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DIFERENCIAÇÃO TAXONÔMICA E FUNCIONAL DE HEPÁTICAS (Marchantiophyta) NO GRADIENTE ALTITUDINAL DA COLÔMBIA

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2022

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Dissertação apresentada ao Programa de Pós-Graduação em Biologia Vegetal do Centro de Biociências do departamento de Botânica da Universidade Federal de Pernambuco, como parte dos requisitos parciais para obtenção do título de mestre em Biologia Vegetal.

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Com muito carinho e gratidão,
a minha madre,
Nubia Sanchez Naranjo
DEDICO

A Karen Suarez, meu porto seguro

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“Uma árvore não é só luz do Sol.
Ela passou pelo adubo,
Pela chuva,
Pela seca,
Pelo vento,
Pelo medo de não conseguir crescer.
Talvez alguém a tenha arrancado do chão quando estava no médio do caminho...
Mas ela conseguiu alcançar a terra com suas raízes de novo.
Ela é todo o processo que levou para ser o que é.
***Tudo tem seu papel no nosso amadurecer**.*

p.s. Cada planta cresce no seu tempo”
Pedro Salomão

RESUMO

A Colômbia é o país da América tropical com a maior riqueza de hepáticas, 705 espécies catalogadas. A partir de estudos florísticos e de taxonomia esta diversidade tem sido atribuída principalmente à heterogeneidade ambiental ao longo do amplo gradiente altitudinal de 0-5000 m. Todavia, ainda é desconhecido o papel deste gradiente altitudinal na diversidade taxonômica e ecológica das hepáticas no país. Assim, nesta pesquisa objetivou-se analisar os padrões de diversidade taxonômica, funcional e a composição funcional ao longo do amplo gradiente altitudinal, de 0-5000 m, da Colômbia, bem como testar a hipótese denominada efeito do domínio médio (i.e., aumento da riqueza de espécies em altitudes intermediárias) neste modelo de estudo. A distribuição das hepáticas e seus respectivos atributos funcionais foram compilados mediante pesquisa bibliográfica e em base de dados online. Foram selecionados atributos morfológicos do gametófito, celular, forma de vida e reprodução, relacionados à captação e manutenção hídrica, bem como a proteção à luminosidade. A diversidade taxonômica e os índices de diversidade funcional foram relacionados ao gradiente altitudinal a partir da One-Way ANOVA. A composição funcional foi calculada para cada faixa altitudinal usando medias ponderadas da comunidade (CWM) e observada por meio de análises de ordenação (PRINCALS). A relação das métricas de diversidade taxonômica, diversidade funcional e composição funcional com as faixas altitudinais foram avaliadas através de One-Way ANOVA. Uma relação unimodal entre as diversidades taxonômica e a funcional e o gradiente altitudinal foi observada, sendo os maiores valores registrados, de modo geral, nas faixas medianas compreendidas entre 14100-2500 m ; com exceção da equabilidade funcional que demonstrou o padrão inverso na faixa de 4100 -5000m. Observou-se substituição de atributos ao longo do gradiente e formação de grupos funcionais característicos de cada faixa altitudinal, tendo em vista que a grande maioria dos atributos analisados apresentou relação positiva ou negativa com o gradiente. O efeito do domínio médio foi explicativo para a distribuição das diversidades taxonômica e funcional ao longo do gradiente altitudinal, provavelmente devido aos filtros ambientais que selecionam os atributos funcionais das hepáticas, em particular àqueles relacionados à proteção contra a incidência de luz e, principalmente, a absorção e retenção hídrica. Neste sentido, as hepáticas respondem aos filtros ambientais e se configuram como um excelente modelo para testar métricas de composição e diversidade em função de gradientes ambientais, dentre eles, o altitudinal.

Palavras chaves: Biodiversidade; Briófitas; Diversidade funcional; Composição de atributos; Ecologia de comunidades; Efeito do domínio médio.

ABSTRACT

Colombia is the country in tropical America with the greatest wealth of liverworts, with 705 cataloged species. From floristic and taxonomic studies this diversity has been mainly attributed to environmental heterogeneity along the wide altitudinal gradient from 0-5000 m. However, the role of this altitudinal gradient in the taxonomic and ecological diversity of liverworts in the country is still unknown. Thus, this research aimed to analyze the patterns of taxonomic, functional diversity and functional composition along the wide altitudinal gradient, from 0-5000 m, in Colombia, as well as to test the hypothesis called mid-domain effect (ie, increase in species richness at intermediate altitudes) in this study model. The distribution of liverworts and their respective functional attributes were compiled through bibliographic research and an online database. Morphological attributes of gametophyte, cell, life form and reproduction were selected, related to water uptake and maintenance, as well as light protection. Taxonomic diversity and functional diversity indices were related to the altitudinal gradient using One-Way ANOVA. The functional composition was calculated for each altitudinal range using community weighted mean (CWM) and observed using ordination analyzes (PRINCALS). The relationship of the metrics of taxonomic diversity, functional diversity and functional composition with the altitudinal ranges was evaluated using One-Way ANOVA. A unimodal relationship between taxonomic and functional diversities and the altitudinal gradient was observed, with the highest values being generally recorded in the median ranges between 14100-2500 m; with the exception of the functional evenness which demonstrated the inverse pattern in the range of 4100 -5000m. There was a substitution of attributes along the gradient and the formation of functional groups characteristic of each altitudinal range, considering that the vast majority of the analyzed attributes presented a positive or negative relationship with the gradient. The effect of the middle domain explained the distribution of taxonomic and functional diversities along the altitudinal gradient, probably due to environmental filters that select the functional attributes of liverworts, in particular those related to protection against the incidence of light and, mainly, the water absorption and retention. In this sense, liverworts respond to environmental filters and are an excellent model to test composition and diversity metrics as a function of environmental gradients, including the altitudinal.

Keywords: Biodiversity; Bryophytes; Functional diversity; Attribute composition; Community ecology; Mid-domain effect.

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1 INTRODUÇÃO

O catálogo de plantas e líquens da Colômbia lista cerca de 24500 espécies de plantas vasculares e 1650 de briófitas, sendo 45% (705 spp.) hepáticas (Marchantiophyta) (BERNAL et al., 2016). Atualmente, a Colômbia é o país da América tropical com a maior diversidade de hepáticas (GRADSTEIN, 2021), seguida pelo Brasil com 633 espécies (COSTA e PERALTA, 2015). Ao longo das Florestas Tropicais, estudos tem reportado diferenciação de diversidade de hepáticas com base na altitude, sendo as florestas de terras baixas, as que apresentam a menor diversidade, comparativamente as florestas montanas, que reúnem maior diversidade de hepáticas, especialmente na região dos Andes, sobre as altitudes compreendidas entre 2000-3000 m (URIBE e GRADSTEIN, 1999). Dessa forma, a distribuição de hepáticas parece estar fortemente relacionada aos filtros ambientais gerados pela variação da altitude, com a tais como umidade relativa do ar, neblina, luz, temperatura e precipitação devem também influenciar a diversidade (CORNELISSEN E TER STEEGE, 1989; ASADA et al., 2003; MOTA DE OLIVEIRA et al., 2009).

As hepáticas têm se configurado como eficientes bioindicadores e biomonitores, sobretudo devido às suas características morfofisiológicas, podendo absorver água, nutrientes e poluentes do ar por toda a extensão do gametófito (GLIME, 2017). Além disso, as hepáticas distribuídas principalmente em habitats úmidos, como nas florestas úmidas tropicais, onde podem produzir alta biomassa, absorver grande quantidade de água da chuva, desempenhando assim um papel importante no balanço hídrico e nos ciclos de nutrientes da floresta (GRADSTEIN, 2021). O conhecimento sobre a flora de hepáticas na Colômbia tem sido enriquecido na taxonomia e ecologia, especialmente na pesquisa da distribuição espacial das espécies e sua abundância nas florestas úmidas tropicais (GRADSTEIN e URIBE, 2016; GRADSTEIN, 2021).

Por outro lado, a aplicação de conceitos ecológicos funcionais no Neotrópico tem sido amplamente utilizada em estudos de plantas vasculares, em comparação com as briófitas, especificamente nas hepáticas que apresenta um campo de pesquisa potencialmente muito promissor, em particular, com seus atributos funcionais que permitem que essas plantas possam viver em situações de mudança climática (AH-PEG et al., 2014). Da mesma forma, a diversidade funcional das hepáticas e sua composição funcional no gradiente altitudinal na Colômbia permanece ainda um tema relevante a ser explorado.

Utilizando a rica base de informações florísticas/taxonômicas disponível sobre as hepáticas da Colômbia este trabalho teve como objetivo geral avaliar a diversidade taxonômica, funcional e a distribuição da composição funcional de hepáticas ao longo dos diferentes tipos de formações vegetacionais do gradiente altitudinal na Colômbia.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 FILTRAGEM AMBIENTAL NA MONTAGEM DAS COMUNIDADES DE BRIÓFITAS

Os conceitos de assembleia de comunidades pressupõem que a dinâmica e a composição das comunidades de escalas locais a globais são influenciadas pelos efeitos combinados de filtros ambientais, interações bióticas e processos neutros (GÖTZENBERGER et al., 2012; OVASKAINEN et al., 2017). De acordo, com a Teoria Neutra Unificada da Biodiversidade e Biogeografia (HUBBELL, 2001), as espécies são ecologicamente semelhantes em termos de dispersão, extinção e especiação. Portanto, todas as espécies presentes no grupo regional têm, em teoria, a mesma probabilidade de colonizar qualquer comunidade, independentemente da sobreposição de nichos (HUBBELL, 2001). Além disso, padrões aleatórios também podem ser observados quando há um desempenho conjunto e equilibrado dos processos de filtragem ambiental e de competição (KEMBEL e HUBBELL, 2006). O filtro ambiental assume que as espécies que compõem uma comunidade são semelhantes em resposta às condições e requisitos ambientais (HUBBELL, 2001) e esse parece ser o processo mais explicativo para a montagem de comunidades de briófitas em ecossistemas tropicais (MOTA DE OLIVEIRA et al., 2009; CAMPOS et al., 2019).

As briófitas são plantas tipicamente de pequeno porte, com ausência de sistema vascular lignificado e cutícula epidérmica (GRADSTEIN et al., 2001), com metabolismo intrinsecamente dependente dos fatores abióticos, principalmente relacionados a umidade e a luminosidade (GLIME, 2017). Estas características as tornam sensíveis as variações ambientais, sendo comumente utilizadas como modelo biológico para detectar variações ambientais nos ecossistemas a curto prazo (HALLINGBACK e HODGETTS, 2000).Neste âmbito, pesquisas vêm sendo desenvolvidas analisando a composição e a riqueza de briófitas em diferentes ambientes, considerando a influência da a altitude, que demonstra gerar filtros ambientais sobre as comunidades de briófitas ao longo do gradiente (FRAHM e GRADSTEIN 1991; ACEBEY et al., 2003; PROCTO, 2003; PHARO et al., 2005; CORRALES et al., 2010).

Vanderpoorten e Engels (2003) usaram os tipos de florestas e solo como preditores de riqueza de briófitas em regiões temperadas, indicando que a estrutura da floresta pode afetar diretamente a composição e riqueza de espécies pela variação do microclima. Outras condições do microhabitat também influenciam a diversidade de briófitas, como o pH da casca das árvores para as briófitas epífitas (HOLZ e GRADSTEIN, 2005; ASADA et al., 2003; WEIBULL e RYDIN, 2005), bem como as taxas de decomposição da serapilheira, que relacionam-se com a diminuição de riqueza das briófitas terrícolas (FRAHM e GRADSTEIN, 1991). De modo general, a montagem de comunidades de briófitas está relacionada aos fatores bióticos e a bióticos, principalmente à disponibilidade de luz e umidade (FRAHM, 2003).

Nesta perspectiva, as espécies e seus adaptações funcionais podem responder aos filtros exercidos pelo ambiente com uma maior sensibilidade, entretanto, a abordagens sobre a diversidade funcional podem nos ajudar a entender as respostas estruturais e funcionais às mudanças nos diferentes tipos de habitat e a variação climática na montagem de comunidades de briófitas (LAVOREL e GARNIER, 2002; CORRALES et al., 2010).

2.2. EFEITO DO DOMÍNIO MÉDIO NAS ESPÉCIES

O entendimento dos padrões de distribuição da diversidade de espécies ao longo de gradientes ambientais tem sido o foco de muitos estudos de ecologia e de biogeografia nas últimas décadas (RAHBEK, 2005). Avaliar os padrões de riqueza de espécies em função da altitude é crucial para a conservação da biodiversidade (LEE et al., 2021). Dentre estes, a maioria dos trabalhos sobre a distribuição da riqueza de espécies ao longo de gradientes altitudinais apresenta um pico de maior riqueza em altitudes intermediárias, denominado efeito de domínio médio (MDE) (COLWELL e LEES, 2000; RAHBEK, 1995, 2005; COLWELL et al., 2004).

Colwell e Lee (2000) demostraram que o MDE pode resultar de limites rígidos, os quais são definidos em relação ao grau de resistência à dispersão e sobrevivência das espécies. Por exemplo, o alcance de uma espécie ao longo de um gradiente altitudinal é geometricamente limitado pelo nível do mar ou o fundo de um vale como limite inferior e o topo de uma montanha ou uma limitação ecofisiológica como limite superior (COLWELL e HURTT, 1994; RAHBEK, 1997).

Grau et al., (2007) relacionaram dados de espécies de briófitas, samambaias e plantas vasculares no gradiente altitudinal no Nepal e evidenciaram que há uma relação unimodal entre a riqueza de espécies e a altitude para cada táxon, por exemplo, os máximos valores de riqueza foram em musgos: 2500m; hepáticas: 2800m; samambaias:1900m e plantas vasculares:1500 e 2500m. Essas diferenças entre os padrões podem ser influenciadas pelas diferentes demandas nas variáveis climáticas como a energia disponível e a água, sendo esta última a principal razão (GRAU et al., 2007).

Similarmente, Watkins et al. (2006) observaram que a distribuição da riqueza em samambaias e licófitas foi maior nas altitudes medias do gradiente (1500-2500). Além disso, esse padrão se repete nessas plantas em toda a região Neotropical em função da altitude (SALAZAR et al., 2015). Em hepáticas, Cacua et al. (2018) evidenciaram em uma floresta úmida nos Andes que a diversidade máxima foi registrada na altitude de 3000m, encontrando uma alta relação entre a maior riqueza de espécies e a baixa temperatura, alta umidade e luz.

Adicionalmente, estudos onde a riqueza de espécies é interpolada em gradientes altitudinais mostraram que um forte MDE não exclui a possibilidade de que outros fatores como o clima, nutrientes do local e a precipitação possam contribuir simultaneamente para os padrões espaciais de riqueza de espécies nos gradientes (COLWELL e LEES, 2000; WATKINS et al., 2006).

Rahbek (2005) destacou, de modo geral, que para diferentes grupos biológicos a riqueza de espécies em escala local em relação ao gradiente altitudinal apresenta um padrão monotônico, diminuindo com o aumento da altitude, embora, este padrão pode se modificar em picos intermediários quando toda a amplitude do gradiente é avaliada. Os estudos sobre a diversidade em hepáticas na Colômbia tendem avaliar a escala local (e.g FEUILLET e TORRES, 2016; CACUA et al., 2018). Portanto, a avaliação da diversidade de espécies e a diversidade funcional em toda a amplitude altitudinal é crucial para analisar os padrões de distribuição das espécies, sobretudo, hepáticas, organismos suscetíveis as alterações ambientais.

2.3 DIVERSIDADE FUNCIONAL NAS BRIÓFITAS

Um componente importante da diversidade funcional é a composição, que descreve a presença e a abundância dos atributos das espécies e geralmente é medida pela presença de grupos funcionais (DÍAZ e CABIDO, 2001). Esses atributos funcionais são características morfológicas, fisiológicas ou fenológicas das espécies que respondem à variabilidade ambiental (CIANCIARUSO et al., 2009). Por sua vez, grupos funcionais são definidos como um conjunto de espécies que compartilham uma resposta semelhante ao ambiente ou têm efeitos semelhantes no funcionamento do ecossistema (DÍAZ e CABIDO, 2001; HOOPER et al., 2005). O estudo da quantificação de atributos funcionais e sua variação entre as espécies pode aumentar a compreensão sobre a montagem de comunidades e os processos ecossistêmicos (SUDING et al., 2008; SHIPLEY, 2010).

Até o momento, os esforços para desenvolver protocolos sobre atributos funcionais, incluindo grandes bancos de dados padronizados, concentraram-se em plantas vasculares, principalmente angiospermas e gimnospermas (CORNELISSEN et al., 2003). Apresentado atributos voltados principalmente às alterações ambientais, que controlam uma variedade de processos dos ecossistemas terrestres, tal como o armazenamento de carbono, ciclagem de nutrientes e requerimento de recursos (DEYN et al., 2008). Entretanto, outros organismos fotossintéticos como cianobactérias, briófitas, líquens e samambaias podem ser funcionalmente importantes nos processos dos ecossistemas (LINDO e GONZÁLEZ, 2010; PORADA et al., 2014).

As briófitas apresentam atributos funcionais distintos das plantas vasculares, muitos dos quais relacionados à reprodução (esporos e propágulos assexuados), morfologia (gametófito) e às relações hídricas (COE e STANTON, 2017). Por exemplo, Batista et al. (2018) encontraram que em uma floresta úmida no nordeste do Brasil, as espécies de briófitas eram predominantemente monóicas (67%), e apenas 21% exibiam reprodução assexuada, incluindo gemas, fragmentos em regeneração e folhas caducas, o que significa que essas características reprodutivas permitem as espécies tolerar condições adversas, sujeitas à baixa disponibilidade de água da floresta sazonal.

Nesse sentido, são poucos os trabalhos que abordam a diversidade funcional em briófitas (TAO e ZHANG 2012; SILVA et al. 2017; MOTA DE OLIVEIRA, 2018; SOUZA et al., 2020). Duckett et al. (2004) reportaram que isso pode ser devido ao desconhecimento das comunidades ecológicas, problemas de identificação taxonômica e obstáculos metodológicos, como as dificuldades de cultivo. Outros temas ainda devem ser desenvolvidos, principalmente nos atributos funcionais relacionados ao balaço hídrico, biomassa, ciclagem de nutrientes e fixação de carbono (HALLINGBACK e HODGETTS, 2000). Tais atributos podem ser usados simultaneamente para explicar as respostas a fatores ambientais bióticos e abióticos e seus efeitos sobre a comunidade e a função dos ecossistemas (CORNELISSEN et al., 2003).

2.4 DIVERSIDADE TAXONÔMICA DE HEPÁTICAS NA COLÔMBIA

O número de espécies de hepáticas no mundo é ca. 7486 (SÖDERSTRÖM et al., 2016), das quais 1350 espécies ocorrem no Neotrópico (GRADSTEIN et al., 2001). A Colômbia apresenta grande diversidade neste grupo de plantas, ou seja, 60 % das espécies (705 spp.) (GRADSTEIN, 2021). As primeiras contribuições mais relevantes sobre o conhecimento das hepáticas no país foram atribuídas aos catálogos feitos por Gradstein e Hekking (1979), Uribe e Gradstein (1998) e Gradstein e Uribe (2016). A primeira edição do catálogo foi feita dos dados extraídos da literatura disponível e principalmente de coletas e determinações inéditas feitas no Herbário Nacional da Colômbia por A.M. Cleef, T. van der Hammen, H. Bischler e outros (GRADSTEIN e HEKKING, 1979). A segunda edição do catálogo de Uribe e Gradstein (1998) foi o resultado das coletas feitas por van Reenen et al., (1984) no âmbito do Projeto ECOANDES (parceria entre Holanda e Colômbia), e os trabalhos de Uribe e Aguirre (1997), do Herbário Nacional da Colômbia, Gradstein (1994, 1995), van Zanten e Gradstein (1988), Meenks (1987), Wolf (1993), e Schuster (1992), além de outras coletas feitas por Churchill e Linares (1995), durante o desenvolvimento do projeto "Flora da Colômbia".

Desde a publicação de Uribe e Gradstein (1998), foram publicados mais de 100 trabalhos contendo correções à flora de hepáticas do país e 91 espécies foram registradas pela primeira vez na Colômbia (GRADSTEIN, 2021). Posteriormente, mais de 200 espécies foram reduzidas à sinonímia ou foram consideradas registros duvidosos (GRADSTEIN e URIBE, 2016). Devido ao número de novidades florísticas e mudanças taxonômicas, se fez necessária a elaboração de uma terceira versão do catálogo, registrando um total de 715 espécies, com vinte e três endêmicas para o país (GRADSTEIN e URIBE, 2016). Na versão mais atualizada do catálogo, Gradstein (2021), compilou 705 espécies de hepáticas.

Esta grande diversidade de hepáticas no país é atribuída à ampla variedade de clima, solos e topografia que a Colômbia apresenta (GRADSTEIN e BORGES, 2019) e resulta em formações vegetais diversas, como as florestas úmidas de terras baixas da Amazônia, a região do Chocó, além dos semidesertos na costa do Caribe, a exuberante floresta montanhosa e os páramos andinos (GRADSTEIN e BORGES, 2019). A diversidade e a abundância das hepáticas no país aumentam das terras baixas (<500 m) em direção as regiões montanhosas até altitudes em torno dos 2500 m, diminuindo até os picos das montanhas mais elevadas (ca. 5000 m) (URIBE e GRADSTEIN, 1999; GRADSTEIN, 1995). Neste sentido, diversos autores de compilação florística têm indicado que a faixa altitudinal entre 2000-3000 m apresenta maior riqueza (URIBE e GRADSTEIN, 1999; FEUILLET e TORRES, 2016; CACUA et al., 2018). Nesta faixa altitudinal, frequentemente há uma alta condensação e as temperaturas como um todo são mais baixas, condições que influenciam o aumento da riqueza das hepáticas (FRAHM e GRADSTEIN, 1991; URIBE e GRADSTEIN, 1999). Outra característica é a maior diversificação dos microhabitats na floresta nesta faixa altitudinal, com inúmeras espécies de briófitas crescendo em bases de árvores, arbustos, troncos, galhos, folhas, troncos caídos e, também no chão úmido (VAN REENEN e GRADSTEIN, 1983; FRAHM e GRADSTEIN, 1991). Em geral, observa-se uma tendência de maior número de espécies com o aumento da umidade e a altitude, o que não surpreende considerando o caráter poiquilohídrico das hepáticas na absorção e retenção da água do ambiente (GLIME, 2017).

3 ARTIGO

A TAXONOMIC AND FUNCTIONAL DIFFERENTIATION OF LIVERWORTS ACROSS AN ALTITUDINAL GRADIENT IN COLOMBIA

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A TAXONOMIC AND FUNCTIONAL DIFFERENTIATION OF LIVERWORTS ACROSS AN ALTITUDINAL GRADIENT IN COLOMBIA

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ABSTRACT

Aim: Liverworts are an excellent model for testing composition and diversity metrics as a function of environmental gradients. We aim to explore the patterns of taxonomic and functional diversity and functional composition of liverworts along an altitudinal gradient (0-5000 m) on a large scale in Colombia, the country with the richest liverwort flora in tropical America.

Location: Colombia.

Taxon: Liverworts – Marchantiophyta.

Methods: Published data on the distribution of 705 liverwort species and functional traits related to gametophyte and cell morphology, life forms, and reproduction were compiled. Taxonomic (= richness) and functional diversity indices were tested for their relationship with the altitudinal gradient, divided into five zones: A1 = 0-500 m, A2 = 501-1400 m, A3 = 1401-2500 m, A4 = 2501-4000 m, and A5 = 4001-5000 m. Functional composition was calculated for each zone using community weighted means and visualized through Categorical Principal Component Analysis and cluster analysis. The relationship of the metrics of taxonomic diversity, functional diversity, and functional composition with the altitudinal zones was evaluated using One-Way ANOVA.

Results: A unimodal hump-shaped relationship between taxonomic and functional diversity and the altitudinal gradient was observed, with the greatest values in general recorded at intermediate zones. As an exception, functional evenness showed an inverse pattern, with greater values at A5. Most of the traits presented a positive or negative relationship with the gradient, resulting in a clear turnover of traits along the gradient. The formation of functional groups typical of each altitudinal zone was also observed.

Main conclusions: The mid-domain effect was explanatory for the distribution of taxonomic and functional diversity along the altitudinal gradient probably due to environmental filters that select the functional traits of liverworts, particularly those related to protection against light incidence and, mainly, water absorption and retention as adaptive strategies.

Key words: biodiversity, bryophytes, functional diversity, trait composition, community ecology, mid-domain effect.

1. INTRODUCTION

The search for patterns in the distribution of species richness (=diversity) and composition is one of the central goals of ecology and biogeography (Lomolino, 2001), and the underlying processes of this patterns have been attributed to climatic, ecological, historical, and geographical variables (Rahbek & Graves, 2001; Grytnes, 2003; Colwell et al., 2004). In this sense, altitude has been used to determine non-random changes in community parameters, mainly because it is considered a surrogate for a set of biotic (e.g., amount of food resources and interspecific interactions) and abiotic (e.g., temperature, primary productivity) factors that influence the structure of communities (Rahbek, 2005).

For a long time, it was believed that there was a universal trend of decline in diversity with increasing altitude (Steven, 1992; Hunter & Yonzon, 1993) attributed to the lower surface area and greater geographic isolation at the higher elevations of the gradient (Siqueira & Rocha, 2013). It has also been demonstrated that there is an increasing overlap of species distributions at intermediate altitudes that leads to a peak of diversity (Terborgh, 1977; Rahbek, 2005), the so-called mid-domain effect (Rahbek, 1995, 2005; Colwell & Lees, 2000; Carvajal et al., 2014). Most studies of plant diversity along altitudinal gradients have confirmed the mid-domain effect (e.g., Parris et al., 1992; Kessler et al., 2001; Kessler, 2002; Watkins et al., 2006; Feuillet & Torres, 2016; Cacua et al., 2018), which appears to be more typical (ca. 50% of cases) than the monotonic decline pattern (ca. 25%) (Rahbek, 1995, 2005; Siqueira & Rocha, 2013). However, a linear decline has been reported for tree communities (Stevens, 1992) and no trend has been recorded for some groups, such as lichens (Soto-Medina et al., 2019).

The knowledge accumulated on the subject over the last two decades has led to a consensus that the relationship between species diversity and composition and altitude is more complex than previously thought and that the patterns depend on the taxonomic group and the scale of the gradient studied (Stevens, 1992; Kessler, 2002). In this sense, one of the biases of most works that investigated this relationship is that they analyzed a small extent of the gradient surveyed. In a review of the effect of scale on species diversity patterns, Rahbek (2005) found that only 16% of the studies had compiled a data set at a broader regional scale. The author also pointed out that, in general, for different biological groups, gradients at a local scale show a monotonic pattern of decreasing diversity with increasing elevation, which can turn into intermediate peaks of diversity when the entire range of the gradient is evaluated.

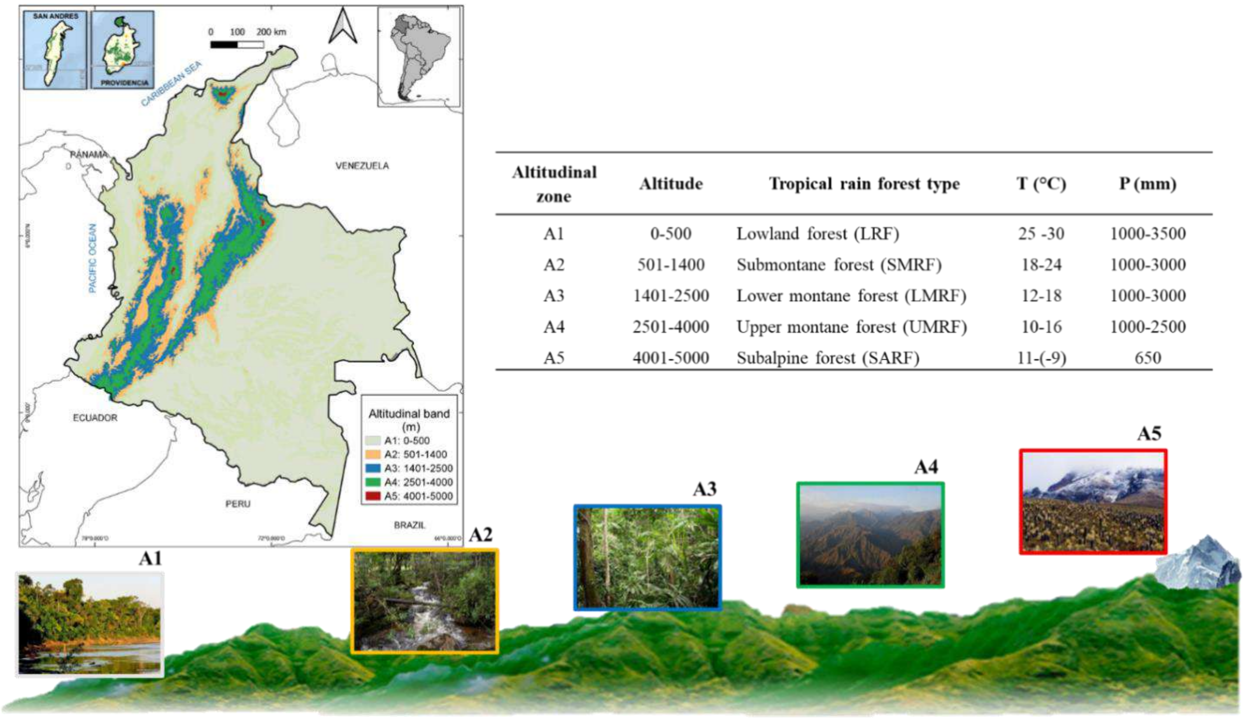
Some studies on the composition and taxonomic and functional diversity of bryophytes, particularly liverworts (Marchantiophyta), have shown that these parameters can significantly increase with altitude (and its associated factors), within the ranges considered at the local scale (Santos et al., 2014; Henriques et al., 2017; Cacua et al., 2018). This efficient response of liverworts to environmental filters in the altitudinal gradient can be due to their intrinsic characteristics, such as the absence of a lignified vascular system and consequent ability of intercepting and retaining water directly from the environment, low desiccation tolerance, and need for wetter conditions in relation to mosses (Bryophyta), which are considered better adapted to water stress (Vanderpoorten & Goffinet, 2009). Thus, it is possible that the distribution patterns of taxonomic and functional diversity and functional composition of liverworts are altered in empirical studies of the altitudinal gradient at large scales.

In this work, we use liverworts as model organisms to assess the functional composition and different diversity metrics (i.e. taxonomic and functional) as a function of altitude on a large scale, considering the whole gradient range in Colombia (0-5000 m), the country with the greatest diversity of these plants in tropical America (705 species – Gradstein, 2021). To the best of our knowledge, this is the first work to empirically assess the taxonomic and functional metrics of diversity along the altitudinal gradient at regional scale. Thus, the goals of this work are: 1) to investigate the potential importance of the mid-domain effect on the taxonomic and functional structure of the community as a function of altitude; 2) to analyze the variation in the functional composition of the community along the entire gradient. We hypothesize that: 1) the taxonomic and functional diversity of liverworts will be concentrated at the intermediate zones of the gradient, influenced by the environmental filtering exerted by altitude, as the extent of species distribution ranges is limited by the highest and lowest elevations, the so-called hard boundaries (Colwell & Hurtt, 1994); 2) since liverworts are efficient indicators of altitude-related environmental filters (Mandl et al., 2009; Ah-Peng et al., 2014; Stanton & Coe, 2021), there will be a turnover of functional traits along the gradient and each zone will present a unique set of functional traits.

2. MATERIAL AND METHODS

2.1 Study area

Five altitudinal zones covering the complete gradient in Colombia were selected: A1: 0-500 m, A2: 501-1400 m, A3: 1401-2500 m, A4: 2501-4000 m, and A5: 4001-5000 m (Fig. 1). This classification followed the guidelines proposed by Frahm & Gradstein (1991), who divided the humid tropical forests of the Neotropics using bryophytes as indicators of altitudinal zones. The scale in which the study fits is large, thus avoiding biases in the estimation of taxonomic and functional metrics.



Altitudinal zone	Altitude	Tropical rain forest type	T (°C)	P (mm)
A1	0-500	Lowland forest (LRF)	25 -30	1000-3500
A2	501-1400	Submontane forest (SMRF)	18-24	1000-3000
A3	1401-2500	Lower montane forest (LMRF)	12-18	1000-3000
A4	2501-4000	Upper montane forest (UMRF)	10-16	1000-2500
A5	4001-5000	Subalpine forest (SARF)	11-(-9)	650

Figure 1. Altitudinal zones A1: 0-500 m, A2: 501-1400 m, A3: 1401-2500 m, A4: 2501-4000 m, and A5: 4001-5000 m (*sensu* Frahm & Gradstein, 1991), with different types of rain forests, temperature and precipitation in Colombia. Temperature and precipitation data extracted from Bernal et al. (2019).

The composition of the vascular vegetation in the forests of each zone is highly variable (Duivenvoorden, 1995). In A1, the forests are dense, lianas are abundant, and there are few epiphytes and vascular hemiepiphytes. They have three or four vegetative strata with numerous herbaceous plants in the understory, among which Marantaceae and Poaceae species with broad leaves stand out, and canopies varying between 20-40 m in height, with some emergent trees reaching 60 m (Galeano et al., 1998). The structure and physiognomy of the forests in A2 is similar to those of A1, but canopies are slightly lower (up to 30 m); trees with tabular roots, arborescent palms, and lianas are less frequent, and plants have, in general, smaller leaves (Cuatrecasas, 1958). The most dominant woody plant families include Fabaceae and Moraceae, and epiphytes - among them, ferns, orchids, bryophytes and lichens - stand out with high diversity (Rangel & Velázquez, 1997). It is a densely populated region with a landscape altered by coffee crops, especially in the Central mountain range (Ideam et al., 2007).

Forests in the zone A3 have canopy heights between 15 and 20 m and thick and leathery leaves. Orchids and bryophytes stand out among the epiphytes. The families Rubiaceae, Melastomataceae, Lauraceae, and tree ferns are the most representative groups in these forests and many species are threatened with extinction (Garcia et al., 2007). These forests have also been heavily transformed, mainly for the establishment of plantations and livestock, so that mature forests are currently scarce. The zone A4 represents an ecotone between upper montane forest and páramos (Rangel, 2000). Upper montane forests are characterized by the presence of fog for at least eight months of the year (Ideam et al., 2007) and epiphytes are abundant, mainly orchids, bromeliads and bryophytes (Van Der Hammen et al., 1983; Rangel, 2000).

On the highest mountain peaks, in the zone A5, páramo and puna vegetation predominates (Rangel, 2000). The arboreal flora is scarce and the herbaceous vascular flora, in turn, is abundant and represented mainly by the families Asteraceae, Orchidaceae, Poaceae, Melastomataceae, Bromeliaceae, and Ericaceae (Morales et al., 2007). In this zone, the number of endemic vascular plants is peculiarly high (Bernal et al., 2019). Colombian páramos are very altered at present, mainly due to the establishment of potato and poppy crops and mining activities, with the original vegetation being completely obliterated in many places (Rangel, 2000).

2.2 Database

An extensive literature search was carried out on the distribution and taxonomy of liverworts along the altitudinal gradient in Colombia in catalogs (Gradstein & Uribe 2016; Bernal et al., 2019; Gradstein, 2021), basic bibliography, and articles published for the country. We also reviewed the following online herbarium databases: National Herbarium of Colombia (COL), Missouri Botanical Garden (MO), New York Botanical Garden (NY), and Herbarium Systematisch-Geobotanisches Institut (GOETHE) and the GBIF (https://www.gbif.org) and Tropicos (https://tropicos.org) pages for complementation and nomenclature updates.

Following specialized literature, fifteen traits of gametophyte and cell morphology, life form and reproduction were selected (Table 1). Traits were computed as a binary variable: 1 indicated presence and 0 absence. Life forms were classified based on their relationship with humidity, according to Glime (2017b). Asexual reproduction was considered to be present when any structure for this purpose was mentioned in the taxonomic description of the species (Kraichak, 2012; Glime & Bisang, 2017).

Table 1. Functional traits of selected liverworts and associated functions.

Traits	Trait states	Associated functions	References
Reproduction	Monoicous Dioicous	Different water requirements for sexual reproduction	(Kraichak, 2012; Glime & Bisang, 2017)
	Production of asexual structures (gemmae, propagules, regenerating leaves)	Water economy	(Kraichak, 2012; Glime & Bisang, 2017)
Life forms	Low humidity (turf) Medium humidity (mat, weft) High humidity (dendroid, flabellate, pendant)	Different water holding capacity and protection against light incidence	(Mägdefrau, 1982; Kürschner, 2004; Glime, 2017b)
G*ametophyte*	Leafy Thallose	Water uptake	(Glime, 2017a)
Leaf	Divided Entire	Different water uptake and holding capacity	(Glime, 2017a)
Lobule	Present Absent	Extracellular water storage	(Kraichak, 2012; Glime, 2017a)
Lobule morphology	Reduced Inflated	Different extracellular water storage	(Kraichak, 2012; Glime, 2017a)
Cell morphology	Dark pigmentation	Protection of chlorophyll from direct light radiation	(Glime, 2017c; Xie & Lou, 2009)
	Papilla	Osmotic regulation and rapid movement of water in the cell	(Proctor, 1979; Kürschner, 2004)

Data analysis

All statistical analyses were performed in the R 4.0.3 environment.

Liverwort richness along the altitudinal gradient was analyzed as taxonomic diversity (SR). Functional diversity was evaluated based on the following indices: Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), Functional Dispersion (FDis), and Functional Redundancy (FRed). The analyses were performed with the ‘vegan’, ‘labdsv’ and ‘FD’ packages (Villéger et al., 2008, 2010; Ah-Peng et al., 2014).

To analyze the effect of altitude on functional and taxonomic diversity metrics, continuous occurrence data of each species along the altitudinal gradient were evaluated. Thus, considering the range mentioned in the literature, a given species could occur more than once within the same altitudinal zone. The relationship of these diversity metrics with the altitudinal zones was measured using One-Way ANOVA and Tukey HSD post hoc test for pairwise comparisons, using the ‘stats’ package.

Spatial patterns of species richness expected under the exclusive influence of geometric constraints were modeled using the RangeModel 5 software (Colwell, 2006). The discrete model was based on the presence and absence of species, by establishing a set of species distribution ranges within a limited domain (in our case, the five altitudinal zones), without substitution. The process was repeated N = 1000 and the expected richness, empirical richness, and 95% confidence interval were reported for each altitudinal zone (Dunn et al., 2006; Colwell, 2008).

The correlation matrix of the traits was visualized with the ‘ggcorrplot’ function (‘ggcorplot’ package), which shows the correlation values and the significance of the traits (see appendix S1) (Kassambara, 2017). Although some traits showed collinearity above ± 0.6, all were kept in the analyses because they presented contrasting biological functionalities and, consequently, different functional responses.

Functional composition was calculated for each altitudinal zone using community weighted means (CWM) and a Categorical Principal Component Analysis (PRINCALS) was performed to observe the relationship of CWM values with the altitudinal zones using the ‘princals’ function (package ‘Gifi’) (Mair et al., 2017). The relationship between the CWM values of the functional traits and the altitudinal zones were evaluated using One-Way ANOVA and Tukey HSD post hoc test for pairwise comparisons, using the ‘stats’ package.

The ‘ggballoonplot’ function of the ‘ggpubr’ package was used to graphically display the representativeness of each trait along the altitudinal gradient. This function creates a graph from a matrix of relative frequency of the traits derived from a contingency table, in which each cell contains a circle whose size reflects the magnitude of the trait in each altitudinal zone (Kassambara, 2017).

3. RESULTS

The 705 species of liverworts that make up the flora of Colombia belong to 131 genera and 41 families. Lejeuneaceae was the family with higher richness, with ca. 30% of the total diversity of species, although unevenly distributed between the altitudinal zones and showing a decrease with elevation: 70% of the diversity was found in A1, 45% in A2, 37% in A3, 24% in A4, and 14% in A5.

The taxonomic diversity was significantly different between the altitudinal zones ($P < 0.001$, $F = 207.6$) (Table 2), with the highest values recorded in the intermediate zones – A3 (487 spp.) followed by A4 (426 spp.) and A2 (368 spp.) – and the lowest in the zones A1 and A5 (340 spp. and 104 spp., respectively), thus exhibiting a unimodal distribution (Fig. 2a). The null model corroborated this distribution, with the empirical richness values being within or above the predicted confidence interval, with the exception of A5, where the observed value was below that predicted by the model (see appendix S2).

The same pattern was found for FRic ($P < 0.001$, $F = 21.99$), FRed ($P < 0.001$, $F = 101.2$), FDiv ($P < 0.001$, $F = 2.811$), FDis ($P < 0.001$, $F = 39.57$) (Fig. 2b, 2c, 2e, 2f, Table 2), but not for FEve, which presented the highest value in A5 (Fig. 2d, Table 2).

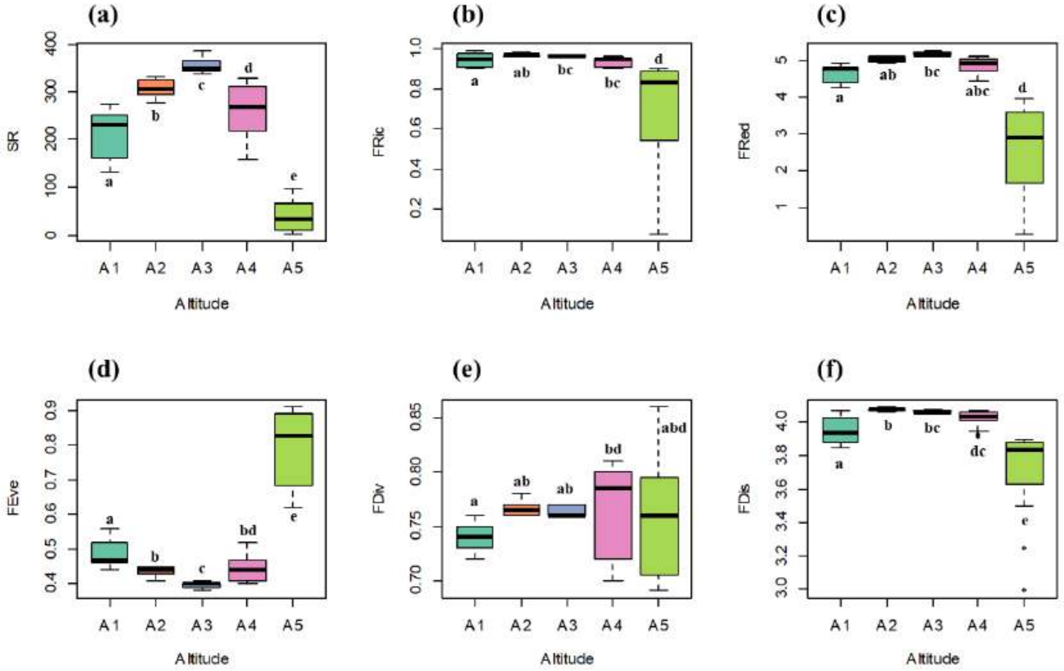


Figure 2. Taxonomic and functional diversity of liverworts in relation to altitude (letters represent the results of post-hoc Tukey comparisons of means for each zone). (a): SR, taxonomic diversity; (b): FRic, functional richness; (c): FRed, functional redundancy; (d): FEve, functional evenness; (e): FDiv, functional divergence; (f): FDis, functional dispersion. Altitudinal zone: A1: 0-500 m, A2: 501-1400 m, A3: 1401-2500 m, A4: 2501-4000 m, and A5: 4001-5000 m.

Table 2. Mean ± SD values of the indices (SR, FRic, FRed, FEve, FDiv and FDis) in the altitude gradient. Values followed by the same lower case letter in a row indicate no statistical difference (one-way ANOVA; Tukey's test, $P \leq 0.05$). SR, taxonomic diversity; FRic, functional richness;

FRed, functional redundancy; FEve, functional evenness; FDiv, functional divergence; FDis, functional dispersion. Altitudinal zone: A1: 0-500 m, A2: 501-1400 m, A3: 1401-2500 m, A4: 2501-4000 m, and A5: 4001-5000 m.

	Altitudinal zone					ANOVA		
	A1	**A2**	**A3**	**A4**	**A5**	***F***	***P***	***df***
SR	215.33±45.46^{a}	306.55±17.83^{b}	353.19±13.83^{c}	259.86±53.78^{d}	41.90±32.61^{e}	207.6	<2e-16	4
FRic	0.948±0.031^{a}	0.968±0.007^{ab}	0.963±0.004^{bc}	0.935±0.021^{bc}	0.705±0.269^{d}	21.99	1.16e-13	4
FRed	4.698±0.224^{a}	5.041±0.062^{ab}	5.193±0.038^{bc}	4.882±0.209^{abc}	2.688±1.118^{d}	101.2	<2e-16	4
FEve	0.482±0.035^{a}	0.436±0.012^{b}	0.398±0.008^{c}	0.443±0.036^{bd}	0.789±0.111^{e}	202.9	<2e-16	4
FDiv	0.742±0.011^{a}	0.766±0.007^{ab}	0.763±0.004^{ab}	0.765±0.039^{bd}	0.754±0.051^{abd}	2.811	0.0284	4
FDis	3.940±0.744^{a}	4.075±0.007^{b}	4.065±0.007^{bc}	4.022±0.049^{dc}	3.728±0.240^{e}	39.57	<2e-16	4

The cumulative variance in the first two axes of the PRINCALS for the cluster of functional traits in the altitudinal zones showed 97.9% (axis 1 = 86.9%, axis 2 = 11%) of significance (Fig. 3). The presence of lobules, reduced lobules, inflated lobules, thalloid gametophytes, and life forms adapted to highly humid conditions were positively correlated with the first axis of the PRINCALS, while leafy gametophytes and life forms tolerant to low humidity showed a negative correlation with this axis (Table 3).

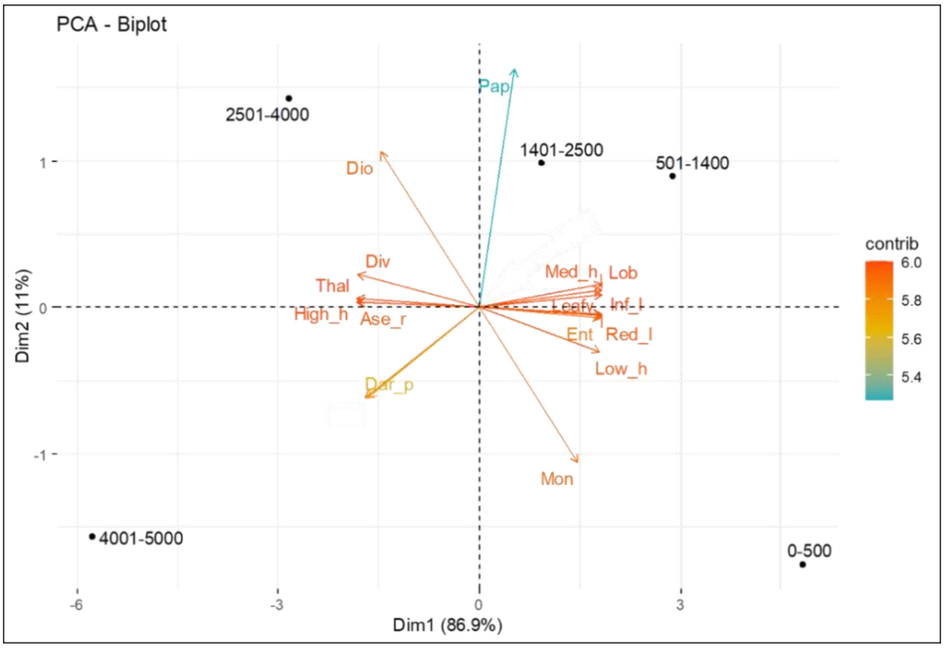


Figure 3. Categorical principal components analysis (PRINCALS) between the functional traits of liverwort species (community weighted means - CWM) and altitudinal zones in Colombia. Mon: Monoicous; Low_h: Low humidity; Red_l: Reduced lobule; Ent: Entire leaf; Lob: Lobule; Inf_l: Inflated lobule; Med_h: Medium humidity; Leafy; Pap: Papilla; Dio: Dioicous; Div: Divided leaf; Thal: Thallose; High_h: High humidity; Dar_p: Dark pigmentation; Ase_r: Asexual reproduction.

Table 3. Pearson correlation between functional traits and the first two axes of the PRINCALS, explanatory variance of each of the axes, and Eigenvalues. Altitudinal zone: A1: 0-500 m, A2: 501-1400 m, A3: 1401-2500 m, A4: 2501-4000 m, and A5: 4001-5000 m.

Altitudinal zone	**Traits**	**Dim.1**	**Dim.2**
A1	Monoicous	-0.817	0.57
	Low humidity	-0.998	0.025
	Reduced lobule	0.995	-0.025
	Entire leaf	0.986	-0.041
A2	Lobule	0.996	0.087
	Inflated lobule	0.998	0.047
	Medium humidity	-0.992	-0.123
	Leafy	-0.998	0.025
A3	Papilla	0.29	0.891
A4	Dioicous	0.817	-0.57
	Divided leaf	-0.988	0.123
	Thallose	0.998	-0.025
A5	High humidity	0.998	0.025
	Dark pigments	0.9	0.387
	Asexual reproduction	0.993	-0.018
	Eigenvalues	14.778	1.867
	% of Variance	86.928	10.985

The analyzed functional traits had a significantly positive or negative relationship with the gradient, confirmed by the ANOVA (see Appendix S3 and Fig. 4). Exceptionally, the presence of cell papillae did not show a significant linear relationship with altitude (P = 0.11, F = 1.925), although it was more pronounced in the intermediate zones (A2 - A4) (Fig. 4c).

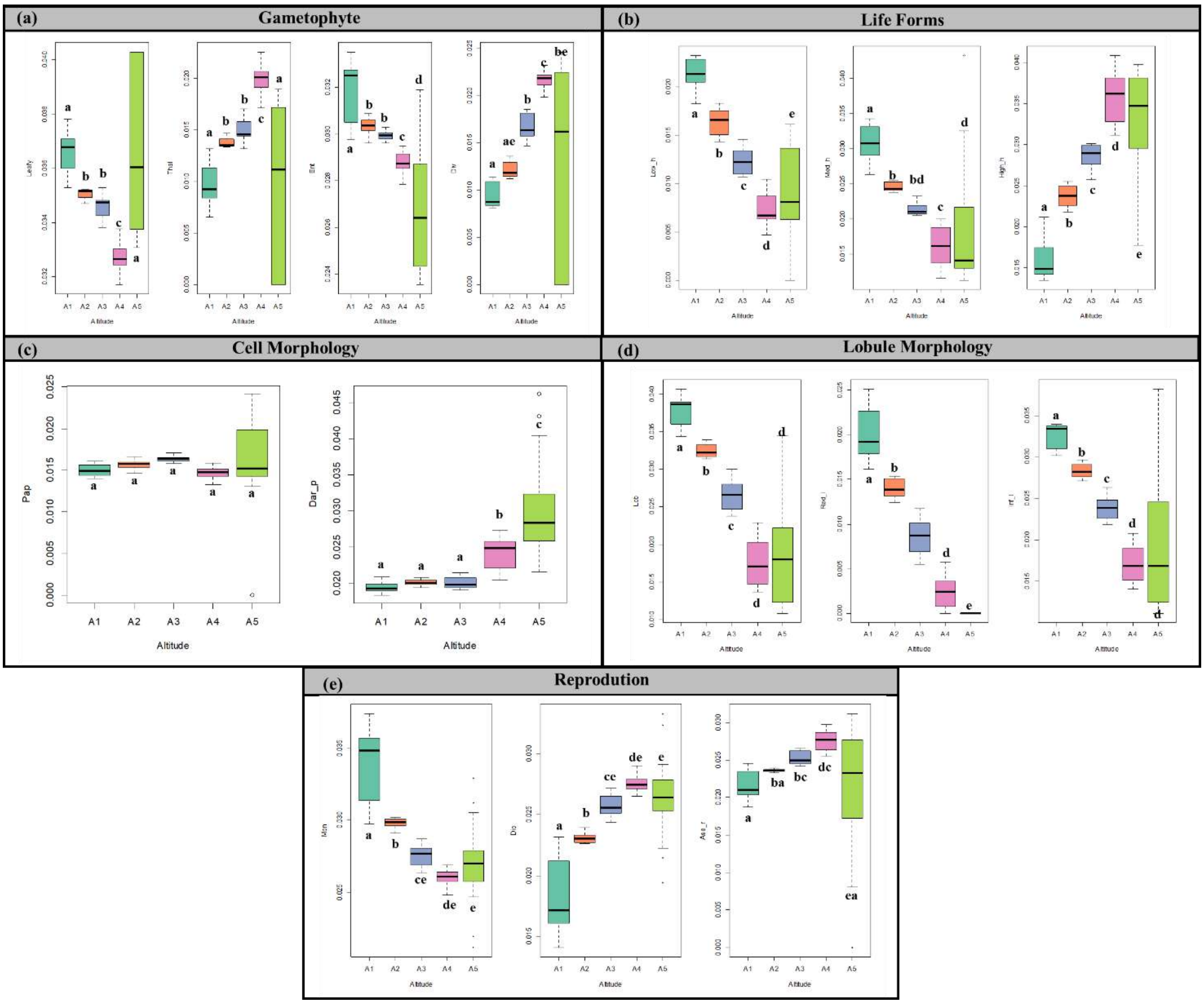


Figure 4. Functional traits per altitudinal zone (letters represent the results of post-hoc Tukey comparisons of the means for each zone). (a): Gametophyte; (b): Life form; (c): Cell morphology; (d): Lobule morphology; (e): Reproduction. Altitudinal zone: A1: 0-500 m, A2: 501-1400 m, A3: 1401-2500 m, A4: 2501-4000 m and A5: 4001-5000 m. Mon: Monoicous; Low_h: Low humidity; Red_l: Reduced lobule; Ent: Entire leaf; Lob: Lobule; Inf_l: Inflated lobule; Med_h: Medium humidity; Leafy; Pap: Papilla; Dio: Dioicous; Div: Divided leaf; Thal: Thallose; High_h: High humidity; Dar_p: Dark pigmentation; Ase_r: Asexual reproduction.

Furthermore, a clear turnover of most traits along the gradient was observed (Fig. 5). The frequency of the attribute leaf lobule progressively decreased along the gradient until reaching the lowest representativeness in A5, while the trait divided leaf showed the inverse pattern. At lower altitudes (A1-A2), the traits that stood out were life form tolerant to low humidity and monoicous reproductive system, which were substituted in higher altitudinal zones (A4-A5) by life form adapted to highly humid conditions and dioicous reproductive system. The traits asexual structures and dark pigmentation were more frequent in A5, confirming the greater functional evenness and specificity of liverworts in this zone.

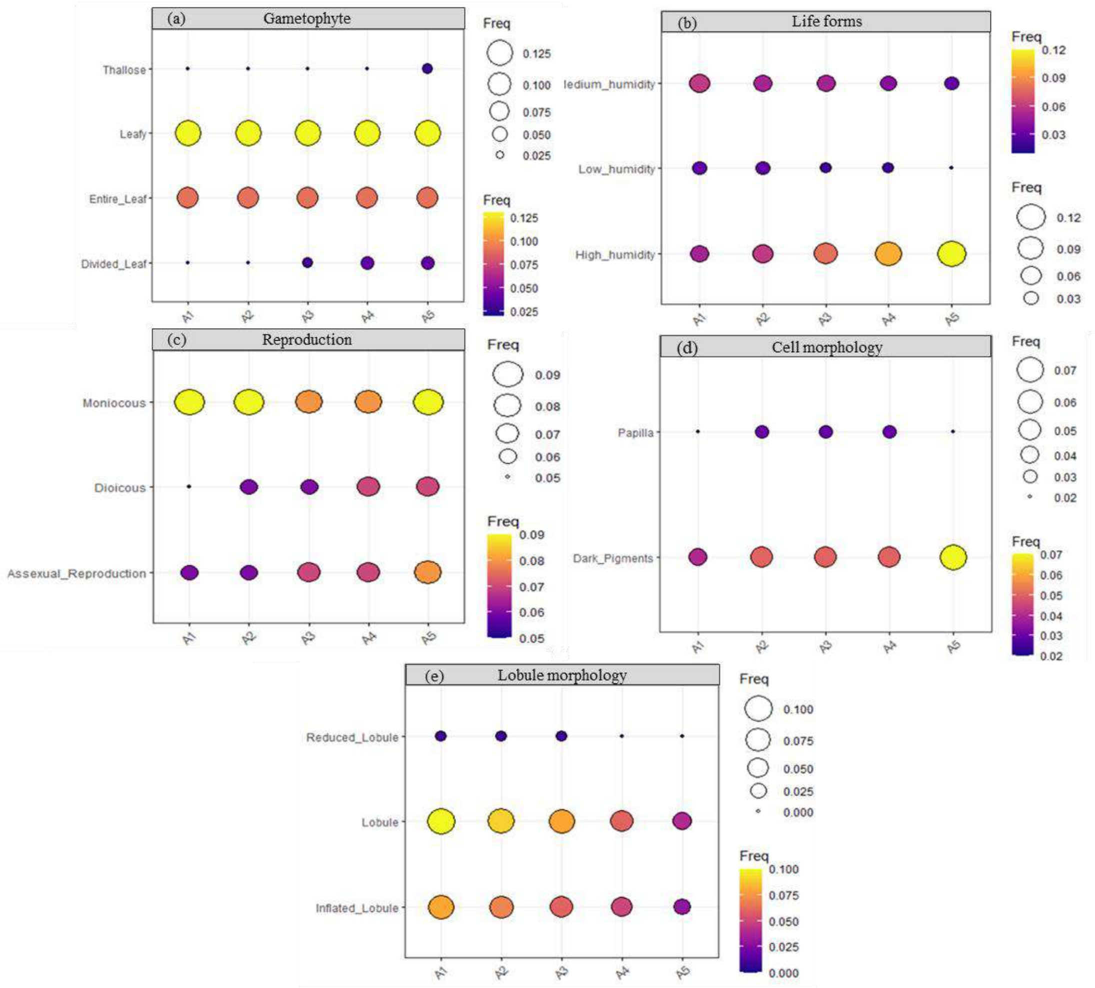


Figure 5. Functional traits with relative frequency values for each altitudinal zone grouped according to gametophyte morphology, cell morphology, reproduction, and life form. (a): Gametophyte; (b): Life form; (c): Reproduction; (d): Cell morphology; (e): Lobule morphology. Altitudinal zone: A1: 0-500 m, A2: 501-1400 m, A3: 1401-2500 m, A4: 2501-4000 m, and A5: 4001-5000 m.

4. DISCUSSION

4.1 Taxonomic and functional diversity

The taxonomic and functional diversity of liverworts along the altitudinal gradient in Colombia showed a unimodal hump-shaped distribution pattern, confirming the prediction of the importance of the mid-domain effect on the community structure as a function of elevation. This pattern has been reported for the taxonomic diversity of different biological groups in tropical forests in meta-analyses (Colwell & Lees, 2000; Rahbek, 2005). Specifically for liverworts, large-scale floristic compilations have indicated that diversity is greatest at intermediate altitudes (Van Reenen & Gradstein, 1983; Gradstein, 1995; Gradstein et al., 1989; Wolf, 2003). For example, the Colombian liverwort flora catalog mentions that diversity peaks between 2000 m and 3000 m in the Andes and decreases in the zone close to sea level and on the tops of mountains, what the authors believe to be due to lack of collections and the more restrictive environmental conditions of the páramo and puna, respectively (Uribe & Gradstein, 1999).

In this work, the mid-domain effect was statistically confirmed. Mid-elevation peaks in richness of species and functional groups can be interpreted as the result of the accumulation of distributions of liverwort species and their functionalities, given the spatial restrictions of the altitudinal domain. These restrictions were clearly evident in the extreme zones, A1 and A5, and the latter, particularly, presented high functional evenness and fewer species than expected by the null model. The synergistic effect of a set of factors is possibly responsible for the diversity patterns observed in this work. The lower richness of liverworts at high altitudes (4001-5000 m) in Colombia can be largely attributed to environmental factors: low arboreal coverage, light incidence that is three-fold higher than that of forested areas, abrupt changes in temperature - reaching 31 °C during the day and falling below zero at night - and strong winds that can increase desiccation and limit the species reproduction and establishment (Cacua et al., 2018).

It is also possible that the lower surface area and geographical isolation of mountain tops, when compared to other altitudinal ranges, result in little area available for species occupation (MacArthur, 1972; Scott, 1976; Uribe & Gradstein, 1999) and explain the decline in taxonomic diversity and abundance of functional traits at the higher zones, leading to greater functional evenness. On the other hand, anthropogenic activities such as deforestation for establishment of subsistence crops, thinning, and conversion of natural areas into livestock pastures have intensified the processes in forests and consequently potentiated the loss of biodiversity in the upper zones of the altitudinal gradient (Rangel, 2000). In this sense, analyzing the whole range of the altitudinal gradient of the study area is important so as to cover as accurately as possible the environmental variation and achieve a better understanding of the distribution patterns of liverworts, as well as of other biological groups.

4.2 Functional composition

Liverworts respond effectively to the altitudinal gradient and can be considered reliable indicators of altitudinal zones because they present more precise responses to the environmental filter than the phanerogamic vegetation in terms of establishment and occupation of habitats

(Frahm & Gradstein, 1991; Santos & Costa, 2010; Santos et al., 2014). The filtering by altitude and its associated factors was evident in the turnover of functional traits along the altitudinal gradient in this work. Contrasting results on the functional composition of liverworts across altitudinal zones indicate that different processes may be acting on the assemblages or that different assemblages have unique sensitivities to abiotic conditions according to their microhabitat (Ah-Peng et al., 2014). Thus, considering the sensitivity of liverworts to altitudinal filters, it is likely that each zone presents numerous specific microenvironmental conditions that play a role in the filtering of the functional traits.

In the studied gradient, the strategies that provide maximum water uptake/storage and protection against desiccation and intense light radiation gained prominence as altitude increased. For example, we found that life forms tolerant to low/medium humidity, e.g., turf and mat, known to be usually more frequent in lowlands (Kürschner & Parolly, 1998), were substituted in the higher zones by life forms adapted to highly humid conditions, e.g. flabellate, dendroid, and pendant. The latter life forms have a relatively solitary habit, with gametophytes attached to the substrate by a single basal point and branches exposed to the atmosphere that play a key role in the interception of cloudwater droplets and condensation of water vapor from occult precipitation frequent on mountain tops (Proctor 2002, 2004; Goldstein et al., 2002; León-Vargas et al., 2006).

It is worth noting that A4 stood out as a transition zone in terms of functional composition, considering that the species shared traits of lower and upper zones of the gradient. This was corroborated by the high functional divergence observed in this zone, generating niche differentiation and reducing competition for resources between liverwort communities.

In turn, in A5, the abiotic conditions tend to be harsher than in the lowlands, mainly due to lower temperature (mean of 11ºC) and lower precipitation rates (650 mm/year on average), in addition to higher light incidence compared lower altitudes (Cacua et al., 2018). In this zone, the predominance of herbaceous vegetation and nearly bare soils resulting from the rocky relief generate a habitat suitable for the development of a rich terrestrial liverwort flora (Gradstein et al., 2001; Frahm, 2003; Hofstede et al., 2003). This environment also favored species with dark pigmentation, which was expected because bryophytes generally show photosynthetic light saturation at moderate irradiance compared to most vascular plants, and excessive luminosity can lead to photoinhibition (Arróniz-Crespo et al., 2004; Marschall & Proctor, 2004; Mota de Oliveira, 2018). Soriano et al. (2019) showed that sun liverwort species exhibit different accessory pigments (e.g., antheraxanthin, zeaxanthin, violaxanthin) compared to shade specialists as a strategy to reduce light absorption and increase photoprotection. This defense mechanism is thought to allow liverworts with dark pigments to exhibit greater tolerance to UV-B radiation than shade species and the vast majority of mosses (Martinez-Albaiger et al., 2003; Soriano et al., 2019).

Generally, high altitudes and the associated abiotic factors also favor plants with conservative strategies (i.e., with greater investment in vegetative growth than in reproduction), demonstrating the important role of the trade-off between reproduction and vegetative growth: plants at higher altitudes usually present low reproductive effort to maintain population growth or establish new individuals (Frey et al., 1995; Hedderson & Longton, 2008; Hautier et al., 2009). In these environments, the maintenance of populations can be ensured through a myriad of structures for clonal propagation, such as gemmae, regenerative gametophyte fragments, and caducous leaves (Glime & Bisang, 2017). In fact, in this work, the reproductive strategy of liverworts at mountain tops (A4-A5) was based on little investment in sexual reproduction in relation to liverworts of lowland forests (A1), and in this assemblage there was a high contribution of dioicous species that invest in asexual reproduction. Furthermore, it has been suggested that low sporophyte production in dioicous species is an adaptive strategy to conserve photosynthates (Frey et al., 1995; Glime & Bisang, 2017). Indeed, populations of upper-Andean liverworts were found to be frequently sterile by Gradstein (2021).

5. CONCLUSION

Liverworts respond efficiently to the altitudinal gradient, and the intermediate zone, between 1401-2500 m, accumulated the highest richness and functional diversity, confirming that the mid-domain effect was explanatory for this group of plants when analyzed on a large scale. Altitude and its associated factors seem to act as environmental filters, providing a myriad of microenvironmental conditions specific to each zone and selecting functional groups and functional traits, particularly those associated with protection against light incidence and temperature variations and, mainly, moisture uptake and water retention as adaptive strategies. As new directions for research on the subject, we suggest to investigate how the patterns of functional diversity found in this study and how phylogenetic diversity may be impacted by ongoing and future climate change, especially in highly vulnerable hotspots such as the tropical Andes.

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BIOSKETCHES

Yeison Jaroc Lombo Sanchez is interested in the functional ecology of bryophytes, the ecology of the community and the distribution patterns of the species in elevational gradients. This article is part of his master's thesis.

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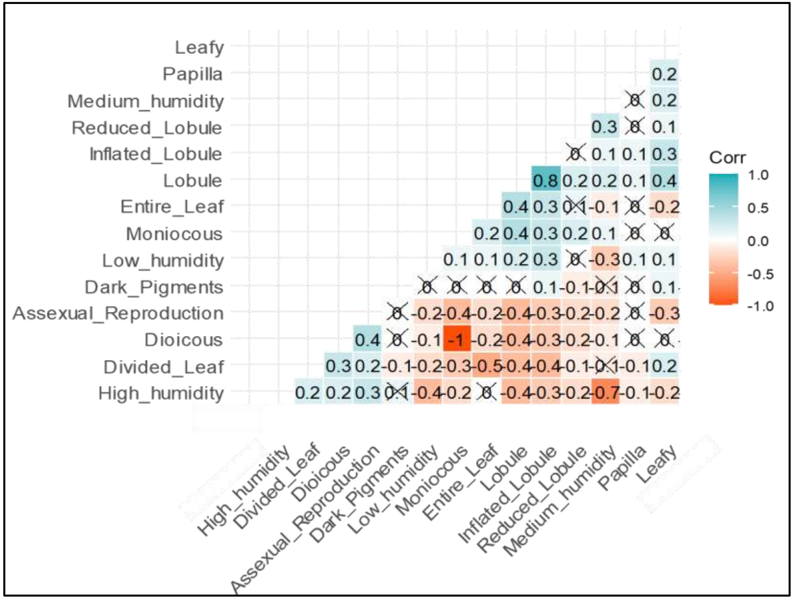
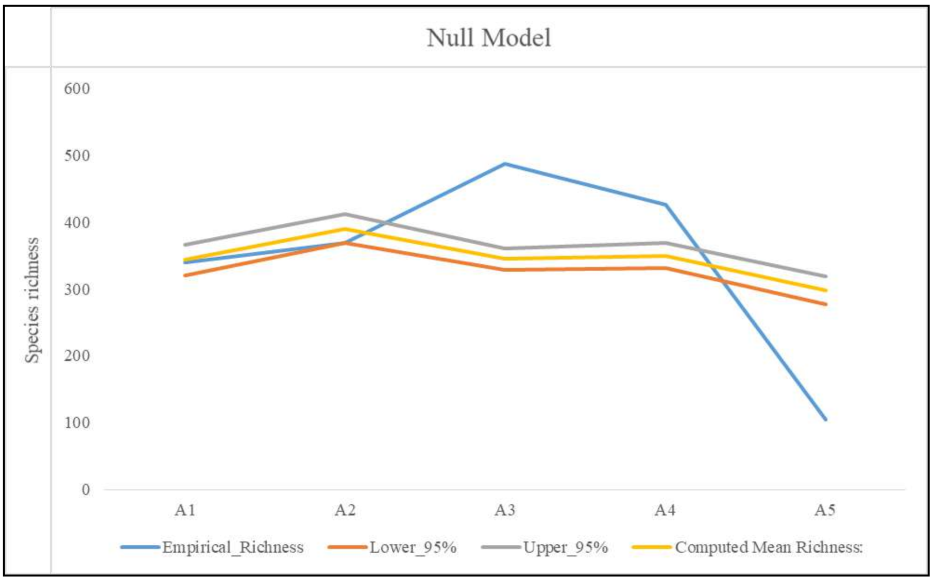
APPENDIX

Appendix S1. Correlogram of functional traits. Positive correlations are shown in blue and negative ones in red. Non-significant correlations are marked with an (X).



Appendix S2. Null model of the observed and predicted distribution of richness and significance values along the altitudinal gradient. Altitudinal zone: A1: 0-500 m, A2: 501-1400 m, A3: 1401-2500 m, A4: 2501-4000 m and A5: 4001-5000 m.



Appendix S3. Mean ± SD values of functional traits as a function of altitudinal zones. Values followed by the same lower case letter in a row indicate no statistical difference (one-way ANOVA; Tukey HSD post hoc test, $P \leq 0.05$). Altitudinal zone: A1: 0-500 m, A2: 501-1400 m, A3: 1401-2500 m, A4: 2501-4000 m, and A5: 4001-5000 m. Mon: Monoicous; Low_h: Low humidity; Red_l: Reduced lobule; Ent: Entire leaf; Lob: Lobule; Inf_l: Inflated lobule; Med_h: Medium humidity; Leafy; Pap: Papilla; Dio: Dioicous; Div: Divided leaf; Thal: Thallose; High_h: High humidity; Dar_p: Dark pigmentation; Ase_r: Asexual reproduction.

	Altitudinal zone					**ANOVA**		
	A1	**A2**	**A3**	**A4**	**A5**	***F***	***P***	***df***
Monoicous	0.0340±0.002^{a}	0.0297±0.00^{b}	0.0275±0.00^{ce}	0.0260±0.002^{de}	0.0269±0.002^{e}	111.4	<2e-16	4
Dioicous	0.0181±0.002^{a}	0.0231±0.00^{b}	0.0257±0.00^{ce}	0.0275±0.00^{de}	0.0264±0.00^{e}	111.4	<2e-16	4
Assexual reproduction	0.0215±0.001^{a}	0.0236±0.00^{ba}	0.0253±0.00^{bc}	0.0276±0.001^{dc}	0.0200±0.0102^{ea}	13.54	3.65e-09	4
Low humidity	0.0214±0.001^{a}	0.0163±0.001^{b}	0.0121±0.001^{c}	0.0072±0.001^{d}	0.0093±0.004^{e}	152.6	<2e-16	4
Medium humidity	0.0214±0.001^{a}	0.0163±0.001^{b}	0.0121±0.001^{bd}	0.0072±0.001^{c}	0.0093±0.004^{d}	152.6	<2e-16	4
High humidity	0.0157±0.002^{a}	0.0237±0.001^{b}	0.0288±0.001^{c}	0.0359±0.003^{d}	0.0329±0.006^{e}	152.6	<2e-16	4
Thallose	0.0095±0.001^{a}	0.0137±0.00^{b}	0.0151±0.001^{b}	0.0199±0.001^{c}	0.0093±0.007^{a}	54.39	<2e-16	4
Leafy	0.0366±0.00^{a}	0.0350±0.00^{b}	0.0345±0.00^{b}	0.0327±0.00^{c}	0.0364±0.001^{a}	54.39	<2e-16	4
Entire leaf	0.0318±0.001^{a}	0.0303±0.00^{b}	0.0299±0.00^{b}	0.0287±0.00^{c}	0.0265±0.002^{d}	58.91	<2e-16	4
Divided leaf	0.0093±0.001^{a}	0.0121±0.00^{ae}	0.0167±0.001^{b}	0.0216±0.00^{c}	0.0131±0.0100^{be}	38.72	<2e-16	4
Lobule	0.0378±0.001^{a}	0.0324±0.00^{b}	0.0263±0.001^{c}	0.0175±0.002^{d}	0.0182±0.001^{d}	193.3	<2e-16	4
Inflated lobule	0.327±0.001^{a}	0.0283±0.00^{b}	0.0236±0.001^{c}	0.0170±0.0016^{d}	0.0191±0.007^{d}	556.5	<2e-16	4
Reduce lobule	0.0202±0.002^{a}	0.0140±0.00^{b}	0.0084±0.001^{c}	0.0023±0.001^{d}	0.0±0.0^{e}	556.5	<2e-16	4
Dark pigments	0.0194±0.00^{a}	0.0201±0.00^{a}	0. 0201±0.00^{a}	0.0241±0.002^{b}	0.0302±0.006^{c}	53.54	<2e-16	4
Papilla	0.0149±0.00^{a}	0.0156±0.00^{a}	0. 0163±0.00^{a}	0.0146±0.00^{a}	0.0155±0.006^{a}	1.925	0.11	4

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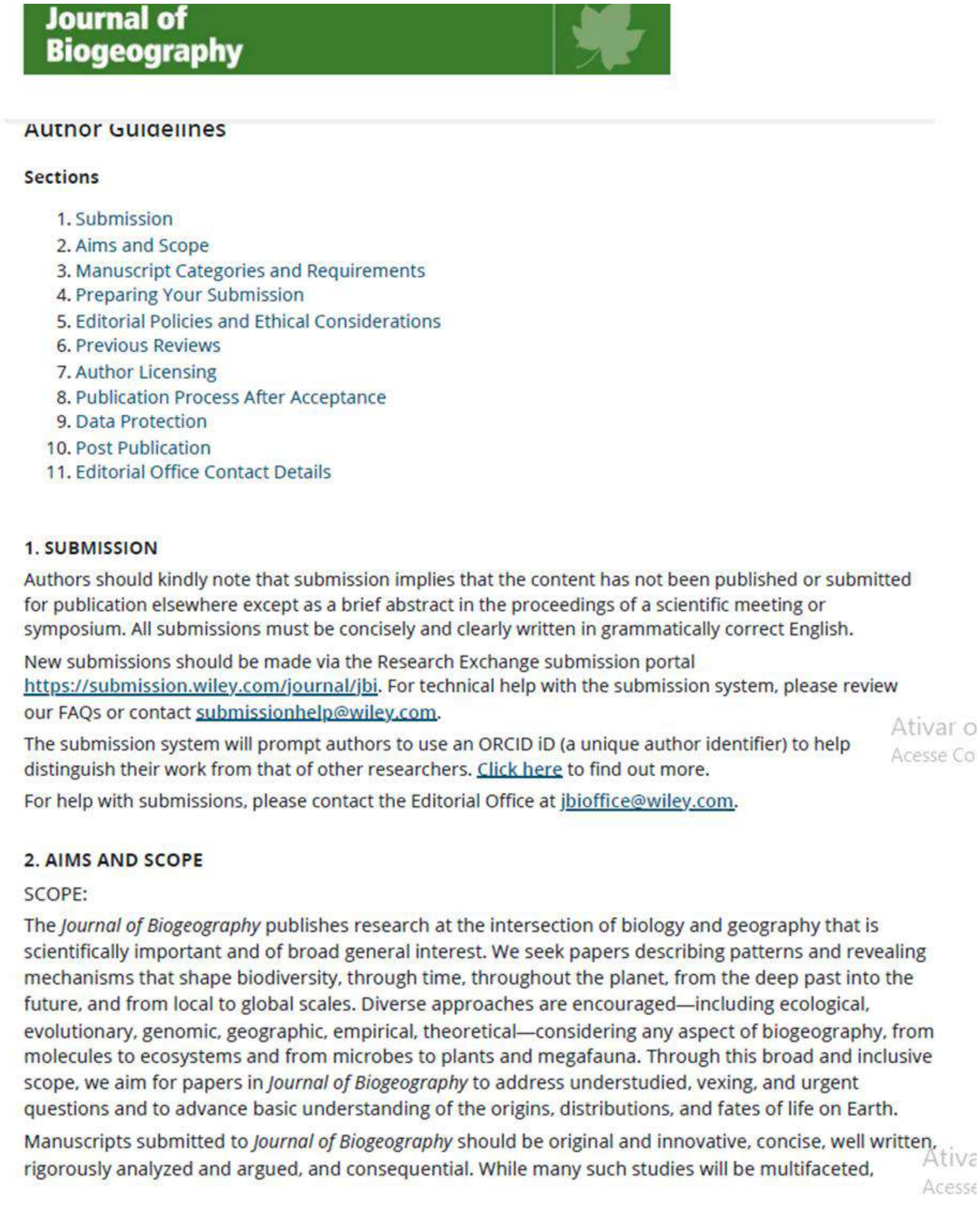

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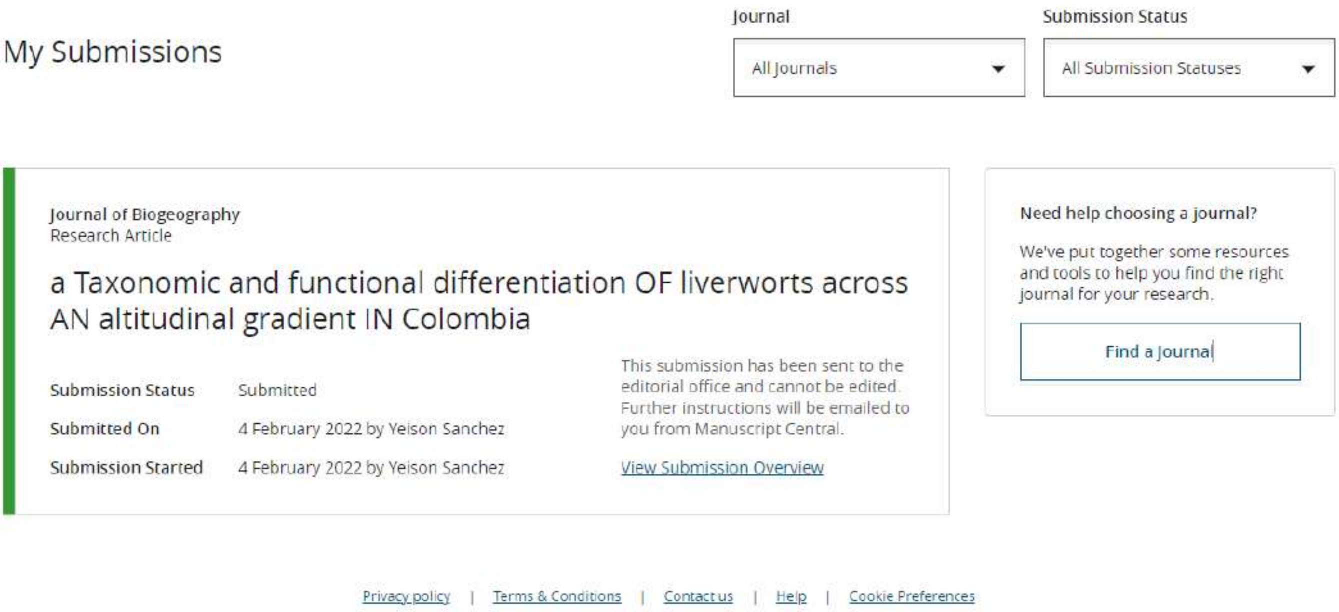

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Journal of Biogeography
Research Article

a Taxonomic and functional differentiation OF liverworts across AN altitudinal gradient IN Colombia

Submission Status	Submitted
Submitted On	4 February 2022 by Yeison Sanchez
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4 CONSIDERACÕES FINAIS

- As hepáticas respondem eficientemente aos filtros ambientais e se configuram como um excelente modelo para testar métricas de composição e diversidade em função de gradientes ambientais, dentre eles, o altitudinal.
- O efeito do domínio médio é explicativo para a riqueza e diversidade funcional das hepáticas, tendo em vista os seus valores máximos ocorrerem na faixa intermediária no gradiente estudado, compreendida entre 1401-2500 m.
- A altitude e os fatores associados parecem atuar como filtros ambientais por fornecer uma gama de condições microambientais específicas para cada faixa e por selecionar atributos e grupos funcionais, em especial aqueles relacionados à proteção contra a incidência luminosa, a variações de temperatura e, principalmente, a absorção de umidade e retenção de água.
- Em futuras investigações sugere-se analisar os padrões de diversidade funcional identificados no presente estudo relacionando-o à de diversidade filogenética de hepáticas, face, por exemplo, às alterações climáticas ora em curso e previstas, sobretudo por ser os Andes tropicais, um hotspot altamente vulnerável.

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