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WANESSA VIEIRA SILVA MENEZES BATISTA

ASSEMBLEIAS DE BRIÓFITAS EM UM CENÁRIO DE PERTURBAÇÕES ANTRÓPICAS NOS BREJOS DE ALTITUDE

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Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de doutora em Biologia Vegetal. Área de Concentração: Ecologia e Conservação

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Se não puder voar, corra. Se não puder correr, ande. Se não puder andar, rasteje, mas continue em frente de qualquer jeito.

Martin Luther King Jr

À minha filha Maria Heloísa e ao meu esposo Henrique

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RESUMO

Os Brejos de Altitude são enclaves de florestas úmidas localizadas em montanhas circundadas por florestas sazonalmente secas de Caatinga. Atuam como refúgio ecológico e abrigam alta diversidade de briófitas. Entretanto, esses ecossistemas têm sido alvos de perturbações antrópicas (PA), onde vários tiveram sua cobertura florestal suprimida ou fragmentada. Para entender as consequências das PA nestas florestas nós avaliamos o grupo das briófitas, por sua importância biológica e seu caráter bioindicador. O objetivo principal desta tese foi investigar os efeitos das PA crônicas e agudas, bem como a influência de condições ambientais de umidade e luminosidade sobre as assembleias de briófitas dos Brejos de Altitude num contexto espaço-temporal. O capítulo 1 investigou mudanças temporais (i.e. dois censos em três localidades) na estrutura taxonômica e funcional da brioflora e a influência de indicadores de PA agudas e crônicas e da cobertura da vegetação. No capítulo 2 nós estudamos o efeito de PA e de fatores ambientais em duas escalas espaciais (local e regional) sobre a composição e diversidade taxonômica e funcional das briófitas epífitas de quatro localidades. Em escala temporal, num cenário de aumento da cobertura florestal aliado ao aumento de PA, a riqueza de espécies aumentou. Contudo, houve perda de diversidade funcional, especialmente relacionada à maior proporção de espécies de hábitos generalistas e à perda das exigentes de umidade e sombra. Por outro lado, o aumento da cobertura florestal aliado a menores níveis de PA resultou em aumento da riqueza de espécies, da diversidade funcional e da proporção de espécies exigentes. Em escala espacial, a composição taxonômica e funcional das assembleias de briófitas epífitas é distinta entre os Brejos de Altitude. Sua montagem é influenciada de forma preponderante pelas condições ambientais. Locais elevados e com maiores aberturas da copa selecionam espécies com estratégias funcionais tolerantes à exposição solar (e.g. especialistas de sol, pigmentação escura) e à desidratação (e.g. lóbulos grandes para acúmulo de água). Nossos resultados indicam que minimizar as formas de PA (especialmente crônicas) que afetam a estrutura e complexidade florestal, também manter a integridade das condições ambientais locais torna-se fundamental para manutenção da diversidade taxonômica e funcional da brioflora dos Brejos de Altitude. Por fim, ao final da tese apresentamos um material didático para popularização científica, para que as informações da tese tornem-se acessíveis para população em geral.

Palavras-chave: Distúrbios antrópicos; Hepáticas; Musgos; Traços funcionais; Floresta tropical úmida.

ABSTRACT

"Brejos de Altitude" are of humid forest enclaves located in mountains originally surrounded by seasonally dry Caatinga forests. They act as ecological refuges and harbor a high diversity of bryophytes. However, these ecosystems have been the target of anthropic disturbances (AD) and many have been fragmented or erased from the map. We evaluated the bryophytes, due to their biological importance and bioindicator potential, to understand the consequences of AD in these forests. The main objective of this thesis was to investigate the effects of AD and the influence of environmental conditions of humidity and luminosity on the bryophyte assemblages of "Brejos de Altitude" in a spatio-temporal context. In Chapter 1, temporal changes (two surveys in three areas) in the taxonomic and functional structure of the bryophyte flora and the influence of acute and chronic AD indicators and vegetation cover were investigated. In Chapter 2, we studied the effect of AD and environmental factors at two spatial scales (local and regional) on the composition and taxonomic and functional diversity of epiphytic bryophytes from four areas. On a temporal scale, in a scenario of increased forest cover combined with increased AD, species richness increased, but there was a loss of functional diversity, especially related to the greater proportion of generalist species regarding tolerance to light incidence and loss of moisture- and shade-demanding species. On the other hand, the increase in forest cover combined with lower levels of AD resulted in an increase in species richness, functional diversity and proportion of demanding species. On a spatial scale, the taxonomic and functional composition of epiphytic bryophyte assemblages differed among the studied "Brejos de Altitude". The assemblage was largely influenced by environmental factors. Elevated sites with greater canopy opening selected species with functional strategies tolerant to sun exposure (e.g. sun specialists, dark pigmentation) and dehydration (e.g. large lobes for water accumulation). Our results indicate that minimizing the forms of AD that affect the structure and complexity of the forest is fundamental for increasing the taxonomic and functional diversity of the bryophyte flora of "Brejos de Altitude".

Keywords: Anthropic disturbances; liverworts; mosses; Functional traits; Wet tropical forest.

SUMÁRIO

1 INTRODUÇÃO

As perturbações antrópicas (PA) têm descaracterizado florestas em escala global, modificando processos naturais ou mesmo simplificando a complexidade do ambiente e, por consequência, têm ocasionado a reorganização das comunidades biológicas e ecossistemas (WESTERN, 2001). As PA podem ser agudas, como o desmatamento florestal, que muda drasticamente a comunidade, ou crônicas (SINGH, 1998). Estas, ocorrem em pequenas escalas e de forma contínua e incluem a exploração de recursos naturais para subsistência familiar (e.g. coleta seletiva de plantas). Ambos os tipos são nocivos às assembleias de plantas e ainda podem atuar de forma sinérgica, intensificando os efeitos deletérios (RITO et al., 2017). A riqueza de espécies, a composição florística e os níveis de diversidade taxonômica, funcional e filogenética são parâmetros afetados por fatores antrópicos, sobretudo de forma negativa, o que compromete a manutenção da biodiversidade, dos serviços ecossistêmicos e da história evolutiva das assembleias de plantas (SANTOS et al., 2010; SOUZA; SILVA; PÔRTO, 2020). Além disso, os efeitos das PA sobre as assembleias podem ser mediados (mini ou maximizados) a depender das condições climáticas/ambientais que atuam concomitantemente (LAURANCE; WILLIAMSON, 2001; RITO, et al., 2017). Portanto, considerar as perturbações agudas e crônicas além da heterogeneidade do ambiente auxilia em interpretações integrais quanto ao efeito de perturbações antrópicas sobre a montagem de comunidades.

Compreender as consequências das PA em florestas de refúgio ecológico torna-se ainda mais urgente para conservação de ambientes únicos globalmente, evitando-se, assim, danos irreversíveis à biodiversidade. Refúgios são florestas úmidas isoladas, originadas após as flutuações climáticas durante o Pleistoceno, onde o aumento do período seco gerou a fragmentação das florestas úmidas resultando em manchas chamadas de refúgios (HAFFER, 1982). Como exemplo de caso, os Brejos de Altitude são resquícios de florestas úmidas localizadas em montanhas originalmente circundadas por florestas sazonalmente secas de Caatinga, que representam um antigo elo entre as florestas Amazônica e Atlântica (LEDO; COLLI, 2017). Contudo, o histórico de PA sobre os Brejos de Altitude suprimiu totalmente alguns destes, restando apenas cerca de 14% (2.626,68 km^2) da cobertura original, considerando todos os Brejos de Altitude (TABARELLI; SANTOS, 2004; LEAL et al., 2005). As principais ameaças agudas são o uso do solo para expansão de atividades agrícolas e a urbanização; entre as crônicas, destaca-se a exploração de recursos vegetais e hídricos (SILVA; LINHARES; CAMPOS, 2011; SEMAS, 2014; GUIMARÃES, 2017; PEREIRA et al., 2019). Em meio a este cenário, cabe ressaltar que os Brejos de Altitude prestam serviços ecossistêmicos chaves para a região semiárida. Essas florestas diferem de suas matrizes principalmente pelas condições amenas de temperatura e maior disponibilidade hídrica, com maiores índices de pluviosidade, chuvas orográficas e presença de nascentes e córregos (ANDRADE-LIMA, 1960; TABARELLI; SANTOS, 2004). Além disso, abrigam táxons endêmicos, raros e de situação vulnerável à extinção da fauna e de diferentes linhagens de plantas vasculares e avasculares (PÔRTO; GERMANO; BORGES, 2004; RODAL; SALES, 2008; SILVA; LINHARES; CAMPOS, 2011). Logo, a conservação destes ambientes implica na sobrevivência de muitas espécies.

A diversidade de briófitas no Nordeste do Brasil é, em parte, mantida pela existência dos Brejos de Altitude apresentando cerca de 30% da flora de briófitas do Brasil. (PÔRTO, 1990; ARAÚJO et al., 2021; BATISTA; PÔRTO; SANTOS, 2021). No entanto, apesar do vasto conhecimento florístico, poucos estudos recentes têm buscado compreender as influências das condições ambientais e dos fatores antrópicos nestes ambientes (ARAÚJO et al., 2021; BATISTA; PÔRTO; SANTOS, 2021). Trabalhos dessa natureza são imprescindíveis para conhecer o *status* de conservação das assembleias de plantas e subsidiar medidas de conservação nestas florestas. É reconhecido que em florestas tropicais as assembleias de briófitas são principalmente moldadas por determinismo ambiental, *i.e.* fatores abióticos (FRAHM; GRADSTEIN, 1991; SANTOS et al., 2014; BATISTA et al., 2021). Ademais, alterações nas condições ambientais (menor umidade e maior luminosidade) geradas por PA agudas (perda de habitat e fragmentação) têm efeito negativo sobre a riqueza, diversidade de espécies e mudanças na composição florística (PÓCS, 1997; ACEBEY; GRADSTEIN; KROMER, 2003; ALVARENGA; PÔRTO, 2007). Quanto ao efeito de perturbações crônicas relacionadas com a exploração de recursos (e.g. através do *proxy* proximidade de núcleos de atividade humana) pouco é abordado, mas estudos também apontam efeitos deletérios sobre as assembleias (PEÑALOZA-BOJACÁ et al., 2018; BATISTA, 2018). Cabe ainda ressaltar que as condições ambientais (e.g. umidade e luminosidade) e diferentes fatores antrópicos podem interagir e gerar diferentes cenários que podem maximizar (e.g. perturbação e maior luminosidade) ou minimizar (e.g. perturbação e maior umidade) os efeitos negativos das PA sobre as briófitas (BATISTA, 2018; ARAÚJO et al., 2021).

Neste sentido, nós realizamos investigações quanto ao efeito de PA (agudas e crônicas) e as interações com as condições ambientais sobre as assembleias de briófitas em escala temporal e espacial nos Brejos de Altitude, abordando temas fundamentais da briologia contemporânea (PATIÑO et al., 2022). Buscamos compreender os fatores que regem as assembleias de briófitas nesses ambientes singulares e historicamente submetidos às PA. Os resultados possibilitaram conhecer como a qualidade ambiental das florestas variou nas últimas décadas e as mudanças nas assembleias de briófitas frente aos cenários de PA vigentes. Por conseguinte, os achados poderão ser utilizados para subsidiar medidas de conservação e restauração nos Brejos de Altitude e recuperação de sua biota. Devido a ampliação do conhecimento quanto a flora de briófitas, suas estratégias funcionais e suas relações com as condições ambientais nestas florestas tropicais. Assim esta Tese está dividida em dois capítulos: o primeiro investigou mudanças temporais (e.g. dois censos em três localidades) na estrutura taxonômica e funcional da brioflora e a relação com indicadores de PA e a cobertura da vegetação. No capítulo 2 foram estudadas a influência das PA e dos fatores ambientais em escala local e regional sobre a composição e diversidade taxonômica e funcional das briófitas epífitas de quatro localidades. Ao final da tese, apresentamos um material didático para popularização do conhecimento científico a ser divulgado gratuitamente. Trata-se de uma cartilha que apresenta uma história para colorir abordando conteúdos da Tese. O cenário da história é uma aula de campo em um Brejo de Altitude, para conhecer na prática a flora de briófitas e suas relações com o ambiente, além de enfatizar a importância de conservar essas florestas.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 PERTURBAÇÕES ANTRÓPICAS ATUAM NA MONTAGEM DE COMUNIDADES DE PLANTAS

Regras de montagem são conceituadas como qualquer processo ecológico que atua a favor ou contra a distribuição espacial das espécies do grupo regional, e assim, determinam a composição da comunidade local (GÖTZENBERGER et al., 2012). Esses processos podem estar associados a regras dependentes de dispersão, *i.e.*, as espécies são igualmente expostas a fatores estocásticos e a distribuição destas é correlacionada com sua capacidade de dispersão (HUBBELL, 2001; WEIHER; KEDDY, 2004). Ainda, processos baseados em nicho ecológico, *i.e.* condições abióticas e interações bióticas, podem atuar como "filtros" para a estruturação das comunidades (KEDDY, 1992; WEIHER; KEDDY, 2004). Além disso, as perturbações antrópicas têm alterado processos ecológicos, provocando mudanças nas condições ambientais, na disponibilidade de recursos e nas interações entre os organismos; por conseguinte, atuando na reorganização das comunidades (WESTERN, 2001).

Em geral, os efeitos das PA sobre as assembleias de plantas são negativos, resultando no aumento do número de espécies dominantes (que resistem ao estresse proveniente das PA), aliado à perda de espécies raras e vulneráveis, o que empobrece a diversidade, seja taxonômica, funcional ou filogenética (RIBEIRO et al., 2016; SFAIR et al., 2018). Desse modo, as PA promovem a homogeneização biótica, o que compromete a manutenção da biodiversidade, os serviços ecossistêmicos e a história evolutiva das comunidades (MCKINNEY; LOCKWOOD, 1999; WEBB, 2000; LÔBO et al., 2011). Ainda, a depender do tipo de PA, os efeitos sobre as comunidades podem ser mais abruptos e em um curto espaço de tempo ou graduais. As PA agudas, como o desmatamento e a fragmentação do habitat, são caracterizadas pela retirada de grandes porções de biomassa de forma abrupta, descaracterizando o habitat em um curto espaço de tempo. Sabe-se que estas perturbações têm gerado principalmente efeitos negativos na estrutura das assembleias de plantas vasculares e avasculares (LAURANCE et al., 1997; ALVARENGA; PÔRTO, 2007). Por outro lado, as PA crônicas, como a exploração de recursos naturais madeireiros e não-madeireiros, acometem as comunidades de forma gradual e contínua (SINGH, 1998). Para as plantas lenhosas, as PA crônicas geram efeitos negativos, positivos ou neutros para a diversidade de espécies (MARTORELL; PETERS, 2005; RITO et al., 2017). Contudo, para as briófitas, os poucos estudos realizados apontam apenas efeitos negativos (PEÑALOZA-BOJACÁ et al., 2018; BATISTA, 2018). Além disso, as PA agudas e crônicas podem atuar de forma sinérgica, intensificando os efeitos acometidos às assembleias de plantas (TABARELLI; SILVA; GASCON, 2004). Ademais, sabe-se que as condições ambientais (e.g.

precipitação) podem interferir neste processo, minimizando ou maximizando os efeitos das PA (LAURANCE; WILLIAMSON, 2001; RITO et al., 2017). Por exemplo, em regiões semiáridas acometidas por perturbações crônicas, uma maior disponibilidade hídrica pode minimizar os efeitos negativos das PA sobre a diversidade de espécies de plantas vasculares (RITO et al., 2017).

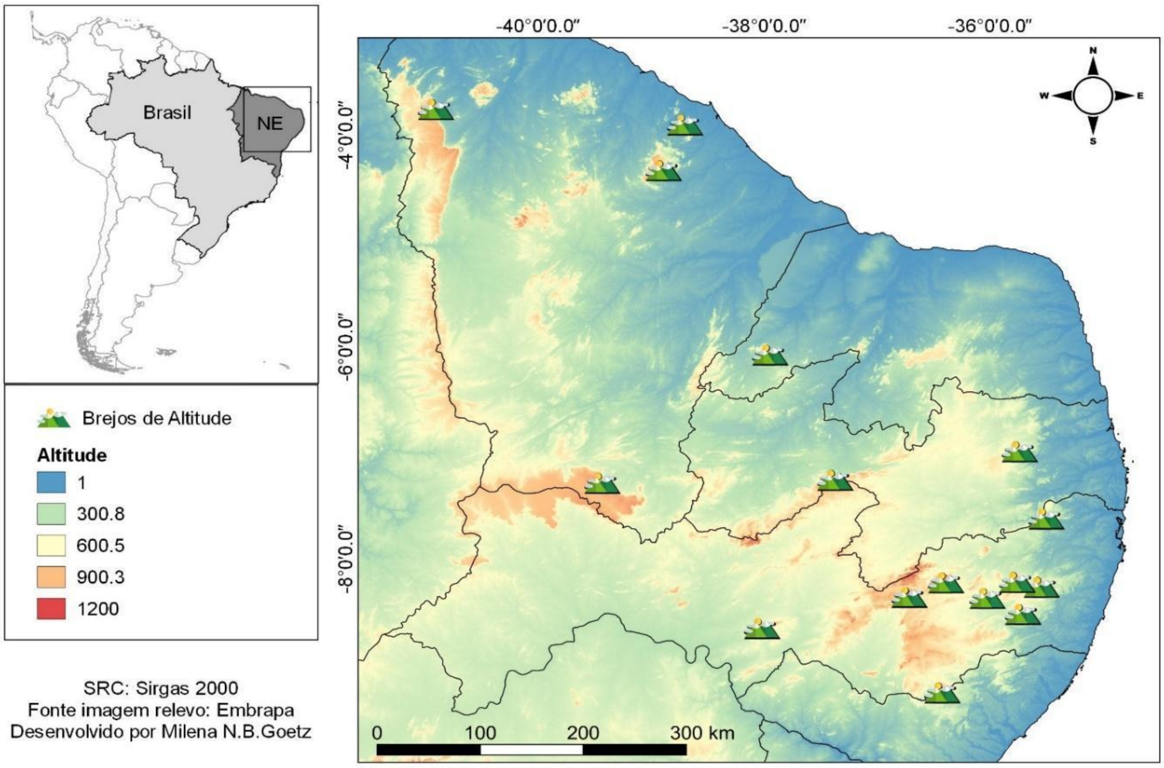
Para compreender como as PA atuam sobre as comunidades biológicas vários parâmetros de comunidade podem ser utilizados, como composição, riqueza e diversidade de espécies. Estas são medidas tradicionais na Ecologia, sendo a riqueza a métrica mais antiga, simples e difundida para comunidades (KREBS, 1999). Tais parâmetros tradicionais, baseados apenas em informações taxonômicas, apesar de extremamente importantes, são limitados quanto ao entendimento da montagem de comunidades, pois não consideram as diferenças funcionais das espécies. Assim, integralizar as informações sobre as funções ecológicas que as espécies desempenham na comunidade às suas exigências ambientais, permite entender os padrões de organização das comunidades de forma mais robusta (GITAY; NOBLE, 1997; PURSCHKE et al., 2013). Além disso, os efeitos de PA podem não ser perceptíveis a depender do parâmetro analisado. Por exemplo, a riqueza de espécies em ambientes perturbados e conservados pode não apresentar diferenças, mas ao analisar os níveis de diversidade taxonômica e funcional pode-se verificar que os efeitos de PA estão além da perda de diversidade de espécies (SANTOS et al., 2010; PURSCHKE et al., 2013). Acessar a estrutura filogenética e funcional das comunidades, além da estrutura taxonômica, é importante para subsidiar planos de conservação, como, por exemplo, definir áreas prioritárias para conservação (SILVA; PÔRTO, 2015).

É válido ressaltar que as PA podem atuar diretamente ou indiretamente na montagem de comunidades, e que seus efeitos deletérios sobre a diversidade funcional implicam diretamente no funcionamento dos ecossistemas (SFAIR et al., 2018; SOUZA; SILVA; PÔRTO, 2020). Alguns estudos, em diferentes cenários de PA, retratam efeitos negativos na estrutura funcional de assembleias de briófitas, plantas sensíveis às alterações ambientais, provocadas por pressão antrópica (COSTA, 1999; SIERRA et al., 2019). De forma geral, a perda de diversidade funcional e de grupos funcionais específicos reflete no desequilíbrio de funções essenciais do ecossistema, como regulação hídrica, ciclagem de nutrientes e disponibilidade de microhabitats (STANTON; COE, 2021), o que acaba gerando comunidades funcionalmente similares. Alvarenga e Pôrto (2007) verificaram que a fragmentação do habitat na Floresta Atlântica afeta negativamente as assembleias de briófitas, em especial com perda de espécies com exigências ecológicas de umidade e sombra (e.g. espécies epífilas e especialistas de sombra). Também na Floresta Atlântica, Souza; Silva; Pôrto (2020) constataram uma mudança na composição funcional de briófitas em direção à borda do fragmento, predominando espécies tolerantes quanto às condições de maior luminosidade e menor umidade (e.g. com pigmentação escura e lóbulos). Na Amazônia, Sierra et al. (2019), em uma paisagem experimental de fragmentação, verificaram mudanças na flora de briófitas epifilas em um intervalo de 15 anos, onde persistiram espécies com maiores capacidades de dispersão (e.g. monoicia e esporos pequenos) e com tolerância fisiológica à dessecação (e.g. pigmentação escura e papilas) especialmente para fragmentos menores.

Em contrapartida, no caso de florestas conservadas, ou ambientes sob menor pressão antrópica, como o interior da floresta, onde há uma maior disponibilidade de nichos, é esperada uma maior diversidade funcional de briófitas (BOUDREAULT et al., 2018; SOUZA; SILVA; PÔRTO, 2020). Comunidades com espécies funcionalmente distintas podem ser resultantes do processo de competição, pois espécies similares competem por nicho e, consequentemente, ocorre exclusão competitiva (KRAFT; VALENCIA; ACKERLY, 2008; PAINE et al., 2011). No entanto, isto é menos provável para briófitas (SLACK, 1990), visto que interações de facilitação dependentes de densidade são, de forma geral, benéficas para a manutenção das espécies (DURING; LLORET, 2001). Por exemplo, o crescimento agregado de indivíduos, ou mesmo de várias espécies de briófitas em uma mancha, pode favorecer a captação de água e nutrientes, e minimizar a dessecação pelo autossombreamento (BATES, 1998). Interação ainda mais necessária quando as condições ambientais são mais restritivas, e.g. redução de umidade e sombra, (GIMINGHAM; BIRSE, 1957), como as que ocorrem em florestas sob pressão antrópica. Também, um cenário de floresta densa ou interior de floresta, onde a umidade e sombra não são fatores limitantes, pode favorecer a diversidade taxonômica e funcional devido às exigências fisiológicas das briófitas, sobretudo por umidade. Entretanto, nestes ambientes, a baixa luminosidade torna-se um fator que restringe as espécies típicas de ambientes ensolarados (TAKASHIMA-OLIVEIRA; MEDEIROS; TAVARES-MARTINS, 2020). Assim, a filtragem ambiental constitui o processo predominante para entender as regras de montagem das assembleias de briófitas (OLIVEIRA; ter STEEGE, 2015). Ainda, sabendo que as PA podem alterar condições ambientais e, assim, impor uma filtragem de espécies ainda mais seletiva, faz-se necessário considerar seus efeitos para entender as regras de montagem de comunidades, em especial para assembleias briófitas.

2.2 BREJOS DE ALTITUDE: ORIGEM, CLIMA E PERTURBAÇÕES ANTRÓPICAS

Enclaves de florestas úmidas localizados em montanhas inseridos no Domínio de Caatinga (Nordeste do Brasil), localmente chamados de Brejos de Altitude (Figura 1). Abrigam plantas vasculares e avasculares de distribuição disjunta com as formações florestais Amazônica e Atlântica (ANDRADE-LIMA, 1960; PÔRTO; GERMANO; BORGES, 2004; RODAL; SALES, 2008; SILVA, 2013; LOIOLA et al., 2015). Este padrão disjunto tem sido atribuído a antigas conexões entre estas formações, *i.e.* vicariância climática, sobretudo para fanerógamas (LEDO; COLLI, 2017). Registros palinológicos suportam que conexões entre a Amazônia e a Floresta Atlântica aconteceram em diversos momentos durante o Quaternário, em regiões atualmente semiáridas (BEHLING et al., 2000; AULER, 2004; LEDRU; MOURGUIART; RICCOMINI, 2009). Os Brejos de Altitude seriam, então, resquícios deste elo, resultantes de processos históricos que fragmentaram as florestas Amazônica e Atlântica, atuando hoje como refúgios para a fauna e flora (AULER, 2004; SIQUEIRA-FILHO; MACHADO, 2004; LINHARES; SILVA, 2015).



SRC: Sirgas 2000
Fonte imagem relevo: Embrapa
Desenvolvido por Milena N.B.Goetz

Fonte: A autora (2022)

Figura 1. Mapa com a distribuição dos principais Brejos de Altitude localizados na região Nordeste do Brasil.

Os Brejos de Altitude caracterizam-se por serem florestas localizadas acima de 500m de altitude, associadas a Planaltos ou Chapadas, podendo chegar a aproximadamente 1.100m de altitude (ANDRADE-LIMA, 1960). As florestas são compostas por fitofisionomia submontana ou montana do tipo Estacional ou Ombrófila, ou ainda Áreas de Tensão Ecológica (SANTOS; TABARELLI, 2004). As matrizes naturais dos Brejos são compostas principalmente por florestas secas de Caatinga, mas podem apresentar-se inseridas em um mosaico de vegetações entre Caatinga e Cerrado (ANDRADE-LIMA, 1982; LINS, 1989), embora sejam atualmente constituídas também por urbanização, plantações e pastagens (GUIMARÃES, 2017). Em geral, os Brejos de Altitude se diferem de suas matrizes principalmente pelas condições amenas de temperatura e a maior disponibilidade hídrica. Eles apresentam maiores índices de pluviosidade, devido ao efeito de chuvas orográficas (Veja Figura 2), presença de nascentes e córregos d’água e ocorrência de neblina (ANDRADE-LIMA, 1982; SALES et al., 1999; CABRAL et al., 2004). Apesar das florestas úmidas de Brejos de Altitude serem perenes ao longo do ano, apresentam marcada sazonalidade de precipitação, sendo estes ambientes caracterizados por duas estações, a seca e a chuvosa, apresentando precipitação média anual entre 600mm e 1.200mm (CABRAL et al., 2004). A distinção climática entre Brejo de Altitude e Caatinga atua como uma barreira para espécies exigentes às condições ambientais. Sabe-se que, para plantas vasculares e avasculares, a distribuição das espécies nestes ambientes é explicada por processos baseados em nicho (LIMA; MANSANO; ARAÚJO, 2012; MONTADE et al., 2016; ARAÚJO et al., 2021; BATISTA; PÔRTO; SANTOS, 2021). Ou seja, afinidades florísticas estão relacionadas com as afinidades climáticas entre as vegetações.

Fonte: Adaptado de Araújo et al. (2021)

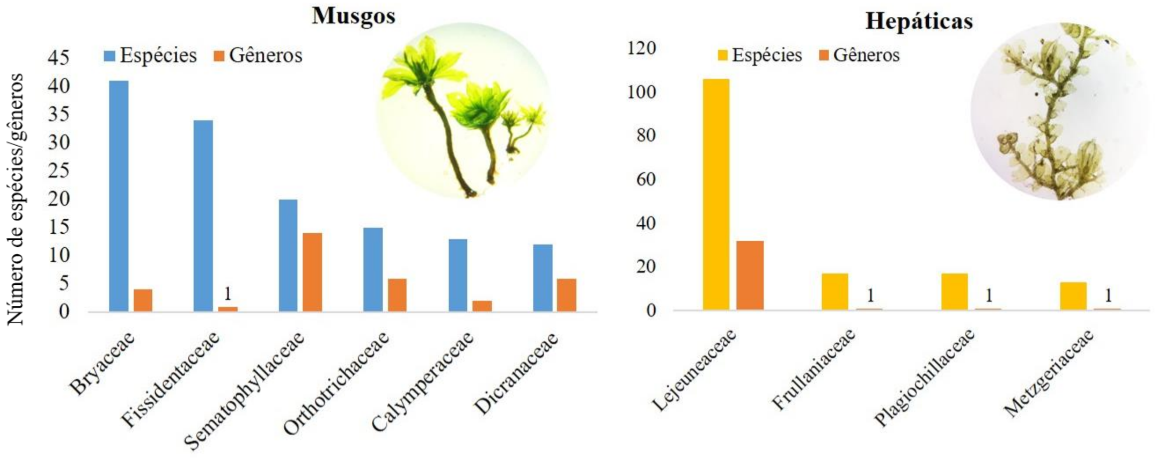
Figura 2. Esquema do perfil estrutural dos Brejos de Altitude, com valores médios de precipitação ilustrativos para cada tipo de vegetação.

Historicamente, os Brejos de Altitude têm sido alvo de perturbações antrópicas agudas e crônicas, onde alguns já foram totalmente dizimados (SANTOS; TABARELLI, 2004). Estima-se que a área original dos Brejos era de 18.589 km^2, distribuídos entre os estados de Alagoas, Ceará, Rio Grande do Norte, Bahia, sendo mais representados na Paraíba e Pernambuco. Entretanto, os remanescentes perfazem um pouco mais de 14% (2.626,68 km), representando um subconjunto de Floresta Atlântica mais ameaçado (TABARELLI; SANTOS, 2004). Conforme Vasconcelos (1971), os estados da Paraíba (oito) e Pernambuco (23) possuem a maior quantidade de Brejos. Entretanto, a maioria encontra-se descaracterizado ambientalmente devido à alta perturbação antrópica (SALES; MAYO; RODAL, 1998). A conservação destes ambientes implica diretamente na manutenção da biodiversidade, pois eles abrigam diferentes linhagens de plantas vasculares e avasculares, com táxons endêmicos, raros e/ou de situação vulnerável à extinção (PÔRTO; GERMANO; BORGES, 2004; RODAL; SALES, 2008). Além disso, sua conservação também implica na manutenção do clima local e na disponibilidade de recursos hídricos para a região. Além destes ambientes atuarem como florestas de “refúgio” para plantas e animais, devido à sua extrema importância hídrica na região semiárida, também representam um refúgio para as populações humanas. Em geral, as cidades se desenvolvem em torno dos Brejos de Altitude, devido à disponibilidade de recursos que estes promovem para as populações humanas do semiárido (e.g. água para consumo e irrigação de plantações), principalmente como fonte de renda (LINS, 1989). Há décadas o desmatamento nos Brejos de Altitude é provocado principalmente pelo uso da terra para práticas agrícolas de subsistência familiar/econômica e pecuária, desenvolvimento de centros urbanos, entre outros (LINS,1989; MONTEIRO; SAWYER, 1999; SANTOS; TABARELLI, 2004; SILVA; LINHARES; CAMPOS, 2011). Além disso, a extração seletiva de plantas (*e.g.,* madeireiras e ornamentais) e a caça comprometem a estrutura da floresta e os recursos naturais (SILVA; TABARELLI, 2000). Apesar do reconhecimento do cenário crítico dos Brejos de Altitude há mais de quinze anos (SANTOS; TABARELLI, 2004), e do entendimento sobre os efeitos da perturbação antrópica sobre a biodiversidade, infelizmente a pressão antrópica ainda persiste, mesmo estando seus remanescentes regidos sob ações de conservação, das florestas naturais e pelos planos de manejo das espécies ameaçadas (SILVA; TABARELLI, 2000; SILVA; LINHARES; CAMPOS, 2011). Contudo, cabe ainda verificar o *status* atual de conservação dos Brejos de Altitude e os efeitos que as perturbações antrópicas têm causado nas assembleias, em particular de plantas.

2.3 BRIÓFITAS

2.3.1 Diversidade e distribuição nos Brejos de Altitude

As briófitas constituem um grupo monofilético (SU et al., 2021; HARRIS et al., 2020) de plantas criptógamas avasculares, basal dentre as Embryophyta (plantas terrestres), que incluem três filos: Anthocerotophyta (antóceros), Bryophyta (musgos) e Marchantiophyta (hepáticas). As briófitas contribuem significativamente para a biodiversidade do planeta, sendo o segundo maior grupo de plantas terrestres, com ca. 15.000 espécies (GRADSTEIN et al., 2001). Nas florestas tropicais úmidas apresentam uma elevada diversidade, devido à complexidade estrutural destas florestas, que possuem uma variedade de microhabitats, sendo estimada a ocorrência de 3.000-4.000 espécies (PÓCS, 1982; GRADSTEIN, 1995; FRAHM, 2001). Para o Brasil são registradas aproximadamente 1.610 espécies (distribuídas em 117 famílias), entre musgos (895 espécies/73 famílias), hepáticas (694/40) e antóceros (18/4) (BRAZIL FLORA GROUP, 2021). No país, as florestas tropicais úmidas apresentam a maior diversidade de briófitas, sendo registradas, para o domínio fitogeográfico da Floresta Atlântica, 1.337 spp., e para o domínio Amazônico, 590 spp. (BRAZIL FLORA GROUP, 2021). Os Brejos de Altitude possuem aproximadamente 518 spp. e cerca de 51 famílias (PÔRTO, 1990; PÔRTO; GERMANO, 2001; PÔRTO; GERMANO; BORGES, 2004; YANO; PÔRTO, 2006; OLIVEIRA, 2008; SILVA; PÔRTO, 2015; GERMANO; SILVA; PERALTA, 2016; BATISTA; PÔRTO; SANTOS, 2021; ARAÚJO et al., 2021). Assim, a riqueza de briófitas nos Brejos de Altitude representa cerca de 32% da diversidade de briófitas do Brasil. Entre as dez famílias mais representativas nos Brejos de Altitude, Lejeuneaceae apresenta a maior riqueza específica e genérica para as hepáticas e, com relação aos musgos, a família Bryaceae possui maior riqueza específica e Sematophyllaceae a genérica (Figura 3).



Fonte: A autora (2022)

Figura 3. Famílias mais diversas de musgos e hepáticas nos Brejos de Altitudes do Nordeste do Brasil.

Além da imensa importância da riqueza de espécies de briófitas presentes nos Brejos de Altitude, alguns táxons apresentam distribuição rara e de situação vulnerável quanto ao seu grau de ameaça de extinção (PÔRTO; GERMANO; BORGES, 2004). Até o presente, 16 Brejos, localizados nos estados de Alagoas (1), Ceará (4), Paraíba (2) e Pernambuco (9), apresentam levantamentos de briófitas. Entretanto, apenas 50% destas áreas apresentam inventários sistemáticos (PÔRTO; GERMANO; BORGES, 2004; SILVA; PÔRTO, 2015; ARAÚJO et al., 2021). O conhecimento florístico dos demais Brejos é limitado a coletas esporádicas e/ou levantamentos florísticos (PÔRTO; GERMANO; BORGES, 2004). Os poucos estudos que abordam a ecologia e os fatores moduladores das assembleias de briófitas nestas florestas de refúgio ecológico demonstram consenso quanto à influência de processos determinísticos sobre as briófitas (SILVA; PÔRTO, 2015; GERMANO; SILVA; PERALTA, 2016; BATISTA; PÔRTO; SANTOS, 2021; ARAÚJO et al., 2021). Informações quanto aos efeitos antrópicos sobre estas plantas nos Brejos de Altitude são ainda mais escassas (ARAÚJO et al., 2021). Araújo et al. (2021) analisaram três Brejos de Altitude, demonstraram que cada área apresenta uma brioflora única e que a conservação destes ambientes implica diretamente na conservação da diversidade de espécies. Ainda, que a altitude é um fator relevante para riqueza e diversidade de espécies em escala regional, enquanto o efeito de borda atua como um fator secundário em escala local.

2.3.2. Ecologia de briófitas

As briófitas são plantas poiquiloídricas, ou seja, seu balanço hídrico é regulado conforme a umidade do ambiente (PROCTOR, 2000; PROCTOR; TUBA, 2002). Por isso, são extremamente dependentes das condições ambientais para sua sobrevivência e a reprodução. Devido à íntima relação destas plantas com o ambiente, atuam como organismos indicadores de condições ambientais (VANDERPOORTEN; GOFFINET, 2009). Diferentes estratégias ecológicas e reprodutivas são adotadas pelas briófitas de forma a garantir seu estabelecimento e permanência no ambiente. Essas estratégias podem ser detectadas através de traços (características ou atributos) ou grupos funcionais (Tabela 1). Os traços funcionais podem ser características morfológicas, fisiológicas ou fenológicas que representem alguma funcionalidade para a espécie e/ou para o ambiente (CIANCIARUSO; SILVA; BATALHA, 2009; DÍAZ et al., 2007). Quanto aos grupos funcionais, estes são conjuntos de organismos que apresentam determinados traços como resposta a fatores externos e/ou traços que possuam efeitos sobre processos ecossistêmicos (De BELLO et al., 2010).

A forma de vida é um grupo funcional para briófitas, pois representa diferentes estratégias adotadas pelas plantas para evitar a evapotranspiração, maximizar o acúmulo de água e minimizar o estresse luminoso sobre o gametófito (BATES, 1998). Algumas formas de vida (e.g. coxim e tufo) são tolerantes à escassez hídrica, ocorrendo amplamente em ambientes xéricos. Outras são generalistas (tapete e trama), ou mesmo exigentes, por exemplo, às condições de florestas úmidas e sombrias (flabelada, dendróide e pendente). Outro grupo funcional reconhecido para as briófitas são as guildas de tolerância à luz (espécies típicas de sol, sombra ou generalistas), onde as espécies são classificadas conforme sua distribuição em ambientes ombrófilos ou abertos (GRADSTEIN, 1992; COSTA, 1999).

Quanto aos traços funcionais relacionados às condições limitantes de baixa umidade e elevada disponibilidade de luz, típicas de florestas úmidas sob perturbação antrópica, destacam-se aqueles que permitem um maior acúmulo de água no gametófito e/ou que confiram proteção contra o estresse luminoso (Veja Tabela 1). Dentre eles, a literatura aponta os filídios esquarosos e gametófitos enegrecidos, que representam uma proteção contra a intensa insolação e elevada temperatura (SEEL; HENDRY; LEE, 1992; MELICK; SEPPEL, 1994; KÜRSCHNER, 2004). Com relação ao acúmulo de água, destacam-se traços como o tamanho do lóbulo e filídios convolutos (OLIVEIRA, 2018; SOUZA; SILVA; PÔRTO, 2020).

Ainda, outros aspectos funcionais como as estratégias reprodutivas (e.g. sistema sexual) também podem garantir o sucesso da chegada ou permanência da espécie no ambiente (BISANG; HEDENAS, 2005). O tipo de sistema sexual das briófitas pode influenciar a capacidade de reprodução e dispersão da espécie dentro e entre os hábitats (LONGTON; SCHUSTER, 1983). Nas espécies monoicas, a proximidade entre os gametângios lhes garante uma maior frequência de fecundação, ou seja, produção de esporófitos (OLIVEIRA; PÔRTO, 1998). Enquanto as dioicas, que possuem gametângios segregados (plantas femininas e plantas masculinas), têm dificuldades na produção de esporófitos; por conseguinte, tendem a manter suas populações realizando exclusivamente reprodução assexuada, sobretudo quando as condições hídricas são limitantes (LONGTON; MILES, 1982; LONGTON, 1997; GLIME; BISANG 2017). Por exemplo, na Caatinga, onde a água é um recurso limitante, as espécies monoicas predominam sobre as dioicas (SILVA; SILVA; PÔRTO, 2014).

Além disso, devido às estratégias reprodutivas e alta capacidade de dispersão dos esporos, as briófitas estão amplamente distribuídas no mundo, desde as regiões polares, onde são o grupo mais rico de plantas, às áreas temperadas e tropicais, incluindo desertos, ambientes aquáticos, exceto marinho (GLIME, 2007; BIERSMA et al., 2017). Apesar do reconhecimento de tantas estratégias adotadas pelas briófitas, são recentes os estudos que investigam traços funcionais a nível de assembleia e suas relações com fatores abióticos ou antrópicos isoladamente (HENRIQUES; AH-PENG; GABRIEL, 2017; SILVA et al., 2017; OLIVEIRA, 2018; SOUZA; SILVA; PÔRTO, 2020). No entanto, sabendo que a estrutura funcional de assembleias de briófitas pode ser moldada tanto fatores abióticos quanto antrópicos, é preciso ainda investigar a importância integrada destes fatores para entender padrões na estrutura funcional de briófitas em florestas tropicais (PATIÑO et al. 2022).

Tabela 1. Grupos e traços funcionais, relacionados às condições de umidade e luminosidade do ambiente para espécies de briófitas utilizados em estudos ecológicos a nível de comunidade. Traços e grupos funcionais que podem ser avaliados para hepáticas e musgos estão destacados em laranja, apenas para musgos em azul e apenas para hepáticas em amarelo.

Traços e Grupos funcionais	Função	Tipo do traço	Referência
Projeção celular do filídio (papilas)	Otimizar a captação de água	Binário (ausência= 0; presença= 1)	Kürschner (2003, 2004)
Célula hialina, cancelinas	Acumular água da célula e transporte hídrico	Binário (ausência= 0; presença= 1)	Glime (2007)
Células com oleocorpos	Organela com conteúdo químico (terpenóides) que confere resistência a dessecação	Binário (ausência= 0; presença= 1)	Pressel; P’NG; Duckett (2010); Chen et al. (2018).
Filídios convolutos	Filídios se curvam quando secos para minimizar a perda de água	Binário (ausência= 0; presença= 1)	Oliveira (2018).
Pigmentação enegrecida	Proteção quanto à radiação solar	Binário (ausência= 0; presença= 1)	Melick; Seppel (1994); Deltoro; Calatayud;

			Gimeno (1998); Oliveira (2018).
Tamanho da costa do filídio.	Otimizar o transporte de água	Classes (ausente= 0; < 1/2= 1; >1/2= 2; excurrente= 3)	Frahm (1985); Zastrow (1934 apud GLIME, 2007); Henriques et al. (2017).
Presença e tipo de costa	Otimizar o transporte de água	Classes (ausente= 0; simples= 1; dupla= 2)	Frahm (1985); Zastrow (1934 apud GLIME, 2007); Henriques et al. (2017).
Tamanho do lóbulo	Armazenamento de água extracelular	Classes (ausente= 0; < 1/2= 1; >1/2= 2)	Renner; Devos; Brown (2013); Renner (2015); Souza (2019).
Formas de vida	Maximizar o acúmulo de água e diminuir a exposição solar e ao vento	Classes (grau de tolerância à dessecação) (pendente= 1; flabelada=2, dendróide= 3; trama= 4; tapete= 5; tufo= 6; coxim= 7)	Mägdefrau, 1982; Bates (1998).

Fonte: A autora (2022)

3 TEMPORAL CHANGES IN THE TAXONOMIC AND FUNCTIONAL STRUCTURE OF BRYOPHYTE ASSEMBLAGES WARN ABOUT THE CONSERVATION STATUS OF BIOLOGICAL REFUGES IN BRAZIL

Manuscript I: to be submitted to Biodiversity Conservation

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Abstract

Tropical rainforests are subject to changes over time, even at faster rates when under anthropic pressure. Modifications in the forest structure imply microclimatic changes that can affect the maintenance of communities. Understanding anthropogenic impacts on ecological refuge forests is urgent to avoid irreversible damage to biodiversity. In this study, temporal changes (time intervals of nine, ten and more than 30 years) were investigated in the taxonomic and functional structure of assemblages of bryophytes – a dynamic group of plants sensitive to environmental changes – in three ecological refuge forests known as "Brejos de Altitude", in Brazil, and the influence of anthropogenic disturbances and vegetation cover. The parameters of the bryophyte flora (Taxonomic and Functional) analyzed were richness, composition and beta diversity. A total of 247 species, corresponding to 128 liverworts and 119 mosses, were recorded in the three "Brejos de Altitude". Temporal changes in the taxonomic (stress = 0.08) and functional composition were observed. Floristic dissimilarity was explained by species turnover, while functional dissimilarity by nestedness and turnover. In general, the species that persisted in the areas have functional characteristics typical of disturbed environments (generalist and sun specialist species and life forms tolerant to desiccation). The most dynamic species among the censuses were the shade specialists and the life forms vulnerable to desiccation, which were less represented in the latter surveys. Most of the parameters of the bryoflora were not related to the predictor variables. However, the increase in species richness was influenced by the increase in matrix forest cover and changes in the degree of chronic anthropogenic disturbance. In scenarios of loss of environmental quality (slight increase in matrix forest cover associated with increase in anthropogenic disturbances), we found a loss of functional diversity due to the loss of moisture- and shade-demanding species, which were replaced with generalist species regarding light requirements and species with high reproductive capacity (monoicous). In turn, in scenarios of improved environmental quality (increase in forest cover and decrease in chronic disturbances), there was an increase in demanding species, which reflects higher functional diversity. The rapid responses to loss of environmental quality typical of bryophytes were evident in the bryophyte flora of most "Brejos de Altitude" studied. Thus, efforts to increase the vegetation cover (e.g. ecological restoration) and decrease anthropogenic pressures, mainly those of chronic nature, to improve environmental quality will favor the conservation of the diversity of more demanding species.

Keyword: Mosses, liverworts, functional groups, tropical rainforest, vegetation cover, disturbances.

Introduction

Tropical rainforests have historically been the target of intense human activities because of their relevance in essential provisioning and regulating ecosystem services such as water and plant resources and climate regulation (Pyles et al. 2018). In recent years, Ecology has witnessed a strong conceptual change in relation to the transformation of natural ecosystems into anthropic ones (Albuquerque et al. 2018). Thus, it is extremely important to consider the influence of anthropic actions on ecological patterns and processes (Liu 2001). Anthropogenic activities such as land use for agriculture, urbanization and other purposes remove the vegetation cover and drastically mischaracterize the forest environment, directly affecting biological communities (Arroyo-Rodríguez et al. 2020). Chronic disturbances such as selective collection of firewood, fruits and seedlings gradually and continuously affect the ecosystem, directly impacting forest regeneration (Singh et al. 1998; Pyles et al. 2018). These disturbances lead to changes in species composition, with loss of species and functions associated with their role in the environment (Morris 2010; Fletcher et al. 2018; Pereira et al. 2021). Understanding the consequences of anthropogenic disturbances in ecological refuge forests is, thus, urgent to preserve these globally unique environments and avoid irreversible damage to biodiversity.

"Brejos de Altitude" are unique areas of highland tropical rainforests inserted in the Caatinga domain in Northeast Brazil, recognized to act as ecological refuges and considered relicts of the past connection between the Amazon and Atlantic Forest (Santos and Tabarelli

2004). The local human populations established around “Brejos de Altitude” have a history of strong dependence on natural resources (e.g. water, firewood, plant products, agriculture) (Leal et al. 2005; Tabarelli and Santos 2004). The resulting acute and chronic anthropogenic disturbances have affected these environments to the point that some of them have already been completely erased from the map – only about 14% (2,626.68 km^2) of their original coverage exists today (Santos and Tabarelli 2004). However, considerable efforts have been made in recent decades to preserve these environments, including the creation of conservation units (Braga and Pôrto 2004). The direct benefits of these efforts to biodiversity include the protection of endemic and rare taxa and of different vascular and non-vascular plant lineages vulnerable to extinction (Pôrto et al., 2004; Rodal and Sales 2008; Terceiro et al. 2021).

The diversity of bryophytes in “Brejos de Altitude” is recognized to be important for the flora of Northeast Brazil, corresponding to almost 30% of the brazilian flora (Pôrto et al. 2004; Yano and Pôrto 2006; Araújo et al. 2021; Batista et al. 2021). These plants are considered model organisms in ecological studies because they are pioneers and show fine responses to anthropogenic disturbances (Souza et al. 2020). Acute disturbances such as habitat loss and fragmentation have reported in the literature to negatively affect bryophyte assemblages, leading to biotic homogenization (Zartman 2003). The main effects include the loss of shade specialist species and pendant life forms and changes in taxonomic and functional composition (Zartman 2003; Alvarenga and Pôrto 2007; Souza et al. 2020). In experimental fragmented landscapes in the Amazon, for example, Sierra et al. (2019) observed changes in the flora of epiphyllous bryophytes on a 15-year time scale, in which species with greater dispersal capacity (e.g. monoicous sexual system and small spores) and physiological tolerance to desiccation (e.g. dark pigmentation and leaf ornamentation) persisted. In addition, indirect measures of chronic disturbances such as proximity to urbanized areas (i.e. indicator of exploitation of natural resources) have proved to be associated with a change in the composition of species and functional groups, with negative effects on groups with greater requirements for moisture and shade (Batista 2018; Peñaloza-Bojacá et al. 2017).

Anthropogenic pressures often alter the vegetation cover of forest environments and consequently the microclimate of the understory (Gehlhausen et al. 2000; Fahrig 2003). Knowing that anthropogenic disturbances gradually change the vegetation cover over time (Fahrig 2003) and that the poikilohydric nature and short life cycles of bryophytes lead them to respond rapidly to such alterations (During 1979; Proctor and Tuba 2002), we investigated the

the changes in the taxonomic and functional structure of bryophyte assemblages in three "Brejos de Altitude" assessed in two moments (time intervals of nine, ten and more than 30 years) and analyzed their relationship with anthropogenic factors (acute and chronic) and vegetation cover. We hypothesize that the increase in acute and chronic anthropogenic disturbances in "Brejos de Altitude" over the past few years has negatively affected the bryophyte assemblages and that the relative importance of the effects is mediated by vegetation cover. Thus, in the worst scenario, we expect that a high degree of anthropogenic disturbances associated with reduced vegetation cover will lead to losses in floristic and functional richness and composition due to the exclusion of vulnerable species (e.g. moisture- and shade-demanding species) and replacement with generalist species. We emphasize that this study is particularly necessary in the context of unique forest formations such as "Brejos de Altitude" to understand the changes that assemblages undergo under constant climate change and anthropic pressure of today's world.

Methodology

Study area

The study was conducted in three "Brejos de Altitude" in Northeast Brazil (Fig. 1) which have been historically subject to anthropic pressure, mainly deforestation to expand agricultural activities (Benevides et al. 2019). Other chronic factors are the selective exploitation of plants, extraction of wood and clay, and the introduction of invasive alien species that have reconfigured the forest understory (Santos and Tabarelli 2004, SEMAS 2014; Guimarães 2017; Benevides et al. 2019).

Professor João Vasconcelos Sobrinho Municipal Park (A1) – This is a conservation unit created in 1983 in the municipality of Caruaru, state of Pernambuco (PE), with an area of 359 hectares including forests and other land-use types, such as plantations, exposed soil and large lakes. The vegetation is classified as Semideciduous Seasonal Forest (Santos and Tabarelli 2004). The average annual rainfall is 1,141 mm, the average annual temperature is 23.2°C and altitudes range between 800 and 1000 m (Cabral et al. 2004; Karger et al. 2017). In the past, the main threat to the forest was deforestation for agricultural expansion (e.g. coffee plantations), but today the main threats are selective plant exploration, clay extraction and agriculture (Guimarães 2017). The park offers local tourism activities as well as environmental education and reforestation practices (Parque V Sobrinho 2017).

Mata do Siriji (A2) – The creation of a conservation unit in this “Brejo the altitude” has been proposed since 2009, but not yet formalized. This area is under the protection of the city hall of the municipality of São Vicente Ferrer, PE. The area has 630 hectares and the vegetation is classified as Open Ombrophilous Forest (Santos and Tabarelli 2004). The average annual rainfall is 1,076 mm, the average annual temperature is 23.1°C and altitudes range between 600 and 750 m (SEMAS 2014; Karger et al. 2017). The threats that affect biodiversity are mainly deforestation, the expansion of family or commercial agriculture, especially of banana and grape crops, and the introduction of exotic species that become invasive and affect the forest understory (SEMAS 2014).

Mata do Pau Ferro State Ecological Reserve (A3) – The reserve was created in 1992, in the municipality of Areia, state of Paraíba (PB), and is under state jurisdiction. The reserve has approximately 607 hectares encompassing dense forest vegetation and other land-use types, such as pastures and plantations. The vegetation is classified as Open Ombrophilous Forest (Santos and Tabarelli 2004). The average annual rainfall is 1,072 mm, the average annual temperature is 22°C, and altitudes range between 500 and 630 m (Karger et al. 2017; Pôrto et al. 2004). In addition to the presence of agricultural activities within the reserve and mainly in the surroundings (e.g. sugarcane mills), frequent visitation, sometimes in a disorderly manner, takes place in the reserve (Benevides et al. 2019; Pereira et al. 2019).

Sampling

The three selected areas are “Brejos de Altitude” that have already been extensively sampled. Floristic surveys were carried out in the first area (A1) in 1987 (Pôrto 1990), in the second area (A2) in 2010 (Silva 2013), and in the third area (A3) in 2009 (Silva 2013). The three areas were resampled in 2018. Thus, the areas were evaluated in different time intervals. Maximum similarity with the previous surveys was sought in the sampling, covering the same trails in the fragments and the same collection time (which varied from 4 [A2 and A3] to 10 days [A1]), and sampling all types of substrate available. The usual material sampling and processing methods in bryology were applied in these collections (Glime 2017).

Vegetation cover and indicators of anthropic disturbance

In each area, we used vegetation cover data for the “Brejo de Altitude”, the matrix and the city. The land areas devoted to agricultural activities and urban infrastructure of the city were used as proxies for acute anthropogenic disturbance and the number of inhabitants and gross domestic product (GDP) were used as proxies for chronic anthropogenic disturbance. All these variables were evaluated in four time series that mainly comprised the time interval between floristic surveys or corresponded to the closest dates.

Land use and land cover data from MapBiomas 5.0 were used to quantify the vegetation cover of the fragments on a temporal scale. These data are produced from the pixel-by-pixel classification of Landsat satellite images and provide a time series from 1985-2019 (MapBiomas 2020). Data were extracted using the Google Earth Engine platform and processed using QGIS 3.14 software. Maps with dates corresponding to the floristic surveys were used. For sampled “Brejos de Altitude” were delimited and at 1 km buffer was established around each “Brejo de Altitude” considering the limits of the forest spot within each environmental protection area to quantify the forest cover of the matrix. The size of the buffer represents the area of influence of species dispersion, because according to Vanderpoorten et al. (2019) bryophytes can disperse through 1 km without interference of long-distance dispersal processes. Acute disturbance data (agriculture and urban infrastructure) were downloaded directly from the MapBiomas 5.0 platform, while indicators of chronic disturbance (number of inhabitants and GDP of the cities) were obtained through the historical series database of the Brazilian Institute of Geography and Statistics (IBGE 2021). Studies point out that urbanization, proximity to human activity nuclei and indicators of society development such as population growth can be proxies for understanding anthropic pressures, especially the exploitation of natural resources (Hill et al. 2002; Liley and Clarke 2003; Martorell and Peters 2005; Ribeiro et al. 2016; Ribeiro-Neto et al. 2016; Sfair et al. 2018). Indicators related to the profile of society such as higher population density and GDP (especially from the Agrarian sector) have recognized influence on the greater demand for forest resources (Liu 2001, Babulo et al. 2009; Medeiros et al. 2012). Therefore, greater human interference in the forest hypothetically incurs greater structural, functional and climatic changes that can affect the maintenance of bryophyte species.

Data treatment

First, the species listed in the original surveys (Pôrto 1990; Silva 2013) and in records from virtual herbarium consulted through the Specieslink platform were compiled (The New York Botanical Garden 2020). Only species that occurred within the areas, that is, within the forest fragments, were included in the floristic matrix. The names of the species were updated according to the literature and consultation of the Flora do Brasil website (Söderström et al. 2016; Brazil Flora Group 2021) in order to exclude possible synonyms.

For the qualitative analysis of the bryoflora, the species were classified into functional groups. Sexual system was used as a proxy for the ability to reproduce. As reproductive organs are not segregated in monoicous plants, sexual reproduction is facilitated, and consequently, spore production is greater, while the opposite occurs in dioicous plants (Bisang and Hedenäs 2005; Stark et al. 2005). Therefore, the species were classified into three categories according to their ability to reproduce/disperse, namely: (0) dioicous species, which have low ability to reproduce; (1) monoicous species, which with better ability to reproduce; and (2) species that have both sexual systems. The species were classified into light-tolerance guilds as sun specialists, shade specialists, and generalists. This classification was used as a proxy for the physiological ability of bryophytes to withstand high light intensities and consequent photooxidative damage. These guilds are known to show fine responses to habitat loss and fragmentation in Atlantic Forest (Alvarenga et al. 2009, 2010). The presence of two functional traits related to protection against solar radiation (dark pigmentation) and optimization of water uptake (leaf papillae) was also noted for the species. And finally, the species were classified according to life forms following Gimingham and Birse (1957) into: tolerant to desiccation (turf and cushion), intermediate tolerance to desiccation (mat and weft), or vulnerable to desiccation (fan, dendroid, pendant) (Glime 2017). Life form is a structural trait that reflects the response of plants to environmental moisture levels as a strategy to avoid desiccation. Light tolerance guild, dark pigmentation, leaf papillae, and life form were recorded as binary data (presence and absence).

Data on functional groups were obtained from specialized literature (Sharp 1994; Costa 1999; Buck 1998; Reiner-Drehwald 1998, 2000; Gradstein et al. 2001; Gradstein and Costa 2003; Pursell, 2007; Alvarenga and Pôrto 2007; Silva and Pôrto 2009; Santos 2011; Oliveira et al. 2011; Bordin 2013; Visnadi 2015; Costa and Peralta 2015), the database of the study group of the authors. In some cases, the opinion of specialists and field observations were also considered to classify the species into light tolerance guilds. Functional data (sexual system, light tolerance guilds, and life forms) were compiled for about 95% of the species.

Data analysis

All analyses were performed in the R statistical environment version 4.1.3 (R Core Team 2021). The following matrices were used: (i) floristic data (presence and absence of species per area and census), (ii) environmental data (seven variables), and (iii) functional data (nine functional characteristics) for the set of species of each area. The species richness of each

“Brejo de Altitude” in each census were calculated (hereafter, ‘past’ refers to the first survey and ‘current’ to the most recent survey). To investigate the taxonomic composition, a Nonmetric Multidimensional Scaling (NMDS) was performed with 1000 permutations and Stress ≤ 0.2, using the metaMDS function of the vegan package (Oksanen et al. 2018). To analyze the functional composition and identify which functional traits and/or functional groups were more representative in the two surveys (past and current) in each area, community-weighted mean (CWM) trait values were first calculated and weighted by presence of species using the FD package. A Principal Component Analysis (PCA) was then carried out to graphically display the functional composition of each “Brejo de Altitude” using the FactoMineR and Factoextra packages

The taxonomic beta diversity and functional beta diversity based on the Sørense index (βsor) were partitioned into the turnover (βsim) and nestedness (βnes) components using the betapart package, based on presence and absence data (Baselga and Orme 2012). The beta.temp and functional.beta.pair functions were used, respectively, to calculate the taxonomic beta and functional diversity. Turnover indicates the replacement of species and nestedness indicates differences between areas resulting from the loss of species in relation to the species pool (Baselga 2010). While functional replacement refers to the dissimilarity of functional richness between assemblages, functional nestedness measures the relative gain or loss of shared functional space between assemblages (Villéger et al. 2013). In addition, the Convex Hull Hyper-Volume (CHull) analysis was added to an NMDS in order to visualize the functional space of the community considering the flora of each area and its functional characteristics. The CHull in a multivariate space is defined based on the irregular form yielded by species occupancy in the trait space (Pla et al. 2012).

To avoid multicollinearity, vegetation cover data (from the four sample series) and of the anthropic disturbance proxies were tested by the Spearman correlation coefficient. Variables presenting correlations > 0.6 were excluded from the subsequent analyses. Also, to help in the choice of variables to be included in the gradient analysis, we investigated their contribution to the sample set through a PCA, prioritizing the variables that contributed the most to the sample set. Generalized Linear Mixed Models (GLMMs) were used to check the relationships between the response variables (species richness, taxonomic beta diversity, and functional beta diversity) and the environmental variables (matrix vegetation cover and number of inhabitants). The identity of the three “Brejos de Altitude” as a random effect in all GLMMs. Species richness was modeled with a Poisson family error distribution, and beta diversity data, were modeled with a gaussian family error distribution. All GLMMs were performed using the lme4 package. The beta diversity variables were simplified for the models and extracted through the first axis of a Principal Coordinate Analysis (PCoA). We performed a PCoA for each paired beta diversity matrix (Coccia and Farinã 2019) for all components of the Sørense index (e.g. βsim, βsne, and βsor) using the vegan package.

Results

We observed variations in acute and chronic anthropogenic disturbance and vegetation cover of the landscape in which the “Brejos de Altitude” are inserted (Fig. 1). Matrix vegetation cover and number of inhabitants were the variables that most contributed to the sample set of data (See Supplementary Material S1). Matrix vegetation cover was also positively correlated with the vegetation cover in the forest patch and in the city. Number of inhabitants, a proxy for chronic disturbance, had a strong positive correlation with the other proxies for anthropogenic disturbances (See Supplementary Material S2). These variables characterize different environmental scenarios for the “Brejos de Altitude” over the time analyzed, possibly creating a short gradient of environmental quality (A3>A1>A2). For example, in A3 there was a decrease in the number of inhabitants, in agriculture, and an increase in the matrix vegetation cover, indicating a scenario of better environmental quality in relation to other locations. In A1, there was a decrease in agriculture and an increase in matrix vegetation cover, but there was an increase in the number of inhabitants (Fig. 1). On the other hand, A2 had a scenario of decrease in environmental quality, in view of the increase in the number of inhabitants, a slight increase in agriculture and stability of the matrix vegetation cover (Fig. 1).

A total of 247 bryophyte species, corresponding to 128 liverworts and 119 mosses, were recorded in the three “Brejos de Altitude” over the evaluated period (See supplementary material S3). Species richness increased over time in all areas. Between 50% and 58% of the species were resampled in the three “Brejos de Altitude” in 2018 (persistent species) and the others were exclusive to the past or to the current survey (Fig. 2). As for functional groups, the dioicous species, generalist species, and life forms with intermediate tolerance to desiccation predominated among the species that persisted in the areas (Fig. 2). Regardind the functional characteristics of the species, the groups that most varied between the past and current surveys in the areas which underwent a decrease in environmental quality (A1 and A2) were the shade specialists and the life forms vulnerable to desiccation, which were mainly represented in the flora of the past survey (Fig. 2). It should be noted that three shade specialist species were lost regionally (i.e. in A1 and A2) and 44 species disappeared at least in one of the areas in the current survey (Table. 1). In addition to these species, moisture-demanding species were also lost, *Pseudocryphaea domingensis* (Spreng.) W.R. Buck and *Thuidium tomentosum* Schimp. in A2. However, in A3 there was no loss of moisture-demanding species and shade specialists.

As for species composition, the NMDS (stress = 0.08) showed that the areas are distinguished in time and space (Fig. 3). The floristic dissimilarity was explained by species turnover between the surveys in A1 (βsim = 0.51, βsne = 0.03, βsor = 0.54), A2 (βsim = 0.41, βsne = 0.05, βsor = 0.46) and A3 (βsim = 0.24, βsne = 0.16, βsor = 0.40). Considering the functional composition of the areas, the cumulative variance in the first two PCA axes was 77.6% (Fig. 4). Life forms with intermediate tolerance to desiccation (0.99) and ability to reproduce (0.98) showed the highest contribution in the first axis, while dark pigmentation (0.95) was more relevant in the second axis, followed by sun specialists (0.63). Changes in functional composition were observed in the time interval studied (Fig. 4). In general, the flora in the past survey was specially characterized by shade specialist species and species with life forms vulnerable to desiccation, while the flora in the current survey was more characterized by generalist species and species with greater reproductive ability (monoicous sexual system). Regarding functional dissimilarity, nestedness explained the difference between the surveys in A2 (βsim = 0, βsne = 0.20, βsor = 0.20) and A1 (βsim = 0.48, βsne = 0.50, βsor = 0.98), while turnover explained it in A3 (βsim = 0.99, βsne = 0, βsor = 0.99). This reflects the functional space occupied by species exclusive to the past vs. exclusive to current survey in each area: only A3 (stress = 0.13) showed low overlap, while in A1 (stress =0.17) and A2 (stress = 0.16), the overlap of the functional space was greater (Fig. 5).

The community parameters evaluated between the surveys had weak relationships with the predictor variables. Matrix vegetation cover and the proxy for chronic disturbance “number of inhabitants” explained in an additive way the change in species richness between the surveys considering all species of bryophytes ($p < 0.05$, $r^2 = 0.77$) and the richness of liverworts ($p < 0.05$, $r^2 = 0.97$) and mosses ($p < 0.05$, $r^2 = 0.85$) separately. Other parameters, such as functional richness and taxonomic and functional beta diversity and their partitioned components of the Sorensen index were not explained by the variables evaluated in the models (Supplementary Material – S4).

Discussion

Environmental scenario in "Brejos de Altitude"

The socio-environmental profile of the areas has changed over time and resulted in different scenarios. Our data indicate that there was an improvement in environmental quality in A3. However, scenarios of decline in environmental quality caused by the synergistic increase in acute and chronic disturbances were more frequent (A2 > A1). In general, the increase in urbanization and GDP over time was evident, indicating advances in the economic development of the Northeast region of Brazil. This fact may conflict with the conservation of biodiversity, considering that in the regions where the "Brejos de Altitude" A2 and A3 are inserted, agribusiness is the main sector of the expanding economy. Furthermore, as farming lands (acute anthropogenic disturbance) decreased in A1 and A3, the forest vegetation cover increased in the city, showing that limiting the expansion of land use for agricultural activities favors forest regeneration over time. Among the variables studied, two were more relevant to understand the different environmental scenarios of the "Brejos de Altitude". First, the number of inhabitants; a decrease in the human population (e.g. in A3) may imply less influence of chronic disturbances. And second, the forest vegetation cover, especially in the matrix of the "Brejos de Altitude". In contrast with reports in recent decades of lack of conservation in "Brejos de Altitude" (Santos and Tabarelli 2004), the forest cover in the matrix, that is, in the landscape where the the areas studied are inserted, has remained stable and even increased over time (especially in A3, followed by A1). This may be an indication of lower acute anthropogenic pressure around the forest, which, when combined with the decrease in chronic disturbances, led to improved environmental quality in the landscape.

Our results confirm the common conflicting relationship between agricultural expansion and the conservation of tropical forests (Arroyo-Rodríguez et al. 2015; Faria and Almeida 2016). In the Amazon territory, for example, considerable loss of forest cover is observed in cities whose economy mainly relies on agricultural activities (Faria and Almeida 2016). Significant urban sprawling, especially close to forests, creates inhospitable environments for many forest species (Fisogni et al. 2020). As the proximity to forests increases, populations are more likely to depend on and use forest resources (Martorell and Peters 2005; Ribeiro et al. 2016). Thus, urbanization may be associated with different acute and also chronic disturbances and brings greater anthropogenic pressure, decreasing the environmental quality of the landscape.

Although less visible, chronic disturbances are present in the studied “Brejos de Altitude”. The literature reports selective collection of firewood and plants of ornamental interest, loose animal rearing within the forest, and disordered tourism (Santos and Tabarelli 2004; Pereira et al. 2019). These chronic pressures imply the high dependence of forest fringe communities on forest resources. Our data are in line with the literature regarding the conflicting relationships between population density and tropical forest cover, in which deforestation rates decrease as population growth, especially rural population growth, slows down (Wright and Muller 2006; Coelho et al. 2020). According to Ferreira et al. (2012), the decline in the human population in A3 is precisely related to social changes in the rural population (emigration) and technological advances in the agricultural sector with consequent decrease in the need of manpower.

The increase in forest cover, even on a short time scale (<10 years), was noticeable in the landscape. These changes in the matrix landscape modify the land used for human activities (agriculture) and improve the quality of the soil, increasing environmental heterogeneity and habitat availability for wildlife species (Arroyo-Rodríguez et al. 2017). The greater the similarity between the matrix and forest patches, the lower the anthropogenic impacts on biodiversity (Laurance et al. 2012; Laurance et al., 2018; Reider et al. 2018). However, increased vegetation cover not always implies improved environmental quality. It is important that forest restoration actions in “Brejos de Altitude” are implemented and expanded on a landscape scale. Recovering the biological and functional diversity of ecosystems is fundamental for successful ecological restoration (Massi et al. 2021). Actions that prioritize environmental inspection to avoid acute disturbances such as agricultural expansion (especially in A2) and disorderly urbanization close to forest patches need to be devised. Furthermore, incentives to environmental education should be implemented as well as solutions that encourage the sustainable use of natural resources. For example, actions should be undertaken to raise awareness among the rural population about the impact of chronic exploitation of the forest, discussing how imbalanced functioning of the ecosystem and loss of species may be directly related to the loss of provisioning ecosystem services in “Brejos de Altitude” (e.g. climate regulation, water supply). In addition, training programs on sustainable management practices and agroforestry for rural farmers can contribute to reduce human pressure in these areas.

Bryophyte flora and relationship with the environment

As expected, moisture- and shade-demanding species, which are vulnerable groups, were the most affected in the time interval between the surveys. Generalist species in terms of light requirements were those that persisted over time, demonstrating their ability to tolerate fluctuations in environmental conditions. Studies indicate that these species are the most representative in scenarios with anthropogenic disturbances (Costa 1999; Alvarenga and Pôrto 2007). The persistent species also had more frequently the mat life form, which is generalist in relation to humidity and luminosity conditions. Mat is a growth form of bryophytes in which the body architecture provides greater adhesion to the substrate, resulting in lower exposure to changes in environmental conditions (Richards 1954; Gradstein 1992; Bates 1998). The persistent species were also mainly dioicous. It should be noted that although the distance between male and female gametangia and the dependence of fertilization on water pose barriers to sexual reproduction, many dioicous species invest in asexual production (Longton 1997; Glime and Bisang 2017). Some examples of such strategy in our study areas were species of the genera *Syrrhopodon* Schwägr., *Drepanolejeunea* (Spruce) Schiffn., and *Cheilolejeunea (*Spruce) Steph.

Variations in flora over time are related to environmental changes. The increase in the matrix vegetation cover and changes in the human population size of the areas significantly influenced the increase in species richness in all sites. It is important to note that parameters solely based on taxonomic information, such as species richness, although extremely important, do not provide a full understanding of community assemblage rules, as they do not encompass the functional differences between the species (Purschke et al. 2013). Thus, species richness alone does not indicate a general positive change in the bryoflora. About 50% of the species were replaced by species with different ecological requirements, indicating important changes in the taxonomic and functional structure of the assemblages. Species turnover also reflects the replacement and loss of functional traits and ultimately the loss or gain of functional diversity. For example, in areas with a scenario of decreased environmental quality (A1 and A2), where there was a slight increase in the matrix vegetation cover and an increase in the number of inhabitants, we observed the loss of vulnerable species and their replacement mainly with generalist species. Still, in the area with the greatest loss of environmental quality (A2), we observed an increase in the proportion of species with monoicous sexual system and thus greater sexual reproduction capacity. The facilitated sexual reproduction induced by greater proximity between reproductive organs (Longton, 1997; Bisang & Hedenäs 2005), in relation to dioicous species, represents an advantage in disturbed forests, where humidity is generally lower. In the scenario of improved environmental quality (A3), where there was an increase in matrix vegetation cover associated with a decrease in the number of inhabitants, positive effects on the bryophyte flora that go beyond species richness were observed. We found an increase in the proportion of moisture- and shade-demanding species, promoting higher diversity and functional space occupied by the assemblages. Another important finding was the occurrence of epiphyllous liverworts in the current census (e.g. *Cololejeunea*, *Diplasiolejeunae*, and *Metzgeria*). Epiphyllous bryophytes are recognized as indicators of good environmental quality and they are drastically affected by anthropogenic disturbances (Alvarenga et al. 2009; Zartman and Nascimento 2006). Our findings regarding temporal changes in the environment and bryophyte flora suggest that the improvement in environmental quality promotes functional diversity and the maintenance of vulnerable species. Our working hypothesis was only partially corroborated, because parameters such as taxonomic and functional dissimilarity did not present significant relationships with the environmental variables evaluated. It is possible that other factors, such as climate (e.g. precipitation) are influential in the context of the study areas because we observed particularly the loss of species with higher ecological requirements regarding humidity.

Some studies in different scenarios of anthropogenic disturbance are in agreement with our findings regarding temporal changes in the structure of the bryophyte flora. For example, Boudreault et al. (2018) analyzed bryophytes assemblages along a chronosequence in a boreal forest (18 to > 200 years) and suggested that species richness was explained by the greater complexity of the stands (e.g., more closed canopy and more woody trees). Even on the small time scale of our study, the increase in vegetation cover had positive effects on species richness, probably derived from larger forested areas and consequent greater availability of niches. Still, in a chronosequence of primary forests in the Brazilian Amazon, Takashima-Oliveira et al. (2020) found that the richness of sun tolerant bryophytes decreased with the progression of the successional stages (0 to > 25 years), while that of shade tolerant species increased. Light tolerance guild showed fluctuations between the surveys in the present study as well, possibly responding to microclimatic changes within the forest. In a fragmented landscape scenario in the Amazon, Sierra et al. (2019) found an increase in the abundance and richness of species and a change in the taxonomic and functional composition of epiphyllous bryophytes on a 15-year time scale. Functional changes associated with greater tolerance to desiccation and greater dispersion capacity (e.g. monoic system) were especially found in smaller fragments, where the effects of fragmentation were more intense. In agreement with their result, we also found higher proportions of monoicous species in the scenario where there was the greatest loss of environmental quality over time (A2).

"Brejos de Altitude" are climatically and biologically unique environments. Conservation actions aimed at them must directly target the protection of their biological and functional diversity. The scenarios evaluated had different degrees of anthropogenic disturbance, especially of chronic nature, but the improvement in vegetation cover over the last decades have apparently minimized the deleterious effects on the richness of bryophytes. The structure of the assemblages was affected by the environmental conditions of the "Brejos de Altitude", with relevant replacement of species. We also found that functional characteristics may determine the persistence (e.g. generalist in light-tolerant species) or elimination (e.g. shade specialists and life forms vulnerable to desiccation) of species. It is worth mentioning that more severe conditions such as higher temperatures and lower precipitation rates in the Caatinga domain, where most "Brejos de Altitude" are located, are predicted for future climate scenarios (Torres et al. 2018). These conditions implicate negative effects on vegetation cover dynamics and potentiate the impact of anthropogenic disturbances, especially on vulnerable species such as moisture- and shade-demanding species, which play a key role in forest environments (Stam et al. 2017). These groups enhance the diversity of bryophyte communities and contribute to the functional quality of habitats in the understory, for example, by regulating water balance, nutrient cycling and the availability of microhabitats (Stanton and Coe 2021). Recovering the vegetation cover through ecological restoration actions, in addition to conservation of forest remnants and minimization of anthropogenic disturbances, seems to be the way to improve the environmental quality and preserce the biodiversity of these forests.

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Figures and tables

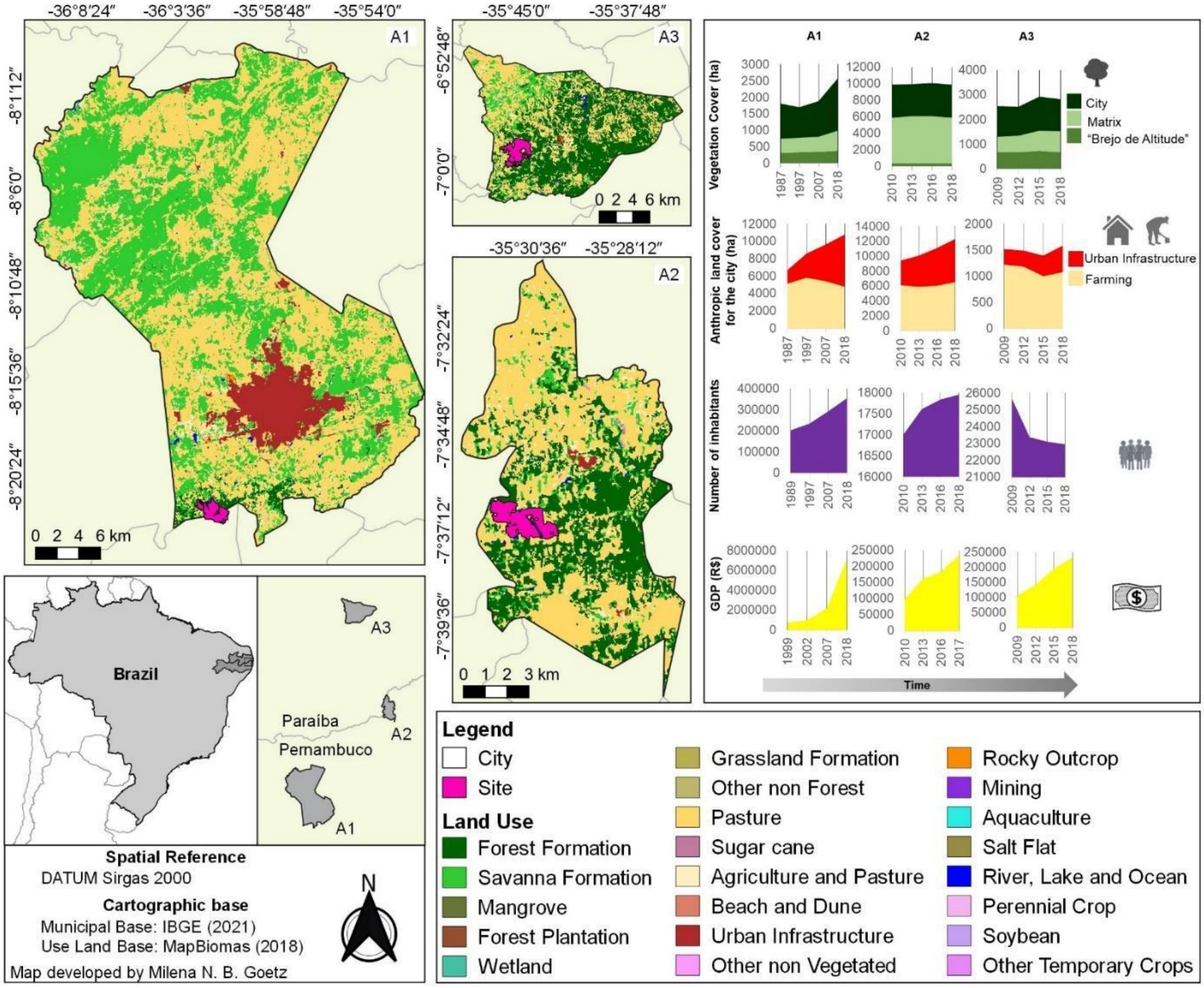


Fig. 1. Location and socio-environmental profile of the areas studied in Northeast Brazil. Colors indicate different land-use types in each city. Pink = "Brejos de Altitude" (A1 located in the city of Caruaru, state of Pernambuco; A2 in São Vicente Férrer, state of Pernambuco; and A3 in Areia, state of Paraíba). The area charts portray the variation in the four time series in each "Brejo de Altitude". Forest vegetation cover was quantified for the forest patch ("Brejo de Altitude"), the matrix of the area, and the city. Acute (farming and urban infrastructure) and chronic (number of inhabitants and gross domestic product - GDP) anthropogenic disturbance variables are also represented.

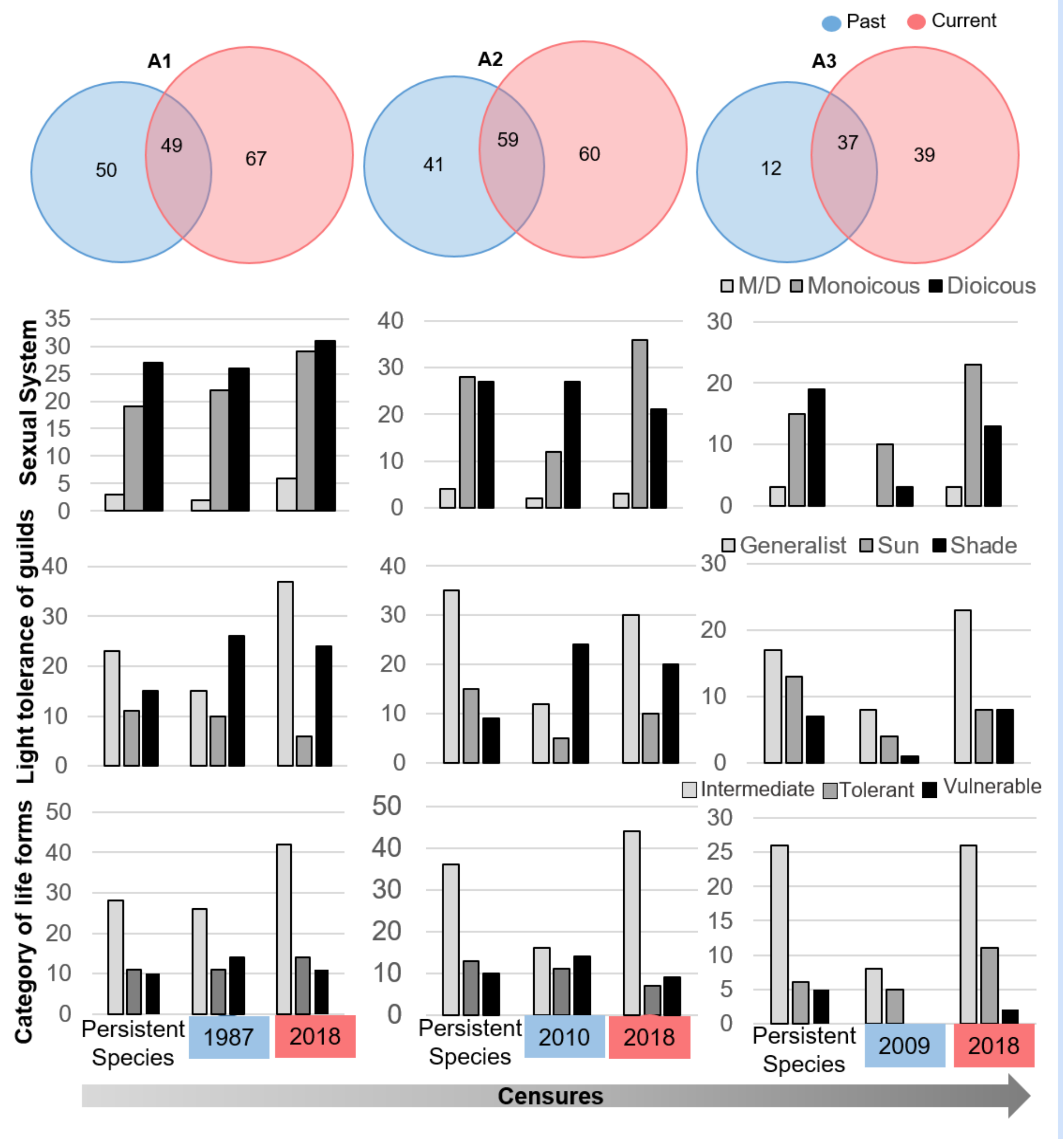


Fig. 2. Venn diagram of the bryophyte flora recorded in the past and current survey for each "Brejo de Altitude" (A1, A2 and A3). Data on functional groups and sexual system of the species exclusive to each survey (past and current) and shared between the surveys (persistent species) are depicted below.

Table. 1. Shade specialists not collected in the current census in A1 and A2. Loss of shade specialists was not recorded in A3. Species lost on a regional scale (which disappeared from both areas) are presented first, and then those that were lost on a local scale.

Lost shade species in current census

Species/Localities					
Meteorium deppei	○	△	*Octoblepharum pulvinatum*	○	
Neurolejeunea breutelii	○	△	*Pelekium schistocalyx*		△
Squamidium brasiliense	○	△	*Phyllogonium fulgens*	○	
Aptychopsis estrellae		△	*Pilotrichella pentasticha*	○	
Ceratolejeunea guianensis	○		*Plagiochila deflexirama*	○	
Cyclodictyon olfersianum		△	*Plagiochila gymnocalycina*		△
Cylindrocolea rhizantha		△	*Porella swartziana*	○	
Daltonia marginata	○		*Radula angulata*	○	
Fissidens goyazensis	○		*Radula flaccida*		△
Fissidens inaequalis		△	*Radula kegelii*		△
Holomitriopsis laevifolia	○		*Radula mexicana*	○	
Lepidolejeunea involuta	○		*Radula tenera*	○	
Lepidopilum caudicaule	○		*Rhodobryum roseum*		△
Lepidopilum muelleri	○		*Squamidium nigricans*		△
Lepidopilum subsubulatum	○		*Symphyogyna aspera*		△
Leucobryum martianum	○		*Telaranea coactilis*	○	
Meteorium nigrescens	○		*Odontolejeunea lunulata*	●	△
Metzgeria brasiliensis		△	*Plagiochila corrugata*	●	△
Monoclea gottschei		△	*Porotrichum mutabile*	●	△
Monodactylopsis monodactyla		△	*Rhodobryum beyrichianum*	●	△
Orthodontium pellucens	○		*Leucoloma cruegerianum*	●	△
Orthostichella pachygastrella	○		*Schwetschkea fabronioides*	●	△
Orthostichella pentasticha	○		*Squamidium leucotrichum*	●	△
Orthostichella versicolor	○				

Localities	**Shade Species**
○ A1	○ Lost
△ A2	● Persisted

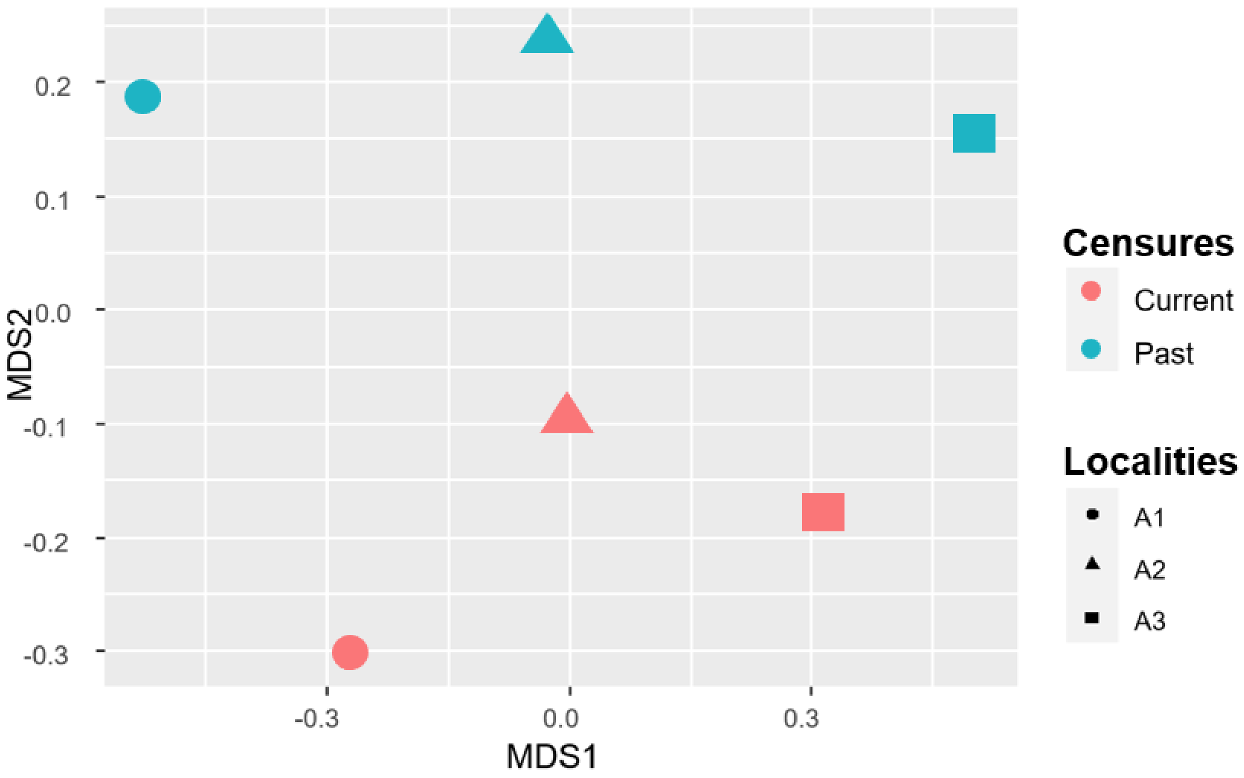


Fig. 3. Nonmetric Multidimensional Scaling (NMDS) ordination plot of the three “Brejos de Altitude” in the past and current survey (stress = 0.08), showing affinities based on floristic composition.

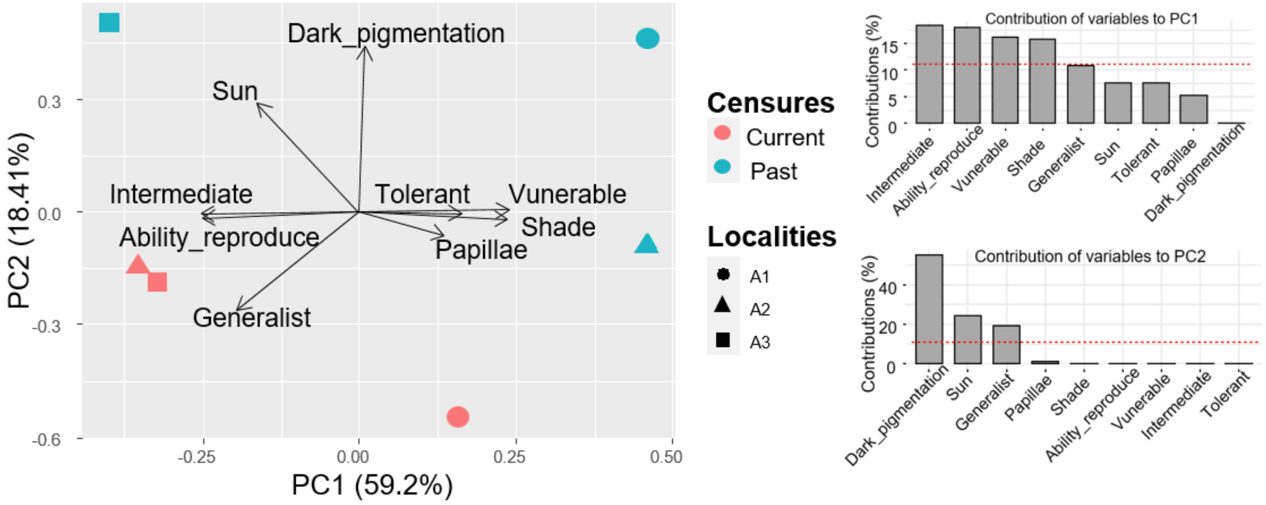


Fig. 4. Principal Component Analysis (PCA) ordination plot of CWM matrices according to functional traits for the past and current survey in each “Brejos de Altitude” (A1, A2 and A3). The percentage contribution of each functional trait to axis 1 (PC1) and axis 2 (PC2) of the PCA is shown at the side.

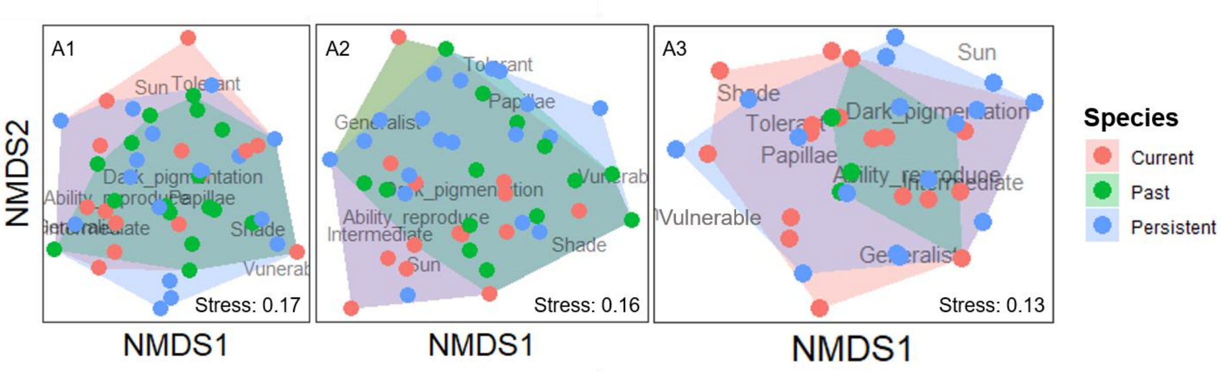
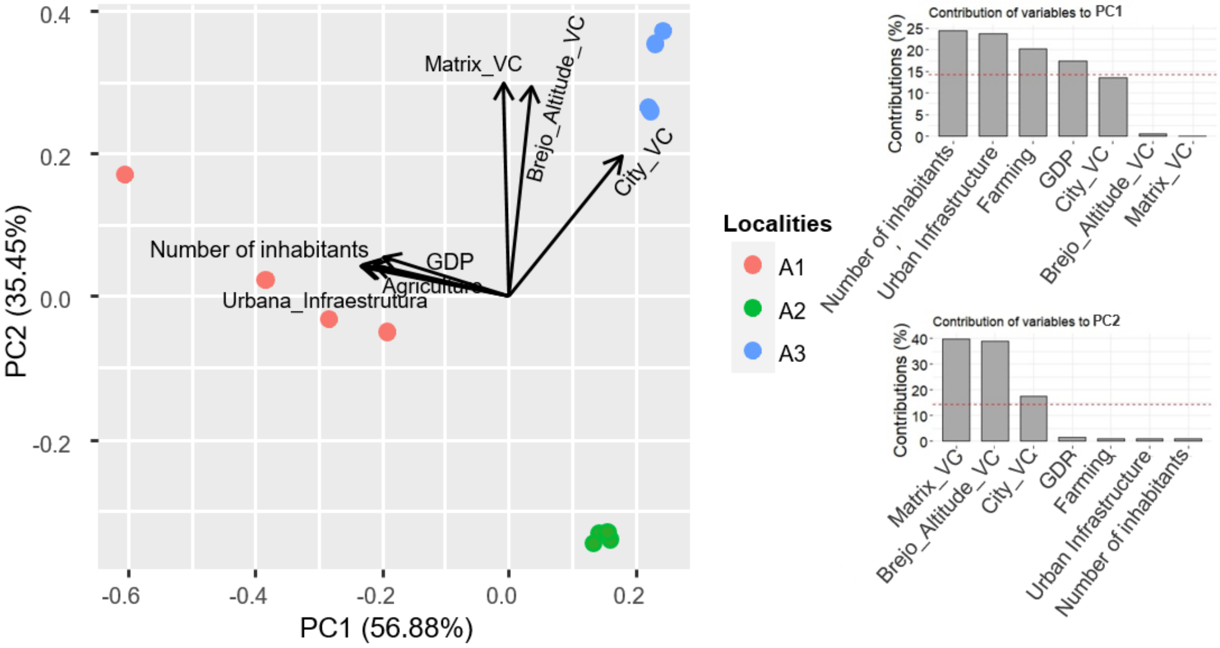
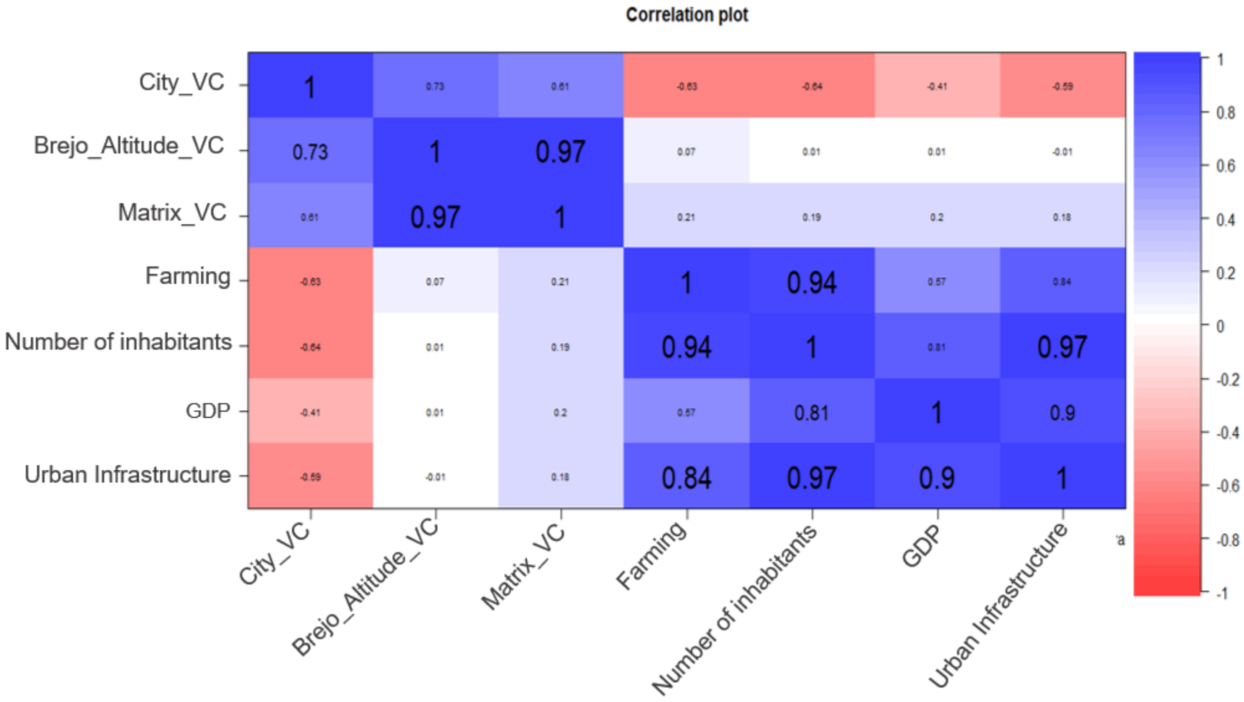


Fig. 5. Nonmetric Multidimensional Scaling (NMDS) ordination plot showing the niche space (based on convex hull area) occupied by the bryophyte assemblages of the three “Brejos de Altitude”. The colors represent the functional space of the species exclusively present in the past survey, the species exclusively present in the current survey, and the species present in the two surveys (persistent).

SUPPLEMENTARY MATERIAL



S1. Principal Component Analysis (PCA) ordination plot of environmental variables in each “Brejo de Altitude” (A1, A2 and A3). VC = Vegetation coverage of the forest patch (“Brejo de Altitude”), the matrix of the area, and the city. Acute (farming and urban infrastructure) and chronic (number of inhabitants and gross domestic product - GDP) anthropogenic disturbance variables are also represented. The percentage contribution of each variable to axis 1 (PC1) and axis 2 (PC2) of the PCA is shown at the side.



S2. Correlation between forest vegetation cover (VC) in the “Brejo de Altitude”, the matrix of the area, and the city. Also, acute (farming and urban infrastructure) and chronic (number of inhabitants and gross domestic product - GDP) anthropogenic disturbance variables. Gradients in red represent negative correlations and in blue represent positive correlations.

S3. Species list and data on sexual system, functional groups and incidence of bryophytes recorded in the "Brejos de Altitude" (A1, A2, and A3) in the past (A1_P, A2_P and A3_P) and current (A1_C, A2_C and A3_C) survey. Group (Gr): Liverwort (L) and Moss (M). Sexual System (S_S): D = Dioicous; M = Monoicous. Light tolerance guilds (L_G): Generalist (G), Shade specialist (Sh), and Sun specialist (S). Life forms (L_F): mat and weft (Intermediate = I); turf and cushion (Tolerant = T); fan, dendroid, and pendent (Vulnerable = V). Dark pigment (D_P): presence (1), and absence (0). Papillae (Pp): presence (1), and absence (0).

Species	**Gr**	**S_S**	**L_G**	**L_F**	**D_P**	**Pp**	**A1_P**	**A1_C**	**A2_P**	**A2_C**	**A3_P**	**A3_C**
Anoplolejeunea conferta (C.F.W.Meissn. ex Spreng.)	L	D	Gen	I	0	0	1	1	1	0	0	0
Aptychopsis estrellae (Hornsch.) Ångström	M	M	Sh	I	0	0	0	0	1	0	0	0
Archidium ohioense Schimp. ex Müll. Hal.	M	M	Sun	T	0	0	0	0	1	0	0	0
Barbula indica (Hook.) Spreng.	M	D	Sun	T	1	1	0	0	0	0	1	0
Bazzania heterostipa (Steph.) Fulford	L	D	Gen	I	0	0	1	0	0	0	0	0
Brachythecium ruderale (Brid.) W.R.Buck	M	D	Gen	I	0	1	0	1	0	0	0	0

Brittonodoxa subpinnata (Brid.) W.R. Buck, P.E.A.S.Câmara & Carv.-Silva	M	M	Gen	I	0	0	1	1	1	1	1	1
Bryohumbertia filifolia (Hornsch.) J.-P. Frahm	M	D	Sun	T	1	0	1	1	0	0	0	0
Bryopteris diffusa (Sw.) Nees	L	D	Sh	V	1	0	1	1	0	0	0	0
Bryopteris filicina (Sw.) Nees	L	M	Sh	V	1	0	1	1	1	1	0	0
Bryum argenteum Broth.	M	D	Gen	T	0	0	1	1	0	0	0	0
Bryum coronatum Schwägr.	M	D	Gen	T	0	0	0	0	0	0	0	1
Bryum limbatum Müll. Hal.	M	D	Sh	T	0	0	0	1	0	0	0	0
Bryum mildeanum Jur.	M	D	Gen	T	0	0	0	0	1	0	0	0
Callicostella apophysta (Hampe) A.Jaeger	M	M	Sh	I	0	0	0	0	0	1	0	0
Callicostella pallida (Hornsch.) Ångström	M	M	Gen	I	0	1	1	1	1	1	0	1

Callicostella rufescens (Mitt.) A.Jaeger	M	D / M	Sh	I	1	0	0	0	0	1	1	1
Calymperes afzelii Sw.	M	D	Gen	T	0	1	0	1	1	1	0	1
Calymperes erosum Müll. Hal.	M	D	Gen	T	1	1	0	0	1	1	0	0
Calymperes palisotii Schwägr.	M	D	Gen	T	0	1	0	1	0	1	1	1
Calypogeia laxa Gottsche & Lindenb.	L	D	Gen	I	0	0	0	1	0	1	0	0
Calypogeia miquelii Mont.	L	D	Gen	I	0	0	1	0	0	0	0	0
Calypogeia peruviana Nees & Mont.	L	D / M	Gen	I	0	0	0	0	1	0	0	0
Campylopus heterostachys (Hampe) A.Jaeger	M	D	Sun	T	1	0	0	1	0	0	0	0
Campylopus surinamensis Müll. Hal.	M	D	Sun	T	1	0	1	0	0	0	0	0

Caudalejeunea lehmanniana (Gottsche) A.Evans	L	M	Sun	I	1	0	0	0	0	0	1	1
Ceratolejeunea atlantica Alvarenga & Ilk.-Borg.	L	M	Gen	I	1	0	0	1	0	0	0	0
Ceratolejeunea ceratantha (Nees & Mont.) Steph.	L	M	Gen	I	1	0	0	1	0	0	0	0
Ceratolejeunea coarina (Gottsche) Schiffn.	L	M	Gen	I	1	0	0	1	0	0	0	0
Ceratolejeunea confusa R.M.Schust	L	M	Gen	I	1	0	0	1	0	1	0	1
Ceratolejeunea cornuta (Lindenb.) Schiffn	L	D / M	Sun	I	1	0	1	1	1	1	0	1
Ceratolejeunea cubensis (Mont.) Schiffn.	L	D / M	Gen	I	1	0	0	0	1	1	0	1
Ceratolejeunea fallax (Lehm. & Lindenb.) Bonner	L	D / M	Gen	I	1	0	0	1	0	0	0	0

Ceratolejeunea filaria (Taylor ex Lehm.) Steph.	L	D	Gen	I	1	0	1	0	0	0	0	0
Ceratolejeunea guianensis (Nees & Mont.) Steph.	L	D/M	Sh	I	1	0	1	0	0	0	0	0
Ceratolejeunea laetefusca (Austin) R.M.Schust.	L	D	Gen	I	1	0	0	1	0	1	0	1
Ceratolejeunea minuta Dauphin	L	D	Gen	I	1	0	0	0	0	1	0	0
Cheilolejeunea acutangula (Nees) Grolle	L	M	Gen	I	0	0	1	1	1	0	0	0
Cheilolejeunea adnata (Kunze) Grolle	L	D	Gen	I	0	0	1	1	1	1	1	0
Cheilolejeunea filiformis (Sw.) W. Ye, R.L. Zhu & Gradst.	L	D	Gen	V	1	0	1	1	1	0	0	0
Cheilolejeunea holostipa (Spruce) Grolle & R.-L.Zhu	L	M	Gen	I	1	0	0	0	0	0	0	1
Cheilolejeunea lobulata (Lindenb.) Gradst. & C.J. Bastos	L	D/M	Gen	I	0	0	0	1	0	0	0	0
Cheilolejeunea oncophylla (Aongström) Grolle & E.Reiner	L	M	Gen	I	1	1	0	0	0	1	0	0
Cheilolejeunea rigidula (Nees ex Mont.) R.M. Schust.	L	D	Gen	I	1	0	1	1	1	1	1	1

Cheilolejeunea trifaria (Reinw. et al.) Mizut.	L	M	Gen	I	1	0	0	1	0	1	0	0
Cheilolejeunea unciloba (Lindenb.) Malombe	L	M	Gen	I	0	0	1	0	0	0	0	1
Cheilolejeunea xanthocarpa (Lehm. & Lindenb.) Malombe	L	M	Sun	I	1	0	1	1	1	1	0	0
Chiloscyphus latifolius (Nees) J.J. Engel & R.M. Schust.	L	D / M	Gen	I	0	0	0	1	0	0	0	0
Lophocolea muricata (Lehm.) Nees in Gottsche et al.	L	M	Sh	I	0	1	1	1	0	0	0	0
Cololejeunea cardiocarpa (Mont.) A.Evans	L	M	Gen	I	0	0	0	0	0	0	0	1
Cololejeunea diaphana A. Evans	L	M	Sh	I	0	1	0	1	0	1	0	1
Cololejeunea microscopica (Taylor) Schiffn.	L	M	Gen	I	0	1	0	0	0	1	0	0
Cololejeunea obliqua (Nees & Mont.) Schiffn	L	M	Gen	I	0	0	1	0	1	1	1	0
Cololejeunea subcardiocarpa Tixier	L	M	Gen	I	0	0	1	0	0	1	1	1
Cololejeunea verrucosa Steph.	L		Sh	I	0	0	0	1	0	0	0	0
Cololejeunea verwimpii Tixier	L	M	Gen	I	0	0	0	1	0	0	0	1

Crossomitrium epiphyllum (Mitt.) Müll. Hal.	M	D	Sh	I	0	0	0	0	0	1	0	0
Crossomitrium patrisiae (Brid.) Müll. Hal.	M	D	Gen	I	0	0	1	1	1	1	0	0
Cryptolophocolea martiana (Nees) L. Söderstr., Crand.-Stotl.	L	M	Sh	I	0	0	1	1	0	0	0	0
Cyclodictyon olfersianum (Hornsch.) Kuntze	M	M	Sh	I	0	0	0	0	1	0	0	0
Cylindrocolea rhizantha (Mont.) R.M.Schust.	L	M	Sh	I	0	0	0	0	1	0	0	0
Daltonia marginata Griff.	M	M	Sh	T	0	0	1	0	0	0	0	0
Daltonia splachnoides (Sm.) Hook. & Taylor	M	M	Gen	T	0	0	0	1	0	1	0	0
Dibrachiella auberiana (Mont.) X.Q. Shi, R.L. Zhu & Gradst.	L	M	Sun	I	1	0	0	0	0	1	1	0
Diplasiolejeunea brunnea Steph.	L	D	Sun	I	0	0	0	1	1	1	0	1
Diplasiolejeunea cavifolia Steph.	L	M	Sun	I	0	0	1	1	0	1	0	1
Diplasiolejeunea rudolphiana Steph.	L	M	Sun	I	0	0	1	0	1	1	0	1
Drepanolejeunea aracauriae Steph	L	D/M	Gen	I	0	0	0	1	0	0	0	0

Drepanolejeunea bidens (Steph.) A.Evans	L	D/M	Gen	I	0	0	1	1	0	0	0	0
Drepanolejeunea fragilis Bischl.	L	D	Gen	I	0	0	0	1	1	1	1	1
Drepanolejeunea mosenii (Steph.) Bischl.	L	D	Sh	I	0	0	1	1	1	1	1	1
Entodontopsis leucostega (Brid.) W.R.Buck & Ireland	M	M	Gen	I	0	0	0	0	0	0	1	1
Entodontopsis nitens (Mitt.) W.R.Buck & Ireland	M	M	Gen	I	0	0	0	0	0	0	0	1
Eulacophyllum cultelliforme (Sull.) W.R.Buck & Ireland	M	M	Sun	I	0	0	0	0	0	1	0	0
Fabronia ciliaris (Brid.) Brid.	M	M	Gen	I	0	0	0	0	0	0	1	0
Fissidens amoenus Müll. Hal.	M	M	Sh	T	0	0	0	1	0	0	0	1
Fissidens elegans Brid.	M	M	Gen	T	1	1	0	0	1	0	0	0
Fissidens goyazensis Broth.	M	M	Sh	T	0	1	1	0	0	0	0	1
Fissidens guianensis Mont.	M	M	Gen	T	1	1	0	0	1	1	1	0
Fissidens hornschuchii Mont.	M	M	Gen	T	0	1	0	0	0	0	1	0

Fissidens inaequalis Mitt.	M	M	Sh	T	1	0	0	0	1	0	0	0
Fissidens juruensis Broth.	M	M	Sh	V	0	0	0	0	1	1	1	1
Fissidens lagenarius Mitt.	M	M	Sh	T	0	1	1	1	0	0	0	0
Fissidens pallidinervis Mitt.	M	M	Sh	T	1	1	0	1	0	1	0	1
Fissidens pellucidus Hornsch.	M	M	Gen	T	1	0	1	0	1	1	0	0
Fissidens radicans Mont.	M	M	Gen	T	1	0	0	0	1	1	0	0
Fissidens scariosus Mitt.	M	M	Sh	T	1	0	1	0	0	1	0	1
Fissidens serratus Müll. Hal.	M	M	Sh	T	1	1	1	1	0	1	1	0
Fissidens zollingeri Mont.	M	M	Gen	T	0	0	0	1	1	1	1	1
Floribundaria flaccida (Mitt.) Broth.	M	D	Sh	V	0	1	0	1	1	1	0	0
Frullania apiculata (Reinw. et al.) Nees	L	M	Sun	V	1	0	0	1	0	1	0	0
Frullania brasiliensis Raddi	L	D	Sun	V	1	0	1	0	0	0	0	0

Frullania caulisequa (Nees) Nees	L	M	Sun	I	1	0	1	0	1	1	1	1
Frullania dusenii Steph.	L	M	Sun	I	1	0	0	0	1	0	1	0
Frullania ericoides (Nees) Mont.	L	D	Sun	I	1	0	0	0	0	0	1	1
Frullania kunzei (Lehm. & Lindenb.) Lehm. & Lindenb.	L	M	Sun	I	1	0	1	0	1	1	1	1
Frullania riojaneirensis (Raddi) Spruce	L	M	Sun	I	1	0	1	0	1	1	1	1
Groutiella apiculata (Hook.) H.A.Crum & Steere	M	D	Sun	T	1	1	1	1	1	0	1	1
Groutiella chimborazensis (Spruce ex Mitt.) Florsch.	M	D	Sun	T	1	1	1	0	0	0	0	0
Groutiella obtusa (Mitt.) Florsch.	M	D	Sun	T	1	0	0	0	0	1	0	0
Groutiella tomentosa (Hornsch.) Wijk & Margad.	M	D	Sun	T	1	0	1	1	1	1	1	1
Harpalejeunea stricta (Lindenb. & Gottsche) Steph.	L	D	Sun	I	0	0	0	1	1	1	1	1
Helicophyllum torquatum (Hook.) Brid.	M	D	Gen	I	1	1	0	0	0	0	1	1
Henicodium geniculatum (Mitt.) W.R.Buck	M	D	Gen	V	0	1	1	1	1	1	1	1

Holomitriopsis laevifolia (Broth.) H. Rob	M		Sh	T	0	0	1	0	0	0	0	0
Holomitrium arboreum Mitt.	M	D	Gen	T	1	0	1	0	1	1	0	0
Homalia trichomanoides (Hedw.) Brid.	M	M	Sh	V	0	0	0	0	0	1	0	0
Hyophila involuta (Hook.) A.Jaeger	M	D	Sun	T	1	1	0	0	0	0	0	1
Isopterygium subbrevisetum (Hampe) Broth.	M	M	Gen	I	0	0	0	1	0	1	0	1
Isopterygium tenerifolium Mitt.	M	M	Gen	I	0	0	0	1	0	1	0	1
Isopterygium tenerum (Sw.) Mitt.	M	M	Gen	I	0	0	1	1	0	1	1	1
Jaegerina scariosa (Lorentz) Arzeni	M	D	Gen	V	0	0	1	1	1	1	0	1
Lejeunea adpressa Nees	L	M	Gen	I	0	0	0	1	0	1	0	1
Lejeunea aphanes Spruce	L	M	Gen	I	0	0	0	1	0	1	0	1
Lejeunea boryana Mont.	L	M	Sh	I	1	0	0	0	0	1	0	0
Lejeunea capensis Gottsche	L	M	Gen	I	0	0	0	1	0	0	0	0

Lejeunea cerina (Lehm. & Lindenb.) Gottsche	L	M	Gen	I	0	0	0	0	1	0	0	0
Lejeunea controversa Gottsche	L	M	Gen	I	0	0	0	0	0	1	0	1
Lejeunea flava (Sw.) Nees	L	M	Gen	I	0	0	1	1	1	1	0	1
Lejeunea glaucescens Gottsche	L	M	Gen	I	0	0	1	1	1	1	1	1
Lejeunea immersa Spruce	L	M	Gen	I	0	0	0	0	0	0	1	0
Lejeunea laeta (Lehm. & Lindenb.) Gottsche	L	M	Gen	I	0	0	0	0	1	0	0	0
Lejeunea laetevirens Nees & Mont.	L	D	Gen	I	0	1	0	1	1	1	1	1
Lejeunea monimiae (Steph.) Steph.	L	M	Gen	I	0	0	0	1	0	0	0	0
Lejeunea parviloba Ångstr.	L	D	Gen	I	0	0	0	0	0	1	0	0
Lejeunea perpapillosa E. Reiner & Pôrto	L	M	Gen	I	0	1	0	1	0	0	0	0
Lejeunea phyllobola Nees & Mont.	L	D	Gen	I	0	0	0	1	1	1	1	1
Lejeunea quinqueumbonata Spruce	L	M	Sh	I	0	0	0	1	0	1	0	0

Lejeunea raddiana Lindenb.	L	M	Gen	I	0	0	0	0	0	1	0	0
Lejeunea serpillifolioides (Raddi) Gradst.	L	M	Gen	I	0	0	0	1	0	1	0	0
Lejeunea sporadica Besch. & Spruce	L	M	Gen	I	0	0	0	0	0	1	0	0
Lejeunea subsessilis Spruce	L	M	Gen	I	0	*0*	0	0	0	1	0	0
Lepidolejeunea involuta (Gottsche) Grolle	L	D	Sh	I	0	0	1	0	0	0	0	0
Lepidopilum amplirete Müll. Hal.	M	M	Sh	I	0	0	0	1	0	0	0	0
Lepidopilum caudicaule (Müll.Hal.) Broth.	M	M	Sh	I	0	0	1	0	0	0	0	0
Lepidopilum muelleri (Hampe) Mitt.	M	M	Sh	V	1	0	1	0	0	0	0	0
Lepidopilum pallidonitens (Müll. Hal.) Broth.	M	M	Gen	I	0	1	0	1	1	1	0	0
Lepidopilum subsubulatum Geh. & Hampe	M	M	Sh	I	1	0	1	0	0	0	0	0
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	L	D/M	Sun	I	1	0	1	0	1	1	1	1
Leptoscyphus porphyrius (Nees) Grolle	L	D	Sh	I	1	0	0	1	0	0	0	0

Leucobryum albicans (Schwägr.) Lindb.	M	D	Sh	T	0	0	0	1	0	0	0	0
Leucobryum martianum (Hornsch.) Hampe ex Müll. Hal.	M	D	Sh	T	0	0	1	0	0	0	0	0
Leucoloma cruegerianum (Müll.Hal.) A.Jaeger	M	D	Sh	T	1	1	1	1	1	0	0	0
Leucoloma serrulatum Brid.	M	D	Sh	T	1	1	1	1	1	1	0	0
Leucomium strumosum (Hornsch.) Mitt.	M	M	Sh	I	1	0	0	0	0	1	0	0
Lophocolea bidentata (L.) Dumort.	L	D	Sh	I	0	0	0	1	0	0	0	0
Lopholejeunea nigricans (Lindenb.) Schiffn.	L	D / M	Sun	I	1	0	0	1	1	1	0	1
Lopholejeunea subfusca (Nees) Schiffn.	L	M	Sun	I	1	0	1	1	1	1	1	1
Lophozia bicrenata (Schmidel) Dumort.	L	M	Sun	I	*1*	*0*	0	0	0	1	0	0
Macromitrium punctatum (Hook. & Grev.) Brid.	M	D	Sun	T	1	0	0	0	1	0	0	0
Marchesinia brachiata (Sw.) Schiffn.	L	D	Sun	I	1	0	1	1	1	1	1	1
Metalejeunea cucullata (Reinw. et al.) Grolle	L	M	Gen	I	0	0	0	1	0	0	0	0

Meteoridium remotifolium (Müll.Hal.) Manuel	M	D	Gen	V	0	1	1	1	1	1	0	0
Meteorium deppei (Hornsch. ex Müll. Hal.) Mitt.	M	D	Sh	V	1	1	1	0	1	0	0	0
Meteorium nigrescens (Sw. ex Hedw.) Dozy & Molk.	M	D	Sh	V	1	1	1	0	0	0	0	0
Metzgeria albinea Spruce	L	D	Gen	I	0	0	0	0	1	0	0	0
Metzgeria aurantiaca Steph.	L	D	Gen	I	0	0	0	0	0	1	0	0
Metzgeria brasiliensis Schiffn.	L	D	Sh	I	0	0	0	0	1	0	0	0
Metzgeria ciliata Raddi	L	D	Gen	I	0	0	1	1	0	1	1	1
Metzgeria furcata (L.) Dumort.	L	D	Gen	I	0	0	0	1	0	1	0	1
Microcalpe subsimplex (Hedw.) W.R. Buck	M	M	Gen	I	0	0	1	1	1	1	1	1
Microlejeunea bullata (Taylor) Steph.	L	D	Sun	I	0	0	0	0	0	0	0	1
Microlejeunea epiphylla Bischl.	L	D	Sun	I	0	0	1	1	0	1	1	1
Mittenothamnium reptans (Hedw.) Cardot	M	M	Gen	I	0	0	1	0	0	0	0	0

Monoclea gottschei Lindb.	L	D	Sh	V	0	0	0	0	1	0	0	0
Monodactylopsis monodactyla (Spruce) R.M.Schust.	L	M	Sh	I	0	1	0	0	1	0	0	0
Neckeropsis disticha (Hedw.) Kindb.	M	M	Sh	V	0	0	0	0	0	1	0	0
Neckeropsis undulata (Hedw.) Reichardt	M	M	Sh	V	0	0	0	1	1	1	0	0
Neurolejeunea breutelii (Gottsche) A.Evans	L	D	Sh	I	1	0	1	0	1	0	0	0
Ochrobryum gardneri (Müll.Hal.) Lindb.	M	D	Sun	T	0	0	0	1	0	0	0	0
Octoblepharum albidum Hedw.	M	M	Gen	T	0	0	0	1	1	1	1	1
Octoblepharum pulvinatum (Dozy & Molk.) Mitt.	M		Sh	T	0	0	1	0	0	0	0	0
Odontolejeunea lunulata (Weber) Schiffn.	L	D/M	Sh	I	1	0	0	1	1	0	0	0
Orthodontium pellucens (Hook.) B.S.G.	M	M	Sh	V	0	0	1	0	0	0	0	0
Orthostichella pachygastrella (Müll.Hal.) B.H.Allen & Magill	M	D	Sh	V	1	0	1	0	0	0	0	0
Orthostichella pentasticha (Brid.) W.R. Buck	M	D	Sh	V	1	0	1	0	0	0	0	0

Orthostichella rigida (Müll.Hal.) B.H.Allen & Magill	M	D	Sh	V	1	0	0	1	0	0	0	0
Orthostichella versicolor (Müll.Hal.) B.H.Allen & W.R.Buck	M	D	Sh	V	1	0	1	0	0	0	0	0
Orthostichidium quadrangulare (Schwägr.) B.H. Allen & Magill	M	D	Sh	V	0	0	0	1	0	0	0	0
Otigoniolejeunea huctumalcensis (Lindenb. & Gottsche)	L	D / M	Gen	I	1	0	0	0	0	1	0	0
Pelekium schistocalyx (Müll.Hal.) A. Touw	M	M	Sh	V	0	1	0	0	1	0	0	0
Phyllogonium fulgens (Hedw.) Brid.	M	D	Sh	V	0	0	1	0	0	0	0	0
Phyllogonium viride Brid.	M	D	Sh	V	0	0	1	1	0	0	0	0
Pilosium chlorophyllum (Hornsch.) Müll. Hal.	M	M	Gen	I	1	0	1	1	1	1	1	0
Pilotrichella pentasticha (Brid.) Wijk & Margad.	M	D	Sh	V	0	0	1	0	0	0	0	0
Pilotrichum evanescens (Müll.Hal.) Müll.Hal.	M	D	Sh	V	0	1	0	1	0	1	0	1
Pinnatella minuta (Mitt.) Broth.	M	D	Sh	V	0	1	0	0	0	1	0	0
Pireella cymbifolia (Sull.) Cardot	M	D	Sh	V	1	0	0	0	0	1	0	0

Pireella pohlii (Schwägr.) Cardot	M	D	Sh	V	1	0	0	0	0	1	0	0
Plagiochila aerea Taylor	L	D	Sh	V	0	0	0	0	1	1	0	0
Plagiochila corrugata (Nees) Nees & Mont.	L	D	Sh	V	0	0	0	1	1	0	0	0
Plagiochila deflexirama Taylor	L	D	Sh	V	0	0	1	0	0	0	0	0
Plagiochila disticha (Lehm. & Lindenb.) Lindenb.	L	D	Sh	V	0	0	0	0	1	0	1	1
Plagiochila gymnocalycina (Lehm. & Lindenb.) Lindenb.	L	D	Sh	V	0	0	0	0	1	0	0	0
Plagiochila lingua Steph.	L	D	Sh	V	0	0	0	0	0	1	0	0
Plagiochila martiana (Nees) Lindenb.	L	D	Sh	V	0	0	0	0	0	0	1	1
Plagiochila montagnei Nees	L	D	Sh	V	0	0	0	1	1	1	1	1
Plagiochila patula (Sw.) Lindenb.	L	D	Sh	V	0	0	0	1	0	0	0	0
Plagiochila raddiana Lindenb.	L	D	Sh	V	0	0	0	1	0	0	0	0
Porella swartziana (Weber) Trevis.	L	D	Sh	V	1	0	1	0	0	0	0	0

Porotrichum mutabile Hampe	M	D	Sh	V	0	0	0	1	1	0	0	0
Porotrichum substriatum (Hampe) Mitt.	M	D	Sh	V	1	0	1	1	0	1	0	0
Prionolejeunea denticulata (Weber) Schiffn.	L	M	Gen	I	0	0	0	0	1	1	0	0
Pseudocryphaea domingensis (Spreng.) W.R.Buck	M	D	Gen	V	1	0	0	0	1	0	0	0
Pterogonidium pulchellum (Hook.) Müll.Hal.	M	M	Gen	I	0	0	0	0	0	1	0	0
Pycnolejeunea contigua (Nees) Grolle	L	D	Sun	I	0	0	0	0	0	1	0	0
Racopilum tomentosum (Hedw.) Brid.	M	M	Gen	I	1	0	1	1	1	1	1	0
Radula angulata Steph.	L	D	Sh	I	0	0	1	0	0	0	0	0
Radula flaccida Lindenb. & Gottsche	L	D	Sh	I	0	0	0	0	1	0	0	0
Radula javanica Gottsche	L	D	Sh	I	0	0	0	0	0	1	0	0
Radula kegelii Gottsche ex Steph.	L	D	Sh	I	0	0	0	0	1	0	0	0
Radula mexicana Lindenb. & Gottsche	L	D	Sh	I	0	0	1	0	0	0	0	0

Radula recubans Taylor	L	D	Sh	I	0	0	0	1	0	1	0	0
Radula tenera Mitt. ex Steph.	L	D	Sh	I	0	0	1	0	0	0	0	0
Rectolejeunea flagelliformis A.Evans	L	D	Gen	I	0	0	1	0	0	0	0	0
Rectolejeunea versifolia (Schiffn.) L.Söderstr. et A.Hagborg	L	D	Gen	I	0	0	0	0	1	1	0	0
Rhacopilopsis trinitensis (Müll.Hal.) E.Britton & Dixon	M	D	Gen	I	1	0	1	1	0	0	0	0
Rhodobryum beyrichianum (Hornsch.) Müll. Hal.	M	D	Sh	T	1	0	0	1	1	0	0	0
Rhodobryum roseum (Hedw.) Limpr.	M	D	Sh	T	1	0	0	0	1	0	0	0
Rhynchostegium serrulatum (Hedw.) A.Jaeger	M	M	Gen	I	0	0	0	1	0	0	0	0
Rosulabryum densifolium (Brid.) Ochyra	M	D	Gen	T	0	0	0	1	0	1	0	1
Schiffneriolejeunea polycarpa (Nees) Gradst.	L	D/M	Sun	I	1	0	1	1	0	1	1	1
Schlotheimia rugifolia (Hook.) Schwägr.	M	D	Sun	T	1	0	1	0	1	1	0	0
Schlotheimia torquata (Hedw.) Brid.	M	D	Sun	T	1	0	1	0	0	0	0	0

Schwetschkea fabronioides (Welw. & Duby) Broth.	M	M	Sh	I	0	0	1	1	0	0	0	1
Sematophyllum adnatum (Michx.) Brid.	M	M	Gen	I	0	0	0	1	0	1	0	1
Sematophyllum beyrichii (Hornsch.) Broth.	M	M	Gen	I	0	0	1	0	0	1	0	1
Sematophyllum swartzii (Schwägr.) W.H. Welch & H.A. Crum	M	M	Gen	I	0	0	1	0	0	0	0	0
Squamidium brasiliense Broth.	M	D	Sh	V	0	1	1	0	1	0	0	0
Squamidium leucotrichum (Taylor) Broth.	M	D	Sh	V	0	1	1	1	1	0	0	0
Squamidium nigricans (Hook.) Broth.	M	D	Sh	V	0	1	0	0	1	0	0	0
Stictolejeunea squamata (Willd. ex Weber) Schiffn.	L	D	Gen	I	1	0	0	1	1	1	0	0
Symbiezidium barbiflorum (Lindenb. & Gottsche) A. Evans	L	M	Gen	I	1	0	1	0	1	1	1	1
Symphyogyna aspera Steph.	L	D	Sh	V	0	0	0	0	1	0	0	0
Syrrhopodon africanus (Mitt.) Paris	M	D	Sun	T	0	1	0	0	1	0	0	0
Syrrhopodon incompletus Schwägr.	M	D	Sh	T	0	0	1	1	1	1	0	1

Syrrhopodon ligulatus Mont.	M	D	Sh	T	0	1	0	1	0	0	1	1
Syrrhopodon parasiticus (Brid.) Besch.	M	D	Sun	T	0	1	1	1	1	1	0	1
Syrrhopodon prolifer (Brid.) Besch.	M	D	Gen	T	0	1	1	1	1	0	0	1
Taxithelium planum (Brid.) Mitt.	M	M	Gen	I	0	1	0	0	1	1	0	0
Telaranea coactilis (Spruce) J.J. Engel & G.L. Merr.	L	M	Sh	I	0	1	1	0	0	0	0	0
Telaranea diacantha (Mont.) Engel & Merr.	L	M	Sh	I	0	0	1	1	0	0	0	0
Thuidium tomentosum Schimp.	M	D	Gen	V	0	1	0	0	1	0	0	0
Vesicularia vesicularis (Schwägr.) Broth.	M	M	Gen	I	0	0	0	0	1	1	0	0
Vitalia galipensis (Müll. Hal.) P.E.A.S.Câmara, Carv.-Silva & W.R. Buck	M	M	Gen	I	0	0	0	1	0	1	0	0
Vitalianthus bischlerianus (Porto & Grolle) R.M.Schust. & Giancotti	L	M	Sun	I	0	0	0	0	0	1	0	0
Xylolejeunea crenata (Nees & Mont.) X.-L. He & Grolle	L	M	Gen	I	0	0	0	0	1	0	0	0
Zelometeorium patulum (Hedw.) Manuel	M	D	Gen	V	0	1	1	1	1	1	0	0

S4. Results of Generalized Linear Mixed Models (GLMMs) of species richness, functional richness and beta diversity components for taxonomic and functional data of the bryophyte assemblages (response variables) as a function of environmental variables [matrix vegetation cover (VC) and the number of inhabitants] and the time factor (past and current survey) in the “Brejos de Altitude”. * = Significant values.

Model Factors		**95% CI**		
	p-value	**Lower**	**Upper**	**R2**
Bryophytes_Richness				**0.77**
Matrix VC	>0.001*	-0.8565	-0.3622	
Number of inhabitants	>0.001*	0.18655	0.6372	
Time	0.005*	0.07338	0.41716	

Model Factors		**95% CI**		
	p-value	**Lower**	**Upper**	**R2**
Liverworts_Richness				**0.97**
Matrix VC	0.001*	-0.8824	-0.2155	
Number of inhabitants	0.05*	-0.0009	0.61766	
Time	>0.001*	0.07713	0.55275	

Model Factors		**95% CI**		
	p-value	**Lower**	**Upper**	**R2**
Moss_Richness				**0.85**
Matrix VC	>0.001*	-1.0501	-0.3131	
Number of inhabitants	0.01*	0.19979	0.85975	
Time	0.1	-0.0814	0.41681	

Model Factors		**95% CI**		
	p-value	**Lower**	**Upper**	**R2**
Functional_Richnss				**-**
Matrix VC	-2.365	-0.6663	-0.0571	
Number of inhabitants	1.5	-0.0601	0.47745	
Time	0.6	-0.1373	0.27099	

Model Factors		**95% CI**		
	p-value	**Lower**	**Upper**	**R2**
βsim_Diversity				**-**
Matrix VC	-0.1494	-0.5791	0.07805	
Number of inhabitants	2.786	0.14591	0.83809	
Time	-2.354	-0.6177	-0.0564	

Model Factors		**95% CI**		
	p-value	**Lower**	**Upper**	**R2**
βnes_Diversity				**-**
Matrix VC	3.53	0.03103	0.10847	
Number of inhabitants	1.226	-0.0465	0.20218	
Time	-4.781	-0.1288	-0.0539	

Model Factors		**95% CI**		
	p-value	**Lower**	**Upper**	**R2**
βsor_Diversity				**-**
Matrix VC	10.06	0.2865	0.42516	
Number of inhabitants	-3.155	-0.5697	-0.1331	
Time	3.498	0.05234	0.18572	

Model Factors		**95% CI**		
	p-value	**Lower**	**Upper**	**R2**
βsim_Functional_Diversity				**-**
Matrix VC	-0.645	-0.7215	0.36417	
Number of inhabitants	-1.863	-1.1152	0.02821	
Time	0.66	-0.3076	0.6197	

Model Factors		**95% CI**		
	p-value	**Lower**	**Upper**	**R2**
βnes_Functional_Diversity				**-**
Matrix VC	1.197	-0.003	0.01252	
Number of inhabitants	-0.282	-0.0164	0.01225	
Time	-1.003	-0.0103	0.00334	

Model Factors		**95% CI**		
	p-value	**Lower**	**Upper**	**R2**
βsor_Functional_Diversity				**-**
Matrix VC	1.485	-0.1251	0.90755	
Number of inhabitants	1.1	-0.2206	0.78475	
Time	-1.618	-0.6968	0.0667	

4 TAXONOMIC AND FUNCTIONAL COMPOSITION ARE COUPLED AND MODULATED BY A SHORT ENVIRONMENTAL GRADIENT IN BRYOPHYTE ASSEMBLAGES

Manuscrito II: to be submitted to FLORA

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Abstract

Bryophyte assemblages of unique forest refuges in Northeastern Brazil have relevant biological diversity. However, the persistence of the species and their functional role in the environment may be compromised in these forests due to the anthropogenic pressures that have affected them over decades. In this study, we investigated the taxonomic and functional composition and diversity of epiphytic bryophyte assemblages and the influence of environmental factors (light and humidity) and human disturbance. Epiphytic bryophytes were collected in the understory of four forest refuges in a total of 58 400-m² plots, in an average of seven phorophytes per plot, keeping a minimum distance of 100 m between plots. The relationships of humidity (elevation and distance to water bodies), light incidence (canopy opening), and disturbance (edge distance) proxies with community parameters and the response of functional traits to abiotic and anthropic factors were analyzed. We used ordination analyses to examine the taxonomic and functional composition. We also used combined RLQ and fourth-corner analyses for the functional data and generalized linear models to verify the relationships between the environment and the taxonomic and functional alpha diversity. The taxonomic and the functional composition were significantly influenced by elevation and canopy opening. In general, environments with greater light incidence (canopy opening) selected sun specialist species, the life form mat (e.g. in mosses), and species with functional traits that promote water accumulation (large lobules in liverworts). The environment did not affect the taxonomic and functional diversity. Nevertheless, our results suggest that higher luminosity in the understory may select a flora increasingly composed of sun specialists to the detriment of more moisture-demanding groups (e.g. liverworts with small lobules, species with pendant life forms, shade

specialists), tacitly implying the disappearance of these taxa and consequently of their functions from the ecosystem.

Keywords: liverworts; mosses; environmental filtering; functional traits; community assembly.

1. Introduction

Anthropogenic disturbances modify the structure of tropical forests and, consequently, the local abiotic conditions, either by simplifying or by adding abiotic filters (Western 2001). These changes, in turn, have repercussions that go from the disappearance of species to a compromised provision of key ecosystem services, such as carbon sequestration and storage (Huang et al. 2020). Investigating functional and even phylogenetic data, added to taxonomic information, allows us to understand the relationships of the species with the environment and the strategies adopted by them to survive (Zou et al. 2016; Chelli et al. 2019; Roos et al. 2019). This approach is particularly relevant in biological communities of unique and fragile ecosystems, such as ecological refuges, where changes in environmental conditions can cause irreversible losses in the communities or even in the ecosystem.

An example of unique ecosystems are the “Brejos de Altitude”, which are unique submontane humid tropical forests embedded in the Caatinga domain in the Northeast of Brazil, recognized to act as ecological refuges. They harbor a high biodiversity and many taxa with endemic and disjunct distribution, occurring in the Amazon and Atlantic Forest (Andrade-Lima 1960; Pôrto et al. 2004; Tabarelli and Santos 2004; Loiola et al. 2015). Historically, “Brejo de Altitude” have been the target of acute and chronic disturbances, and some have already been totally decimated (Santos and Tabarelli 2004). It is estimated that only 14% (2,626.68 km) of their original area persists and are now the most threatened rainforest remnants in Northeast Brazil (Santos and Tabarelli 2004). Despite the recognition of their biological relevance, they are still very vulnerable to anthropic pressure due to the exploitation of wood and water resources and the growth of agricultural activities and urbanization (Monteiro and Sawyer 1999; Santos and Tabarelli 2004). These factors can change the forest structure (e.g. increase canopy opening, create new edges - Tabarelli and Silva 2004) and alter local environmental conditions (e.g. reduce humidity, increase light incidence and temperature - Pohlman et al. 2007), generating negative effects on biological communities, particularly in assemblages of typical understory plants, such as bryophytes (Alvarenga and Pôrto 2007).

The understory of “Brejo de Altitude” presents, in general, a complex structure, with a high diversity of climbing plants, and epiphytes (including pedant plants), especially bryophytes, which provide shelter for the microbiota and contribute to water regulation and nutrient cycling (Pôrto et al. 2004; Glime 2017; Terceiro et al. 2021). The bryophyte species growing in “Brejo de Altitude” correspond to about 34% of the bryophyte flora of the country and are mostly representatives of liverworts, epiphytes and epiphylls - groups that are typical of humid tropical forests (see database by Batista et al. 2021). The knowledge of the bryophyte flora of “Brejo de Altitude” comes mainly from floristic surveys (Pôrto 1990; Pôrto et al. 2004; Yano and Pôrto 2006) and few studies addressing the relationships of the species with the environment (Araújo et al. 2021; Batista et al. 2021).

Bryophytes are poikilohydric (i.e. have their water content directly regulated by ambient humidity) and are extremely dependent on environmental conditions for survival and reproduction (Proctor 1999; Proctor and Tuba 2002). Poikiloidry may justify the fact that bryophyte assemblages are strongly shaped by niche-based processes at different spatial scales (Frahm and Gradstein 1991; Oliveira and Ter Steege 2015; Batista et al. 2021). Some main factors that govern bryophyte assemblages in tropical forests include the vegetation type, climate, and elevation (Santos et al. 2014; Amorim et al. 2017; Garcia et al. 2020). Yet, anthropogenic factors also act as selectors (Souza et al. 2020). The loss of original habitats and consequent edge effects cause a decrease in species richness and diversity (Alvarenga and Pôrto 2007; Silva and Pôrto 2015) and change the taxonomic and functional composition of bryophyte communities, depending on the degree of disturbance (Souza et al. 2020; Riffo-Donosco et al. 2021). It should be noted that only a handful of studies have examined the functional ecology of bryophytes in rainforests (Henriques et al. 2017; Souza et al. 2020), and even less have considered anthropogenic factors (Souza et al. 2020). It is still necessary to investigate how anthropic and abiotic factors affect the taxonomic and functional structure of bryophyte assemblages, bearing in mind that these parameters may present responses in opposite directions (Vieira et al. 2012; Souza et al. 2020). Moreover, evaluating the taxonomic and functional structure of bryophytes in unique ecosystems subject to anthropogenic threats and forthcoming climate change in the Caatinga domain, including “Brejo de Altitude” (Torres et al. 2018), makes it possible to predict possible changes in the assemblages and plan management or mitigation actions.

In this study, we investigated the influence of abiotic (elevation, distance to water bodies, and canopy opening) and anthropogenic (edge distance) factors on the taxonomic and functional composition and diversity of epiphytic bryophytes in “Brejo de Altitude” in Northeastern Brazil. First, we checked for the existence of environmental variation between the study localities to better understand possible environmental gradients imposed on species in these forests. We sought to understand how these factors act in the organization of the taxonomic and functional structure of the assemblages. We also investigated which functional traits of the species respond to the environmental filtering posed by abiotic and/or anthropic factors. We hypothesized that abiotic and anthropic factors modulate the taxonomic and functional composition and diversity of bryophyte assemblages at a local and regional scale. We expect that environments with higher environmental quality for bryophytes (i.e., higher humidity, lower light incidence, and lower disturbance) will have a different taxonomic and functional composition compared to lower quality environments (i.e., lower humidity, higher light incidence, and higher disturbance). We expect, for example, a greater representation of generalist species and traits that optimize water uptake (e.g., costae, papillae, and lobules) and protect against solar radiation (dark pigmentation) in sites of lower environmental quality. As for the taxonomic and functional diversity, we expect them to be greater in sites of higher environmental quality.

2. Methodology

2.1 *Study area*

The data set of this study corresponds to four “Brejo de Altitude” in Northeastern Brazil (Fig. 1, also see in Supplementary material – S1). Two localities are located in the state of Pernambuco, Brazil: Professor João Vasconcelos Sobrinho Municipal Park (A1), in Caruaru, and Mata do Siriji (A2), in São Vicente Férrer. The Mata do Pau Ferro State Ecological Reserve (A3) is located in the municipality of Areia, state of Paraíba, and the Chapada do Araripe Environmental Protection Area is located in the municipalities of Crato, Barbalha and Missão Velha, state of Ceará (A4). The vegetation of A1 and A4 is classified as seasonal semideciduous forest and the vegetation of A2 and A3 as open rainforest (A2) (Santos and Tabarelli 2004; Loiola et al. 2015). The localities are at elevations varying between 510 and 940 m and are under the effect of orographic rains (Andrade-Lima 1960). The four “Brejo de Altitude” have historically been subject to anthropic pressure, mainly deforestation for expansion of agricultural activities (Santos and Tabarelli 2004; Linhares and Silva 2015). Other chronic factors are the selective exploitation of plants, extraction of wood and clay, and introduction of invasive alien species which change the structure of the forest understory (Santos and Tabarelli 2004; SEMAS 2014; Guimarães 2017; Albuquerque et al. 2017). These localities have a high diversity of bryophytes and are biologically important for the Northeast of Brazil (Pôrto et al. 2004). They also harbor species of bryophytes vulnerable to extinction, as well as other endemic vascular plants and animals (Pôrto et al. 2004; Silva et al. 2011).

2.2 *Sampling and processing of floristic data*

We analyzed a total of 58 400-m² (20 x 20 m) plots: eight in A1; 13 in A2 and A3; and 24 in A4. All plots were established at a minimum distance of 100 m from each other. The number of plots per localities was variable because we aimed at a comprehensive representation of the heterogeneity of the environments in each of the localities. We inventoried between six and eight phorophytes in each plot for collection of bryophytes. Phorophytes were inspected up to a maximum height of 2 m, and thus sampled species that live in the forest understory. Excursions for collections in A4 were conducted in 2017, and in A1, A2 and A3 in 2018. All collections were carried out during the rainy season in each locality. Bryophyte species were identified in the Bryophyte Biology Laboratory in the Federal University of Pernambuco using specific literature (Sharp et al. 1994, Buck 1998 Gradstein and Costa, 2003; Gradstein and Ilkiu-Borges 2009). The classification adopted follows that proposed by Crandall-Stotler et al. (2009) for the Division Marchantiophyta, by Goffinet et al. (2009) for the Division Bryophyta.

2.3 *Functional data*

For a qualitative analysis of the bryophyte flora, the species were classified into functional groups as to humidity and light conditions. The species were classified according to light-tolerance guilds into sun specialists, shade specialists, and generalists. It should be noted that these functional groups show fine responses to acute disturbances such as habitat loss and fragmentation in the Atlantic Forest (Alvarenga et al. 2009, 2010). The species were also classified according to life forms following Gimingham and Birse (1957), who related environmental moisture levels to life forms as a response of plants to avoid desiccation. Thus, the life forms were divided in classes of tolerance to desiccation as follows: tolerant (turf and cushion), intermediate (mat and weft), and vulnerable (fan, dendroid, pendant).

We also analyzed the presence of functional traits (Table 1) related to the limiting conditions of low humidity (e.g. papillae, large lobules in liverworts and costae in mosses) and high light incidence (e.g. dark pigmentation). These conditions are common on the edges of forest fragments or in sites with greater canopy opening (Didham and Lawton 1999), that is, environments of lower environmental quality for bryophytes. It is worth noting that in these environments, bryophytes may adopt multiple functional strategies to maximize water accumulation and protection against solar radiation (Silva et al. 2017), including the functional traits selected in this study.

All functional data were obtained from specialized studies (Sharp 1994; Costa 1999; Buck 1998; Reiner-Drehwald 2000; Gradstein et al. 2001; Gradstein and Costa 2003; Pursell 2007; Alvarenga and Porto 2007; Silva and Pôrto 2009; Oliveira et al. 2011; Bordin 2013; Visnadi 2015; Costa and Peralta 2015), and the database of the study group of the authors. In the case of some species, we considered the opinions of experts and field observations to classify the species as to light-tolerance guilds.

2.4 *Sampling of environmental factors*

Edge distance was considered an anthropic variable; canopy opening, an abiotic variable indicator of light incidence; and elevation and distance to water bodies, abiotic variables indicators of humidity. All variables were measured in relation to the center of each plot. Edge distance was measured using the ruler tool in the Google Earth Pro software, considering the nearest edge. Canopy opening was measured through hemispheric photographs (two per plot) taken at twilight time at each plot at a vertical angle of 90º using a NIKON digital camera and analyzed in the Gap Light Analyzer 2.0 software (Frazer et al. 1999). Elevation and distance to the nearest water bodies were measured with a GPS Gamin 60CSX. In this study, canopy opening was considered to be a proxy for light incidence, although this variable may also reflect chronic anthropogenic disturbance which, consequently, further intensifies the luminosity in the understory (Silva and Vibrans 2019). In turn, the variable distance was used to evaluate edge effects and represents a proxy for acute anthropic disturbance; the greater the distance from the edge, the smaller the edge effect (Didham and Ewers 2012). Distance to water bodies and elevation were considered as proxies for humidity; the shorter the distance to water bodies and the higher the elevation, the greater the air humidity conditions (Batista 2018).

2.5 *Data analysis*

All analyses were performed in the R statistical environment version 3.6.3 (R Development Core Team, 2020). The following matrices were used: (i) floristic data (incidence of species per localities, except for taxonomic diversity), (ii) environmental data (four environmental variables per localities), and (iii) functional data (traits and functional groups, considering the incidence of species) from each localities. The significance level of 5% was adopted in all statistical tests.

2.5.1 *Environmental data*

The presence of strong collinearities between the environmental variables (abiotic and anthropic) was checked through the calculation of the Variance Inflation Factor (VIF). VIF values greater than 10 are large and indicate the existence of a serious problem of multicollinearity in the model (Chatterjee and Price 1991). In this analysis, we also included localities (A1, A2, A3, A4) as a factor and vegetation type of the localities (seasonal forest or ombrophilous forest) for possible *a posteriori* tests. However, vegetation type had VIF > 10 (10.549136) and was excluded from the analyses. The other variables were included in the analyses; they had the following VIF values: canopy opening = 1.175167; elevation = 9.977011; edge distance = 1.378303; distance to water bodies = 1.197309; and locality = 2.355838. Elevation had a VIF close to 10, but we decided to keep this variable because of its recognized importance for the assembly of bryophyte communities (Santos et al. 2014; Amorim et al. 2017). To assess the environmental profile of the localities, data in the environmental matrix were standardized (range) and then assessed through a Principal Component Analysis (PCA) using the FactoMineR and Factoextra packages.

2.5.2 *Taxonomic and functional composition*

To investigate the taxonomic composition and its relationship with the environment, firstly, a Nonmetric Multidimensional Scaling (NMDS) was performed with 1000 permutations and Stress ≤ 0.2, using the metaMDS function of the vegan package (Oksanen et al. 2018). After the NMDS, we tested the correlation between the environmental variables and the floristic composition summarized in the NMDS ordination scores, with 1000 permutations, using the envfit function of the vegan package (Oksanen et al., 2018). This method calculates the centroid of the samples for each factor and determines their statistical significance by permutations. Only the significant variables were plotted in the graph.

For the analysis of functional data, we used two levels of organization. First, data were analyzed at the community level, including traits common to all bryophyte species. Then, the assemblage of liverworts was analyzed separately, including the functional data of this group only, and finally, the assemblage of mosses separately. To analyze the functional composition and identify which functional traits (traits and/or functional groups) were related to environmental filtering (abiotic and anthropic factors), community-weighted mean (CWM) trait values were first calculated, weighted by abundance (incidence on phorophytes) in each plot using the FD package. A PCA was then carried out to graphically display the functional composition of the “Brejo de Altitude”. And finally, we used the combined RLQ and fourth-corner method (with 1000 permutations) to investigate, respectively, the simultaneous and individual relationships between the functional traits and the environmental variables, using the ade4 package (Dray and Dufour 2007). Both analyses cross information from three data matrices (R: environmental, L: species and Q: functional characteristics), considering the abundance (frequência) of species in the samples (Dray et al. 2014).

2.5.3 *Taxonomic and functional diversity*

We adopted Rao’s quadratic diversity index (Q) (Rao 1982) to calculate the taxonomic (Rao_T) and functional (Rao_F) diversity because this index is not very sensitive to sample size. The index incorporates the relative abundances of the species and the distances between species pairs, in which two individuals are randomly selected. As a measure of functional diversity, this index is independent of the taxonomic component and reflects functional richness and divergence (Mouchet et al. 2010).

Generalized Linear Models (GLMs) were used to verify the relationships between taxonomic and functional diversity and the environmental variables. The identity of the four “Brejo de Altitude” was considered as a fixed effect factor in all GLMs in order to verify possible relationships on a local and regional scale. A significant interaction between “Brejos de Altitude” identity and a given environmental variable is regarded to indicate that this variable acts on a local scale, while a significant relationship between an abiotic and/or anthropic variable and the response variable, without interaction with “Brejos de Altitude” identity, suggests that this variable acts on a regional scale, that is, independently from “Brejos de Altitude” identity. The models were tested with the quasipoisson family of error, as data were not normally distributed and were overdispersed. GLMs were performed using the stats package.

3. Results

3.1 *Are abiotic or anthropic factors the most relevant environmental conditions in the studied ecological refuges?*

The abiotic and anthropogenic factors showed a wide range of variation at a local scale and were not distinctive enough to separate the four studied “Brejo de Altitude”. The cumulative variance in the first two PCA axes was 64.30% (Fig. 2). Edge distance (-0.71) and distance to water bodies (-0.58) showed the highest contribution in the first axis, while elevation (-0.64) was more relevant in the second axis, followed by canopy opening (-0.63). Few plots had high distance values to forest edges and water bodies (Fig. 2). It is noteworthy that elevation and canopy opening values were relevant on a macro scale, because “Brejo de Altitude” that had the same type of vegetation had close environmental characteristics (namely, A1 and A4, which are seasonal forests; and A2 and A3, which are rainforests). A2 showed greater cohesion between plots (upper right quadrant), reflecting greater local homogeneity, and proved to be the most distinct localities from an environmental point of view.

3.2 *How do abiotic and anthropogenic factors act in the organization of the taxonomic and functional structure of bryophyte assemblages?*

3.2.1 *Taxonomic and functional composition*

A total of 121 species were evaluated (Species details see in Supplementary material – S2 and S3), being 68 liverworts and 53 mosses. The most representative family was Lejeuneaceae (48 liverwort species), followed by the equal contribution of the moss families Fissidentaceae, Pterobryaceae, and Sematophyllaceae (7 taxa per family). The “Brejos de Altitude” A1 was the richest with 75 species, followed by A2 with 54 species, A3 with 47 species and A4 with 34 species.

The taxonomic composition (NMDS, stress = 0.15) was explained by elevation and canopy opening (Fig. 3). Plots in A4 had a more differentiated composition and formed a more cohesive group (Fig. 3). This “Brejo de Altitude” also presented the highest canopy opening values (See Fig. 1). As for functional composition, the cumulative variance in the first two PCA axes was 72.3% in the analyses of the species altogether, 80.3% for the liverwort assemblage, and 69.8% for the moss assemblage (Fig. 4). The life forms with intermediate tolerance to desiccation were the most correlated with the PCA axis 1 (0.94) considering all species (Table 2); the trait large lobules was the most relevant (0.88) for liverworts; and the generalist guild (0.91) was the most relevant for mosses (Table 2). It should be noted that the “Brejos de Altitude” A4 had a functionally distinct flora (greater cohesion between plots) in relation to the others, with the most relevant species presenting functional traits typical of sites with lower environmental quality such as dark pigmentation, large lobules, and life forms with intermediate tolerance to desiccation and belonging to the generalist guild (Fig. 4). The results of the RLQ test did not reveal global correlations between the environment and the set of functional traits for all bryophytes (Model LxQ, $p = 0.2$), mosses (Model 4 LxQ, $p = 0.1$), or liverworts (LxQ, $p = 0.1$) (See in Supplementary material – S4). However, the results of the fourth-corner analysis indicated a positive relationship of intermediate life forms with canopy opening for all bryophytes (r = 0.10, p = 0.04) and mosses (r = 0.17, p = 0.01). In the case of liverworts, the trait “large lobule” had a positive correlation with elevation (r= 0.25, p = 0.04) and canopy opening (r = 019, p = 0.01), and sun specialist species (r = 0.20, p = 0.02) had a positive relationship with canopy opening (Fig. 5).

3.2.2 Taxonomic and functional diversity

The analyzed environmental variables did not presente significant relationships with functional and taxonomic diversity índices, although the pattern of taxonomic diversity differed according to the identity of the localities (See in Supplementary material – S5).

4. Discussion

We confirmed that environmental filters shape the taxonomic and functional composition of epiphytic bryophytes and that the main drivers were canopy opening and elevation. These drives were responsible for the floristic differentiation between the localities and selected a functional composition typical of sites with lower environmental quality for bryophytes, with lower humidity and greater luminosity. This was indicated by the greater representation of sun specialists, the life forms mat and weft, and liverworts with large lobules [e.g. *Frullania ericoides* (Nees) Mont. and *Schiffneriolejeunea polycarpa* (Nees) Gradst.], especially in environments with greater canopy opening, as expected. Differently from what was expected, however, elevation did not act as a proxy for humidity in this study because localities at higher elevations presented greater canopy opening, which was in line with the finding of liverworts with large lobules in these localities. In fact, a bryophyte flora typical of open environments, and dark colored species, often prevails in sites at higher elevations and with more open vegetation (Santos et al. 2017). Higher light incidence levels in the understory may compromise the environmental quality for bryophytes in “Brejo de Altitude” at higher elevations by reducing the atmospheric humidity. Large lobules are essential for liverworts in these environments, as they enhance the accumulation of water by the plant (Renner et al. 2013). Brighter environments also select sun specialist and species growing as mats, especially in the case of mosses. This life form avoids external exposure to the substrate and allow greater adherence to vertical substrates, favoring the uptake of moisture in the bark of trunks, for example (Bates 1998). Although the environmental parameters measured did not modulate the taxonomic and functional diversity of bryophytes, they acted on the taxonomic and functional composition. This combination of results suggests that the environment may not affect the quantitative parameters of diversity, but alters the quality of the assemblages, selecting certain species and functional traits.

Studies carried out with tropical bryophytes indicate that some community parameters, such as species richness and diversity, may sometimes not show deterministic relationships with the environment (Silva and Pôrto 2009; Sporn et al. 2009; Jiang et al. 2018). However, taxonomic and functional composition is commonly shaped by environmental filters (Vieira et al. 2012; Peñaloza-Bojacá et al. 2018; Souza, et al. 2020; Garcia et al. 2020). For example, in a fragmented landscape of the Atlantic Forest in Northeastern Brazil, environmental variations resulting from horizontal (edge-core) and vertical (base-canopy) gradients had no effects on species diversity, but on composition and functional diversity (Silva and Porto 2009; Souza et al. 2020). Souza et al. (2020) highlighted that liverwort species with lobules predominated in environments with high light incidence and that the size of the lobule increased as height in the phorophyte increased, as a strategy to enhance water uptake and accumulation. This pattern was confirmed by our findings: brighter environments selected liverworts with large lobules. This trait is relevant for liverworts, as they are the more representative group in humid tropical forests (Gradstein et al. 2001) and are more sensitive than mosses and less frequent in microhabitats exposed to intense light (Mandl et al. 2009). The taxonomic and functional composition of epiphytic bryophytes was shaped along vertical (light and humidity) and altitudinal gradients also in the Amazon forest (Oliveira and ter Steege 2015; Oliveira 2018). Oliveira (2018) noted that dark pigmentation (photoprotection) and convoluted leaves (water loss minimization) were important traits for the assemblage of liverworts in habitats with high light incidence, such as in the forest canopy, and were less frequent at the base of the trunks.

The composition of bryophyte assemblages is altered especially through high turnover rates (Roos et al. 2019; Araújo et al. 2021; Batista et al. 2021), directly implying the loss of biodiversity, functional groups and ecosystem functions (Stanton and Coe 2021). However, the taxonomic and the functional composition of bryophytes may not respond to environmental conditions in the same direction. In peatland ecosystems, high taxonomic turnover was seen along precipitation and temperature gradients, but the functional composition and functional redundancy of the community as a whole remained unchanged (Robroek et al. 2017). Species of the genus *Sphagnun* predominate in this type of ecosystem, and their morpho/functional similarities allow them to maintain the functioning of the ecosystem. However, tropical forests have high environmental and microenvironmental heterogeneity and this is reflected variable species composition and functional strategies (Frahm 2003). Thus, we corroborate that changes in the environment generate changes in taxonomic and functional composition.

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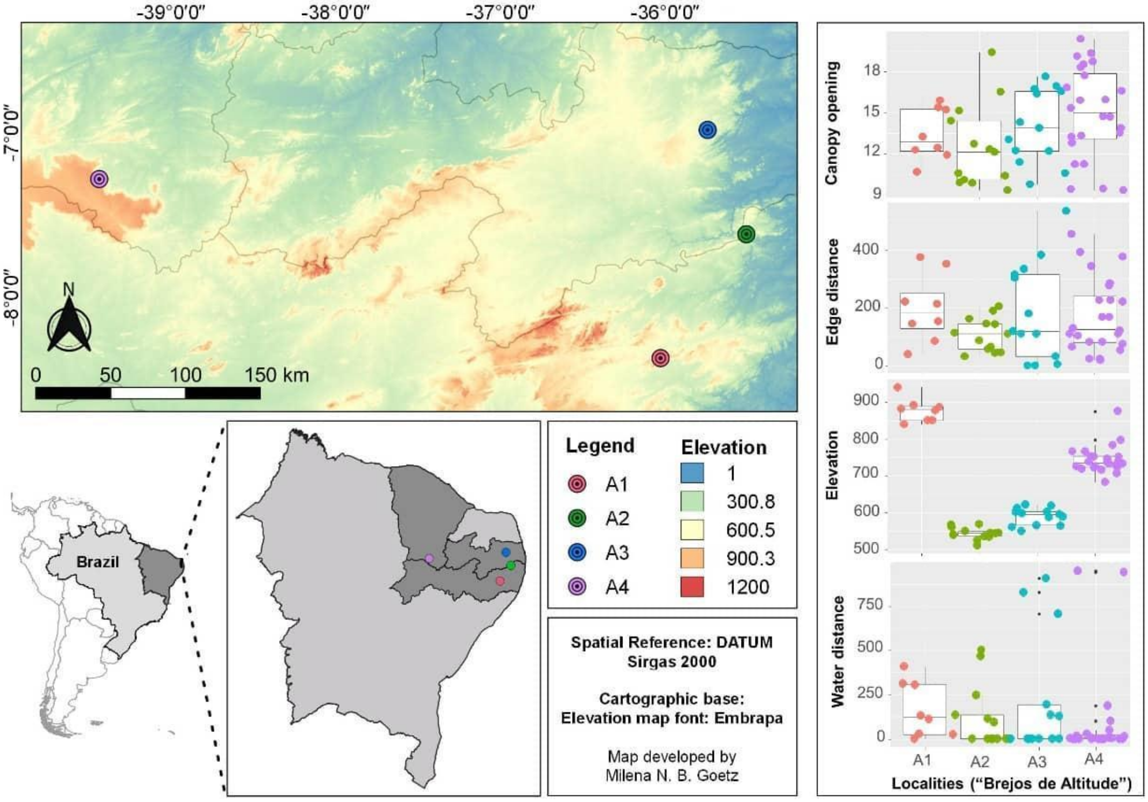


Fig. 1. Location of the "Brejos de Altitude studied in Northeast Brazil. Colors indicate different localities (A1 - Professor João Vasconcelos Sobrinho Municipal Park, state of Pernambuco; A2 - Mata do Siriji, state of Pernambuco; A3 - Mata do Pau Ferro State Ecological Reserve, state of Paraíba; and A4 - Chapada do Araripe Environmental Protection Area,state of Ceará). To the left, the charts portray the variation the environmental data from the four localities. Proxies of humidity (Elevation and Distance to water bodies), light incidence (canopy opening), and disturbance (Edge distance).

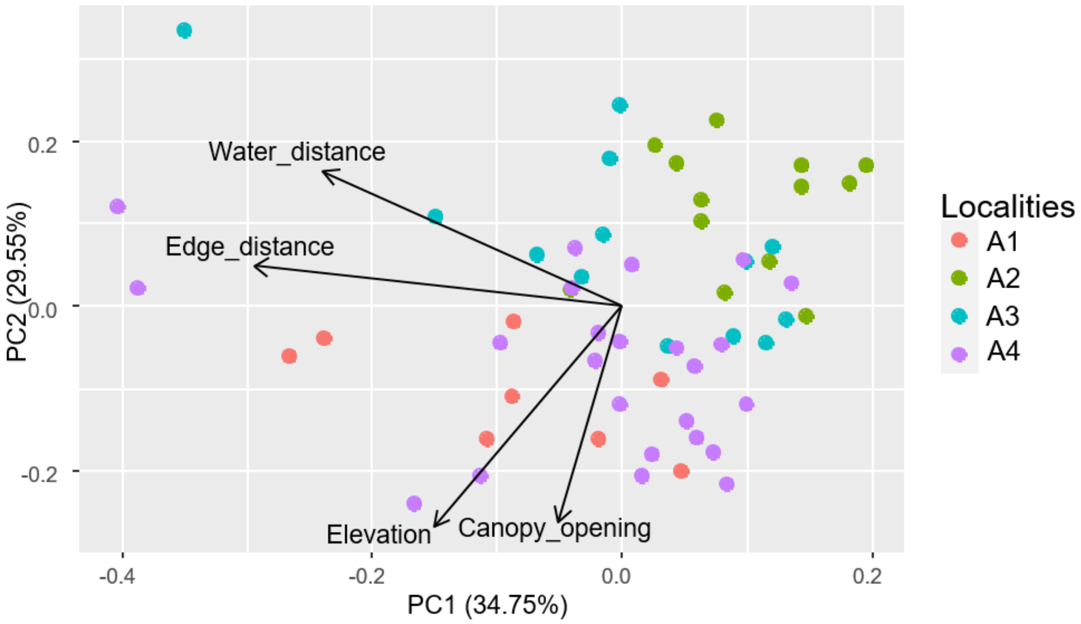


Fig. 2. Principal Component Analysis (PCA) ordination diagram of the environmental data from the four studied "Brejo de Altitude".

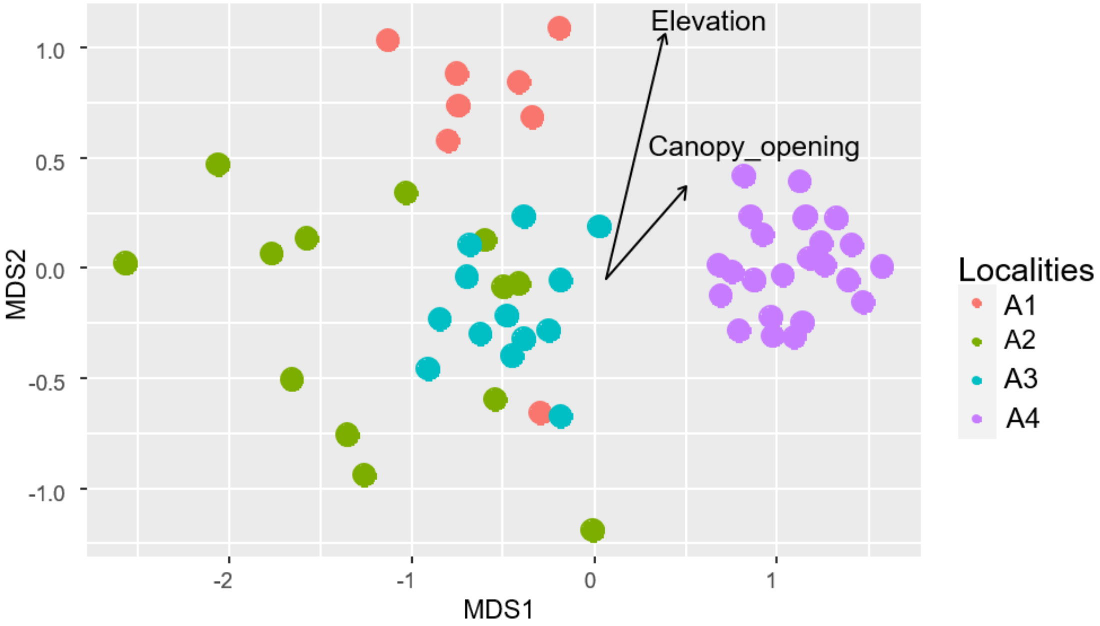


Fig. 3. Nonmetric Multidimensional Scaling (NMDS) ordination diagram of the four "Brejo de Altitude" showing affinities based on floristic composition. Black vectors represent significant correlations ($p<0.05$) between NMDS scores and abiotic factors (Canopy opening and Elevation).

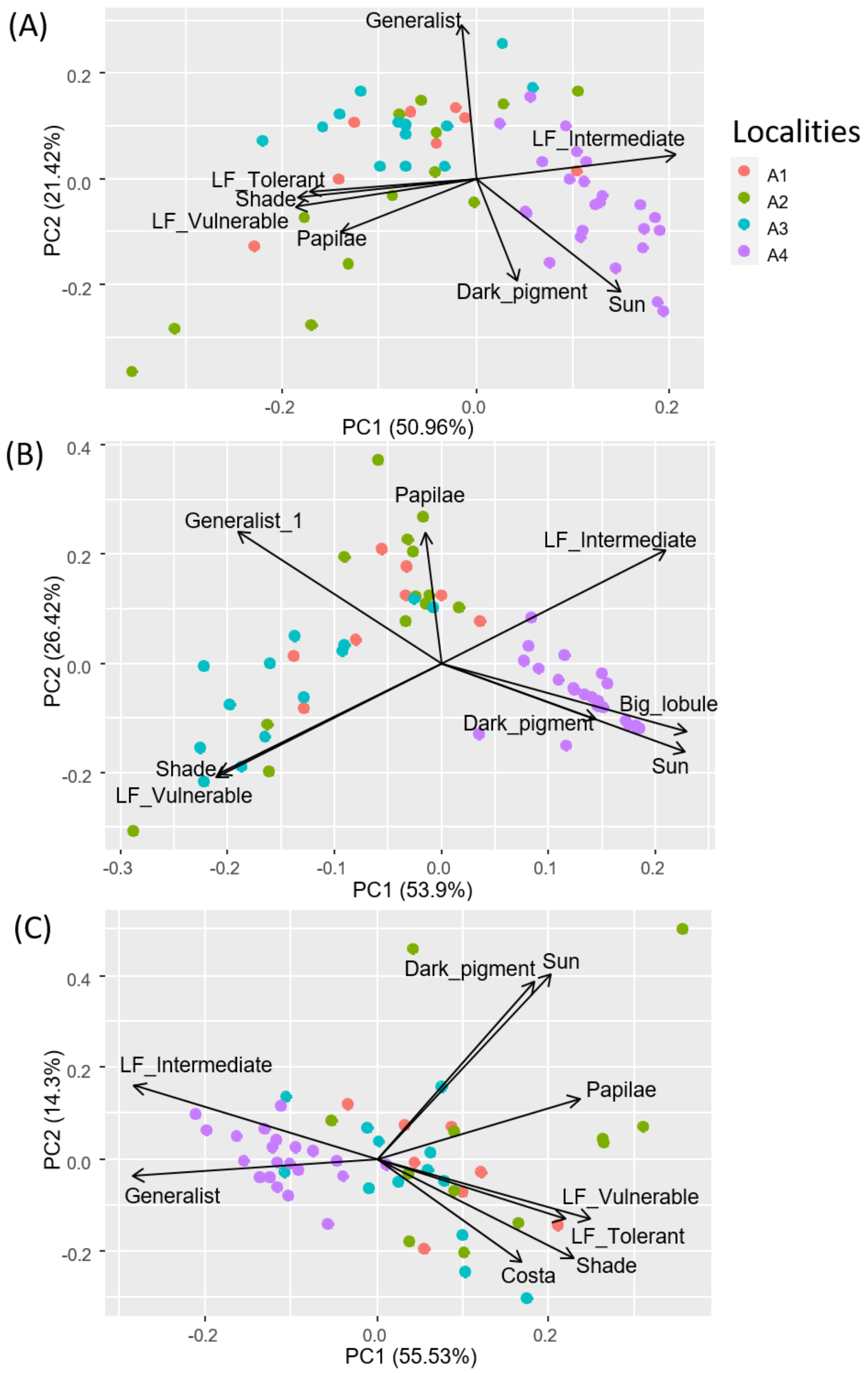


Fig. 4. Principal Component Analysis (PCA) ordination diagrams of CWM matrices according to functional traits. (a) All bryophytes; (b) liverwort assemblage; and (c) moss assemblage.

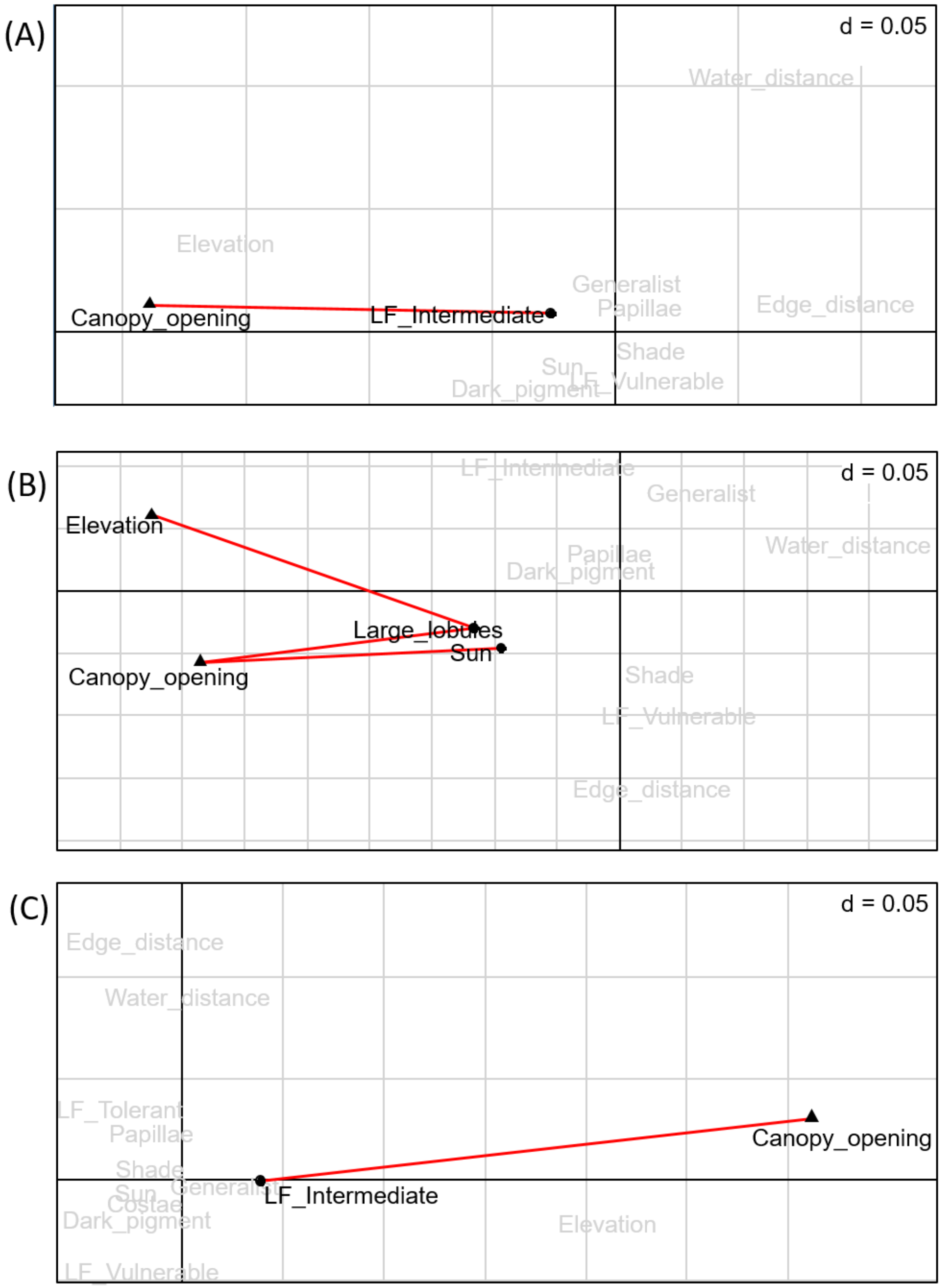


Fig. 5. Results of the combined RLQ and fourth-corner analyses. Red lines indicate positive associations ($p < 0.05$) identified by the fourth-corner method on the factorial map of the RLQ analysis. (a) all bryophytes; (b) liverworts; (c) mosses.

Table 1. Functional traits selected and compiled for analysis of presence/absence in the species.

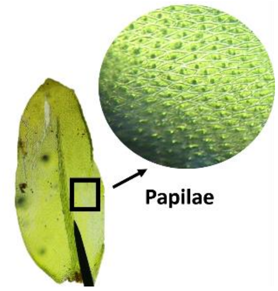
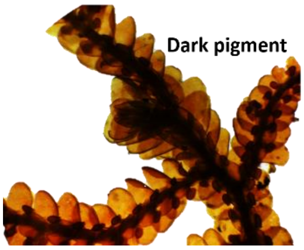
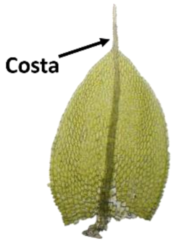
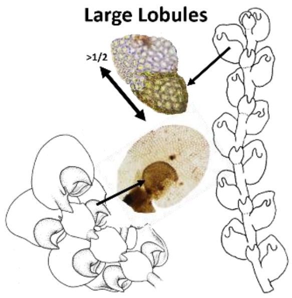
	Traits	Function	Reference
	**Papillae** (cellular projection of the leave) **In liverworts and Mosses.**	Optimization of water intake and regulation	Kürschner (2004).
	**Dark pigment** (secundary pigment) **In liverworts and Mosses.**	Mitigation of damages caused by solar radiation	Melick and Seppel (1994); Deltoro et al. (1998); Oliveira (2018).
	**Costa** (elongate cells) **In Mosses.**	Rapid water absorption and transport	Frahm (1985); Zastrow (1934); Henriques et al. (2017).
	**Large lobules** (lobules ≥ 1/2 lobe length or presence of saccate lobe) **In liverworts.**	Storage of extracellular water	Renner et al. (2013); Renner (2015); Souza et al. (2020).

Table 2. Correlation between community-weighted mean (CWM) trait values and the first two PCA axes, explanatory variance of each of the axes, and eigenvalues. Stronger correlations with each axis are in bold.

	All bryophytes		Liverworts		Mosses	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Large lobules	-	-	**0.89**	0.33	-	-
Costa	-	-	-	-	0.54	-0.36
Dark pigmentation	-0.20	0.59	0.55	0.27	0.59	0.62
Papillae	0.65	0.31	-0.05	-0.63	0.76	0.21
LF Tolerant	**0.80**	0.074	-	-	0.70	-0.21
LF Intermediate	**-0.97**	-0.13	**0.80**	-0.55	**-0.91**	0.25
LF Vulnerable	**0.88**	0.16	**-0.80**	0.55	0.79	-0.21
Generalist	0.06	**-0.89**	-0.72	-0.64	**-0.91**	-0.05
Sun specialist	-0.70	0.65	**0.87**	0.43	0.65	0.65
Shade specialist	**0.86**	0.10	-0.79	0.54	0.73	-0.35
Explanatory variance (%)	50.96	21.42	53.9	26.42	55.53	14.3
Eigenvalues	4.08E+00	1.71E+00	4.31E+00	2.11E+00	5.00E+00	1.29E+00

Supplementary material

S1 Table. Characteristics of the “Brejo de Altitude” included in the study.

“Brejos de Altitude”	Size (ha)	Annual Precipitation (mm)	Annual Mean Temperature (°C)	Maximum Elevation (m)
A1	359	630	23,2	950
A2	630	1.076	23,1	750
A3	607	1.072	22	600
A4	4.485	1.033	25	950

Data source: WolrdClim database and published studies conducted in the selected “Brejos de Altitude”.

S2 Table. List of liverwort (L) and moss (M) species occurring in the four “Brejos de Altitude” (A1, A2, A3, and A4).

Species	Group	A1	A2	A3	A4
Anoplolejeunea conferta (C.F.W.Meissn. ex Spreng.)	L	1	0	0	0
Brachythecium ruderale (Brid.) W.R.Buck	M	1	0	0	0
Brittonodoxa subpinnata (Brid.) W.R. Buck, P.E.A.S.Câmara & Carv.-Silva	M	1	1	0	1
Bryopteris filicina (Sw.) Nees	L	1	1	0	0
Bryum capillare Hedw.	M	0	0	0	1
Calymperes afzelii Sw.	M	1	1	1	1

Calymperes palisotii Schwägr.	M	1	1	1	1
Campylopus heterostachys (Hampe) A.Jaeger	M	1	0	0	0
Caudalejeunea lehmanniana (Gottsche) A.Evans	L	0	0	1	0
Ceratolejeunea ceratantha (Nees & Mont.) Steph.	L	1	0	0	0
Ceratolejeunea confusa R.M.Schust	L	1	1	1	0
Ceratolejeunea cornuta (Lindenb.) Schiffn	L	1	1	1	0
Ceratolejeunea cubensis (Mont.) Schiffn.	L	0	1	1	0
Ceratolejeunea fallax (Lehm. & Lindenb.) Bonner	L	1	0	0	0
Ceratolejeunea laetefusca (Austin) R.M.Schust.	L	1	1	1	0
Ceratolejeunea minuta Dauphin	L	0	1	0	0
Cheilolejeunea adnata (Kunze) Grolle	L	1	1	0	0
Cheilolejeunea holostipa (Spruce) Grolle & R.-L.Zhu	L	0	0	1	0
Cheilolejeunea oncophylla (Aongström) Grolle & E.Reiner	L	0	1	0	0
Cheilolejeunea rigidula (Nees ex Mont.) R.M. Schust.	L	1	1	1	1
Cheilolejeunea trifaria (Reinw. et al.) Mizut.	L	1	1	0	0
Cheilolejeunea unciloba (Lindenb.) Malombe	L	0	0	1	0
Cheilolejeunea xanthocarpa (Lehm. & Lindenb.) Malombe	L	1	1	0	0
Cololejeunea camillii (Lehm.) A. Evans	L	0	0	0	1
Cololejeunea contractiloba A. Evans	L	0	0	0	1
Cololejeunea verwimpii Tixier	L	1	0	1	0
Crossomitrium patrisiae (Brid.) Müll. Hal.	M	1	1	0	0

Cryptolophocolea martiana (Nees) L. Söderstr., Crand.-Stotl.	L	1	0	0	0
Cylindrocolea rhizantha (Mont.) R.M.Schust.	L	0	0	0	1
Daltonia splachnoides (Sm.) Hook. & Taylor	M	1	1	0	0
Dibrachiella auberiana (Mont.) X.Q. Shi, R.L. Zhu & Gradst.	L	0	1	0	0
Donnellia commutata (Müll.Hal.) W.R.Buck	M	0	0	0	1
Drepanolejeunea aracauriae Steph	L	1	0	0	0
Drepanolejeunea bidens (Steph.) A.Evans	L	1	0	0	0
Drepanolejeunea fragilis Bischl.	L	1	1	1	0
Entodontopsis leucostega (Brid.) W.R.Buck & Ireland	M	0	0	1	1
Entodontopsis nitens (Mitt.) W.R.Buck & Ireland	M	0	0	1	0
Erpodium coronatum (Hook. & Wilson) Mitt.	M	0	0	0	1
Fabronia ciliaris (Brid.) Brid.	M	0	0	0	1
Fabronia macroblepharis Schwägr.	M	0	0	0	1
Fissidens brevipes Besch.	M	0	0	0	1
Fissidens elegans Brid.	M	0	0	0	1
Fissidens gardneri Mitt.	M	0	0	0	1
Fissidens lagenarius Mitt.	M	1	0	0	0
Fissidens pallidinervis Mitt.	M	1	1	1	1
Fissidens radicans Mont.	M	0	1	0	1
Fissidens serratus Müll. Hal.	M	1	1	0	0
Floribundaria flaccida (Mitt.) Broth.	M	1	1	0	0

Frullania dusenii Steph.	L	0	0	0	1
Frullania ericoides (Nees) Mont.	L	0	0	1	1
Frullania kunzei (Lehm. & Lindenb.) Lehm. & Lindenb.	L	0	1	1	1
Frullania platycalyx Herzog	L	0	0	0	1
Groutiella apiculata (Hook.) H.A.Crum & Steere	M	1	0	1	0
Harpalejeunea stricta (Lindenb. & Gottsche) Steph.	L	1	1	1	0
Henicodium geniculatum (Mitt.) W.R.Buck	M	1	1	1	0
Isopterygium subbrevisetum (Hampe) Broth.	M	1	1	1	0
Isopterygium tenerifolium Mitt.	M	1	1	1	0
Isopterygium tenerum (Sw.) Mitt.	M	1	1	1	1
Jaegerina scariosa (Lorentz) Arzeni	M	1	1	1	1
Lejeunea adpressa Nees	L	1	1	1	0
Lejeunea aphanes Spruce	L	1	1	1	0
Lejeunea controversa Gottsche	L	0	1	1	0
Lejeunea flava (Sw.) Nees	L	1	1	1	1
Lejeunea glaucescens Gottsche	L	1	1	1	1
Lejeunea laetevirens Nees & Mont.	L	1	1	1	0
Lejeunea parviloba Ångstr.	L	0	1	0	0
Lejeunea perpapillosa E. Reiner & Pôrto	L	1	0	0	0
Lejeunea phyllobola Nees & Mont.	L	1	1	1	1
Lejeunea quinqueumbonata Spruce	L	1	1	0	0

Lejeunea subsessilis Spruce	L	1	1	0	0
Lepidopilum amplirete Müll. Hal.	M	1	0	0	0
Lepidopilum pallidonitens (Müll. Hal.) Broth.	M	1	1	0	0
Leucoloma cruegerianum (Müll.Hal.) A.Jaeger	M	1	0	0	0
Lophocolea bidentata (L.) Dumort.	L	1	0	0	0
Lophocolea liebmanniana Gottsche	L	1	0	0	0
Lopholejeunea nigricans (Lindenb.) Schiffn.	L	1	1	1	0
Lopholejeunea subfusca (Nees) Schiffn.	L	1	1	1	0
Marchesinia brachiata (Sw.) Schiffn.	L	1	1	1	0
Metalejeunea cucullata (Reinw. et al.) Grolle	L	1	0	0	0
Metzgeria aurantiaca Steph.	L	0	1	0	0
Metzgeria ciliata Raddi	L	1	1	1	0
Metzgeria furcata (L.) Dumort.	L	1	1	1	0
Microcalpe subsimplex (Hedw.) W.R. Buck	M	1	1	1	1
Microlejeunea bullata (Taylor) Steph.	L	0	0	1	1
Microlejeunea epiphylla Bischl.	L	1	1	1	1
Myriocoleopsis minutissima (Sm) R.L.Zhu, Y.Yu & Pócs	L	0	0	0	1
Neckeropsis disticha (Hedw.) Kindb.	M	0	1	0	0
Neckeropsis undulata (Hedw.) Reichardt	M	1	1	0	0
Ochrobryum gardneri (Müll.Hal.) Lindb.	M	1	0	0	1
Octoblepharum albidum Hedw.	M	1	1	1	1

Orthostichidium quadrangulare (Schwägr.) B.H. Allen & Magill	M	1	0	0	0
Otigoniolejeunea huctumalcensis (Lindenb. & Gottsche)	L	0	1	0	0
Pilosium chlorophyllum (Hornsch.) Müll. Hal.	M	1	1	0	0
Pilotrichum evanescens (Müll.Hal.) Müll.Hal.	M	1	1	1	0
Pinnatella minuta (Mitt.) Broth.	M	0	1	0	0
Pireella pohlii (Schwägr.) Cardot	M	0	1	0	0
Plagiochila disticha (Lehm. & Lindenb.) Lindenb.	L	0	0	1	0
Plagiochila martiana (Nees) Lindenb.	L	0	0	1	0
Plagiochila montagnei Nees	L	1	1	1	0
Plagiochila patula (Sw.) Lindenb.	L	1	0	0	0
Plagiochila raddiana Lindenb.	L	1	0	0	1
Porotrichum substriatum (Hampe) Mitt.	M	1	1	0	0
Pterogonidium pulchellum (Hook.) Müll.Hal.	M	0	1	0	0
Pycnolejeunea contigua (Nees) Grolle	L	0	1	0	1
Radula recubans Taylor	L	1	1	0	0
Rectolejeunea versifolia (Schiffn.) L.Söderstr. et A.Hagborg	L	0	1	0	0
Rhynchostegium serrulatum (Hedw.) A.Jaeger	M	1	0	0	0
Schiffneriolejeunea polycarpa (Nees) Gradst.	L	1	1	1	1
Schwetschkea fabronioides (Welw. & Duby) Broth.	M	1	0	1	0
Sematophyllum adnatum (Michx.) Brid.	M	1	1	1	0
Stereophyllum radiculosum (Hook.) Mitt.	M	0	0	0	1

Stictolejeunea squamata (Willd. ex Weber) Schiffn.	L	1	1	0	0
Symbiezidium barbiflorum (Lindenb. & Gottsche) A. Evans	L	0	1	1	0
Syrrhopodon incompletus Schwägr.	M	1	1	1	0
Syrrhopodon ligulatus Mont.	M	1	0	1	1
Syrrhopodon parasiticus (Brid.) Besch.	M	1	1	1	1
Syrrhopodon prolifer (Brid.) Besch.	M	1	0	1	0
Taxithelium planum (Brid.) Mitt.	M	0	1	0	0
Telaranea diacantha (Mont.) Engel & Merr.	L	1	0	0	0
Vitalia galipensis (Müll. Hal.) P.E.A.S.Câmara, Carv.-Silva & W.R. Buck	M	1	1	0	1
Zelometeorium patulum (Hedw.) Manuel	M	1	1	0	0

S3. Functional characteristics (functional groups and traits) of the species recorded for the four "Brejos de Altitude". Light tolerance guilds: Generalist (G), Shade specialist (Sh), and Sun specialist (S). Life forms: mat and weft (Intermediate = I); turf and cushion (Tolerant = T); fan, dendroid, and pendent (Vulnerable = V). Presence of functional traits: Dark pigment, Papillae, Large lobules, and Costa.

Species	**Light-tolerance guilds**	**Life forms**	**Dark pigmentation**	**Papillae**	**Large lobules**	**Costae**
Anoplolejeunea conferta	Generalist	Intermediate	0	0	1	0
Brachythecium ruderale	Generalist	Intermediate	0	1	0	1
Brittonodoxa subpinnata	Generalist	Intermediate	0	0	0	0
Bryopteris filicina	Shade	Vulnerable	1	0	1	0
Bryum capillare	Generalist	Tolerant	0	0	0	1
Calymperes afzelii	Generalist	Tolerant	0	1	0	1
Calymperes palisotii	Generalist	Tolerant	0	1	0	1
Campylopus heterostachys	Sun	Tolerant	1	0	0	1
Caudalejeunea lehmanniana	Sun	Intermediate	1	0	1	0
Ceratolejeunea ceratantha	Generalist	Intermediate	1	0	0	0
Ceratolejeunea confusa	Generalist	Intermediate	1	0	0	0
Ceratolejeunea cornuta	Sun	Intermediate	1	0	0	0
Ceratolejeunea cubensis	Generalist	Intermediate	1	0	0	0
Ceratolejeunea fallax	Generalist	Intermediate	1	0	0	0

Ceratolejeunea laetefusca	Generalist	Intermediate	1	0	0	0
Ceratolejeunea minuta	Generalist	Intermediate	1	0	0	0
Cheilolejeunea adnata	Generalist	Intermediate	0	0	1	0
Cheilolejeunea holostipa	Generalist	Intermediate	1	0	1	0
Cheilolejeunea oncophylla	Generalist	Intermediate	1	1	1	0
Cheilolejeunea rigidula	Generalist	Intermediate	1	0	0	0
Cheilolejeunea trifaria	Generalist	Intermediate	1	0	0	0
Cheilolejeunea unciloba	Generalist	Intermediate	0	0	0	0
Cheilolejeunea xanthocarpa	Sun	Intermediate	1	0	1	0
Cololejeunea camillii	Generalist	Intermediate	0	0	0	0
Cololejeunea contractiloba	Generalist	Intermediate	0	1	1	0
Cololejeunea verwimpii	Generalist	Intermediate	0	0	0	0
Crossomitrium patrisiae	Generalist	Intermediate	0	0	0	0
Cryptolophocolea martiana	Shade	Intermediate	0	0	0	0
Cylindrocolea rhizantha	Shade	Intermediate	0	0	0	0
Daltonia splachnoides	Generalist	Tolerant	0	0	0	1

Dibrachiella auberiana	Sun	Intermediate	1	0	1	0
Donnellia commutata	Generalist	Intermediate	0	0	0	0
Drepanolejeunea aracauriae	Generalist	Intermediate	0	0	1	0
Drepanolejeunea bidens	Generalist	Intermediate	0	0	1	0
Drepanolejeunea fragilis	Generalist	Intermediate	0	0	1	0
Entodontopsis leucostega	Generalist	Intermediate	0	0	0	1
Entodontopsis nitens	Generalist	Intermediate	0	0	0	1
Erpodium coronatum	Generalist	Intermediate	0	0	0	0
Fabronia ciliaris	Generalist	Intermediate	0	0	0	1
Fabronia macroblepharis	Sun	Intermediate	0	0	0	1
Fissidens brevipes	Generalist	Tolerant	1	1	0	1
Fissidens elegans	Generalist	Tolerant	1	1	0	1
Fissidens gardneri	Shade	Tolerant	1	1	0	1
Fissidens lagenarius	Shade	Tolerant	0	1	0	1
Fissidens pallidinervis	Shade	Tolerant	1	1	0	1
Fissidens radicans	Generalist	Tolerant	1	0	0	1
Fissidens serratus	Shade	Tolerant	1	1	0	1

Floribundaria flaccida	Shade	Vulnerable	0	1	0	1
Frullania dusenii	Sun	Intermediate	1	0	1	0
Frullania ericoides	Sun	Intermediate	1	0	1	0
Frullania kunzei	Sun	Intermediate	1	0	1	0
Frullania platycalyx	Sun	Intermediate	1	0	1	0
Groutiella apiculata	Sun	Tolerant	1	1	0	1
Harpalejeunea stricta	Sun	Intermediate	0	0	0	0
Henicodium geniculatum	Generalist	Vulnerable	0	1	0	1
Isopterygium subbrevisetum	Generalist	Intermediate	0	0	0	0
Isopterygium tenerifolium	Generalist	Intermediate	0	0	0	0
Isopterygium tenerum	Generalist	Intermediate	0	0	0	0
Jaegerina scariosa	Generalist	Vulnerable	0	0	0	1
Lejeunea adpressa	Generalist	Intermediate	0	0	1	0
Lejeunea aphanes	Generalist	Intermediate	0	0	1	0
Lejeunea controversa	Generalist	Intermediate	0	0	0	0
Lejeunea flava	Generalist	Intermediate	0	0	0	0
Lejeunea glaucescens	Generalist	Intermediate	0	0	0	0
Lejeunea laetevirens	Generalist	Intermediate	0	1	0	0

Lejeunea parviloba	Generalist	Intermediate	0	0	0	0
Lejeunea perpapillosa	Generalist	Intermediate	0	1	0	0
Lejeunea phyllobola	Generalist	Intermediate	0	0	0	0
Lejeunea quinqueumbonata	Shade	Intermediate	0	0	0	0
Lejeunea subsessilis	Generalist	Intermediate	0	*0*	*0*	0
Lepidopilum amplirete	Shade	Intermediate	0	0	0	1
Lepidopilum pallidonitens	Generalist	Intermediate	0	1	0	1
Leucoloma cruegerianum	Shade	Tolerant	1	1	0	1
Lophocolea bidentata	Shade	Intermediate	0	0	0	0
Lophocolea liebmanniana	Shade	Intermediate	0	0	0	0
Lopholejeunea nigricans	Sun	Intermediate	1	0	0	0
Lopholejeunea subfusca	Sun	Intermediate	1	0	1	0
Marchesinia brachiata	Sun	Intermediate	1	0	0	0
Metalejeunea cucullata	Generalist	Intermediate	0	0	1	0
Metzgeria aurantiaca	Generalist	Intermediate	0	0	0	0
Metzgeria ciliata	Generalist	Intermediate	0	0	0	0
Metzgeria furcata	Generalist	Intermediate	0	0	0	0

Microcalpe subsimplex	Generalist	Intermediate	0	0	0	0
Microlejeunea bullata	Sun	Intermediate	0	0	1	0
Microlejeunea epiphylla	Sun	Intermediate	0	0	1	0
Myriocoleopsis minutissima	Generalist	Intermediate	0	0	1	0
Neckeropsis disticha	Shade	Vulnerable	0	0	0	1
Neckeropsis undulata	Shade	Vulnerable	0	0	0	1
Ochrobryum gardneri	Sun	Tolerant	0	0	0	1
Octoblepharum albidum	Generalist	Tolerant	0	0	0	1
Orthostichidium quadrangulare	Shade	Vulnerable	0	0	0	0
Otigoniolejeunea huctumalcensis	Generalist	Intermediate	1	0	0	0
Pilosium chlorophyllum	Generalist	Intermediate	1	0	0	0
Pilotrichum evanescens	Shade	Vulnerable	0	1	0	1
Pinnatella minuta	Shade	Vulnerable	0	1	0	1
Pireella pohlii	Shade	Vulnerable	1	0	0	1
Plagiochila disticha	Shade	Vulnerable	0	0	0	0
Plagiochila martiana	Shade	Vulnerable	0	0	0	0
Plagiochila montagnei	Shade	Vulnerable	0	0	0	0

Plagiochila patula	Shade	Vulnerable	0	0	0	0
Plagiochila raddiana	Shade	Vulnerable	0	0	0	0
Porotrichum substriatum	Shade	Vulnerable	1	0	0	1
Pterogonidium pulchellum	Generalist	Intermediate	0	0	0	1
Pycnolejeunea contigua	Sun	Intermediate	0	0	0	0
Radula recubans	Shade	Intermediate	0	0	1	0
Rectolejeunea versifolia	Generalist	Intermediate	0	0	0	0
Rhynchostegium serrulatum	Generalist	Intermediate	0	0	0	1
Schiffneriolejeunea polycarpa	Sun	Intermediate	1	0	1	0
Schwetschkea fabronioides	Shade	Intermediate	0	0	0	1
Sematophyllum adnatum	Generalist	Intermediate	0	0	0	0
Stereophyllum radiculosum	Generalist	Intermediate	0	1	0	1
Stictolejeunea squamata	Generalist	Intermediate	1	0	0	0
Symbiezidium barbiflorum	Generalist	Intermediate	1	0	0	0
Syrrhopodon incompletus	Shade	Tolerant	0	0	0	1
Syrrhopodon ligulatus	Shade	Tolerant	0	1	0	1

Syrrhopodon parasiticus	Sun	Tolerant	0	1	0	1
Syrrhopodon prolifer	Generalist	Tolerant	0	1	0	1
Taxithelium planum	Generalist	Intermediate	0	1	0	0
Telaranea diacantha	Shade	Intermediate	0	0	0	0
Vitalia galipensis	Generalist	Intermediate	0	0	0	0
Zelometeorium patulum	Generalist	Vulnerable	0	1	0	1

S4 Table. Results of RLQ analysis

	Bryophytes	**Liverworts**	**Mosses**
Inertia % Axis 1	75.2	86.6	75.1
Correlation	0.18	0.31	0.2
p Model 2 (RxL)	0.09	0.01	0.2
p Model 4 (LxQ)	0.2	0.1	0.1

S5 Table. GLM results for taxonomic (Rao_T) and functional (Rao_F) diversity.

				95% CI	
Model Factors	**p-value**	**β**	**SE**	**Lower**	**Upper**
Rao_T					
Elevation	0.6068	1.461e-04	2.821e-04	-4.087904e-04	6.968690e-04
Edge_distance	0.2623	-7.982e-05	7.040e-05	-2.179102e-04	5.804903e-05
Water_distance	0.2757	3.618e-05	3.283e-05	-2.837358e-05	1.003356e-04
Canopy_opening	0.1548	-3.914e-03	2.710e-03	-9.225257e-03	1.396251e-03
factor(Brejo)A2	0.7273	-3.349e-02	02 9.551e-02	-2.212445e-01	1.531429e-01
factor(Brejo)A3	0.8589	1.511e-02	8.457e-02	-1.511436e-01	1.803546e-01
factor(Brejo)A4	0.0258 *	-1.034e-01	4.500e-02	-1.918046e-01	-1.540395e-02
Rao_F					
Elevation	0.14099	1.038e-03	6.938e-04	-3.347856e-04	2.384755e-03
Edge_distance	0.15201	2.585e-04	1.777e-04	-9.038148e-05	6.063007e-04
Water_distance	0.34230	-8.041e-05	8.387e-05	-2.462172e-04	8.262621e-05
Canopy_opening	0.77021	-1.998e-03	6.803e-03	-1.533764e-02	1.133215e-02
factor(Brejo)A2	0.12997	3.622e-01	2.352e-01	-1.023623e-01	8.198229e-01
factor(Brejo)A3	0.27492	2.308e-01	2.091e-01	-1.821271e-01	6.375564e-01
factor(Brejo)A4	0.68374	-4.548e-02	1.110e-01	-2.642215e-01	1.709391e-01

Rao_T: Observations = 58

Residual Deviance = 0.14352 (df=50); Null Deviance =0.28069 (df = 57)

Rao_F: Observations = 58

Residual Deviance = 0.47899 (df=50); Null Deviance =0.71639 (df = 57)

Note: $*p<0.05$

5 CONCLUSÕES

Constatamos que a brioflora apresenta singularidades florísticas regionais e que está sujeita a mudanças ao longo do tempo. Isto reforça ainda mais a importância da conservação destas florestas, pois implica diretamente na manutenção da riqueza, composição taxonômica e funcional das assembleias de briófitas. Compreendemos nesta tese a importância de avaliar a influência de fatores antrópicos, especialmente crônicos, como também estruturais da floresta (e.g. cobertura da vegetação e abertura do dossel) que refletem variações nas condições de luz e umidade em que as briófitas do sub-bosque são submetidas.

Observamos mudanças especialmente na composição taxonômica e funcional, que, em geral, reagem de forma acoplada em escala temporal e espacial. Isto é, a substituição de espécies é dada por táxons com características funcionais distintas, o que reflete na alteração do espaço funcional da comunidade. A falta de relação entre os fatores ambientais e a diversidade beta taxonômica e funcional ao longo do tempo, ainda assim sugere que condições climáticas (e.g. umidade, pluviosidade) sejam relevantes para compreender a montagem das assembleias de briófitas. Uma prova disto, seria a substituição de espécies que exigem umidade e sombra por espécies de hábitos generalistas. Em relação ao aumento da riqueza de espécies constatado nas três áreas estudadas, as consequências de perturbações antrópicas, sobretudo crônicas (e.g. número de habitantes da região) demonstram ser minimizadas com o aumento da cobertura da vegetação da paisagem (devido ao acréscimo de espécies exigentes de umidade e sombra) ou mais severas quando a cobertura da vegetação é estável (devido a maior proporção das espécies de hábitos generalistas).

Em escala espacial, mudanças na composição de espécies de briófitas epífitas e nas características funcionais estão associadas predominantemente aos fatores ambientais (e.g. abertura da copa e altitude) e não por pressão antrópica (distância da borda). Locais elevados e com maior abertura da copa selecionam uma flora distinta, incluindo espécies típicas de sol e hepáticas que possuem atributos que minimizam a dessecação (e.g. lóbulos grandes). Estes resultados sugerem que mesmo ambientes distantes da borda podem apresentar condições locais de maior luminosidade, o que implica na filtragem de espécies. Fato preocupante para conservação, pois é possível que efeitos que intensifiquem a abertura da copa (e.g. especialmente de origem antrópica) favoreçam apenas as espécies tolerantes à intensa luminosidade e dessecação, em substituição das que demandam maior qualidade ambiental (e.g. especialistas de sombra).

Por fim, verificamos que, apesar da importância biológica dos Brejos de Altitude, estes estão sujeitos a mudanças temporais e espaciais. Nossos achados sugerem que cenários com aumento da perturbação antrópica impõem filtros como maior luminosidade e menor umidade, selecionando espécies com atributos mais resistentes à dessecação (e.g. generalistas em relação à luz, especialistas de sol, pigmentação escura, formas de vida tapete, hepáticas de lóbulos grandes). Cenário que implica na perda de espécies vulneráveis, que demandam umidade e sombra (e.g. especialistas de sombra, formas de vida pendentes e flabeladas e hepáticas de lóbulos pequenos). Estas espécies exercem um papel funcional importante no balanço hídrico dos microambientes e sevem de abrigo para pequenos organismos, aumentando a complexidade estrutural da floresta.

Destacamos que é relevante que ações de restauração florestal nos Brejos de Altitude sejam implementadas e ampliadas em escala de paisagem para manter a brioflora. Também, ações que priorizem a fiscalização ambiental para evitar perturbações agudas, como a expansão do uso da terra para atividades agrícolas (especialmente em A2, Mata do Siriji em São Vicente Férrer-PE), e da urbanização desordenada no entorno das manchas florestais. Especialmente, promover incentivos em educação ambiental que conscientizem a sociedade sobre o impacto negativo das perturbações antrópicas, inclusive crônicas, para a biodiversidade (e.g. perda de espécies vulneráveis e de serviços ecossistêmicos relacionados à regulação do clima e provimento hídrico). Além disso, programas de capacitação dos agricultores rurais com práticas de manejo sustentável e implementação de agroflorestas são atividades que podem contribuir para diminuir a pressão antrópica nessas localidades, encorajando o uso sustentável dos recursos naturais. Por fim, tais ações conduzem a um caminho de melhora na qualidade ambiental dos Brejos de Altitude que reflete positivamente para as briófitas e, de forma geral, para a conservação destas florestas.

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APÊNDICE. A AVENTURA DE JÉSSICA EM UM BREJO DE ALTITUDE

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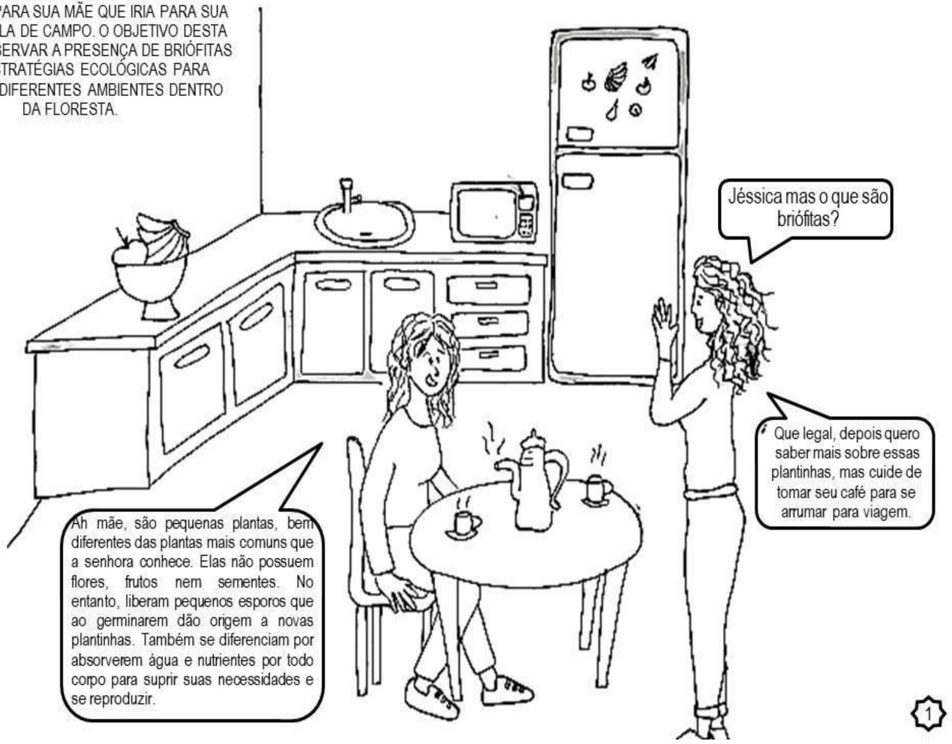
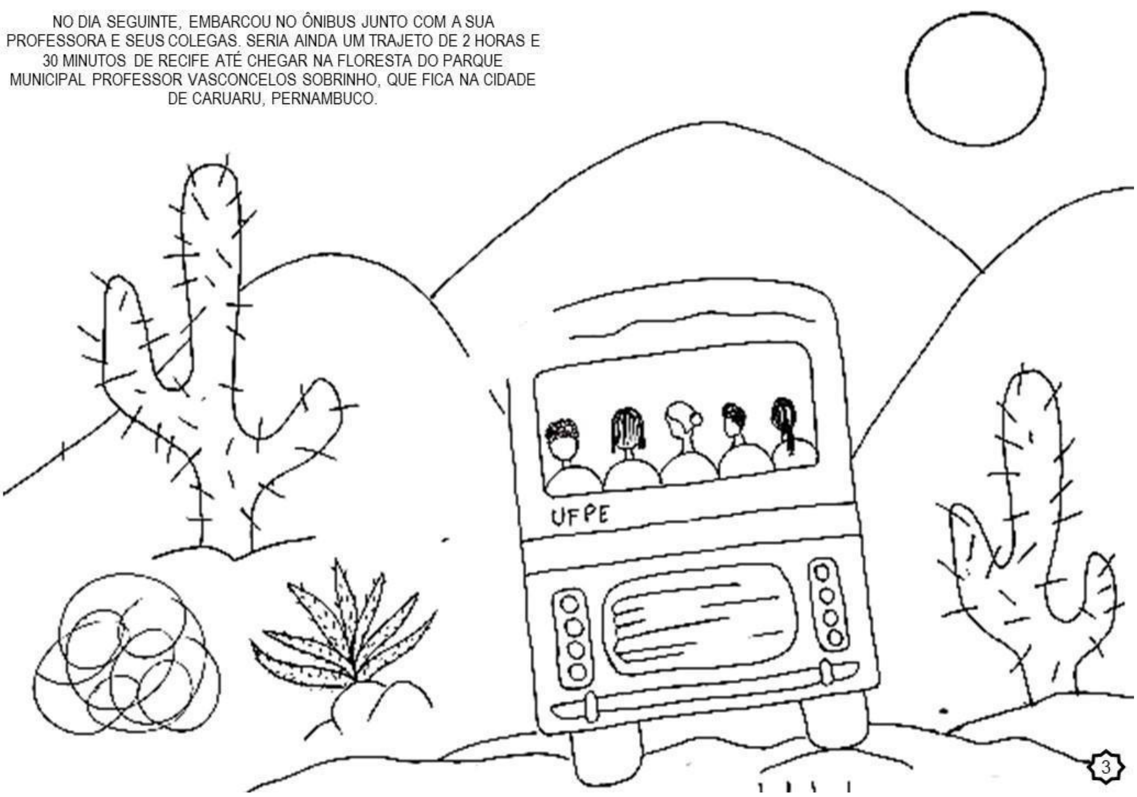
JÉSSICA É ESTUDANTE DE BIOLOGIA DA UNIVERSIDADE FEDERAL DE PERNAMBUCO (UFPE). ELA ESTAVA MUITO EMPOLGADA CONTANDO PARA SUA MÃE QUE IRIA PARA SUA PRIMEIRA AULA DE CAMPO. O OBJETIVO DESTA AULA FOI OBSERVAR A PRESENÇA DE BRIÓFITAS E SUAS ESTRATÉGIAS ECOLÓGICAS PARA COLONIZAR DIFERENTES AMBIENTES DENTRO DA FLORESTA.



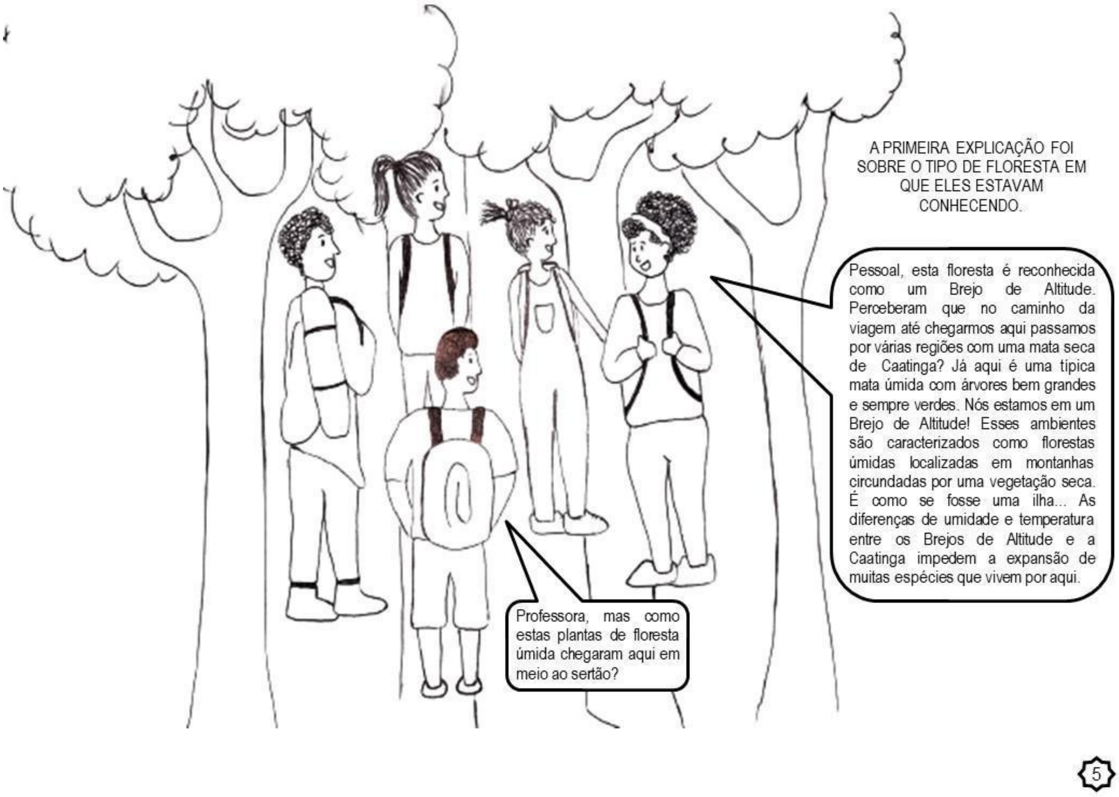
ELA PREPAROU TUDO, MOCHILA, EQUIPAMENTOS DE CAMPO COMO LUPA, FITA, CANETA, CADERNETA E LANTERNA. TAMBÉM SEPAROU MANTIMENTOS E ÁGUA. JÉSSICA NÃO QUERIA SE ATRASAR PORQUE O ÔNIBUS IRIA SAIR LOGO CEDO E DECIDIU DORMIR JÁ PRONTA PARA VIAGEM.

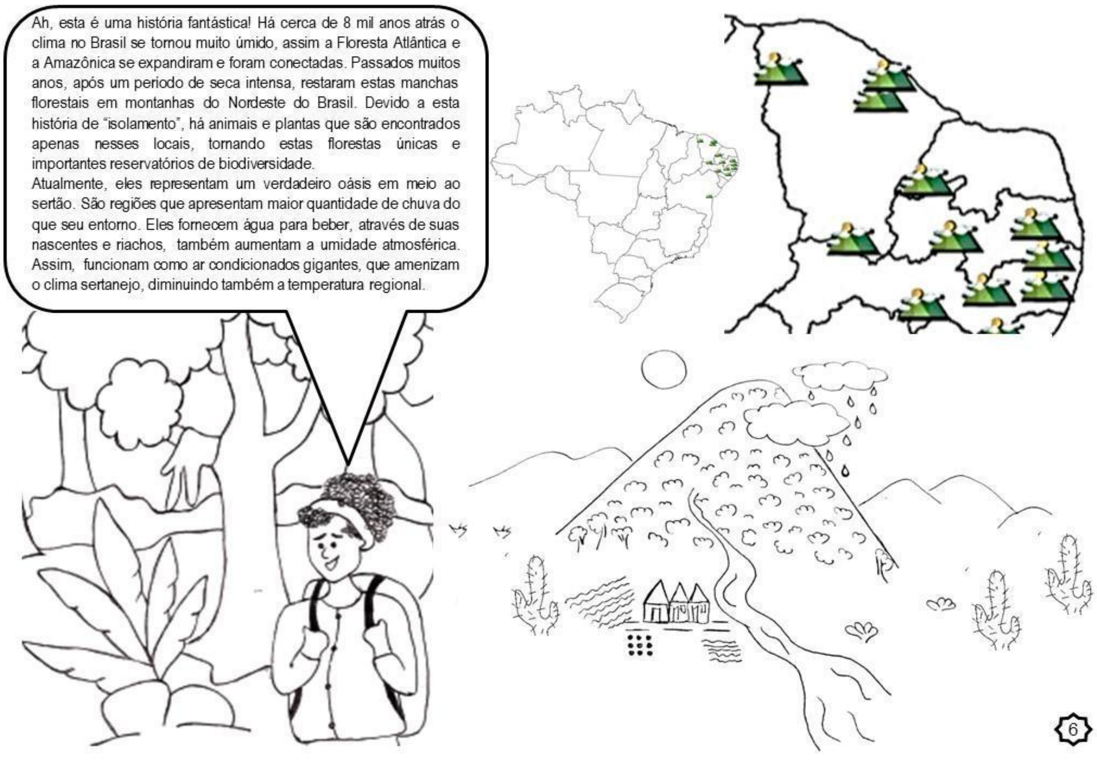


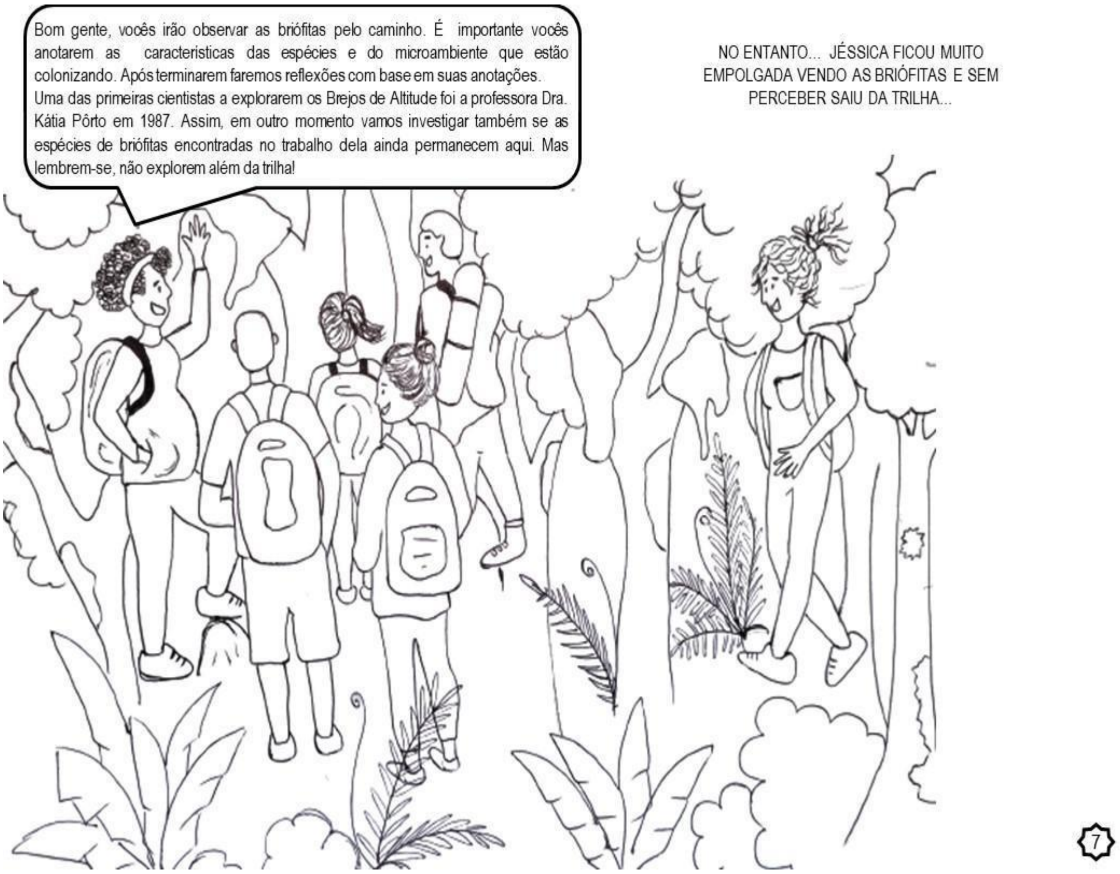
NO DIA SEGUINTE, EMBARCOU NO ÔNIBUS JUNTO COM A SUA PROFESSORA E SEUS COLEGAS. SERIA AINDA UM TRAJETO DE 2 HORAS E 30 MINUTOS DE RECIFE ATÉ CHEGAR NA FLORESTA DO PARQUE MUNICIPAL PROFESSOR VASCONCELOS SOBRINHO, QUE FICA NA CIDADE DE CARUARU, PERNAMBUCO.

CHEGANDO LÁ NO PARQUE A PROFESSORA EXPLICOU ALGUMAS ORIENTAÇÕES PARA A AULA NA FLORESTA. UMA DAS PRIMEIRAS: A IMPORTÂNCIA EM SEGUIR JUNTOS PELO TRAJETO, ESTAR ATENTOS AOS SONS NATURAIS, CHECAR O AMBIENTE ANTES DE SEGURAR EM ALGUMA PLANTA, PARA EVITAR POSSÍVEIS ACIDENTES COM ANIMAIS VENENOSOS E, PRINCIPALMENTE, RESPEITAR TODOS OS SERES DA FAUNA, FLORA E MICROORGANISMOS INVISÍVEIS QUE OCORREM NO SOLO E SOBRE ÁRVORES DA FLORESTA.

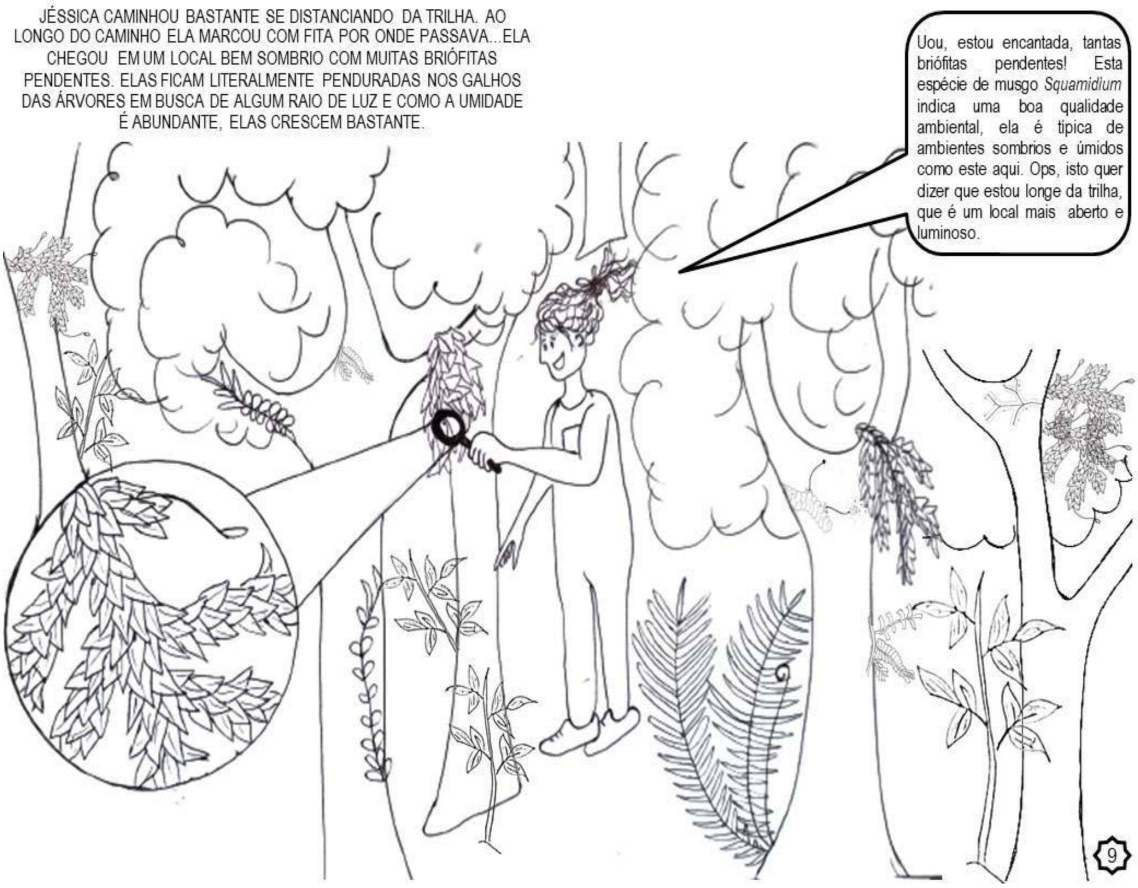
ASSIM INICIARAM A AULA PELA TRILHA...

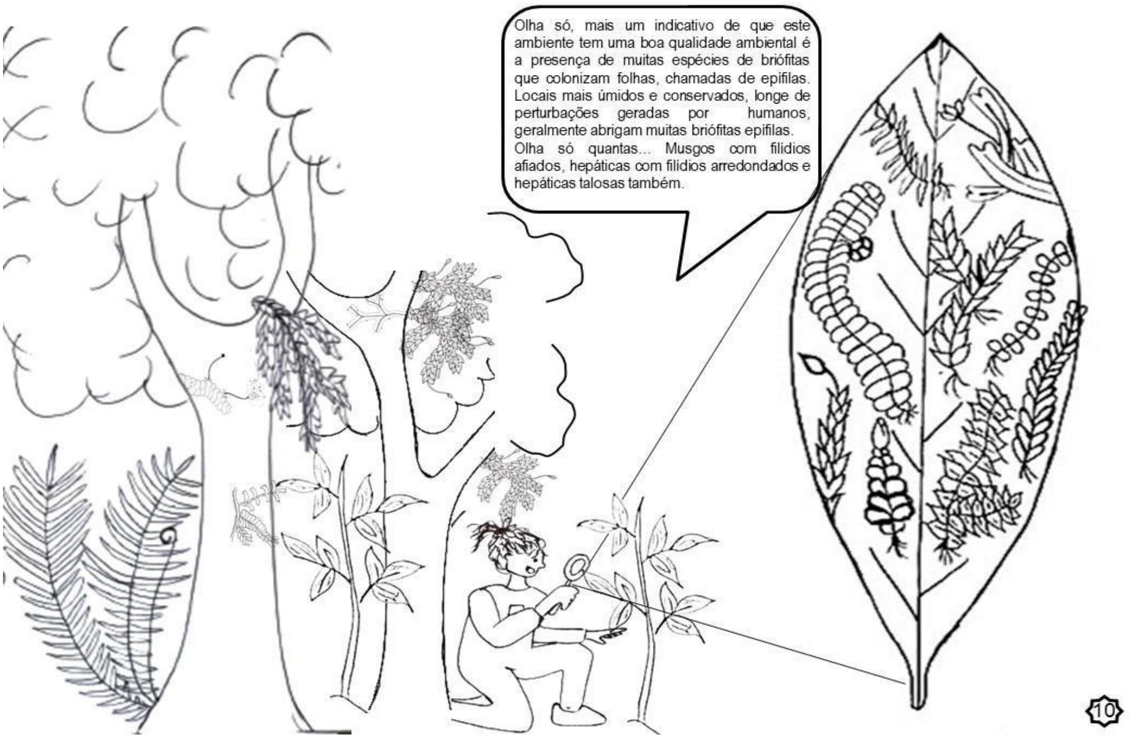

A PRIMEIRA EXPLICAÇÃO FOI SOBRE O TIPO DE FLORESTA EM QUE ELES ESTAVAM CONHECENDO.
Pessoal, esta floresta é reconhecida como um Brejo de Altitude. Perceberam que no caminho da viagem até chegarmos aqui passamos por várias regiões com uma mata seca de Caatinga? Já aqui é uma típica mata úmida com árvores bem grandes e sempre verdes. Nós estamos em um Brejo de Altitude! Esses ambientes são caracterizados como florestas úmidas localizadas em montanhas circundadas por uma vegetação seca. É como se fosse uma ilha... As diferenças de umidade e temperatura entre os Brejos de Altitude e a Caatinga impedem a expansão de muitas espécies que vivem por aqui.
Professora, mas como estas plantas de floresta úmida chegaram aqui em meio ao sertão?
5


Ah, esta é uma história fantástica! Há cerca de 8 mil anos atrás o clima no Brasil se tornou muito úmido, assim a Floresta Atlântica e a Amazônica se expandiram e foram conectadas. Passados muitos anos, após um periodo de seca intensa, restaram estas manchas florestais em montanhas do Nordeste do Brasil. Devido a esta história de "isolamento", há animais e plantas que são encontrados apenas nesses locais, tornando estas florestas únicas e importantes reservatórios de biodiversidade.
Atualmente, eles representam um verdadeiro oásis em meio ao sertão. São regiões que apresentam maior quantidade de chuva do que seu entorno. Eles fornecem água para beber, através de suas nascentes e riachos, também aumentam a umidade atmosférica. Assim, funcionam como ar condicionados gigantes, que amenizam o clima sertanejo, diminuindo também a temperatura regional.
6

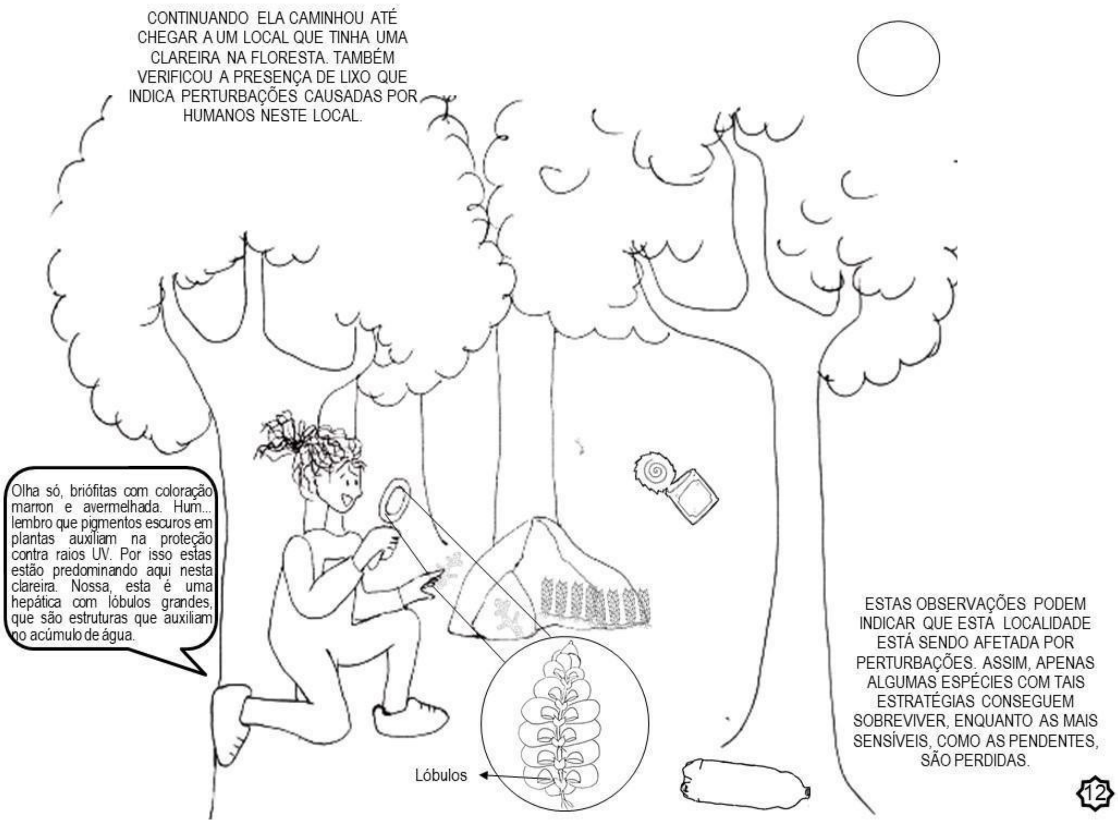

Bom gente, vocês irão observar as briófitas pelo caminho. É importante vocês anotarem as caracteristicas das espécies e do microambiente que estão colonizando. Após terminarem faremos reflexões com base em suas anotações.
Uma das primeiras cientistas a explorarem os Brejos de Altitude foi a professora Dra. Kátia Pôrto em 1987. Assim, em outro momento vamos investigar também se as espécies de briófitas encontradas no trabalho dela ainda permanecem aqui. Mas lembrem-se, não explorem além da trilha!
NO ENTANTO... JÉSSICA FICOU MUITO EMPOLGADA VENDO AS BRIÓFITAS E SEM PERCEBER SAIU DA TRILHA...
7


FOI SE DISTANCIANDO DA TURMA... QUANDO NOTOU ESTAVA PERDIDA.
E agora o que vou fazer?
8

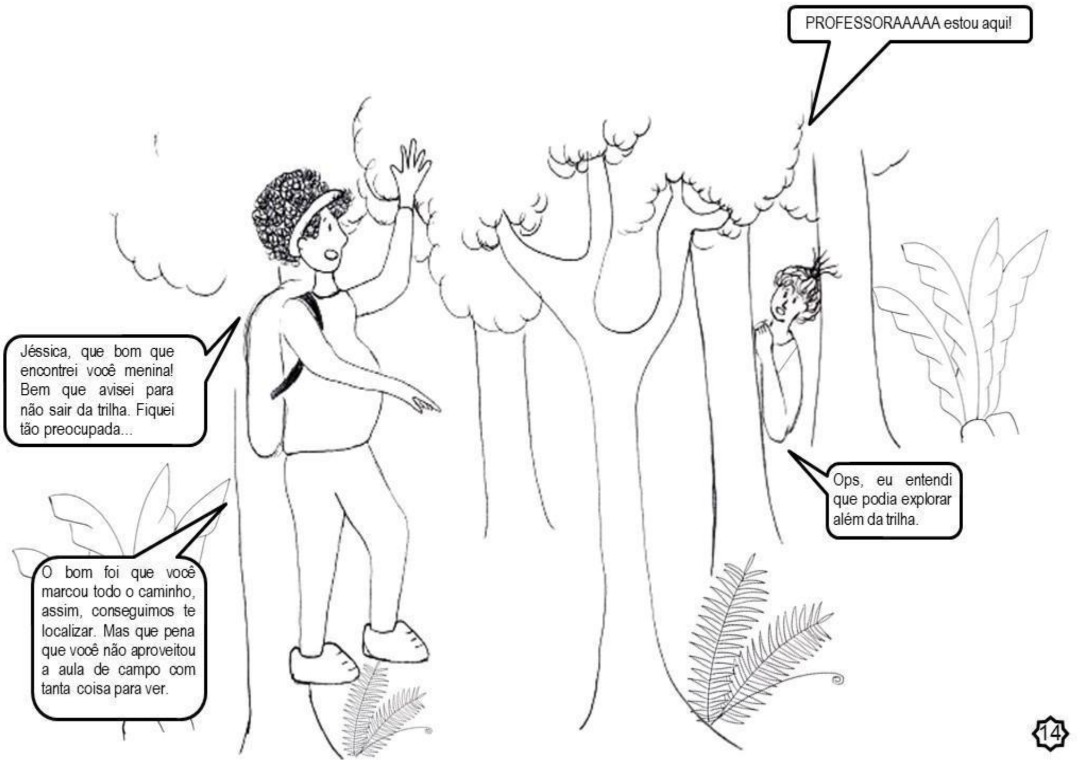

JÉSSICA CAMINHOU BASTANTE SE DISTANCIANDO DA TRILHA. AO LONGO DO CAMINHO ELA MARCOU COM FITA POR ONDE PASSAVA...ELA CHEGOU EM UM LOCAL BEM SOMBRIO COM MUITAS BRIÓFITAS PENDENTES. ELAS FICAM LITERALMENTE PENDURADAS NOS GALHOS DAS ÁRVORES EM BUSCA DE ALGUM RAIO DE LUZ E COMO A UMIDADE É ABUNDANTE, ELAS CRESCEM BASTANTE.
Uou, estou encantada, tantas briófitas pendentes! Esta espécie de musgo *Squamidium* indica uma boa qualidade ambiental, ela é típica de ambientes sombrios e úmidos como este aqui. Ops, isto quer dizer que estou longe da trilha, que é um local mais aberto e luminoso.
9

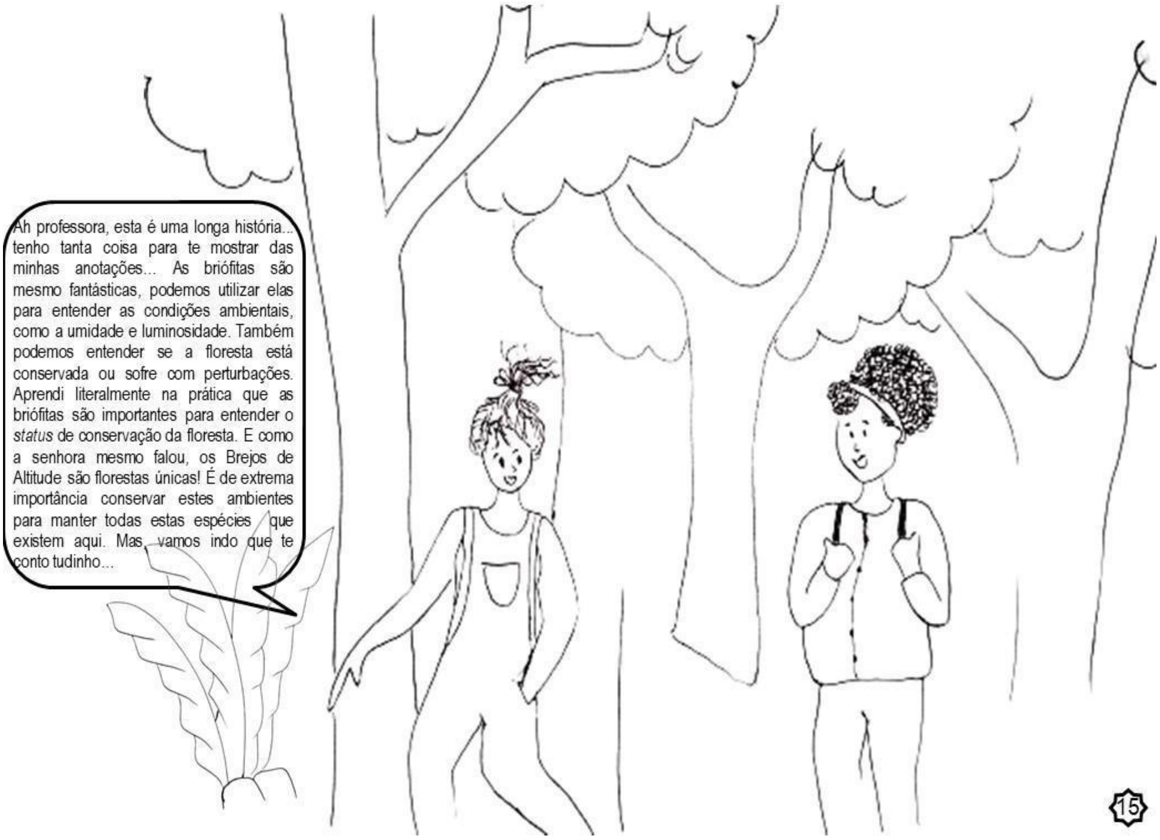

Olha só, mais um indicativo de que este ambiente tem uma boa qualidade ambiental é a presença de muitas espécies de briófitas que colonizam folhas, chamadas de epífilas. Locais mais úmidos e conservados, longe de perturbações geradas por humanos, geralmente abrigam muitas briófitas epífilas. Olha só quantas... Musgos com filídios afiados, hepáticas com filídios arredondados e hepáticas talosas também.
10

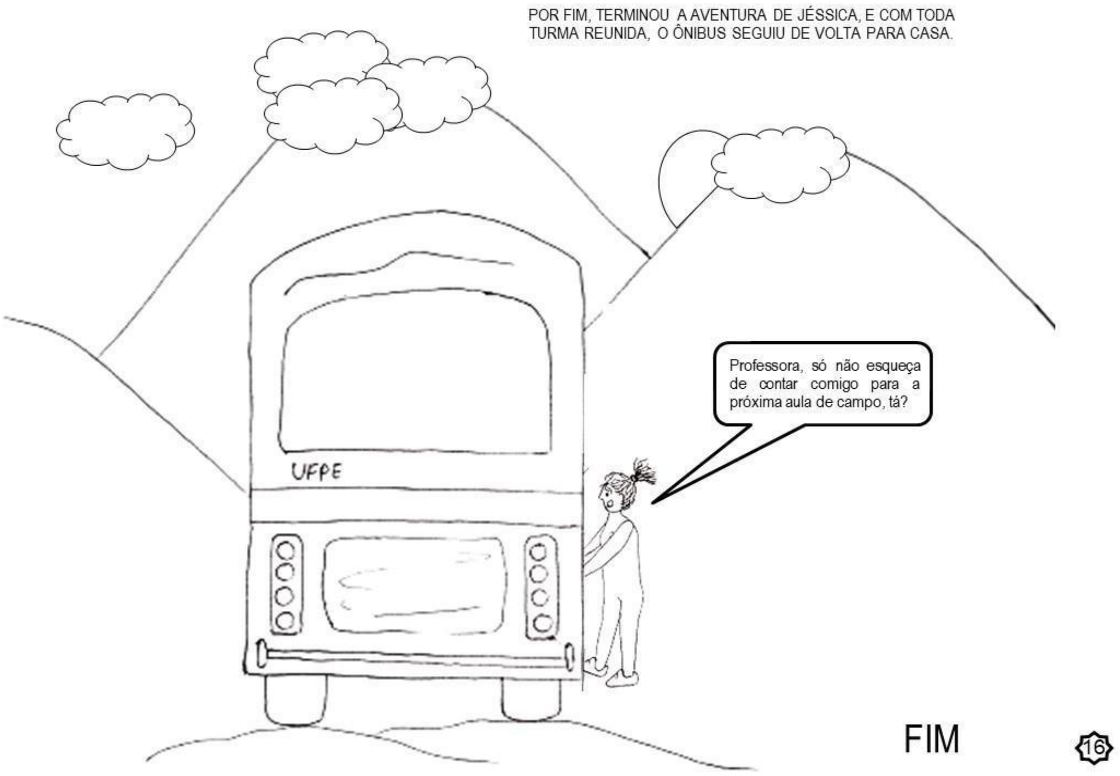

JÉSSICA SEGUIU ADIANTE...PERCEBEU QUE AS BRIÓFITAS PENDENTES ESTAVAM SUMINDO. E FEZ MAIS UMA OBSERVAÇÃO...
Nossa, que lago lindo, olha só as briófitas aqui são do tipo tapete, que crescem bem aderidas ao substrato. Hum, lembro que as espécies que têm este crescimento geralmente podem estar em diferentes tipos de ambientes, não possuem preferências de habitats. Olha só, mas elas estão crescendo apenas em um lado das árvores, por que?
Bom, sabendo que as briófitas são muito dependentes de umidade... Já sei, é possível que a umidade do lago esteja favorecendo o crescimento delas mais deste lado do mais próximo ao lago. Que legal!
11


CONTINUANDO ELA CAMINHOU ATÉ CHEGAR A UM LOCAL QUE TINHA UMA CLAREIRA NA FLORESTA. TAMBÉM VERIFICOU A PRESENÇA DE LIXO QUE INDICA PERTURBAÇÕES CAUSADAS POR HUMANOS NESTE LOCAL.
Olha só, briófitas com coloração marron e avermelhada. Hum... lembro que pigmentos escuros em plantas auxiliam na proteção contra raios UV. Por isso estas estão predominando aqui nesta clareira. Nossa, esta é uma hepática com lóbulos grandes, que são estruturas que auxiliam no acúmulo de água.
Lóbulos
ESTAS OBSERVAÇÕES PODEM INDICAR QUE ESTÁ LOCALIDADE ESTÁ SENDO AFETADA POR PERTURBAÇÕES. ASSIM, APENAS ALGUMAS ESPÉCIES COM TAIS ESTRATÉGIAS CONSEGUEM SOBREVIVER, ENQUANTO AS MAIS SENSÍVEIS, COMO AS PENDENTES, SÃO PERDIDAS.
12


JÉSSICA SEGUIU ADIANTE... ENCANTADA COM TANTAS BRIÓFITAS, MAS ASSUSTADA POR NÃO ENCONTRAR A TRILHA. EMBAIXO DE UMA SOMBRA, PAROU PARA DESCANÇAR UM POUCO, QUANDO, DE REPENTE, ELA OUVIU UM BARULHO DE ALGO QUE ESTAVA SE APROXIMANDO. ELA FICOU QUIETINHA ESCONDIDA.
ATÉ QUE...
13


PROFESSORAAAAA estou aqui!
Jéssica, que bom que encontrei você menina! Bem que avisei para não sair da trilha. Fiquei tão preocupada...
Ops, eu entendi que podia explorar além da trilha.
O bom foi que você marcou todo o caminho, assim, conseguimos te localizar. Mas que pena que você não aproveitou a aula de campo com tanta coisa para ver.
14


Ah professora, esta é uma longa história... tenho tanta coisa para te mostrar das minhas anotações... As briófitas são mesmo fantásticas, podemos utilizar elas para entender as condições ambientais, como a umidade e luminosidade. Também podemos entender se a floresta está conservada ou sofre com perturbações. Aprendi literalmente na prática que as briófitas são importantes para entender o *status* de conservação da floresta. E como a senhora mesmo falou, os Brejos de Altitude são florestas únicas! É de extrema importância conservar estes ambientes para manter todas estas espécies que existem aqui. Mas, vamos indo que te conto tudinho...
15


POR FIM, TERMINOU A AVENTURA DE JÉSSICA, E COM TODA TURMA REUNIDA, O ÔNIBUS SEGUIU DE VOLTA PARA CASA.
UFPE
Professora, só não esqueça de contar comigo para a próxima aula de campo, tá?
FIM
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