ecology 89: 2290-2301.

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! Oikos 116: 882-892.

Werner FA, Homeier J, Oesker M, Boy J. 2012. Epiphytic biomass of a tropical montane forest varies with topography. Journal of Tropical Ecology 28(1): 23-31.

Supplementary material 1 - Updated list of epiphytic bryophyte species in the forest remnant located at the Murici Ecological Station, Alagoas, Brazil. Total occurrence and occurrence per height zone in the host trees and edge distance classes. Numbers in parentheses reflect the number of genera and species, respectively, per family. Acronym: Z1 = base; Z2 = trunk; Z3 = first ramification; Z4 = second ramification; and Z5 = outer canopy. C1 = 0-200 m, C2 = 201-400 m, C3 = 401-600 m, C4 = 601-800 m and C5 = 801-1100 m.

		Height zone					Edge distance class				
Family/*species*	Total	Z1	Z2	Z3	Z4	Z5	C1	C2	C3	C4	C5
Cephaloziellaceae (1/1)											
Cylindrocolea rhizantha (Mont.) R.M. Schust.	2			1	1					2	
Frullaniaceae (1/6)											
Frullania apiculata (Reinw. et al.) Nees	13		1	4	2	6	4	5		4	
Frullania caulisequa (Nees) Nees	8			2	1	5	2		1	5	
Frullania dusenii Steph	1					1				1	
Frullania kunzei (Lehm. & Lindenb.) Lehm. & Lindenb.	3				2	1		1		1	1
Frullania riojaneirensis (Raddi) Ångstr.	3					3	2	1			
Frullania setigera Steph.	6	2	1	1	1	1	2	4			
Lejeuneaceae (17/39)											
Anoplolejeunea conferta (Meissn.) A. Evans	6	1	1			4		1	1	2	2
Archilejeunea fuscescens (Hampe ex Lehm.) Fulford	2	2						1	1		
Bryopteris filicina (Sw.) Nees	11	3	2	2	1	3	7	2		2	
Ceratolejeunea ceratantha (Nees & Mont.) Steph.	2		1	1			1	1			
Ceratolejeunea coarina (Gottsche) Steph.	3		2			1	2	1			
Ceratolejeunea cornuta (Lindenb.) Schiffn.	23	2	4	3	7	7	4	8	2	4	5
Ceratolejeunea cubensis (Mont.) Schiffn.	14	3	3	3	3	2		2	8	4	
Ceratolejeunea laetefusca (Austin) R.M. Schust.	1	1					1				
Cheilolejeunea adnata (Kunze) Grolle	8	2	3	1	1	1			1	6	1

		Height zone					Edge distance class				
Family/*species*	Total	Z1	Z2	Z3	Z4	Z5	C1	C2	C3	C4	C5
Cheilolejeunea filiformis (Sw.) W. Ye, R.L. Zhu & Gradst.	2			1	1		2				
Cheilolejeunea holostipa (Spruce) Grolle & R-L. Zhu	1	1									1
Cheilolejeunea rigidula (Mont.) R.M. Schust.	26	4	4	8	7	3	3	1	12	5	5
Cheilolejeunea trifaria (Reinw. et al.) Mizut.	8		1	2	2	3	3	2		3	
Cololejeunea diaphana A. Evans	1		1					1			
Colura tortifolia (Nees & Mont.) Steph.	1					1				1	
Diplasiolejeunea brunnea Steph.	3					3		1		1	1
Diplasiolejeunea rudolphiana Steph.	1					1	1				
Drepanolejeunea fragilis Bischl.	12		2	1	2	7		3	2	5	2
Drepanolejeunea mosenii (Steph.) Bischl.	2		1	1					2		
Harpalejeunea stricta (Lindenb. & Gottsche) Steph.	8			2	3	3	3	1	1	1	2
Harpalejeunea tridens (Besch. & Spruce) Steph.	1	1					1				
Lejeunea caespitosa Lindenb.	1				1						1
Lejeunea caulicalyx (Steph.) M.E. Reiner & Goda	2	1			1		1	1			
Lejeunea cerina (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees	6	2	1	3			4	1		1	
Lejeunea controversa Gottsche	1				1						1
Lejeunea aphanes Spruce	1					1		1			
Lejeunea flava (Sw.) Nees	5				1	4	1	1	1	2	
Lejeunea grossitexta (Steph.) E. Reiner & Goda	4	2		1	1		1	3			
Lejeunea laetevirens Nees & Mont.	1					1		1			
Lejeunea oligoclada Spruce	2		1	1			2				
Lepidolejeunea involuta (Gottsche) Grolle	6		2	2	1	1	2	3	1		
Lopholejeunea subfusca (Nees) Schiffn.	1					1				1	
Microlejeunea epiphylla Bischl.	5					5		1	1	2	1

		Height zone					Edge distance class				
Family/*species*	Total	Z1	Z2	Z3	Z4	Z5	C1	C2	C3	C4	C5
Prionolejeunea aemula (Gottsche) A. Evans	1	1								1	
Prionolejeunea denticulata (Weber) Schiffn.	6	4	2					2	2	2	
Prionolejeunea scaberula (Spruce) Steph.	1		1							1	
Symbiezidium barbiflorum (Lindenb. & Gottsche) A. Evans	19	5	2	3	3	6	6	5	3	4	1
Taxilejeunea obtusangula (Spruce) A. Evans	2	1	1					2			
Vitalianthus bischlerianus (Pôrto & Grolle) R.M. Schust. & Giancotti	1			1					1		
Metzgeriaceae (1/2)											
Metzgeria albinea Spruce	6	1	1	1	2	1	1	5			
Metzgeria ciliata Raddi	1					1		1			
Plagiochilaceae (1/4)											
Plagiochila aerea Tayl.	6	3	2		1				3	3	
Plagiochila disticha (Lehm. & Lindenb.) Lindenb.	3	1	1	1			3				
Plagiochila distinctifolia Lindenb.	1					1				1	
Plagiochila montagnei Nees	4		1	2		1		1	2	1	
Radulaceae (1/1)											
Radula kegelii Gottsche ex Steph.	4	2	1	1			4				
Brachytheciaceae (2/2)											
Squamidium brasiliensis (Hornsch.) Broth.	5	1	1		2	1	4	1			
Zelometeorim patulum (Hedw.) Manuel	2		1			1	1				1
Calymperaceae (3/7)											
Calymperes lonchophyllum Schwägr.	1	1								1	
Calymperes palisotii Schwägr.	1		1							1	
Octoblepharum albidum Hedw.	12	1	2	5	4			1	4	1	6
Syrrhopodon incompletus Schwägr.	3	2		1				1			2

Family/*species*	Total	Height zone					Edge distance class				
		Z1	Z2	Z3	Z4	Z5	C1	C2	C3	C4	C5
Syrrhopodon ligulatus Schwägr.	3		1	1	1				1		2
Syrrhopodon parasiticus (Sw. ex Brid.) Paris	13	2	2	2	5	2	1	1	3	3	5
Syrrhopodon prolifer Schwägr	1	1							1		
Dicranaceae (1/1)											
Leucoloma serrulatum Brid.	7	2	3	1	1		3	4			
Fissidentaceae (1/2)											
Fissidens guianensis Montagne	1	1							1		
Fissidens ramicola Broth.	1	1						1			
Hypnaceae (2/2)											
Isopterygium tenerum (Sw.) Mitt.	1				1					1	
Ectropothecium leptochaeton (Schwägr.) W.R. Buck	2				1	1	1	1			
Neckeraceae (1/1)											
Porotrichum substriatum (Hampe) Mitt.	2	1	1					2			
Orthotrichaceae (2/3)											
Groutiella apiculata (Hook.) Crum & Steere	2			1		1	2				
Groutiella mucronifolia (Hook. & Grev.) H.A. Crum & Steere	2				2		1				1
Macromitrium punctatum (Hook. & Grev.) Brid.	3		1	2			1			2	
Phyllogoniaceae (1/1)											
Phyllogonium viride Brid.	5	2	1	1	1		1	4			
Pilotrichaceae (3/3)											
Crossomitrium patrisae (Brid.) Müll. Hal.	2		1			1	1	1			
Lepidopilidium brevisetum (Hampe) Broth.	2				1	1				1	1
Lepidopilum scabrisetum (Schwägr.) Steere	1	1								1	
Pterobryaceae (1/1)											

		Height zone					Edge distance class				
Family/*species*	Total	Z1	Z2	Z3	Z4	Z5	C1	C2	C3	C4	C5
Jaegerina scariosa (Lorentz) Arzeni	3		1	1		1	2	1			
Sematophyllaceae (4/4)											
Acroporium estrellae (Müll. Hal.) W.R. Buck & Schäf. -Verw.	1			1				1			
Brittonodoxa subpinnata (Brid.) W.R. Buck, P.E.A.S.Câmara & Carv.-Silva	16	1	2	3	6	4	1	2	1	4	8
Microcalpe subsimplex (Hedw.) W.R. Buck	4	3		1					1		3
Taxithelium planum (Brid.) Mitt.	1		1							1	
Total	359	65	62	69	71	92	82	85	57	82	53

4 CONCLUSÕES

Os traços funcionais lóbulo, pigmento, papila e as formas de vida mostraram-se preditores eficientes para distribuição espacial do grupo na Floresta Atlântica. A variação na composição de traços ao longo do gradiente vertical foi explicativa, demonstrando existência de filtragem de traços específicos para os microhabitats desde o sub-bosque até o dossel em forófitos, bem como o requerimento de recursos, tendo em vista que o sub-bosque possui maior umidade e menor entrada de luz, inversamente ao dossel. O núcleo e a borda do fragmento apresentaram as maiores distinções funcionais, sem apresentar um efeito de borda linear, bem como a borda associada a traços alusivos à estresse abiótico. O lóbulo das hepáticas folhosas mostrou-se como um caractere funcionalmente relacionado com a distribuição espacial do grupo, com significativas variações no tamanho ao longo dos gradientes, associado a necessidade de requerimento de água, principalmente no dossel e na borda do fragmento. Assim sendo, constatamos que os diferentes microhabtats em ambos os gradientes impõem filtros ambientais, e estes selecionam traços funcionais específicos e suas variações morfológicas.

REFERÊNCIAS

ACEBEY A, GRADSTEIN SR, KRÖMER T. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. **Journal of Tropical Ecology**, v. 19, p. 9-18. 2003.

AH-PENG, C.; CARDOSO, A.W.; FLORES, O.; WEST, A.; WILDING, N.; STRASBERG, D.; HEDDERSON, T.A. The role of epiphytic bryophytes in interception, storage, and the regulated release of atmospheric moisture in a tropical montane cloud forest. **Journal of Hydrology**, v. 548, p. 665-673. 2017.

ALVARENGA, L. D. P.; LISBOA, R. C. L. Contribuição para o conhecimento da taxonomia, ecologia e fitogeografia de Briófitas da Amazônia Oriental. **Acta Amazonica**, v. 39, p. 495-504. 2009.

ALVARENGA, L.D.P.; PÔRTO, K.C. Patch size and isolation effects on epiphytic and epiphyllous bryophytes in the fragmented Brazilian Atlantic forest. **Biological Conservation**, v. 134, p. 415-427. 2007.

ALVARENGA, L.D.P.; PÔRTO, K.C., SILVA, M.P.P. Relations between Regional-Local Habitat Loss and Metapopulation Properties of Epiphyllous Bryophytes in the Brazilian Atlantic Forest. **Biotropica**, v. 41, p. 682-691. 2009.

AMORIM, M.W.; JÚNIOR, J.C.F.M. Plasticidade morfológica de *Myrcia splendens* (S.w.) CD. (Myrtaceae) ocorrente em Mata Atlântica e Cerrado. **Iheringia - Serie Botanica,** v.71, p. 261–268. 2016.

BATAGIN, K.D.; ALMEIDA, C.V.; TANAKA F.A.O. et al. Alterações morfológicas foliares em abacaxizeiros cv. IAC “Gomo-de-mel” micropropagados e aclimatizados em diferentes condições de luminosidade. **Acta Botanica Brasilica**, v. 23, p. 85–92. 2009.

BATISTA, W.V.S.M.; PÔRTO, K.C.; SANTOS, N.D.D. Distribution, ecology, and reproduction of bryophytes in a humid enclave in the semiarid region of northeastern Brazil. **Acta Botanica Brasilica**, v. 32, p. 303-313. 2018.

BRITO, E.D.S.; ILKIU-BORGES, A.L. Bryoflora of the municipalities of Soure and Cachoeira do Arari, on Marajó Island, in the state of Pará, Brazil. **Acta Botanica Brasilica**, v. 27, p. 124-141. 2013.

CAMPANILI, M.; SCHÄFFER, W. B. **Mata Atlântica: Manual de adequação ambiental**. Ministério do Meio Ambiente - Série Biodiversidade 35, 96p. 2010.

CARRIÉ, R.; ANDRIEU, E.; CUNNINGHAM, A.S. et al. Relationships among ecological traits of wild bee communities along gradients of habitat amount and fragmentation. **Ecography**, v. 40, p. 85-97. 2016.

CHAPIN, F.S. Effects of plant traits on ecosystem and regional processes: A conceptual framework for predicting the consequences of global change. **Annals of Botany,** v. 91, p. 455-463. 2003.

CHEN, J.; SAUNDERS, S.C.; CROW, T.R. et al. Microclimate in Forest Ecosystem and Landscape Ecology: Variations in local climate can be used to monitor and compare the effects of different management regimes. **BioScience**, v. 49, p. 288–297. 1999.

CIANCIARUSO, M.V.; SILVA, I.A.; BATALHA, M.A. Diversidades filogenética e funcional: novas abordagens para a Ecologia de comunidades. **Biota Neotropica**, v. 9, p. 93–103. 2009.

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

COSTA, D.P. Epiphytic Bryophyte Diversity in Primary and Secondary Lowland Rainforests in Southeastern Brazil. **Bryologist**, v. 102, p. 320-326. 1999.

DEANE-COE, K.K.; STANTON, D. Functional ecology of cryptogams: scaling from bryophyte, lichen, and soil crust traits to ecosystem processes. **New Phytologist**, v. 213, p. 993–995. 2017.

DELTORO, V.I.; CALATAYUD, A.; GIMENO, C. et al. Changes in chlorophyll a fluorescence, photosynthetic CO2 assimilation and xanthophyll cycle interconversions during dehydration in desiccation-tolerant and intolerant liverworts. **Planta**, v. 207, p. 224-228. 1998.

DEYN, G.B.; CORNELISSEN, J.H.C.; BARDGETT, R.D. Plant functional traits and soil carbon sequestration in contrasting biomes. **Ecology Letters,** v. 11, p. 516–531. 2008.

DIAS-FILHO, M.B.D.F. Competição e sucessão vegetal em pastagens. **Embtapa**. 2006.

DÍAZ, S.; LAVOREL, S.; BELLO. F. et al. Incorporating plant functional diversity effects in ecosystem service assessments. **PNAS**, v. 104, p. 20684–20689. 2007.

ESSEEN, P.; RENHORN, K. Edge effects on an epiphytic lichen in fragmented forests. **Conservation biology,** v. 12, p. 1307–1317. 1998.

FAHRIG, L. Effects of habitat fragmentation on biodiversity. **Annual review of ecology, evolution, and systematics,** v. 34, p. 487-515. 2003.

FLORA DO BRASIL 2020 EM CONSTRUÇÃO. **Jardim Botânico do Rio de Janeiro**. [accessed 2018 May 16]. http://floradobrasil.jbrj.gov.br/.

FOLEY, J.A.; DEFRIES, R.; ASNER, G.P. et al. Global consequences of land use. **Science** v. 309, p. 570–574. 2005

FRAHM, J. P. The effect of light and temperature on the growth of the bryophytes of tropical rain forests. **Nova Hedwigia**, v. 51, p. 151-164. 1990.

FRAHM, J.P. The ecological significance of the costal anatomy in the genus Campylopus. **Abstracta Botanica**, v. 2, p. 159-169. 1985.

GIRÃO, L.C.; LOPES, A.V.; TABARELLI, M. et al. Changes in tree reproductive traits reduce functional diversity in a fragmented Atlantic forest landscape. **PLoS ONE,** v. 2, p. 908. 2007.

GLIME, J.M. Water Relations: Plant Strategies. Chapt. 7-3. In: Glime JM. **Bryophyte Ecology**. Volume 1. Physiological 7-3-1 Ecology. Ebook sponsored by Michigan Technological University and the International Association ofBryologists. 2017a. Last updated 7 March 2017 and available at. [accessed 2018 May 18]. http://digitalcomoons.mtu.edu/bryophyte-ecolog/.

GLIME, J.M. Water Relations: Leaf Strategies – Structural. Chapt. 7-4a. In: Glime JM. **Bryophyte Ecology**. Volume 1. Physiological Ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. 2017b. Last updated 9 March 2017 and available at. [accessed 2018 May 18]. http://digitalcomoons.mtu.edu/bryophyte-ecolog/.

GOFFINET, B.; SHAW, A.J. Bryophyte Biology. 2 ed. **Cambridge: Cambridge University Press**, p. 565, 2008.
GRADSTEIN, S.R.; CHURCHILL, S.T.; SALAZAR-ALLEN, N. Guide to the bryophytes of Tropical America. **Memoirs of the New York Botanical Garden**, v. 86, p. 1-577. 2001.

GRADSTEIN, S.R.; COSTA, D.P. The Hepaticae and Anthocerotae of Brazil. **Memoirs of the New York Botanical Garden**, v. 87, p. 1-318. 2003.

HALLINGBACK, T.; HODGETTS, N. Status Survey and Conservation Action Plan for Bryophytes: Mosses, Liverworts and Hornworts: p 106. In: IUCN/SSC Bryophyte Specialist Group. IUCN, Gland-Switzerland-Cambridge. 2000.

HARPER, K.A.; MACDONALD, S.E.; BURTON, P.J. et al. Edge Influence on Forest Structure and Composition in Fragmented Landscapes. **Conservation Biology**, v. 19, p. 768–782. 2005.

HAUTIER, Y.; TILMAN, D.; ISBELL, F. et al., 2015. Anthropogenic environmental changes affect ecosystem stability via biodiversity. **Science** v. 349, p. 316-320. 2015.

HENDERSON-SELLER, A.; DURBIDGE, T.B.; KENNEDY, P.J. et al. 1993. Tropical Deforestation: Modeling Local- to Regional-Scale Climate Change. **Journal of Geophysical**, v. 98, p. 7289–7315. 1993.

HENRIQUES, D.S.; RIGAL, F.; BORGES, P.A.; AH-PENG, C.; GABRIEL, R. Functional diversity and composition of bryophyte water-related traits in Azorean native vegetation. **Plant Ecology & Diversity**, v. 10, p. 127-137. 2017.

HOLZ, I.; GRADSTEIN, S.R.; HEINRICHS, J.; KAPPELLE, M. Bryophyte diversity, microhabitat differentiation, and distribution of life forms in Costa Rican upper montane Quercus forest. **The Bryologist**, v. 105, p. 334-348. 2002.

KRAFT, N.J.; ADLER, P.B.; GODOY, O. et al. Community assembly, coexistence and the environmental filtering metaphor. **Functional Ecology**, v. 29, p. 592-599. 2015.

KRAICHAK, E. Asexual propagules as an adaptive trait for epiphylly in tropical leafy liverworts (Lejeuneaceae). **American Journal of Botany**, v. 99, p. 1436-1444. 2012.

KÜRSCHNER, H. Epiphytic bryophyte communities of southwestern Arabia-phytosociology, ecology and life strategies. **Nova Hedwigia**, v. 77, p. 55-71. 2003.

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

LAVOREL, S.; GARNIER, É. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. **Functional ecology**, v. 16, p. 545-556. 2002.

LIMA, C.M.G; GARCIA, R.A. Dinâmica da Mata Atlântica 510 anos após o descobrimento: Tendências e drivers atuais. **Cadernos do LESTE**, v. 10, p. 17-34. 2018.

LOPES, A.V.; GIRÃO, L.C.; SANTOS, B.A. et al. Long-term erosion of tree reproductive trait diversity in edge-dominated Atlantic forest fragments. **Biological Conservation**, v. 142, p. 1154–1165. 2009.

MACHADO-FILHO, H.O.; COUTO, E.A.; BEZERRA, C.P. et al. Composição e similaridade da flora associada a sítios antropizados do município de João Pessoa - Paraíba. **Planta Daninha**, v. 33, p. 57–66. 2015.

MAGNAGO, L.F.S.; EDWARDS, D.P.; EDWARDS, F.A. et al. 2014. Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. **Journal of Ecology**, v. 102, p. 475-485. 2014.

MAGURA, T. Ignoring functional and phylogenetic features masks the edge influence on ground beetle diversity across forest-grassland gradient. **Forest Ecology and Management**, v. 384, p. 371-377. 2007.

MANDUJANO, M.C.; GOLUBOV, J.; HUENNEKE, L.F. Effect of reproductive modes and environmental heterogeneity in the population dynamics of a geographically widespread clonal desert cactus. **Population Ecology**, v. 49, p. 141–153. 2007.

MELICK, D.R.; SEPPEL, R.D. Seasonal Investigations of Soluble Carbohydrates and Pigment Levels in Antarctic Bryophytes and Lichens. **American Bryological and Lichenological Society**, v. 97, p. 13-19. 1994.

MITTERMEIER, R.A.; TURNER, W.R.; LARSEN, F.W.; BROOKS, T.M.; GASCON, C. Global biodiversity conservation: the critical role of hotspots. In: ZACHOS, F.E.; HABEL, J.C. (Eds.), **Biodiversity Hotspots: Distribution and Protection of Priority Conservation Areas**. Springer-Verlag, Berlin, p. 3–22. 2011.

MOGENSEN, G.S. The biological significance of morphological characters in Bryophytes. The spore. **The Bryologist**, v. 84, p. 187-207. 1981.

MOTA-DE-OLIVEIRA, S.; 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, p. 441-450. 2015.

MOTA-DE-OLIVEIRA, S.; TER STEEGE, H.; CORNELISSEN, J.H.; GRADSTEIN, S.R. Niche assembly of epiphytic bryophyte communities in the Guianas: a regional approach. **Journal of Biogeography**, v. 36, p. 2076-2084. 2009.

MYERS, N.; MITTERMEIER, R.A.; MITTERMEIER, C.G. et al. Biodiversity hotspots for conservation priorities. **Nature**, v. 40, p. 853-858. 2000.

NEWTON, A.E.; MISHLER, B.D. The evolutionary significance of asexual reproduction in mosses (Proceedings of the Symposia on Bryology and Lichenology at the 15 International Botanical Congress)-(Reproductive Biology of Bryophytes). **Journal of the Hattori Botanical Laboratory**, v. 76, p. 127-145. 1994.

ØKLAND, R.H. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. 5. Vertical dynamics of individual shoot segments. **Oikos**, v. 88, p. 449-469. 2000.

OLIVEIRA, M.A.; GRILLO A.S.; TABARELLI, M. Forest edge in the Brazilian Atlantic forest: drastic changes in tree species assemblages. **Oryx**, v. 38, p. 389-394. 2004.

OLIVEIRA FILHO, A.T.; CARVALHO, W.A.C.; MACHADO, E.L.M. et al. Dinâmica da comunidade e populações arbóreas da borda e interior de um remanescente florestal na Serra da Mantiqueira, Minas Gerais, em um intervalo de cinco anos (1999-2004). **Revista Brasileira de Botânica**, v. 30, p. 149–161. 2007.

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

OLIVEIRA, J.R.P.M.; PÔRTO, K.C.; SILVA, M.P.P. Richness preservation in a fragmented landscape: a study of epiphytic bryophytes in an Atlantic forest remnant in Northeast Brazil. **Journal of Bryology**, v. 33, p. 279-291. 2011.

PANTOJA, A.C.C.; ILKIU-BORGES, A.L.; TAVARES-MARTINS, A.C.C. et al. Bryophytes in fragments of Terra Firme forest on the great curve of the Xingu River, Pará state, Brazil. **Brazilian Journal of Biology**, v. 75, p. 238-249. 2015.

PONCE-REYES, R.; NICHOLSON, E.B.; PETER, W.J. et al. Extinction risk in cloud forest fragments under climate change and habitat loss. **Diversity and Distributions**, v. 19, p. 518–529. 2013.

PRESSEL, S.; DUCKETT, J.G.; LIGRONE, R.; PROCTOR, M.C. Effects of de-and rehydration in desiccation-tolerant liverworts: a cytological and physiological study. **International Journal of Plant Sciences**, v. 170, p. 182-199. 2009.

PROCTOR, M.C.F. Surface wax on the leaves of some mosses. **Journal of Bryology**, v. 10, p. 531-538. 1979.

REESE, W.D. *Calymperaceae*. **Memoirs of the New York Botanical Gardens**, v. 58, p. 1-102. 1993.
RENNER, M.A.M. Lobule shape evolution in *Radula* (Jungermanniopsida): One rate fits all? **Botanical Journal of the Linnean Society**, v. 178, p. 222-242. 2015.

RENNER, M.A.M.; DEVOS, N.; BROWN, E.A. et al. Three modes of heterochrony explain lobule diversity in *Radula* subgenus Cladoradula (Porellales: Jungermanniopsida), a small lineage of early land plants today. **Botanical Journal of the Linnean Society**, v. 173, p. 153-175. 2013.

RIBEIRO, M.C.; METZGER, J.P.; MARTENSEN, A.C. et al. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. **Biological Conservation**, v. 142, p. 1141–1153. 2009.

RICHARDS, P.W. The ecology of tropical forest bryophytes. in: Schuster R. M. (ed.) New Manual of Bryology. **The Hattori Botanical Laboratory, Miyazaki**, p. 1233-1270. 1984.

RICOTTA, C. From theoretical ecology to statistical physics and back: Self-similar landscape metrics as a synthesis of ecological diversity and geometrical complexity. **Ecological Modelling**, v. 125, p. 245-253. 2000.

RICOTTA, C. Through the jungle of biological diversity. **Acta Biotheoretica**, v. 53, p. 29-38. 2005.

SHAW, A.J.; GOFFINET, B. Bryophyte Biology. 2nd. edn. **Cambridge: Cambridge University Press**. 2009.

SILVA, J.B.; SFAIR, J.C.; SANTOS, N.D.; PÔRTO, K.C. 2017. Different trait arrangements can blur the significance of ecological drivers of community assembly of mosses from rocky outcrops. **Flora**, v. 238, p. 43-50. 2017.

SILVA, M.P.P; PÔRTO, K.C**.** Bryophyte communities along horizontal and vertical gradients in a human-modified atlantic forest remnant. **Canadian Journal of Zoology**, v. 91, p. 155-166. 2013.

SILVA, M.P.P; PÔRTO, K.C**.** Effect of fragmentation on the Community structure of epixylic bryophytes in Atlantic Forest remnants in the northeast of Brazil. **Biodiversity Conservation**, v. 18, p. 317–337. 2009.

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, p. 101-112. 2010.

SLADE, E.M.; MANN, D.J.; VILLANUEVA, J.F. et al. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. **Journal of Animal Ecology**, v. 76, p. 1094–1104. 2007.

SOS MATA ATLÂNTICA, INPE. Atlas dos remanescentes florestais da Mata Atlântica, Período 2016-2017. Fundação SOS Mata Atlântica & INPE, São Paulo. **Fundação SOS Mata Atlântica/INPE**. 2018.

SPORN, S.G.; BOS, M.M.; KESSLER, M.; GRADSTEIN, S.R. Vertical distribution of epiphytic bryophytes in an Indonesian rainforest. **Biodiversity and Conservation**, v. 19, p. 745-760. 2010.

TABARELLI, M.; AGUIAR, A.V.; RIBEIRO, M.C. et al. Prospects for biodiversity conservation in the Atlantic Forest: Lessons from aging human-modified landscapes. **Biological Conservation**, v. 143, p. 2328–2340. 2010.

TAO, Y.; ZHANG, Y. M. Effects of leaf hair points of a desert moss on water retention and dew formation: Implications for desiccation tolerance. **Journal of Plant Research**, v. 125, p. 351-360. 2012.

TAVARES-MARTINS, A.C.C.; LISBOA, R.C.L.; COSTA, D.P. 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**, v.28, p. 46-58. 2014.

TILMAN, D. Functional Diversity. **Encyclopedia of biodiversity**, v. 3, p. 109-120. 2001.
VIOLLE, C.; LECOEUR, J.; NAVAS, M.L. How relevant are instantaneous measurements for assessing resource depletion under plant cover? A test on light and soil water availability in 18 herbaceous communities. **Functional Ecology**, v. 21, p. 185-190. 2007.

WALTHER, G.R.; POST, E.; CONVEY, P. et al. Ecological responses to recent climate change. **Nature**, v. 416, p. 389-395. 2002.

WERNER, F.A.; HOMEIER, J.; OESKER, M.; BOY, J. Epiphytic biomass of a tropical montane forest varies with topography. **Journal of Tropical Ecology**, v. 28, p. 23-31. 2012.

WILLI, Y.; VAN BUSKIRK, J.; SCHMID, B. et al. Genetic isolation of fragmented populations is exacerbated by drift and selection. **Journal of Evolutionary Biology**, v. 20, p. 534-542. 2007.

YOUNG, A.; BOYLE, T.; BROWN, T. The population genetic consequences of habitat fragmentation for plants. **Trends in Ecology & Evolution**, v. 11, p. 413-418. 1996.

ZARTMAN, C.E. Habitat fragmentation impacts on epiphyllous bryophyte communities in central Amazonia. **Ecology**, v. 84, p. 948-954. 2003.

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

ZARTMAN, C.E.; SHAW, A.J. Metapopulation extinction thresholds in rain forest remnants. **The American Naturalist**, v. 167, p. 177-189. 2006.

ZAÚ, A.S. Fragmentação da Mata Atlâtica: Aspectos teóricos. **Floresta e Ambiente**, v. 5, p. 160-170. 1998.

ANEXO A – NORMAS DO PERIÓDICO *PLANT ECOLOGY & DIVERSITY*

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