CARLOS MARIO GALVÁN CISNEROS

FILTRAGEM AMBIENTAL, COMPETIÇÃO E FACILITAÇÃO EM COMUNIDADES DE PLANTAS ALPINAS E FLORESTAIS DE MONTANHAS TROPICAIS

Tese apresentada à Universidade Federal de Viçosa como parte das exigências do Programa de Pós-Graduação em Botânica para obtenção do título de *Doctor Scientiae*.

Orientador: João Augusto Alves Meira Neto

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Projeto apresentado à Universidade Federal de Viçosa como parte das exigências do Programa de Pós-Graduação em Botânica para obtenção do título de *Doctor Scientiae*.

APROVADA: 6 de março de 2024.

Assentimento:

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Autor

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Orientador

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ABSTRACT

GALVÁN CISNEROS, Carlos Mario D.Sc., Universidade Federal de Viçosa, March, 2024. **Environmental Filtering, Competition, and Facilitation in Alpine and Forestry plant communities in Tropical Mountains.** Advisor: João Augusto Alves Meira Neto.

Understanding the mechanisms that influence the assembly of natural communities has become a central issue in ecological studies, especially because of the influence of diversity on ecosystem functioning. These mechanisms may be related to niche and neutral processes. Niche-related processes include selection imposed by the abiotic environment and biotic interactions, whereas neutral effects are related to chance or historical events. Mountain ecosystems are among the most suitable models for unraveling the interactions between the facets of biodiversity. The overall aim of this project was to understand the assembly processes of alpine and forest plant communities through phylogenetic and functional diversity across altitudinal gradients in tropical mountains. To respond to this approach, we selected areas from several tropical mountains worldwide. We used lists with altitude records from three tropical montane mountains of tropical ecosystems: Mount Puracé, Colombia; Mount Kilimanjaro, Tanzania; and Mount Haleakalā, Hawaii, USA (CAP. 1). In addition, six sampling sites were established along an elevation gradient of (3200-4100 m). At each station, 10 plots measuring 2.5 m x 4 m were established (CAP. 2 and 3). In addition, 28 isolated individuals of *Espeletia lopezii* (Asteraceae) were selected; a 70 cm diameter metal ring was centered on each caulescent rosette. In addition, 28 rings were established in the open areas (control) (CAP. 4). The alpha taxonomic diversity was estimated using Hill's numbers (q=0, q=1, q=2) (CAP. 2 and 4). For phylogenetic diversity, six phylogenetic metrics were calculated: lineage diversity as the total length of the phylogenetic branch (PD), mean pairwise phylogenetic distance (MPD), mean nearest taxon phylogenetic distance (MNTD), and standardized effect size of these metrics (CAP. 1, 2 and 4). To determine the functional responses that drive the assembly of communities along the elevation gradient, five functional traits were measured: leaf area, leaf length, leaf thickness, leaf dry matter content, and maximum plant height. The weighted community mean (CWM) of the traits and functional diversity (FD) were estimated (CAP. 3). Different statistical models were used to test the main effects of altitude and soil depth on taxonomic, phylogenetic, and functional metrics. In the three tropical mountains, an environmental filtering effect was observed with increasing altitude, causing phylogenetic clustering, decreasing phylogenetic diversity, and decreasing species richness. The decreasing phylogenetic distances between close relatives are congruent with neo-endemism, suggesting recent diversification of plants at high altitudes in tropical mountains, possibly driven by geographical isolation and environmental heterogeneity (CAP. 1). In Chapter 2, the results showed that as soil depth decreased and altitude increased, *páramo* plant communities showed a general pattern of decreasing phylogenetic diversity. These results are consistent with the general expectation that community assemblage attributes become more closely related as stressful environmental conditions increase along a gradient. In Chapter 3, the results showed that several functional traits (CWM) and several indices of functional diversity varied significantly along the altitude and soil gradient in the area. Three of the five functional traits showed the potential to describe how the functional composition of páramo communities responded to increasing environmental severity along these environmental gradients. The two functional diversity indices, FDis and FRic, significantly decreased with increasing elevation and decreasing soil depth. In Chapter 4, the vegetation under the canopy of the facilitator plants (*E. lopezii*) was found to have a positive impact on taxonomic diversity, compared to the control areas. Regarding phylogenetic diversity, the dominant pattern observed was mainly random. These results suggest that, at these altitudes, the metacommunity is strongly filtered by climatic and edaphic factors, and despite the benefits of the facilitation exerted by stem rosettes, it is difficult to detect a pattern of phylogenetic overdispersion. In Chapter 5, as a general trend, a greater number of species were found in locations at higher altitudes, decreasing in locations at lower altitudes, and where climatic seasonality is more marked and filters out species from lineages that are less tolerant to stressful environments. Nitrogen-fixing Fabaceae species were prominent among the important species, especially at low altitudes and more stressful sites.

Keywords: Tropical mountains, altitudinal gradient, phylogenetic diversity, functional diversity, plant-plant interaction, community assembly.

RESUMO

GALVÁN CISNEROS, Carlos Mario D.Sc., Universidade Federal de Viçosa, março, 2024. **Filtragem ambiental, competição e facilitação em comunidades de plantas alpinas e florestais de montanhas tropicais.** Orientador: João Augusto Alves Meira Neto.

Compreender os mecanismos que influenciam a montagem das comunidades naturais tornou-se um assunto central nos estudos de ecologia, especialmente pela influência da diversidade no funcionamento ecossistêmico. Estes mecanismos podem estar relacionados a nichos e processos neutros. Os processos relacionados a nichos incluem a seleção imposta pelo ambiente abiótico e interações bióticas, enquanto os efeitos neutros estão relacionados ao acaso ou eventos históricos. Os ecossistemas de montanha são um dos modelos mais adequados para desvendar a interação entre as facetas da biodiversidade. Neste contexto, o objetivo geral deste projeto for compreender os processos de montagem das comunidades de plantas alpinas e florestais por meio da diversidade filogenética e funcional em gradientes altitudinais em montanhas tropicais. Para responder a esta abordagem, foram selecionadas áreas em várias montanhas tropicais ao redor do mundo. Foram usadas listas com registros de altitude de três montanhas tropicais montanas de ecossistemas tropicais: do Monte Puracé, Colômbia; do Monte Kilimanjaro, Tanzânia; e do Monte Haleakalā, Havaí, EUA (CAP. 1). Também, foram estabelecidas seis cotas de amostragem em um gradiente de elevação (3200-4100 m). Em cada estação se estabeleceram 10 parcelas de 2.5 m x 4 m (CAP. 2 e 3). Além disso, foram selecionados 28 indivíduos isolados de *Espeletia lopezii* (Asteraceae); um anel de metal de 70 cm de diâmetro foi centrado em cada roseta caulescente. Também, foram estabelecidos 28 anéis em áreas abertas (controle) (CAP. 4). A diversidade taxonômica alfa foi estimada usando os números de Hill (q=0, q=1, q=2) (CAP. 2 e 4). Para a diversidade filogenética foram calculados seis métricas filogenéticas: a diversidade da linhagem como o comprimento total do ramo filogenético (PD); a distância filogenética média de pares (MPD); a distância filogenética média do táxon mais próximo (MNTD) e tamanho do efeito padronizado dessas métricas (CAP. 1, 2 e 4). Para determinar as respostas funcionais que impulsionam a montagem das comunidades ao longo do gradiente de elevação foram medidos cinco traços funcionais: área foliar, comprimento foliar, espessura foliar e conteúdo de matéria seca foliar e altura máxima de planta, e, posteriormente, foram estimadas a média ponderada da comunidade (CWM) dos traços e a diversidade funcional (DF) (CAP. 3). Foram utilizados diferentes modelos estatísticos para testar os principais efeitos da altitude e a profundidade do solo em diferentes métricas taxonômicas, filogenéticas e funcionais. Nas três montanhas tropicais, foi encontrado um efeito de filtragem ambiental com o aumento da altitude, causando agrupamento filogenético, diminuição da diversidade filogenética e diminuição da riqueza de espécies. As distâncias filogenéticas decrescentes entre parentes mais próximos são congruentes com as neo-endemismos, sugerindo uma recente diversificação de plantas em grandes altitudes de montanhas tropicais, possivelmente impulsionada pelo isolamento geográfico e pela heterogeneidade ambiental (CAP. 1). Para o capítulo 2, os resultados mostraram que, à medida que a profundidade do solo diminuía e a altitude aumentava, as comunidades de plantas do páramo apresentavam um padrão geral de diminuição da diversidade filogenética. Estes resultados são consistentes com a expectativa geral de que os atributos da montagem comunitária estão mais intimamente relacionados à medida que as condições ambientais estressantes aumentam ao longo de um gradiente. Para o capítulo 3, os resultados mostraram que vários traços funcionais (CWM) e vários índices da diversidade funcional variaram significativamente ao longo do gradiente de altitude e de solo no *páramo* em estudo. Três dos cinco traços funcionais revelaram o potencial para descrever como a composição funcional das comunidades de páramo respondeu ao aumento da severidade ambiental ao longo destes gradientes ambientais. Os dois índices de diversidade funcional, FDis e FRic, diminuíram significativamente com o aumento da elevação e a diminuição da profundidade do solo. Para o capítulo 4, se encontrou que a vegetação sob a copa das plantas facilitadoras (*E. Lopezii*) teve um impacto positivo na diversidade taxonômica, em comparação com as áreas de controle. Em relação à diversidade filogenética, foi observado que o padrão dominante foi principalmente aleatório, esses resultados sugerem que, nessas altitudes, a metacomunidade é fortemente filtrada por fatores climáticos e edáficos, e que apesar dos benefícios da facilitação exercida pelas rosetas caulescentes, é difícil detectar um padrão de sobredispersão filogenética. Para o Capítulo 5, como tendência geral, foi encontrado um número maior de espécies em locais de altitudes mais elevadas, diminuindo em locais de altitudes mais baixas e onde a sazonalidade climática é mais acentuada e filtra espécies de linhagens menos tolerantes a ambientes estressantes. As espécies de Fabaceae fixadoras de nitrogênio se destacaram entre as espécies importantes, especialmente em locais de baixa altitude e mais estressantes.

Palavras-chave: Montanhas tropicais, gradiente altitudinal, diversidade filogenética, diversidade funcional, interação planta-planta, montagem de comunidades.

SUMÁRIO

1. INTRODUÇÃO GERAL

Compreender as relações entre biodiversidade e o funcionamento dos ecossistemas tornou-se um assunto central nos estudos de ecologia, especialmente quando essas relações estão ligadas às mudanças climáticas globais, à extinção de espécies e aos serviços ecossistêmicos (HAO et al., 2018; WEISKOPF et al., 2020). Uma das principais necessidades, é compreender os fatores, mecanismos e processos que influenciam a montagem das comunidades naturais (TILMAN, 2004). Teorias de montagem de comunidade deterministas afirmam que as condições ambientais ditam a presença de espécies, e que processos como distúrbios ambientais ou seleção de nichos são os mecanismos predominantes que ditam a adesão à comunidade (KRAFT; ACKERLY, 2010; PERRONNE et al., 2017). Em contraste, teorias de montagem da comunidade estocásticas postulam que as espécies são funcionalmente equivalentes e que a estrutura da comunidade é altamente influenciada por mecanismos aleatórios como a limitação da dispersão e a deriva ecológica (HUBBELL, 2001). Nos últimos anos tem-se aumentado o interesse em múltiplos atributos da biodiversidade, além da riqueza e abundância de espécies (diversidade taxonômica) (HILLEBRAND et al., 2018). Aumentaram-se as pesquisas na diversidade de linhagens evolutivas (diversidade filogenética) e as características relacionadas à estratégia de uso de recursos (diversidade funcional), atributos que, simultaneamente influenciam o funcionamento dos ecossistemas (CADOTTE; CARSCADDEN; MIROTCHNICK, 2011; CHUN; LEE, 2017; CRAVEN et al., 2018; SWENSON, 2013). Estas duas últimas, são as abordagens mais poderosas desenvolvidas recentemente para avaliar os mecanismos subjacentes à construção e dinâmica das comunidades (KRAFT et al., 2015; SWENSON & ENQUIST, 2009).

Os ecossistemas montanhosos são um dos modelos mais adequados para desvendar a interação entre as facetas da biodiversidade (CHUN; LEE, 2018; KESSLER; KLUGE, 2008; LÓPEZ-ANGULO et al., 2020). As montanhas mostram mudanças ambientais acentuadas e previsíveis com a elevação, fator altamente correlacionado com a variação no clima (QIAN; HAO; ZHANG, 2014). Estas mudanças resultam em diferentes habitats e zonas climáticas que podem ser os limites de dispersão e de sobrevivência de muitas espécies (MONTAÑO-CENTELLAS; MCCAIN; LOISELLE, 2020). Portanto, esses gradientes são reconhecidos como fatores importantes que determinam os padrões de diversidade nas montanhas (CULMSEE; LEUSCHNER, 2013; LOMOLINO, 2001), permitindo fazer previsões sobre os efeitos das mudanças climáticas globais a longo prazo sobre o funcionamento ecossistêmico e o futuro da biodiversidade (MCCAIN; COLWELL, 2011).

Estudos abrangentes da diversidade taxonômica (DT), da diversidade filogenética (DFi) e da diversidade funcional (DF) são necessários para compreender melhor os mecanismos subjacentes aos padrões de biodiversidade (CUI et al., 2021; PAVOINE; BONSALL, 2011; WANG et al., 2019). Há evidencias, por exemplo, de que ao longo de gradientes de elevação, os padrões de diversidade filogenética e funcional são estruturados por processos determinísticos baseados em nicho, incluindo interações bióticas (por exemplo, exclusão competitiva e facilitação) e abióticas (por exemplo, filtragem ambiental por fatores climáticos) (CHUN; LEE, 2017; DUARTE et al., 2021; QI et al., 2015; QIAN; HAO; ZHANG 2014). Ao longo dos gradientes de altitude, espera-se que as interações competitivas sejam mais intensas em comunidades em altitudes mais baixas, com competição fortemente assimétrica por luz e presença de maior número de táxons, gerando comunidades de plantas filogeneticamente sobredispersas. Enquanto o efeito da filtragem ambiental deve aumentar em altitudes mais elevadas, onde as baixas temperaturas diminuem a produtividade e os táxons não adaptados a ambientes frios são progressivamente excluídos, levando a comunidades filogeneticamente agrupadas (CULMSEE; LEUSCHNER, 2013; MANISH; PANDIT, 2018; QIAN et al., 2014, 2019; WORTHY et al., 2019; XU et al., 2017). As espécies de alta altitude são mais isoladas do que as espécies em elevações mais baixas, devido a uma maior descontinuidade de terrenos sob uma mesma zona climática (GRAHAM; FINE, 2008). Se as características dos organismos forem em geral conservadas em relação aos seus nichos ambientais, isso deve promover o isolamento entre habitats de alta elevação e, portanto, aumentar o potencial de especiação alopátrica. Como resultado, parentes próximos devem ser encontrados em regiões climáticas semelhantes, como o topo das montanhas, separadas por regiões de baixa aptidão (GRAHAM; FINE, 2008; ZHAO et al., 2017). Daí a importância da informação filogenética em ecologia para detectar padrões de distribuição das espécies diferentes aos aleatórios em relação aos gradientes espaciais e ambientais (GONZÁLEZ-CARO et al., 2014; GRAHAM; FINE, 2008; SALADIN et al., 2019).

O conhecimento dos traços funcionais oferece uma grande oportunidade para entender e prever como as propriedades e a composição da vegetação mudam ao longo dos gradientes geográficos (FAJARDO; PIPER, 2011; MASON et al., 2012). As altas montanhas tropicais oferecem condições ambientais que resultam em ecossistemas únicos, onde as plantas apresentam inúmeras estratégias de adaptação (RADA; AZÓCAR; GARCÍA-NÚÑEZ, 2019).

Ajustes comuns nos traços funcionais das plantas em altitudes mais altas incluem, por exemplo, redução da área foliar específica (AFE) (XU et al., 2017), e aumento do conteúdo de matéria seca da folha (CMSF) (KICHENIN et al., 2013), essas são adaptações ao aumento das condições estressantes com o aumento da altitude. Dados sobre vários traços podem permitir monitorar de forma abrangente as mudanças funcionais nas comunidades como resposta a mudanças ambientais que alterem o funcionamento dos ecossistemas (JUNKER; LARUE-KONTIĆ, 2018). A diversidade funcional fornece um meio poderoso de abordar as questões persistentes da ecologia, por meio de seu duplo papel como indicador de mecanismos que impulsionam a montagem de comunidades e como preditor de processos em nível de ecossistema (MASON; DE BELLO, 2013; PAKEMAN, 2014).

Duas medidas são principais utilizadas na ecologia funcional: a Média Ponderada da Comunidade (MPC) (GARNIER et al., 2004), que é a média dos valores de cada traço funcional numa comunidade ponderada pela abundância das espécies (MILLER; DAMSCHEN; IVES, 2019), e refere-se ao grau de comunidades dominadas por uma estratégia de planta única (ALI et al., 2017); e a Diversidade funcional (DF) (VILLÉGER et al., 2008), que é uma medida multidimensional da distribuição dos traços na comunidade, permitindo estimar como funcionam os ecossistemas (DÍAZ; CABIDO, 2001; LAURETO; CIANCIARUSO; SAMIA, 2015) Em gradientes ambientais conforme aumentam as condições estressantes (por exemplo, diminuição da temperatura), espera-se que as condições climáticas prevalecentes devem exercer uma filtragem ambiental, afetando principalmente o CWM (DE BELLO et al., 2013; DI BIASE et al., 2021). De acordo com a hipótese de produtividade, o número de nichos disponíveis deve aumentar em direção à parte benigna de um gradiente, sugerindo que a diversidade funcional também deve aumentar, por tanto, a diversidade funcional deve declinar em direção a extremos ambientais devido a uma filtragem abiótica mais forte (SCHELLENBERGER COSTA et al., 2017).

Interações bióticas positivas como a facilitação também interferem na diversidade funcional e filogenética. A facilitação ocorre quando uma espécie impacta positivamente a aptidão de outra e tem sido predominantemente estudada em espécies de vida livre, como as plantas (VALIENTE-BANUET; VERDÚ, 2013). A facilitação de plantas é uma interação planta-planta positiva na qual uma espécie facilitadora fornece a outra espécie facilitada um nicho de regeneração (CALLAWAY, 1997; VALIENTE-BANUET; VERDÚ, 2007). Este processo aumenta não apenas o número de espécies na comunidade, mas também a diversidade filogenética, porque podem facilitar espécies funcionalmente diferentes, promovendo assim montagens com maiores distâncias filogenéticas (CARRIÓN et al., 2017; NAVARRO-CANO et al., 2016). Duarte et al. (2021), observaram que em florestas esclerófilas montanas, as plantas facilitadoras aumentam a riqueza de espécies da comunidade de plantas e que as interações facilitadoras são mais frequentes do que as interações competitivas. Além disso, a intensidade da facilitação aumentou com a elevação para as interações que envolvem linhagens distantemente relacionados, seguindo o gradiente de severidade ambiental. Embora haja uma ampla gama de estudos buscando compreender a influência da facilitação direta e indireta sobre as mudanças na diversidade taxonômica e diversidade funcional em comunidades de plantas alpinas ao longo de gradientes de elevação (BALLANTYNE; PICKERING, 2015; BUENO; LLAMBÍ, 2015; CALLAWAY, 1998; CHOLER; MICHALET; CALLAWAY, 2001; LIU et al., 2020; LLAMBÍ et al., 2020; MORA; LLAMBÍ; RAMÍREZ, 2019), ainda há poucos trabalhos indagando sobre a influência da facilitação sobre a diversidade filogenética nestes ambientes.

No contexto dos atuais cenários globais de mudanças climáticas que afetam e ameaçam aos ecossistemas montanos e alpinos, procura-se responder por meio do estudo das relações evolutivas (filogenéticas) e dos traços funcionais, os mecanismos de montagem de comunidades de plantas sujeitas à severidade ambiental de montanhas altas. Para isso as seguintes hipóteses foram testadas: 1) o aumento da altitude funciona como um filtro ambiental, provocando a diminuição da riqueza de espécies, a diminuição da diversidade filogenética e o aumento do agrupamento filogenético em montanhas tropicais **(Capitulo 1)**; 2) e se as comunidades vegetais de alta altitude nas montanhas tropicais também são resultado da recente diversificação, com muitas espécies vegetais recentemente divididas encurtando as distâncias filogenéticas entre as espécies relacionadas mais próximas **(Capitulo 1)**. 3) o aumento da altitude intensifica a filtragem ambiental em um tipo de vegetação adaptada a grandes altitudes, gerando um padrão gradualmente mais agrupado ao longo do gradiente. **(capitulo 2)**. 4) A altitude é uma variável agregadora de outras variáveis ambientais, como temperatura, profundidade do solo, fertilidade do solo, disponibilidade de água; sob este argumento, espera-se que a altitude seja uma variável explicativa mais poderosa do que uma variável ambiental, como a profundidade do solo **(capitulo 2)**. 5) Assumindo-se a conservação de nicho, à medida que a diferença de altitude entre amostras aumenta (as condições abióticas, inclusive a temperatura, se tornam mais diferentes), a dissimilaridade taxonômica e filogenéticas beta aumentam **(capitulo 2)**. Em um gradiente de elevação o aumento da altitude (o que inclui a diminuição da temperatura) é um forte filtro ambiental que atua na estrutura funcional das comunidades de plantas alpinas (de Páramo). Espera-se encontrar 6) os traços funcionais relacionados com tamanho de folha e tamanho de planta tenderão a diminuir com a altitude, isto também refletirá em uma Média Ponderada da Comunidade (MPC) decrescente nestes traços (**Capitulo 3**); 7) há uma redução na diversidade funcional na medida que aumenta a altitude, como resultado da filtragem climática **(Capitulo 3)**. 8) A roseta, *Espeletia lopezii,* atua como engenheiro do ecossistema (*nurse plants*), melhorando as condições do micro-habitat local e aumentando a abundância de plantas e a diversidade de espécies em comparação com as áreas abertas (controle) sem as espécies focais **(Capitulo 4)**; 9) as comunidades de plantas sob a copa da roseta são sobredispersas filogeneticamente, assumindo-se que haja conservantismo de nicho nas linhagens filogenéticas das espécies de plantas amostradas, como efeito da diversificação de nicho promovida pela facilitação. Abordaram-se essas hipóteses concentrando-se na influência das espécies de plantas facilitadoras na diversidade taxonômica e filogenética de espécies locais alpinas **(Capitulo 4)**. Também, abordou-se a estrutura fitossociológica e a composição da vegetação lenhosa de sete Florestas Tropicais Secas ao longo de um gradiente topográfico na região de Cúcuta e arredores, na cordilheira oriental dos Andes colombianos **(Capitulo 5)**.

2. OBJETIVO GERAL

- Compreender os processos de montagem das comunidades de plantas alpinas e florestais por meio da diversidade filogenética e funcional em gradientes altitudinais em montanhas tropicais.

Objetivos específicos

I. Testar se o aumento da altitude funciona como um filtro ambiental, provocando a diminuição da riqueza de espécies, a diminuição da diversidade filogenética e o aumento do agrupamento filogenético em três montanhas tropicais, cobrindo florestas montanas e ecossistemas alpinos.

II. Avaliar se nos Páramos do norte dos Andes, o aumento da altitude e a diminuição da profundidade do solo atuam como filtros ambientais, causando diminuição da riqueza de espécies e o aumento do agrupamento filogenético.

III. Avaliar se nos Páramos do norte dos Andes, a diversidade funcional (FD) e a média ponderada da comunidade (CWM) de traços funcionais diminuem na medida que aumenta a altitude e diminui a profundidade do solo, como resultado da filtragem ambiental.

IV. Estimar se uma roseta caulescente atua como facilitadora causando o aumento da riqueza de espécies e da diversidade filogenética a nível comunitário, e testar se as interações planta-planta nestas elevações (4500 m) dependem da relação evolutiva entre a facilitadora e suas espécies associadas.

V. Determinar a estrutura fitossociológica e a composição da vegetação lenhosa de sete Florestas Tropicais Secas ao longo de um gradiente topográfico na região de Cúcuta e arredores, na cordilheira oriental dos Andes colombianos.

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CHAPTER 1: Altitude as environmental filtering influencing phylogenetic diversity and species richness of plants in tropical mountains*

Running title: Altitude filtering in tropical mountains

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Abstract

Elucidating how multiple factors affect biodiversity and plant community assembly is a central issue in ecology, especially in vulnerable ecosystems such as tropical mountains. These studies are more relevant in global warming scenarios that induce the upward displacement of plant species towards reduced habitats and hostile environments in tropical mountain. This study aimed to analyze how altitude affects taxonomic and phylogenetic diversity in plant communities of tropical mountains. Thus, we tested if (i) increased altitude works as an environmental filtering promoting decreased species richness, decreased phylogenetic diversity, and increased phylogenetic clustering in these tropical mountains; and if (ii) plant communities of high altitude in tropical mountains are also result of recent diversification with plant species recently split shortening phylogenetic distances between closest related species. We tested effects of altitude on species richness and phylogenetic metrics using linear mixed-effects models. Mount Haleakala presented 114 species, Mount Kilimanjaro presented 231 species and Mount Purace presented 280 species. We found an environmental filtering effect with increasing altitude causing phylogenetic clustering, decreased phylogenetic diversity and decreased species richness. The decreasing phylogenetic distances between closest relatives are congruent with neo-endemics, suggesting recent plant diversification in high altitudes of tropical mountains, possibly driven by geographic isolation and environmental heterogeneity. Consequences of global warming should be monitored in tropical mountains focusing on distribution shifts.

Keywords: tropical mountains, global warming, environmental filtering, phylogenetic ecology, assembly rules, conservation, mountaintop vegetation.

1 Introduction

Understanding how multiple factors determine the spatial variation of biodiversity is a central issue in ecology and biogeography (Anderson et al. 2011; Machac et al. 2011), which becomes more relevant under the global warming scenario (IPCC 2021a, b). Thus, the basic understanding of the causes and consequences of global warming in plant community assembly also becomes more relevant (Cavender-Bares et al. 2009) especially as rapid climate change challenges species in which evolutionary responses may not be rapid enough to cope with the change, being replaced by other species of warmer climates (Bradshaw and Holzapfel 2006). Mountain ecosystems have been recognized as highly threatened by climate change, and as remarkable distinct systems to evaluate ecological patterns, and their mechanisms (Körner et al. 2017). Thus, there is evidence of upward displacement of many plant and animal species in mountains caused by global warming (Feeley et al. 2011; Telwala et al. 2013; Zu et al. 2021) which alters the community composition, and ecosystem functioning (Fadrique et al. 2018; Gastauer et al. 2020). Consequently, habitat displacement and environmental filtering caused by shift of altitudinal zonal bands can induce many species extinctions (Galván-Cisneros et al. 2021; Zu et al. 2021). However, most previous studies on the altitudinal gradient in mountain ecosystems have been focused on taxonomic species diversity or distribution of few species responding to altitude. Most of these studies point out that there is a tendency to decrease the number of species as altitude increases, and, sometimes, showing a richness peak at intermediate altitudes (Villalba et al. 2005; Chawla et al. 2008; Toledo et al. 2012; Zhao et al. 2017a; Maharjan et al. 2022). Although a pattern emerges from these findings, they do not depict the environmental filtering of altitude as an evolutionary and ecological process that assembles communities.

One of the main causes of the altitudinal gradient in the mountain ecosystems being a driver of community assembly and plant adaptation is because altitude affects temperature (Seastedt & Oldfather 2021). Typically, tropical mountains have more uniform and stable temperature regimes than mountains in temperate regions (Fadrique et al. 2018) because summer and winter for them hardly change temperatures throughout the year, as they are close to the equator. Consequently, temperature stability in the tropics causes sharp temperature barriers in between zonal bands, creating an evolutionary scenario for tropical species with narrower niches and more limited distribution (Janzen 1967) similar to continental islands (Qian et al. 2021). These stable bands can lead to the so-called ‘Wallace Effect’ prompting speciation because, differently from geographically isolated populations, isolation mechanisms between species may arise through natural selection between bands where incipient species overlap (Sawyer & Hartl 1981). In tropical mountains, vegetation above the forest line consists of dense shrub vegetation and herbaceous grasslands and is considered biogeographically as continental islands (Sklenář et al. 2014). These cold-climate plant communities are inserted within warm tropics with plant lineages originating from temperate regions contributing to the composition with plant lineages from tropical regions (Sklenář et al. 2014) possibly because of recent diversification in tropical lineages (Campos et al. 2021a, 2021b). Therefore, alpine vegetation bands compared to lower tropical vegetation bands have less species richness with most endemic species (Myers et al. 2000; Hofstede 2003; Carbutt & Edwards 2015) that may maximize phylogenetic effects in their communities. Thus, studying phylogenies of alpine plant communities in tropical mountains and their neo-endemic species can be a way to study altitude as an evolutionary/ecological factor. Morevover, temperature change in mountains can promote a detectable vertical migration in altitude of plant distributions, since 500 m upwards counteract an increase of 3°C (Peñuelas et al. 2002) enabling studies of vegetation displacement caused by climate change.

Evolutionary and ecological processes interact assembling plant communities and, thus, phylogenetic diversity can help to evidence processes from the evolutionary proximity between species of these communities (Webb et al. 2002; Cavender-Bares et al. 2009) generating hypotheses from the niche theory and neutral theory (Hubbell 2001; Webb et al. 2002; Soberón 2007). Phylogenetic diversity is a component of biodiversity measured in millions of years of each phylogenetic branch of a phylogenetic tree and expresses the set of evolutionary relationships between species and may reflect the diversity of traits (e.g., phenotypic and genetic) that they possess (Faith 1992). The neutrality-based hypothesis postulates that species are equivalent and that community assembly is driven by dispersal limitation and neutral drift within biogeographical spaces (Hubbell 2001). The niche-based hypothesis suggests that competitive exclusion and environmental filtering are important processes in community assembly at a local scale (Kraft et al. 2015). This hypothesis postulates that abiotic filtering increases under environmental stress (e.g., temperature stress) and resource-limited scenarios (e.g., shallow soils), whereas competition increases as environmental stress decreases (Swenson & Enquist 2009; Violle et al. 2011; Götzenberger et al. 2012). The niche-based hypothesis postulates that species are more likely to be ecologically similar through relationship and niche conservatism (Losos 2008). Thus, less related species coexisting in a community tend to differ in their functional traits allowing resource partitioning (Leibold & McPeek 2006).

When niches are conserved within evolutionary lineages, a filtering promoted by the environment can select closely related, and ecologically similar species (Baraloto et al. 2012; Gastauer & Meira-Neto 2013). Under this assumption, environmental filtering would cause phylogenetic clustering, and species richness decreasing (Table 1), while competition would cause phylogenetic overdispersion and species richness decreasing (Webb et al. 2002). Alternatively, neutral theories suggest stochastic assembly of the community through a neutral process such as dispersal limitation, speciation, or local extinction (Hubbell 2001) that should result in a community that neither differs from the null expectation of random phylogenetic structure nor differs in species richness (Webb et al. 2002; Kembel & Hubbell 2006, Table 1). However, communities shaped by various deterministic processes operating simultaneously in species selection, such as environmental filtering and biotic interactions, can result in the same pattern of random phylogenetic structure (Webb 2000; Cavender-Bares et al. 2009) but species richness decreases. As taxonomic diversity variation along altitudinal gradients results from ecological and evolutionary processes as well (Lomolino 2001; Culmsee & Leuschner 2013), altitude can be a predictor for testing plant diversity patterns and community assembly under the environmental filtering hypothesis if species richness decreasing is observed along with phylogenetic clustering (Qian et al. 2014; Manish & Pandit

2018; Galván-Cisneros et al. 2021). Environmental filtering has been reported causing phylogenetic clustering downwards in dry environments in mountains, assembling communities dominated by lineages adapted to hot and dry climates (Cornwell and Ackerly 2009; González-Caro et al. 2014; Galván-Cisneros et al. 2021). Upwards, the environmental filtering promotes phylogenetic clustering because it selects lineages adapted to cold environments and shortens phylogenetic distances (Li et al. 2014; Qian et al. 2014; Zhu et al. 2019). Additionally to phylogenetic clustering, the environmental filtering downwards or upwards also causes decreased species richness as less tolerant species are filtered out from communities (Laliberté et al. 2014; Galván-Cisneros et al. 2021).

This study aimed to analyze how altitude alone affects taxonomic and phylogenetic diversity in plant communities of three tropical mountain ecosystems on two continents and on an oceanic island. We tested if (i) increased altitude works as an environmental filtering triggering decreased species richness, decreased phylogenetic diversity, and increased phylogenetic clustering in these tropical mountains; and if (ii) plant communities of high altitude in tropical mountains can be a result of recent diversification with plant species recently split shortening phylogenetic distances between closest related species

2 Materials and methods

2.1 Data collection

We used three mountains in this study because, to the best of our knowledge, they were the only studies with the appropriate published results to fulfill the meta-analysis that we performed. Checklists with altitude records from three tropical mountains were used as samples in Mount Puracé, Colombia (Rangel & Lozano 1986); Mount Kilimanjaro, Tanzania (Hemp 2006); and Mount Haleakalā, Hawaii, USA (Kitayama & Mueller-Dombois 1992) (Figure 1). The survey of Mount Puracé (Rangel & Lozano 1986) aimed to describe the vegetation along the altitudinal gradient and consisted of a series of samples with species checklists of the vegetation in 11 different altitudes, from sub-Andean forests at 1020m ASL up to upper Paramo band at 4050m ASL. Only trees, shrubs, lianas and herbaceous species were considered; epiphytes and parasites were excluded. The Mount Kilimanjaro survey aimed to describe the vegetation, find endemic species and elucidate the absence of bamboos band (Hemp 2006); that survey consisted of 21 species checklists of vegetation in different altitudes, from Lowland Forests at 889m ASL up to subalpine heathlands with *Erica* shrubs at 3893m ASL. The survey of Mount Haleakalā (Kitayama & Mueller-Dombois 1992) aimed to describe the vegetation and to study the similarity patterns between altitudinal zonal bands, from lowland forests at 350m ASL up to alpine deserts at 3055m ASL, presenting checklists for each of the eight altitudinal zonal bands (Table 2). As far as we know, these are the only studies in tropical mountains with detailed checklists of many different zonal bands and vegetation types in a range of altitude suitable to test our hypotheses. Altitude was used directly as an environmental factor, although it is a proxy for many associated environmental variables, such as temperature, humidity and soil depth.

2.2 Taxonomic and Phylogenetic diversities and structure

In order to test the hypotheses of Table 1 concerning clustering, overdispersion or eveness of phylogenetic diversity and structure, we build phylogenetic trees and calculate the indices as described below.

A phylogeny of the studied species was generated from the largest dated mega-tree for vascular plants (Open Tree of Life) using the '*V.PhyloMaker*' package (Jin and Qian 2019). This mega-phylogeny was derived from two recently published, dated mega-trees, which were based on molecular markers and included 74,533 species representing all the families of extant vascular plants (Jin and Qian 2019). We used the *phylo.maker* function that makes phylogenetic hypotheses under scenario 3, whereby the tips of a new genus or species not included in the mega-tree are bound at the half-point of the family or genus branch, representing the branch between the family and genus root node and the basal node (for further details, see Jin and Qian 2019). Scenario 3 adds species as polytomies within their parental clades and assigns branch lengths using BLADJ (Jin and Qian 2019).

For each vegetation strip or zone a taxonomic list was extracted. From each phylogenetic tree, we calculated the lineage diversity as the total phylogenetic branch length [phylogenetic distance (PD)] for each vegetation zonal band (Faith 1992). We standardized PD for genus-level richness [i.e. standardized effect size of PD (ses.PD)]. The standardized PD measures how PD deviates from a null expectation generated by randomly shuffling the tips of the phylogeny and recalculating the PD in communities (Kembel 2015). We calculated mean pairwise phylogenetic distance (MPD) as a measure of the average phylogenetic distance between all combinations of pairs of individuals (including conspecifics); we calculated mean nearest taxon distance (MNTD) to be the mean phylogenetic distance from each taxon to its closest relative in the community (Webb 2000; Webb et al. 2002). We also evaluated the standardized effect size of MPD (ses.MPD) and the standardized effect size of MNTD (ses.MNTD). These derived metrics are equivalent to the inverse of the net relatedness index (NRI) and nearest taxon index (NTI), respectively, described by Webb (2000). Positive standardized effect size (ses) values indicate phylogenetic overdispersion (species more distantly related to each other than expected by chance), whereas negative values indicate clustering (species more closely related to each other than expected by chance). For the standardized effect size calculations, our tree was compared with 10,000 null model randomizations using the algorithm '*phylogeny pool*'. We calculated these metrics using the '*picante*' package (Kembel 2015). All phylogenetic analyzes were performed in R 4.0.4 (R Development Core Team 2021).

2.3 Statistical analysis

We used linear mixed-effects models (LMMs, with random and fixed effects) to test the main effects of altitude on different phylogenetic metric (PD, MPD, ses.MNTD) and species richness (response variables). Predictors with fixed effects (continuous explanatory variables) were grouped into two categories of diversity dimensions, such as taxonomic (i.e. species richness), and phylogenetic metrics (PD, MPD, ses.MNTD). The three mountains were considered as a random effect (1 | Mountain) in all models (i.e. Campos et al. 2021a, b). The most suitable distribution and function was tested (i.e., normality was confirmed by the Q-Q graph and Shapiro–Wilk test); after that the distributions of residuals were checked. Thus, the Gaussian error distribution could be confirmed (Crawley 2009; Zuur et al. 2009).

The main effect of altitude as explanatory variable on each response variable using the following equation:

lmer(formula = ntaxa ~ Altitude + (1 | mountain) (Equation 1)

where ntaxa= species richness that can be changed by phylogenetic metrics as response variable. Each response variable was used in different univariate models based on the LMM (equation1). All models were calculated using the package “lme4” (Bates et al. 2014) in the platform R (R Development Core Team 2021). We also used the estimates of the predictors' coefficients to interpret parameter estimates on a comparable scale using the “jtools” package (Long 2021). For example, Adjusted R2 is a corrected goodness-of-fit (model accuracy) measure for classical linear models. To produce the graphs for this study, we used the “ggplot2” package (Hadley, 2015). All analyses were run in R 4.0.1 (R Development Core Team 2021).

3 Results

3.1 Species richness

A total of 626 angiosperms species were compiled across all the vegetation surveys of the three mountains. A total of 114 angiosperms species were compiled in samples of the Mount Haleakalā, which belonged to 81 genera, 40 families and 22 orders; the most species-rich families in the Mount Haleakalā species pool were Poaceae (N = 14), Cyperaceae (N = 10), and Rubiaceae (N = 9) (Fig. 2, Fig. S1). A total of 280 angiosperms species were compiled in samples of the Mount Puracé, which belonged to 181 genera, 78 families and 39 orders; the most species-rich families in the Mount Puracé species pool were Asteraceae (N = 28), Rubiaceae (N = 18) and Poaceae (N = 18) (Fig. 3, Fig. S2). A total of 232 angiosperms species were compiled in the samples of the Mount Kilimanjaro, which belonged to 176 genera, 72 families and 33 orders; the most species-rich families in the Mount Kilimanjaro species pool were Asteraceae (N = 22), Rubiaceae (N = 21) and Poaceae (N = 14) (Fig. 4, Fig. S3).

3.2 Phylogenetic diversity and structure

We found a phylogenetic clustering associated with the altitude based on the tested model. Thus, species richness, ses.PD, ses.MPD and ses.MNTD are explained by the altitude, which consistently suggested a significative and negative effect in all tested models (Fig. 5; Table 3). The first model show that altitude significantly and negatively affected the species richness (LMM, Estimate = -0.01, t = -4.83, p = 0.001) (Figure 5A, Table 3). The ses.PD was negatively (i.e., phylogenetic clustering) influenced by the altitude (LMM, Estimate = -0.01, t = -3.73, p = 0.001) (Fig. 5B). Moreover, we observed that variation of ses.MPD was significantly and negatively affected by Altitude (LMM, Estimate = -0.01, t = -3.84, $p < 0.001$) (Fig. 5C; Table 3). Finally, the altitude had a weak negative effect on ses.MNTD (LMM, Estimate = -0.001, t = -2.86, p = 0.01) (Fig 5D, Table 3).

4 Discussion

We used only three mountains to produce results, the only three studies with adequate data to use. Although there is no statistical limitation in terms of repetition, the few tropical mountains in this study require that the interpretation be made recognizing its limitations. The results show that as altitude increases in the studied tropical mountains, the plant communities show a general pattern of decreasing species richness, decreasing phylogenetic diversity, decreasing mean phylogenetic distance between species and decreasing phylogenetic distances between the closest related species. Therefore, the results suggest that the two working hypotheses were confirmed. The results show expected effects of environmental filtering in high altitudes of tropical mountains that are commonly referred as harsh (Bremer & Sander 2000; Neri et al. 2017; Gastauer et al. 2020). Therefore, the results are congruent with the environmental filtering promoted by increasing altitude with negative effects on species richness, phylogenetic diversity and phylogenetic distances (Laliberté et al. 2014; Aldana et al. 2017). Congruent results of taxonomic diversity and phylogenetic structure were found in some temperate mountains (Qian et al. 2014, 2020; Zhao et al. 2017b; Xu et al. 2017; Manish & Pandit 2018), and to a lesser extent in tropical mountains (Cuesta et al. 2017; Worthy et al. 2019). Especially relevant in our results is that the environmental filtering at high altitudes generates plant communities with shortened phylogenetic distances between closest relatives. This is an expected pattern in communities with many species originated from recent diversification (see Beaman & Beaman 1990). Additionally, as high altitude regions tend to be more sensitive to the global warming forecasted for the 21st century than low altitude regions (Rangwala and Miller 2012), the results suggest a highly adapted mountaintop flora facing a strong influence of global warming. However, further studies are needed to deepen our understanding of the status of the threatened tropical mountaintop flora.

Our results suggest that in tropical mountains the pronounced environmental filtering in high altitudes assembles communities with shortened phylogenetic distances between closest relatives (Machac et al. 2011). Although more studies are needed to reaffirm the causes of such shortened phylogenetic distances, our results are congruent with the hypothesized recent diversification in these continental islands of cold climate surrounded by warm tropical zones. These neighboring zones can generate areas of quick speciation and one of the possible causes is the 'Wallace Effect' that split incipient species occupying bordering zones that quickly isolate from each other due to strong selective pressure for reproductive isolation where their distributions overlap (Sawyer & Hartl 1981). A recurrent generation of species in higher altitudes coming from the same phylogenetic lineages of lower altitudes could explain the expressive number of species arisen recently (neo-endemics) (see Beaman & Beaman 1990) as well as could explain the closest phylogenetic distances among closest relatives found in communities of high altitudes. These findings are congruent with mountains as major centers of endemism at a global scale influenced by the high environmental heterogeneity and strong geographic isolation (Trigas et al. 2013; Noroozi et al. 2018).

The phylogenetic trees show that the environmental filtering promoted by the altitude allows that most of the species occur only in one or two zonal bands, suggesting an upwards decreasing species richness, as well as suggesting a specialized flora of each zonal band. The environmental filtering promoted by the increasing altitude in tropical mountains suggest that other factors associated with altitude, such as temperature, are drivers (Buytaert et al. 2006; Rada et al. 2019) which affect community composition and species richness patterns (Kerkhoff et al. 2014; Klanderud et al. 2015; Bagousse-Pinguet et al. 2017; Qian et al. 2021). Congruently with other findings, our results suggest that as altitude varies, temperature varies in tropical mountains, causing downward or upward environmental filtering (Galván-Cisneros et al. 2021). Environmental filtering downwards is an observed pattern for forests in dry and hot environments in zonal bands of low altitudes (Cornwell & Ackerly 2009; González-Caro et al. 2014), and was not suggested by our results in the three studied sites possibly because it is not the predominant environmental filtering or because the altitude range of this study was not suitable to detect the environmental filtering in the lowest zonal bands (see Galván-Cisneros et al. 2021). Our results suggest an environmental filtering that increases upwards from communities that have high species richness and high phylogenetic diversity below forest lines (Qian et al. 2014; Campos et al. 2021a) contrasting with alpine vegetation of higher altitudes, and above the forest line with lower species richness, lower phylogenetic diversity, and phylogenetically clustered (Li et al. 2014; Qian et al. 2014; Zhu et al. 2019). Therefore, the suggested environmental filtering in the studied tropical mountains associated with the increasing altitude could be caused by other environmental factors as decreasing temperatures that negatively affect species richness, phylogenetic diversity, and phylogenetic distances.

Downwards, below the treeline, phylogenetic overdispersion of plant communities is possibly caused by the increasing abundance of eudicots and magnoliids clades. Below the treeline, the Rubiaceae family (eudicot) showed the highest number of species. Below the treeline, Rubiaceae was followed in number of species by Piperaceae (magnoliid) on Mount Kilimanjaro and Mount Haleakala. The importance of the Rubiaceae family in mountain forest systems is widely known, having representation as trees, shrubs and herbs (Anderson 1995; Richter 2008; Cirimwami et al. 2019). However, Asteraceae was the dominant family in our analyses because it is the best represented family in alpine ecosystems of the world (Pegoraro et al. 2020; Lencinas et al. 2021; Brochmann et al. 2021). The species richness of Asteraceae is assigned to their ability to colonize harsh environments under severe stress conditions with a broad array of adaptations (Knox & Palmer 1995; Ornellas et al. 2019; Zhang et al. 2021). Monocots as Poaceae, Cyperaceae, and Juncaceae stood out in the alpine vegetation of the three mountains, where genus such as *Carex* and *Luzula* were common. These lineages are diversified and dominant above the treeline in phylogenetically clustered communities of alpine vegetation (Ndiribe et al. 2013; Venn et al. 2014; Schubert et al. 2020).

The results show some species of high altitude closely related to other of lower altitudes in the three studied mountains suggesting neo-endemisms, as *Carex* species in Mount Haleakala, *Senecio* species in Mount Kilimanjaro and *Lachemilla* species in Mount Puracé. Another example of possible neo-endemism in Andes is the genus *Lupinus*, Fabaceae, that has at least 81 endemic species in Andes (Hughes and Eastwood 2006), with three species occurring in Mount Puracé. It is also remarkable that Asterales, Poales and Ericales orders (all eudicots) have many adapted species to high altitude in the three studied mountains. These examples are among many others that can be observed in the presented phylogenetic trees. Although it is not certain that these examples are actual neo-endemics, the results of the phylogenetic trees with shortened phylogenetic distances between closest relatives are congruent with neo-endemisms. If this congruence is true, such evolutionary feature could be prompted because the temperature stability in tropical mountains harbors species with narrow niches and limited distribution driven by sharp temperature barriers in between band zones (Janzen 1967; Cuesta et al. 2020).

A possible explanation of the different species number among the studied mountains is given by the classical model of species number provided by the Island Biogeography Theory (MacArthur & Wilson 1967). For example, the Hawaian Mount Haleakala has the fewer surveyed plant species by far (114 species) compared to Mount Kilimanjaro (231 species) and Mount Purace (280 species), congruently to a tropical mountain that creates an island of cold climate in tropics inside an oceanic island. Species richness of Mount Kilimanjaro in Africa and Mount Puracé in South America might be boosted during glacial periods when alpine vegetation occupied lower altitudes in a much larger continental area with merging alpine islands that mixed floras and promoted rapid species diversification (Madriñán et al. 2013). Such species richness booster would not be possible in Mount Haleakala, an island in the middle of the largest ocean on Earth.

Global warming can be a major conservation threat to the specialized flora of the tropical mountains, especially on mountaintops (Hamid et al. 2020; Steinbauer et al. 2022; Kidane et al. 2022). Firstly, as the zonal bands move upwards they would face a decreasing distribution area, a threat *per se* because species-area relationships states the smaller the area, the smaller the species number (see Rosenzweig 1995). Secondly, the zonal bands of vegetation besides smaller with their upwards displacement would be more disconnected, with lower immigration rates and with higher extinction rates (Sklenář et al. 2014), decreasing the species richness (MacArthur & Wilson 1963, 1967) in an opposite way to the glacial periods. During the glacial periods, the downward displacement of zonal bands possibly merged islands of mountain vegetation on much larger areas (Madriñán et al. 2013). Finally, if global warming is causing an upward movement of zonal bands, plants populations could be displaced to recently deglaciated areas with thin, poor and exposed soils, a situation that initiates centuries-long primary successions (FAO - Food and Agriculture Organization of the United Nations 2015; Llambí et al. 2021). For many purposes, including conservation and restoration, the boundaries of species distributions will be especially useful to check range shifts (Parmesan & Yohe 2003). For example, habitat suitability models predicted an altitude increase of trees species distributions in mountains and a concomitant decrease in cover of tussock grasses, caulescent rosettes and small-leaved sclerophyllous shrubs (Arzac et al. 2019). The Tropical Andean alpine species showed highest vulnerability to climate change because the spatially more restricted species near the equator (e.g., Páramo endemics) are at the same time the most vulnerable to warming (Cuesta et al. 2020). Altitudinal changes in zonal bands of tropical mountains could occur in a time scale that may overwhelm ecological and evolutionary processes, especially among mountaintop species (see Parmesan 2006) of the most specious families and orders. Thus, some threats could not to be overcome only by ecological and evolutionary processes and the scenario is that the tropical mountain vegetation could be highly impacted with loss of evolutionary history. More studies, efforts and actions are needed to deepen the knowledge of the current threatened status of tropical mountain flora, especially the mountaintop flora. Global warming and its consequences should be monitored in tropical mountains worldwide, focusing on range shifts and prioritizing mountain vegetation's highest zonal bands. If the worst scenario discussed above is true, dead-ends around tropics will threaten mountaintop floras very soon.

5 Conclusions

Our results of taxonomic and phylogenetic diversity analyses suggest that environmental filtering could be the predominant force that structures the distribution of plant communities along elevational gradients in three tropical mountains, two continental and one oceanic. As a general result, increasing altitude could cause negative effects on species richness, phylogenetic diversity, and phylogenetic distances promoting phylogenetic clustering.

The findings highlight the patterns of diversity and phylogenetic structure as essential in tropical mountains conservation especially because these ecosystems are increasingly more susceptible to climatic changes and anthropic pressures. Tropical mountains harbor a rich endemic flora, and the distribution of plant species would be changing triggered by global temperature changes. As a consequence, plant species located in the highest bands of vegetation might be threatened as they would not have higher altitudes to move to. Therefore, plant lineages occurring at high altitudes, many of them endemic and recently originated might be at greater risk of succumbing to climate change. For this reason, the selection of areas for protection should consider the prioritization of communities with high endemism, high taxonomic and high phylogenetic diversity to improve the chances of biodiversity conservation, especially the mountaintop vegetation of tropical mountains.

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Table 1. Phylogenetic structure and species richness of communities under different evolutionary backgrounds of ecological traits and ecological processes

Ecological processes	**Conserved Traits**	**Convergent Traits**	**Species richness**
Niche theory: Environmental filtering	Cluster dispersion	Overdispersion	Decreased species richness
Niche theory: Limiting similarity	Overdispersion	Clustered or random dispersion	Decreased species richness
Neutral theory: Neutral assembly	Random dispersion	Random dispersion	Unchanged species richness

Table 2. Mountains' location and altitude range of the data used in the analyses.

References	**Mountain**	**Location**	**Altitude (m)**
Rangel-Ch & Lozano, 1986	Puracé	Huila, Colombia	1020-4050
Hemp, 2006	Kilimanjaro	Kilimanjaro Region, Tanzania	998-3893
Kitayama & Mueller-Dombois, 1992	Haleakalā	Maui Island, Hawai, EUA	350-3055

Table 3. Linear mixed models (LMM) explain the relationships between phylogenetic metrics (PD, MPD, MNTD, ses.PD, ses.MPD, ses.MNTD) altitude. ses.PD: standard effective size of phylogenetic diversity; ses.MPD: standard effect size of mean pairwise distance); ses.MNTD: the standard effective size of mean nearest taxon. Models with significant effects (*) are indicated.

Random effects (variance)	**Model**	**R^2**	**Estimate**	**t**	**p**
0.50	Richness ~ Altitude	0.63	-0.01	-4.83	0.001*
0.54	PD ~ Altitude	0.68	-0.90	-5.76	0.001*
0.09	ses.PD ~ Altitude	0.24	-0.01	-3.73	0.01*
0.38	MPD ~ Altitude	0.58	-0.01	-5.14	0.001*
0.02	ses.MPD ~ Altitude	0.34	-0.01	-3.84	0.001*
0.30	MNTD ~ Altitude	0.29	-0.010	-0.20	0.84
0.05	ses.MNTD ~ Altitude	0.23	-0.001	-2.86	0.01*

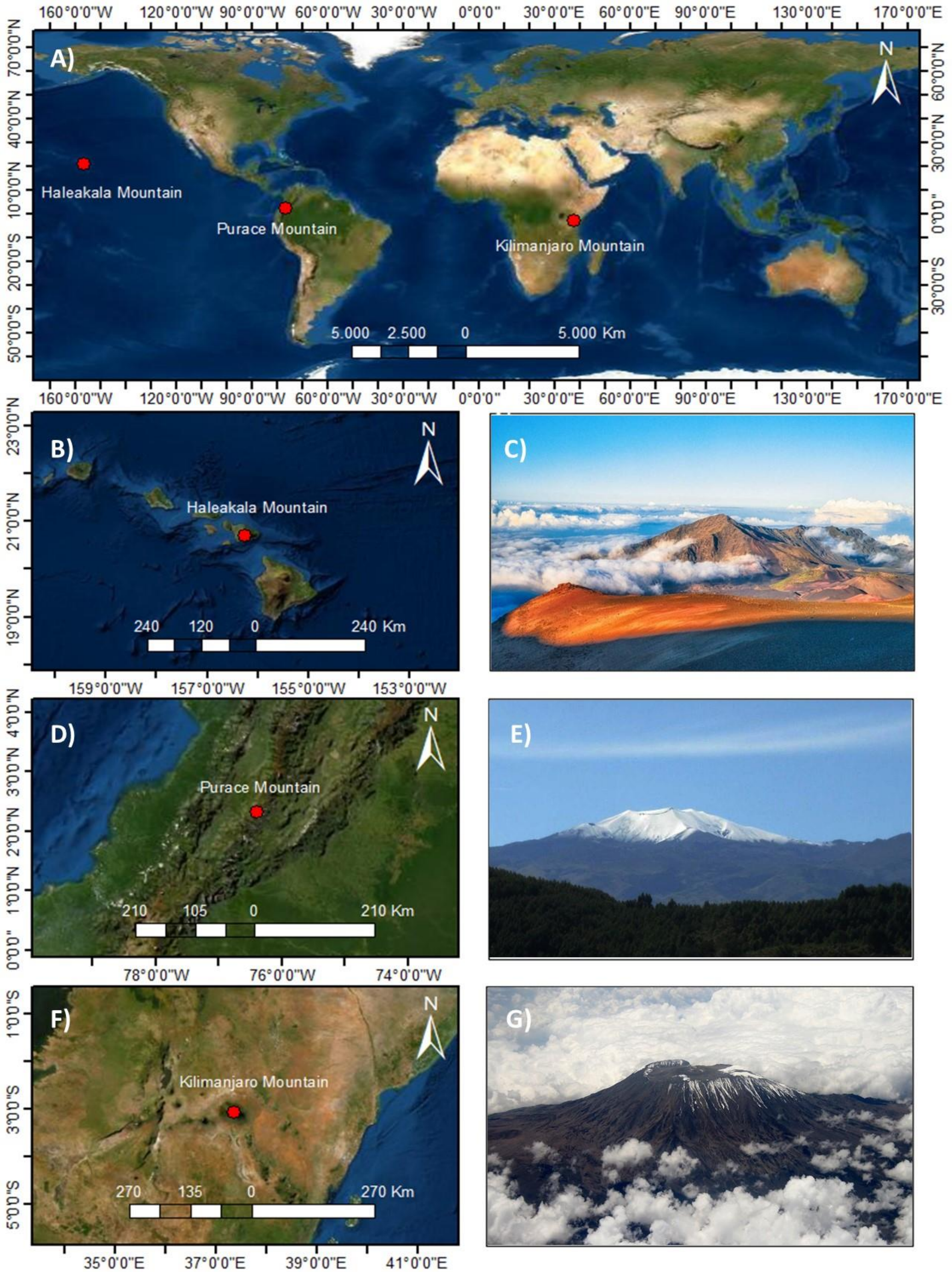

Figure 1 – Location of the study area. Global map (A), Hawaiian Islands indicating the Haleakalā volcano (B), Haleakalā volcano (Photographed by: Fernando Margolles, shutterstock) (C), Andean region of Colombia indicating the Puracé volcano (D), Puracé volcano (Photographed by: Diesalcedo, CC BY-SA 3.0) (E), Tanzania indicating the Mount Kilimanjaro (F) and Mount Kilimanjaro (Photographed by: Muhammad Mahdi Karim, GFDL 1.2) (G).

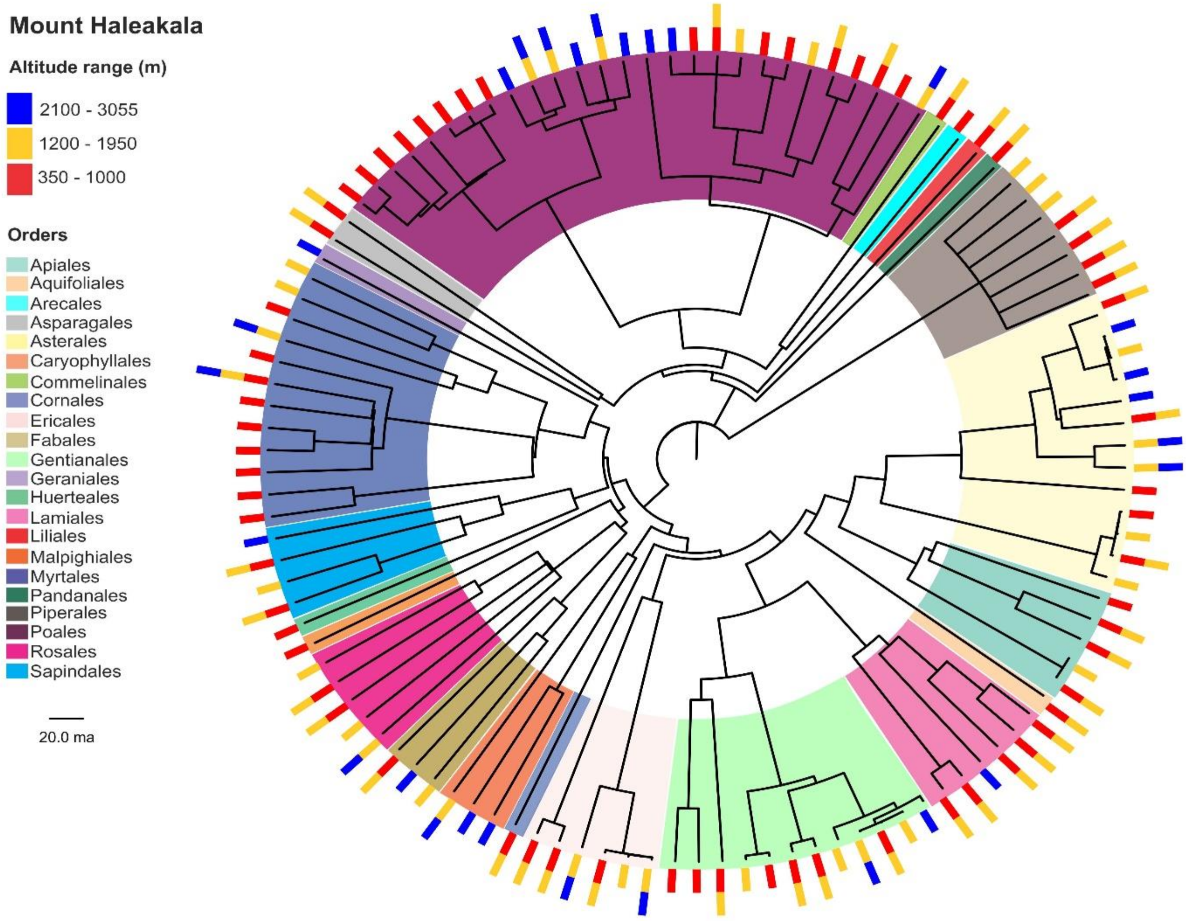

Figure 2 – Phylogenetic tree of plant communities of Mount Haleakala. Orders and altitudinal ranges are indicated by colors, and lineages ages are indicated by branch lengths according to the legend. Phylogenetic divergence scale is indicated in millions of years (ma).

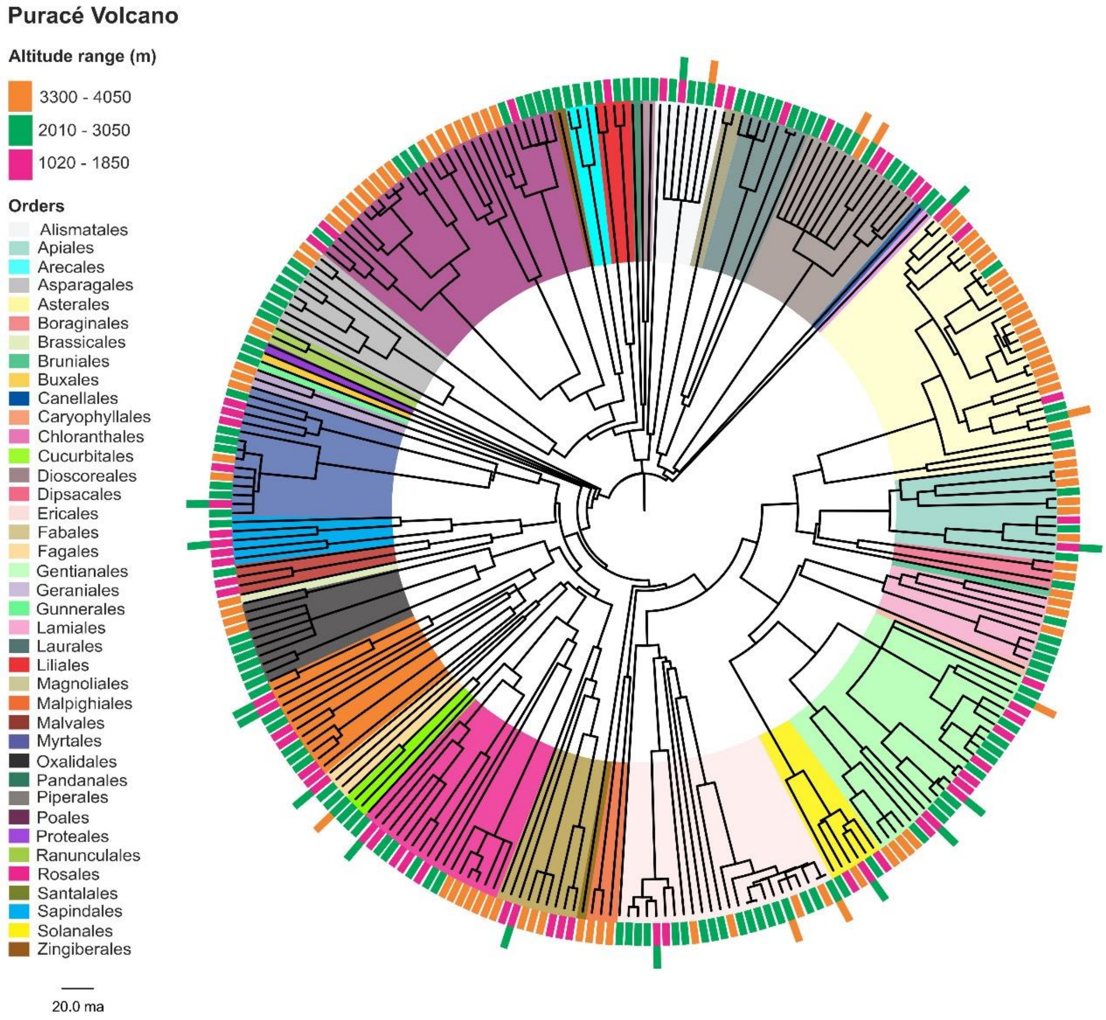

Figure 3 – Phylogenetic tree of plant communities of Mount Puracé. Orders and altitudinal ranges are indicated by colors, and lineages ages are indicated by branch lengths according to the legend. Phylogenetic divergence scale is indicated in millions of years (ma).

Figure 4 – Phylogenetic tree of plant communities of Mount Kilimanjaro. Orders and altitudinal ranges are indicated by colors, and lineages ages are indicated by branch lengths according to the legend. Phylogenetic divergence scale is indicated in millions of years (ma).

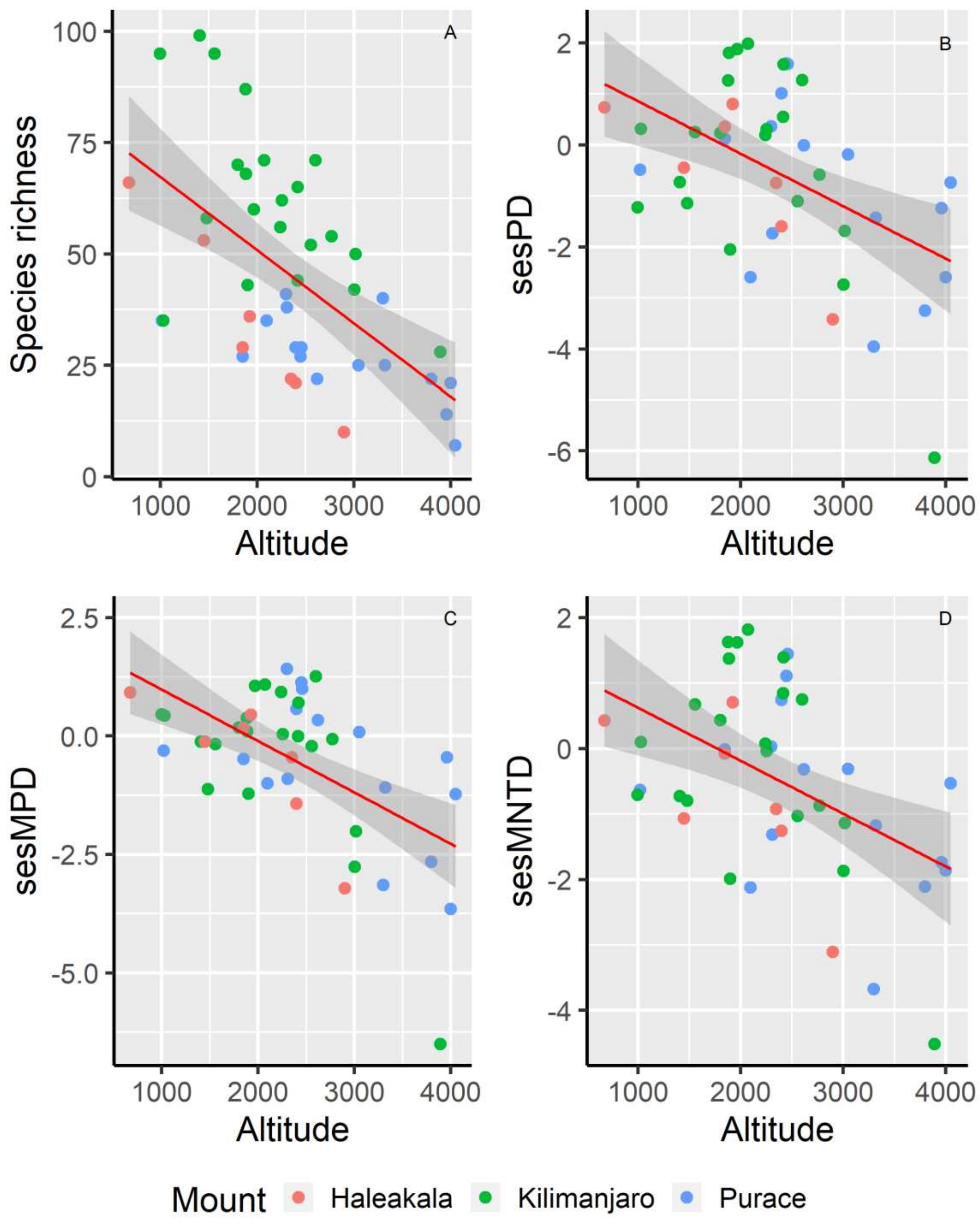

Figure 5 - Relationships between altitude and (A) species richness, (B) standardized effect size of phylogenetic distance - ses.PD, (C) standardized effect size of mean pairwise phylogenetic distance - ses.MPD, and (D) standardized effect size of mean nearest taxon - ses.MNTD. Solid lines represent fitted (predicted) model's values, and the shaded polygons are the 95% confidence interval associated with the modeled predictions.

Supplementary data

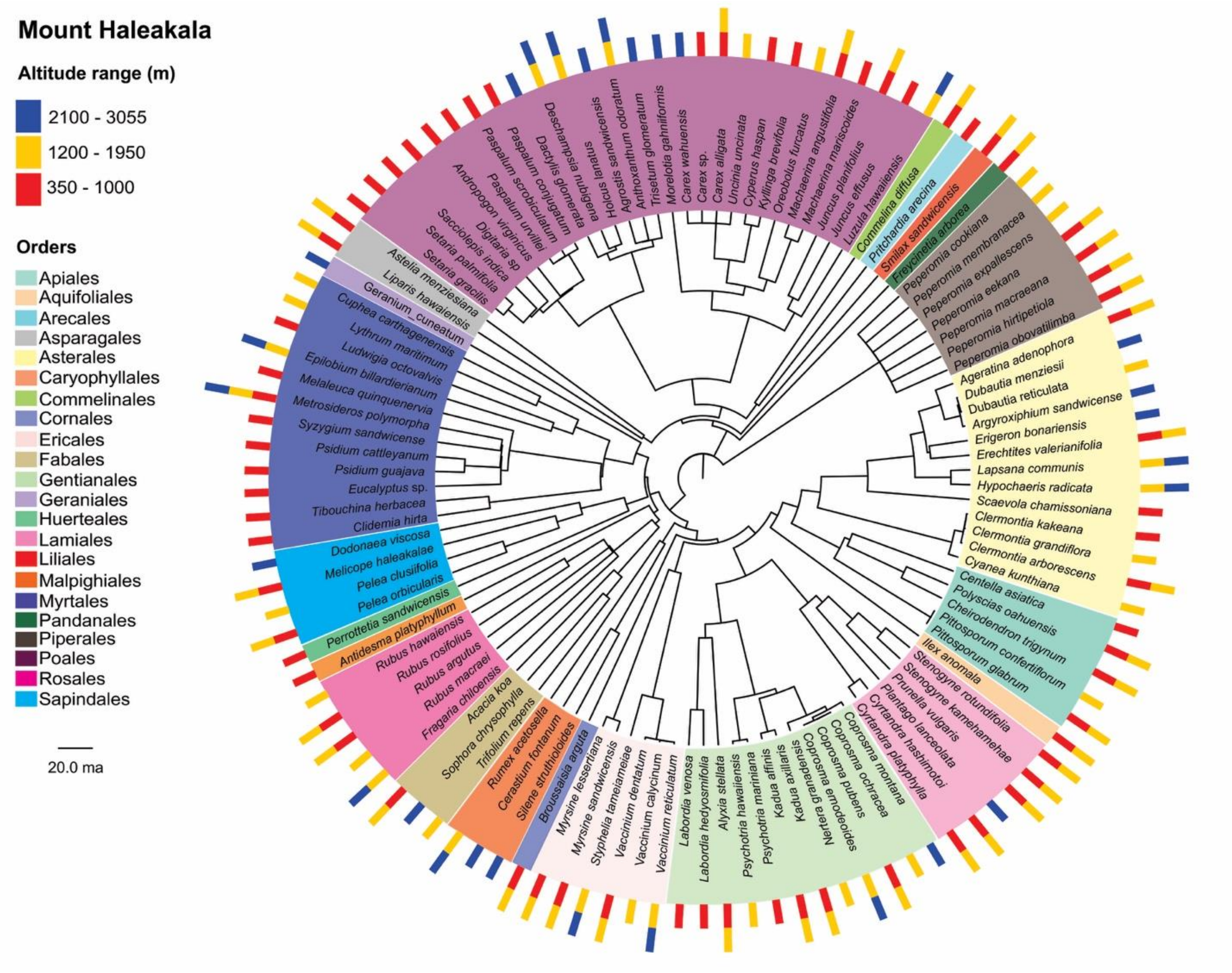

Figure S1 – Phylogenetic tree with species names of the Mount Haleakala, Hawaii.

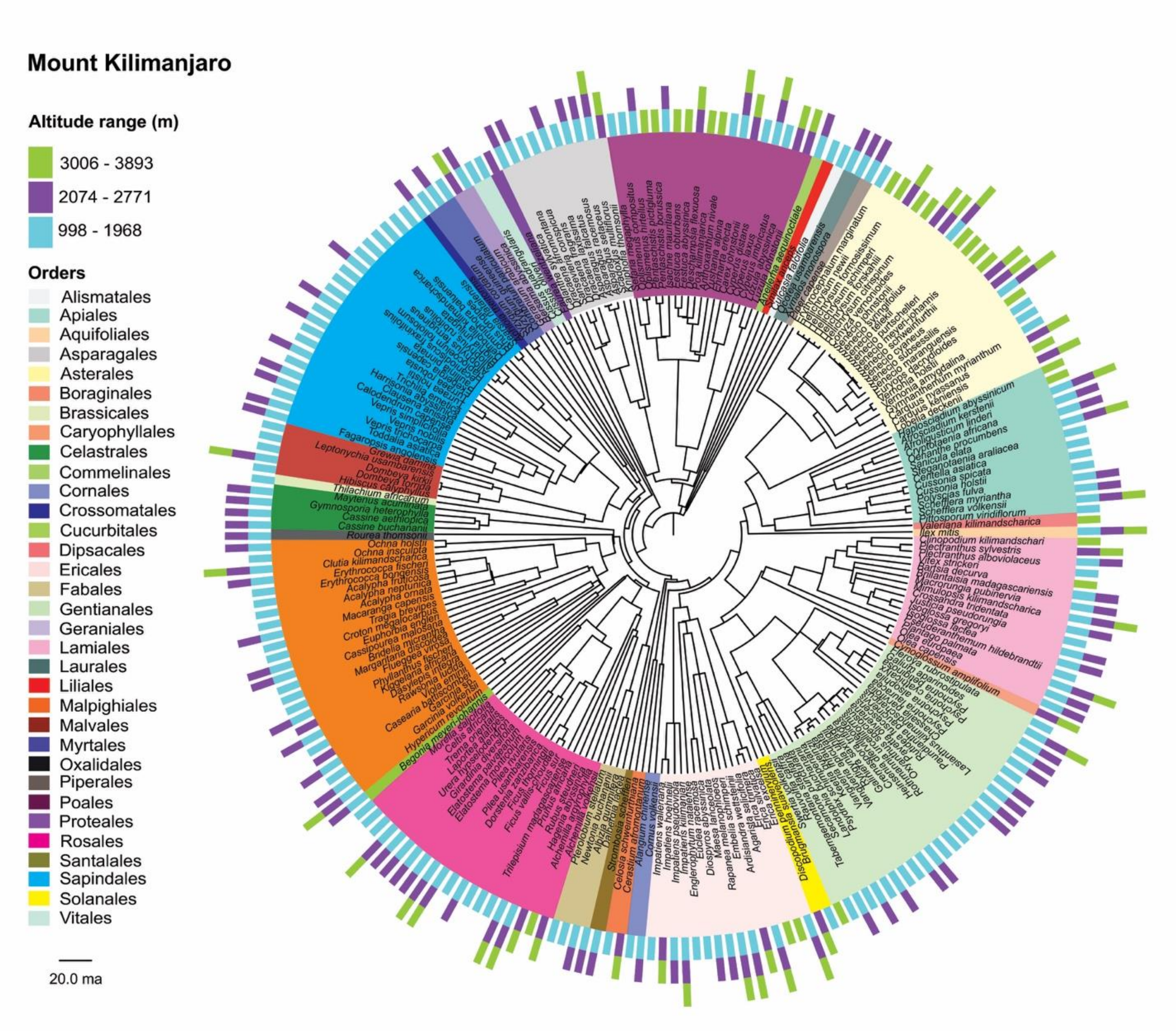

Figure S2 – Phylogenetic tree with species names of the Mount Kilimanjaro, Tanzania.

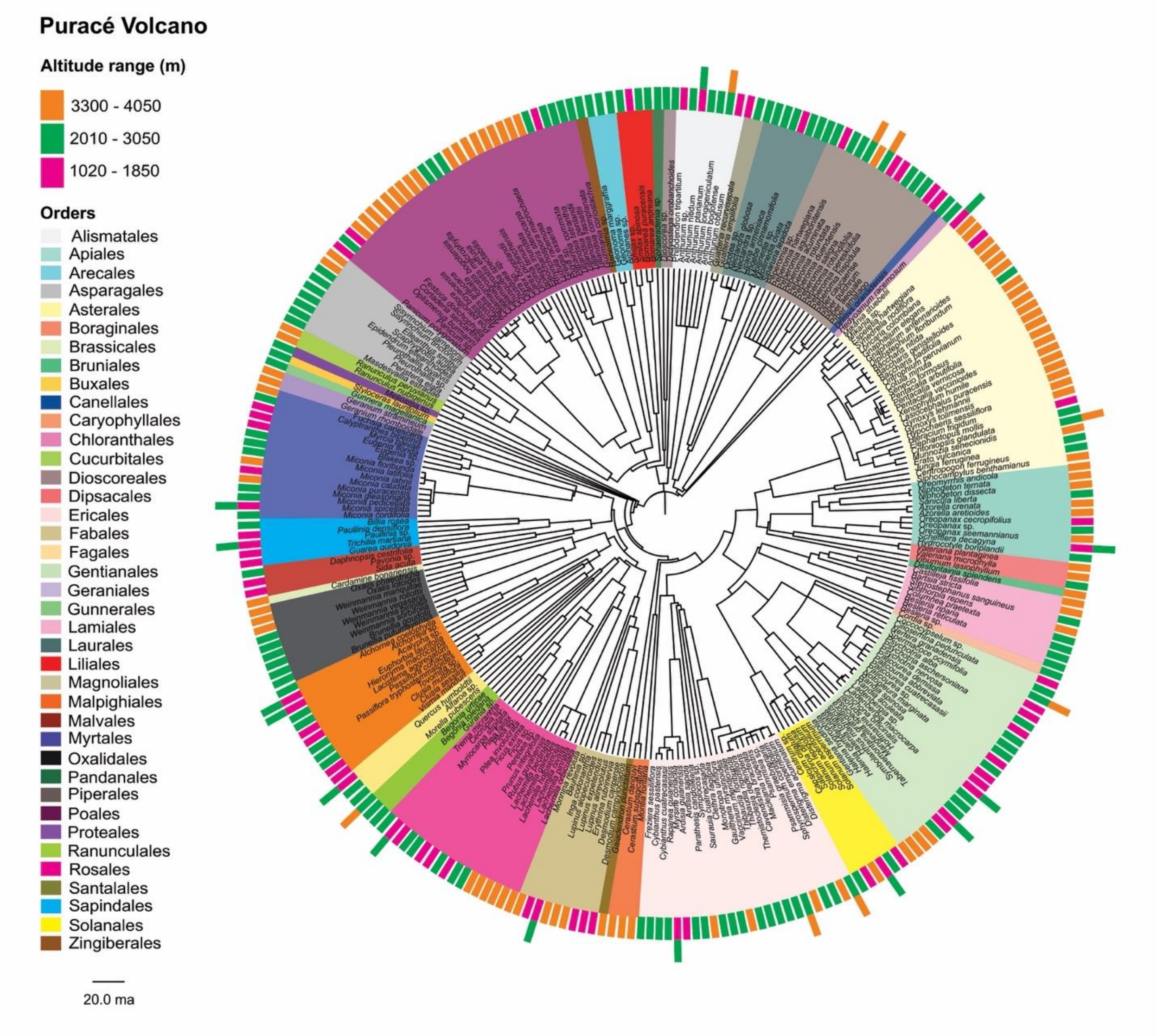

Figure S3 – Phylogenetic tree with species names of the Mount Puracé, Colombia.

Chapter 2: Phylogenetic diversity in Andean tropical grasslands communities along an altitudinal gradient

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Abstract

Phylogenetic information from studies of diversity patterns along elevation gradients can provide new insights into how ecological and evolutionary processes act to form communities in alpine tropical ecosystems. Elevation gradient is an excellent system for conducting ecological studies because of its steeper environmental gradients over short geographical distances. Thus, we addressed the following questions:1) Does increasing altitude continue to cause increasing environmental filtering in a vegetation type adapted to high altitudes? 2) Is altitude a variable that aggregates other environmental variables, such as temperature, soil depth, soil fertility, water availability; because altitude is an aggregating variable, is it expected to be a more powerful explanatory variable than an environmental variable such as soil depth? 3) Assuming niche conservation, as the altitude difference between altitudinal stations (levels) increases (generally meaning that the difference in environmental conditions between plots becomes greater), will beta phylogenetic dissimilarity also increase? The study area was located in the Eastern Cordillera of Colombia, in the Santurbán *páramos* complex. Hill numbers and phylogenetic metrics were used to calculate the taxonomic and phylogenetic components. Linear mixed-effects models (LMMs) were used to test the main effects of soil depth and altitude on different phylogenetic metrics. A total of 110 angiosperm species were compiled, belonging to 30 families. As a general trend, as taxonomic diversity decreases as altitude increases. For the phylogenetic component, the results showed that, as soil depth decreased and altitude increased, *páramo* plant communities showed a general pattern of decreasing phylogenetic diversity. These results are consistent with the general expectation that community assemblage attributes are more closely related as stressful environmental conditions increase along a gradient; that is, environmental filtering promoted by decreasing soil productivity and increasing altitude has negative effects on species richness and phylogenetic diversity.

Key words: Andes mountains, *páramo*, environmental filtering, taxonomic diversity, soil depth

INTRODUCTION

The phylogenetic relationships between organisms show several underlying mechanisms of evolutionary, biogeographical and ecological processes in communities assembly (Butterfield et al., 2013; Cavender-Bares et al., 2009; Qian et al., 2019). Under the classical structure of communities assembly, two main theories: the niche theory and the neutral theory, are the basis that attempt to explain the coexistence of species within a community (Chase & Myers, 2011; Kembel & Hubbell, 2006). The main niche-based deterministic processes are: environmental filtering and biological interactions (mainly competition causing limiting similarity) (Cadotte et al., 2011; Cavender-Bares et al., 2009). It is suggested that neutral processes shape the community when there is an absence of phylogenetic structure (Kembel & Hubbell, 2006). Phylogenetic information in studies of diversity patterns along altitudinal gradients can provide new insights into how ecological and evolutionary processes act to assemble communities in alpine ecosystems (Chun & Lee, 2017; Hoiss et al., 2012; Li et al., 2014; Qian et al., 2014). Knowledge of the phylogenetic pattern of species and the sensitivity of communities to environmental change may allow predictions to be made of their responses to climate change (Hoiss et al., 2012; McCain & Colwell, 2011).

A combination of several processes determines the structure of mountain plant communities and the diversity of associated species (Zhu et al., 2019). Several studies have suggested that environmental factors, such as those linked to soil properties, change drastically along environmental gradients (Perrigo et al. 2019; Schreeg et al. 2010); affecting the phylogenetic structure of plant communities (Luo et al. 2023; Shi et al. 2020; Ulrich et al. 2014). One factor that is widely used as a proxy for direct environmental factors is altitude (McVicar & Korner, 2013). Altitudinal gradient is an excellent system to study because of its steeper environmental gradients over a short geographic distance (Li et al., 2014; Qian et al., 2014; Worthy et al., 2019). Altitudinal gradients can adequately reflect the transition from competition to environmental filtering. In alpine plant communities over the tree line, studies have shown that communities fall into the phylogenetic clustering range, near the tree line these communities tend to show a random pattern or be less clustered (Qian et al., 2021), while at higher altitudes environmental filtering increases its influence because of increasing climate severity showing a clear pattern of phylogenetic clustering (Machac et al., 2011; Manish & Pandit, 2018; Xu et al., 2017; Zhao et al., 2017).

On altitudinal gradients, environmental conditions change rapidly as one ascends and the severity of the climate increases. These changes result in many different climatic and productivity zones, providing unique opportunities to explore the mechanisms involved in the assembly of plant communities (Montaño-Centellas et al., 2020). Most studies on phylogenetic patterns in plant communities on altitudinal gradients have focused on temperate regions, both in woody plant communities (Manish & Pandit, 2018; Qian et al., 2014, 2019, 2020; Zhou et al., 2021), and in alpine communities (Li et al., 2014; Marx et al., 2017; Ndiribe et al., 2013; Xu et al., 2017; Zhao et al., 2017). The most common result of these studies is that plant species tend to be more closely related to each other at higher altitudes, and tend to be more distantly related to each other at lower altitudes. In tropical regions of South America, some studies have explored the phylogenetic structure patterns of tree plant communities along altitudinal gradients, with mixed results. For instance, in Andean forests of Ecuador, Worthy et al., (2019), found that tree species of angiosperms tend to be more phylogenetically clustered at higher altitudes, and more overdispersed at lower altitudes; in contrast, Qian & Ricklefs, (2016) based on a large database of tree species from South America, found that angiosperm tree species tend to be more overdispersed at higher altitudes; Griffiths et al., (2021), in an altitudinal gradient between Amazonia and Peruvian Andean forests, found that tree species tend to be more overdispersed at mid-altitudes; Galván-Cisneros et al., (2023) in a study covering montane forests and alpine ecosystems in three tropical mountains on two continents (one in South America) and on an oceanic island, showed that as altitude increases plant communities show a general pattern of decreasing species richness and decreasing mean phylogenetic distance between species. These contrasting patterns of phylogenetic structure and focus on tree communities suggest the need for studies above the tree line, i.e., Andean tropical grasslands (*Páramo*), to gain insight into the mechanisms involved in assembling communities on Andean mountaintops.

The neotropical *páramos* are isolated on top of several mountain ranges, at altitudes between 3000 and 4700 m above sea level, forming a kind of archipelago (Londoño et al., 2014; Sklenář et al., 2014). In these *Páramos*, the number of endemic genera is low and that of endemic species is high; more than fifty percent of plant species are endemic (Luteyn, 1999; Rangel-Ch, 2000; Sklenář et al., 2014), with close relatives in lowland tropical forests and savannas, and temperate zones in the northern hemisphere and the Patagonian-Antarctic region in the south (Cleef, 2013; Madriñán et al., 2013; Segovia et al., 2020; van der Hammen & Cleef, 1986), a fact related to the recent uplift of the northern Andes (Cleef, 2013; Gregory-Wodzicki, 2000). The Andean flora of the *Páramos* is considered the most species-rich high mountain flora in the world (Smith & Cleef, 1988). The vegetation of the *Páramo* is subject to a unique set of stressful conditions: lower temperatures, high 24-hour temperature variability, high wind speed, lower atmospheric pressure, higher radiant energy (Rada et al., 2019). Furthermore, this unique flora is threatened by current climate changes (Buytaer et al., 2014). It is therefore important to deepen the research on the processes that allow understanding as well as explain the patterns of the relationship between the diversity, functioning and ecosystem services of the *Páramos* (Llambí & Cuesta, 2014). Although the phylogenetic information of *Páramo* plant species has been used in recent years for phylogeny studies (Madriñán et al., 2013; Särkinen et al., 2012), its implementation in phylogenetic ecology study is scarce.

Most of studies on the phylogenetic structuring of plant communities in altitudinal gradient have been approached mainly with an alpha phylogenetic diversity approach, with little attention on phylogenetic beta diversity. In recent years, studies with this approach have increased (Swenson, 2013; Yakimov et al., 2020), with a few studies in alpine ecosystems (Cubino et al., 2022; Wang et al., 2021). Phylogenetic turnover measures phylogenetic dissimilarity between communities (Graham & Fine, 2008; Leprieur et al., 2012), connecting local processes with regional and evolutionary processes (Yakimov et al., 2020). Understanding the interaction between local and regional biodiversity processes is important for theoretical studies, and may allow better prediction of how human-induced changes in climate and land use will influence biodiversity patterns (Graham & Fine, 2008).

Here, we will examine patterns of phylogenetic community structure in Andean tropical grasslands (*Páramo*), on an altitudinal gradient in the Colombian Andes, to assess how competition and abiotic filtering may influence community assembly in the equatorial Andean high-mountain. In tropical mountains there is environmental filtering towards the top. Galván-Cisneros et al., (2023) found that higher altitudes increase environmental filtering, including montane forests and alpine vegetation. In this work, if we analyze only alpine vegetation, 1) the increase in altitude intensifies environmental filtering in a type of vegetation adapted to high altitudes, generating a gradually more clustered pattern along the gradient; 2) altitude is a variable that aggregates other environmental variables, such as temperature, soil depth, soil fertility, and water availability; is therefore expected to be a more powerful explanatory variable than an environmental variable such as soil depth; 3) assuming niche conservation, as the altitude difference between altitudinal levels increases (generally meaning that the difference in environmental conditions between plots becomes greater), beta phylogenetic dissimilarity also increase.

MATERIALS AND METHODS

Study Site

The study area is located on the eastern slope of the Eastern Ranges of Colombia, in the *Páramos* of Santurbán complex, in the Norte de Santander department (province). The altitudinal ranges of the study gradient from 3100 to 4100 m above sea level. This *Páramo* complex shows that precipitation has a bimodal regime, with high periods between the months of April and May, and September and November, and with average rainfall values that vary between 600 and 2,500 mm. The multi-year average minimum temperature values are between 0.3 and 4.6 °C, and the multi-year average values range between 6 and 12 °C. The soils are very shallow, limited by rocks, moderately deep and has a loamy texture. In addition, they are excessively drained, with very strong acidic reaction (pH 4.5 to 5.0) and very low to moderate natural fertility. The main taxonomic classes of soils are Udorthents, Dystrudepts, Fluvaquents and Udifolists (Morales et al., 2007).

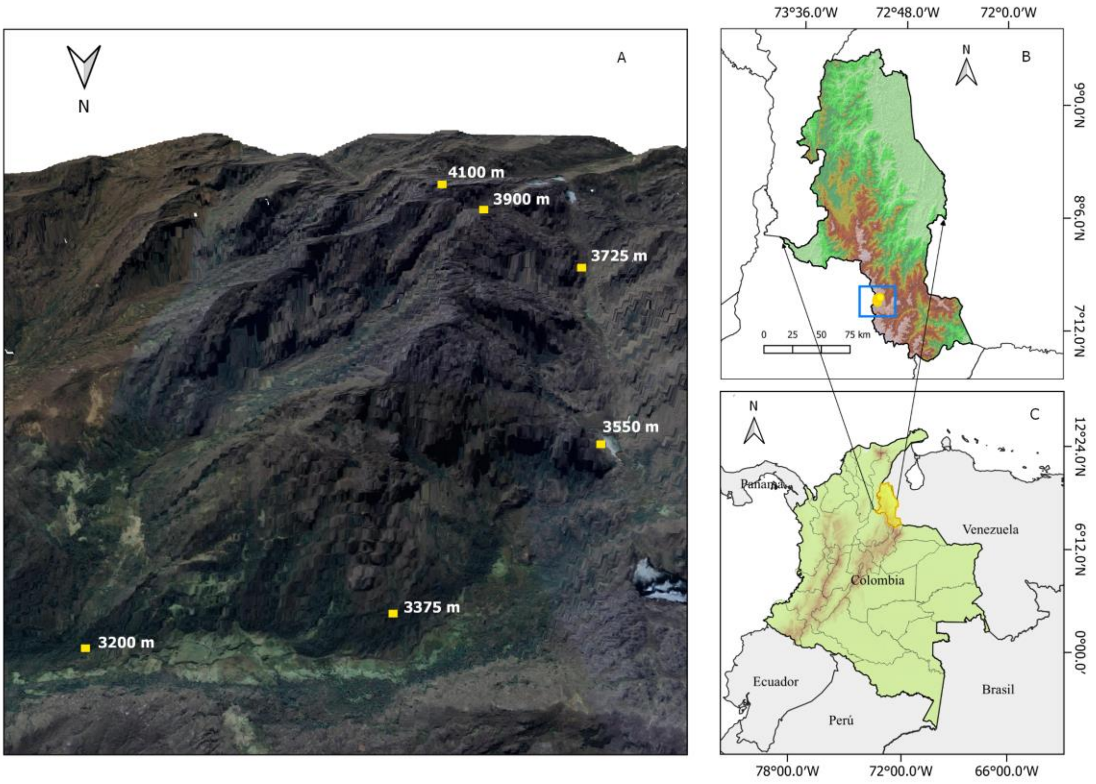

Figure. 1 Map of the study area, located in the Andean region of Colombia.

Sampling

In the altitudinal gradient six sampling stations (altitudinal levels) were established: 3200 m, 3325 m, 3550 m, 3725 m, 3900 and 4100 m. In each station, 10 plots of 2.5 m x 4 m were established, spaced every 40 m (N = 60 plots). In each plot, the total height and percentage of coverage of each species were taken in relation to each plot.

Soil depth

In each altitudinal level the soil depth was measured using a sharp metal rod; one measurement was made for each plot (N = 60 measurements).

Taxonomic and phylogenetic diversity

Alpha taxonomic diversity: For each altitudinal station, was estimated using true diversity indices: ^{0}D (species richness), ^{1}D (represented by relative abundance) Shannon (exp H´) and ^{2}D (represented by species abundance) (inverse Simpson) with the help of the package iNext in the R environment (R Core Team 2021).

To construct the phylogenetic tree, a taxonomic list was prepared according to APG IV (2016). The list of all species in the study was attached to the phylogenetic tree *GBOTB.extended.TPL.tre* incorporated in the package 'V.PhyloMaker2' (Jin & Qian, 2022) implemented in the R environment.

Alpha phylogenetic diversity: For each altitudinal station, four phylogenetic metrics were calculated based on coverage, which was used as a proxy for abundance: mean phylogenetic distance (MPD), mean phylogenetic distance to nearest taxon (MNTD). We also evaluated the standardized effect size of MPD (ses.MPD) and the standardized effect size of MNTD (ses.MNTD). MPD and MNTD are given in millions of years, and ses.MPD and ses.MNTD in standard deviation units. For the standardized effect size calculations, our phylogeny was compared with 10,000 null model randomizations using the algorithm '*phylogeny pool*', using the '*picante*' package.

Beta phylogenetic diversity: To examine this diversity we calculated the phylogenetic distance, four metrics were calculated β MPD, β ses.MPD, β MNTD and β ses.MNTD, for each pair of plots within each altitudinal station and between each altitudinal station. β MPD and β MNTD were estimated with the COMDIST and COMDISTNT algorithms, β ses.MPD and β ses.MNTD were estimated with the ses.COMDIST and ses.COMDISTNT algorithms implemented in the *MicEco* package (Russel, 2021) and applying 10,000 randomizations under the phylogeny pool of the null model (Kembel & Hubbell, 2006). β MPD and β MNTD are analogous to alpha metrics MPD and MNTD, where β MPD calculates the mean phylogenetic distances for each pair of individuals between two communities, β MNTD calculates the mean phylogenetic closest neighbor between individuals of two communities (Fine & Kembel, 2011).

Data analysis

The distribution of the alpha phylogenetic diversity and beta phylogenetic diversity data was assessed with the Q-Q graph, the Shapiro-Wilk and Kolmogorov-Smirnov tests to determine normality.

We analyzed the effects of soil depth and altitude on richness using a generalized linear model (GLM), with the Gaussian error, using the 'glm' command in environment R using lme4 package (Bates et al., 2015). We, also, used linear mixed-effects models (LMMs) using the lme4 package in R (Bates et al., 2015), to test the main effects of soil depth and altitude on different phylogenetic metric (PD, ses.PD, MNTD, ses.MNTD, MPD and ses.MPD); to test this, each phylogenetic metrics was used as the dependent factor, "soil depth" as a fixed effect, and "altitude" as a random effect. The goodness of fit for the models was calculated using the adjusted R^2, this is a measure of corrected goodness-of-fit for classical linear models (Piepho, 2019).

Differences in beta phylogenetic structure between different combinations of communities (groups) were verified using one-way non-parametric analysis of similarity (ANOSIM) with 1000 permutations using 'vegan' R package. The ANOSIM was performed using Euclidean and Bray-Curtis distances and Bonferroni correction for multiple a posteriori comparisons (M. J. Anderson & Walsh, 2013).

All phylogenetic analyzes were performed in R 4.0.4 (R Core Team 2021)

RESULTS

Floristic composition

A total of 110 angiosperms species were compiled, which belonged to 70 genera, 30 families and 18 orders. Asterales and Poales were the most important orders. The families with the highest number of species were Asteraceae with 24 species, Poaceae with 11 species, Rosaceae with 10 species, Cyperaceae and Ericaceae with 8 species each one, and Hypericaceae with 7 species. The 8 species with the highest percentage cover in the data set were, in descending order, *Calamagrostis effusa*, *Chusquea tessellata*, *Cortaderia* *hapalotricha*, *Arcytophyllum nitidum*, *Diplostephium* (*Linochilus*) *rosmarinifolium*, *Gaultheria myrsinoides*, *Geranium sibbaldioides* and *Arcytophyllum muticum* (Figure 2).

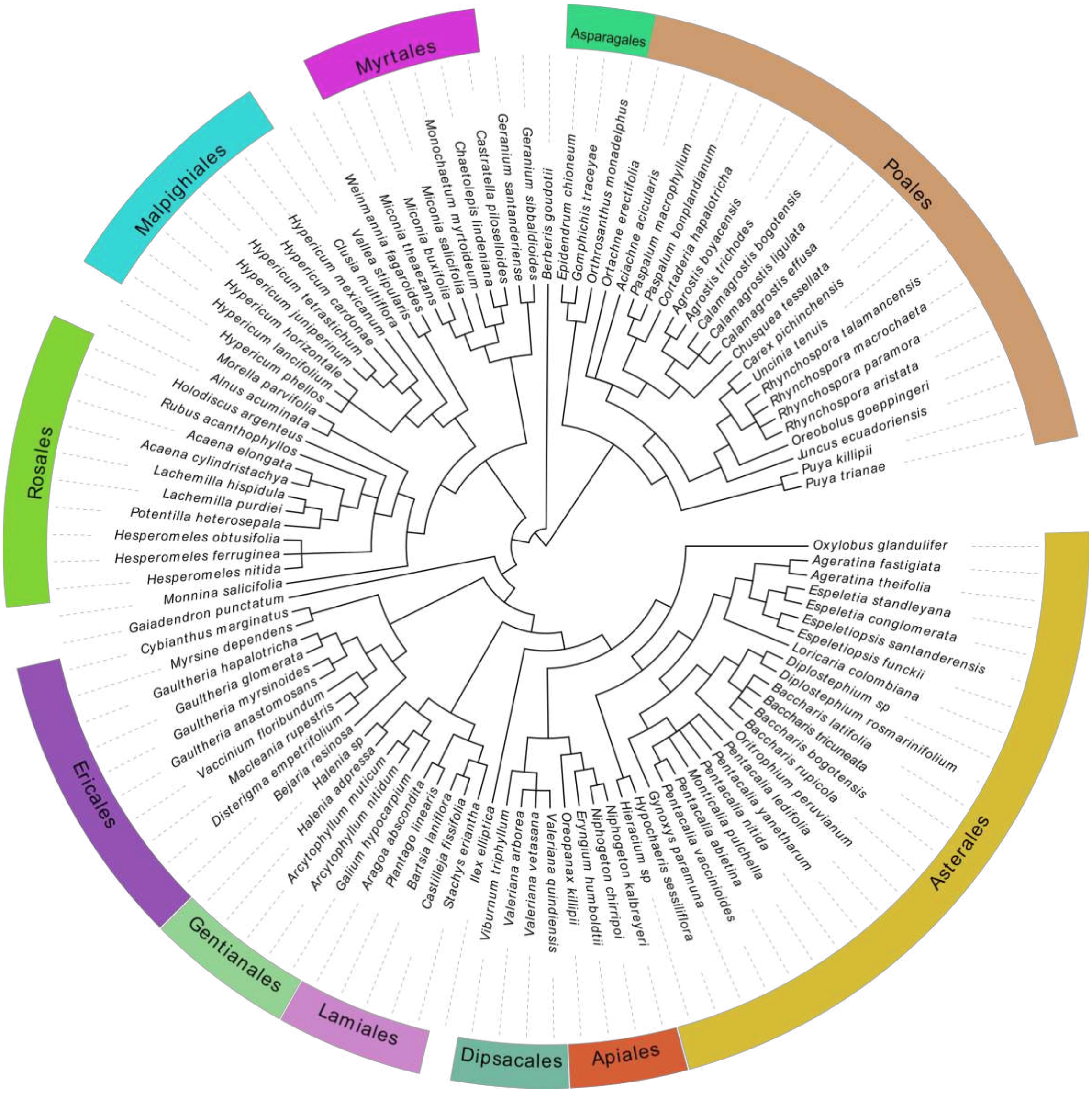

Figure 2. Phylogenetic tree of plant communities of the *páramo* of Santurbán in the tropical Andes. The main orders are highlighted in the tree.

Taxonomic diversity

Species Richness (q0 diversity), Shannon's diversity index (q1 diversity) and inverse Simpson's index (q2 diversity) were calculated for each altitudinal level. As a general tendency, as altitude increases, species richness decreases or as altitude decreases, species richness increases (Figure 3). The altitudinal level at 3200 m a.s.l. -the lowest of all-, was the richest in species with 55; then followed by the altitudinal level at 3375 m a.s.l., with 51 species; then the altitudinal level at 3550 m a.s.l., with 47 species; consecutively the altitudinal level at 3725 m a.s.l., with 32 species; further on the altitudinal level at 3900 m a.s.l., with 24 species and, finally, the altitudinal level at 4100 m a.s.l., with 24 species (Figure 3).

As a general tendency, as altitude increases the Shannon's and inverse Simpson's diversity decreases. The greatest first order diversity was recorded in altitudinal level at 3200 m a.s.l. (1D= 23.32), and the altitudinal level at 3375 m a.s.l. (1D = 16.33), meanwhile the altitudinal levels with the lowest values were at 3900 m a.s.l (1D = 7.33), and at 3725 m a.s.l. (1D = 9.01); the altitudinal levels at 3550 m a.s.l and at 4100 m a.s.l. presented intermediate values. The greatest diversity of second order was found in altitudinal level at 3200 m a.s.l. (2D= 12.92), meanwhile the altitudinal level with the lowest values were at 3725 m a.s.l. (2D = 4.30), at 3900 m a.s.l. (2D = 4.40) and at 3550 m a.s.l. (2D = 5.84); the altitudinal levels at 4100 m a.s.l and at 3375 m a.s.l. presented intermediate values (Figure 3).

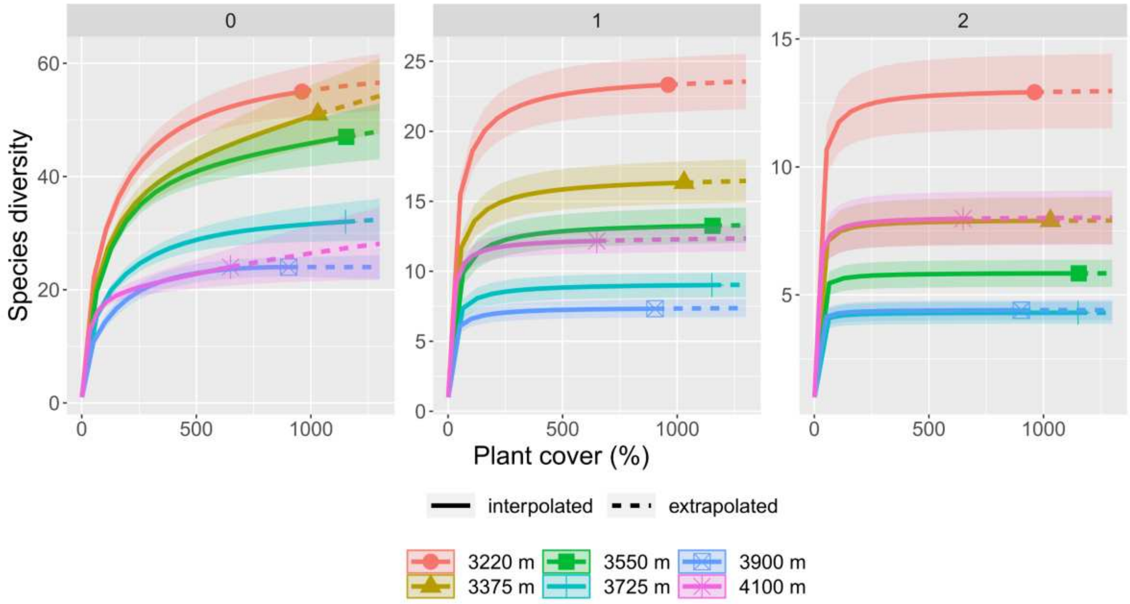

Figure 3. Diversity of plant species of plant communities of the *páramo* of Santurbán in the tropical Andes. 0- q0 diversity (Species Richness), 1- q1 diversity (Shannon's diversity index), 2- q2 diversity (inverse Simpson's index).

Species richness patterns

The generalized linear model, revealed that soil depth had a significant positive effect on species richness (Est. = 0.494, T val. = 2.17, p = 0.034) and altitude had a negative, but not significant effect on it (Est. = -0.1466, T val. = -0.64, p = 0.521). Thus, as soil depth increases (and altitude decreases), species richness in *páramo* plant communities increases (S1).

Alpha phylogenetic diversity

Our results show that as soil depth decreases (and altitude increases) in the altitudinal gradient studied, *páramo* plant communities show a general pattern of decreasing phylogenetic diversity. Thus, PD, ses.PD, MPD, ses.MPD and ses.MNTD are explained by the soil depth, which suggests a significant effect, positive of the soil and negative of the altitude, in the models tested (Figure 4, Table 1). The first model show that depth soil affected significantly and positively the PD (LMM, Estimate = 10.23, t = 5.88, $p < 0.000$) (Figure 4A, Table 1). The ses.PD was significantly and positively influenced by the depth soil (LMM, Estimate = 0.025, t = 3.33, $p < 0.007$) (Figure 4B, Table 1). The MNTD was not significantly (LMM, Estimate = 0.14, t = 0.74, p = 0.46) (Figure 4C, Table 1). The ses.MNTD was significantly and positively influenced by the depth soil (LMM, Estimate = 0.02, t = 3.12, $p < 0.003$) (Figure 4D, Table 1). The MPD was significantly and positively influenced by the depth soil (LMM, Estimate = 0.25, t = 2.66, $p < 0.018$) (Figure 4E, Table 1). Finally, the ses.MPD was significantly and positively influenced by the depth soil (LMM, Estimate = 0.021, t = 2.90, $p < 0.012$) (Figure 4F, Table 1).

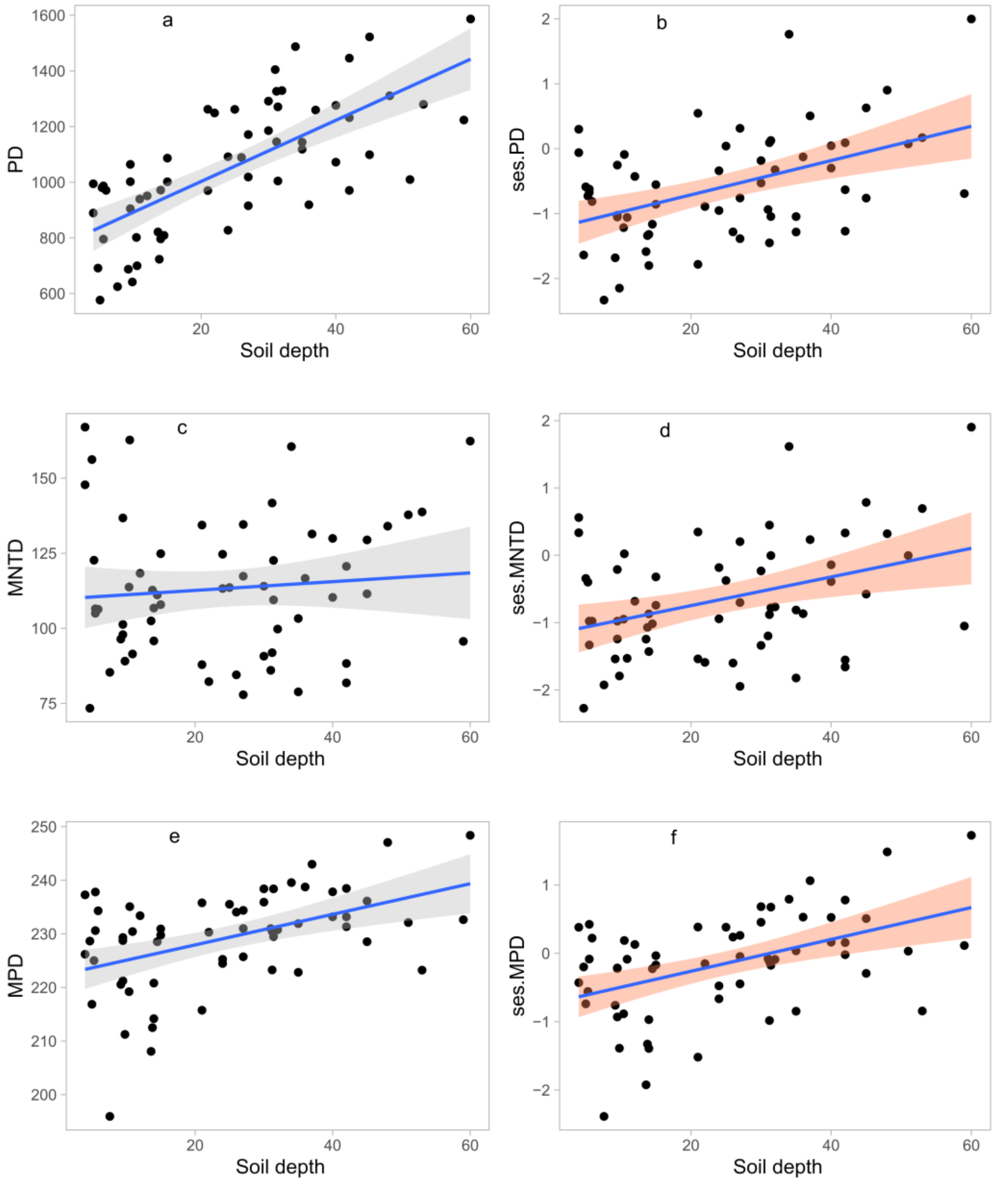

Figure 4. Relationships between soil depth (cm) and (A) Phylogenetic diversity, (B) standardized effect size of phylogenetic distance - ses.PD, (C) phylogenetic distance of the nearest taxon, (D) standardized effect size of mean nearest taxon distance - ses.MNTD, (E) mean pairwise phylogenetic distance and (F) standardized effect size of mean pairwise phylogenetic distance - ses.MPD. Solid lines represent fitted (predicted) model's values, and the shaded polygons are the 95% confidence interval associated with the modeled predictions.

Table 1. Linear mixed models (LMM) explain the relationships between phylogenetic metrics (PD, ses.PD, MNTD, ses.MNTD, MPD, ses.MPD) and depth soil. ses.PD: standard effective size of phylogenetic diversity; ses.MPD: standard effect size of mean pairwise distance; ses.MNTD: the standard effective size of mean nearest taxon. Models with significant effects (*) are indicated.

Random effects (variance)	Model	R^2	Estimate	t	p
0.089	PD ~ Soil	0.68	10.23	5.88	0.000*
0.065	ses.PD ~ Soil	0.26	0.025	3.33	0.007*
0.00	MNTD ~ Soil	0.009	0.146	0.74	0.46
0.00	ses.MNTD ~ Soil	0.14	0.021	3.12	0.003*
0.152	MPD ~ Soil	0.30	0.25	2.66	0.018*
0.121	ses.MPD ~ Soil	0.29	0.021	2.9	0.012*

Beta phylogenetic diversity

Beta phylogenetic diversity indices showed similar trends to those of alpha phylogenetic diversity, i.e., there is an increase in phylogenetic turnover as the difference in altitude between altitudinal levels (communities) increases, and as altitude increases, phylogenetic turnover between altitudinal levels decreases (Table 2). This indicates that as altitude increases, plant communities are assembled by close relatives, represented in a few lineages.

This increase in phylogenetic turnover with increasing spatial distance between communities, for example, can be observed for the comparison between 3200-4100 -the lowest and the highest altitudinal level-, this combination presents the highest phylogenetic turnover, evidenced in the four phylogenetic indices. Comparisons between the altitudinal levels closest to the mountain top show the lowest values of phylogenetic turnover (Table 2, Figures S2-S3).

The phylogenetic turnover towards the tip of the phylogenetic tree (β MNTD, β ses.MNTD) between the lowest altitudinal level -3200 m a.s.l.- and the rest of the levels, presented a quite heterogeneous behavior, this indicates that within the plots of the lowest altitudinal level there is a greater phylogenetic distancing between species (Figure S3).

Table 2. Mean values of phylogenetic turnover and their standard deviations between pairs of altitudinal levels. Different superscript letters indicate statistically significant differences according to ANOSIM pairwise post-hoc tests. β ses.MNTD: standardized effect size of MNTD (mean nearest taxon distance) separating taxa in two communities; β ses.MPD: standardized effect size of MPD (mean pairwise distance) separating taxa in two communities.

Comparison	β MNTD	β ses.MNTD	β MPD	β ses.MPD
3200-3200	60.64 ± 25.24^{dfgh}	-1.589 ± 0.858^{efgh}	216.81 ± 12.07^{d}	-0.932 ± 0.869^{d}
3200-3375	67.99 ± 35.68^{def}	-1.242 ± 1.189^{de}	226.16 ± 12.18^{c}	-0.216 ± 0.752^{c}
3200-3550	71.00 ± 39.65^{cde}	-1.121 ± 1.367^{cd}	226.12 ± 15.30^{b}	-0.166 ± 1.005^{b}

3200-3725	85.97 ± 47.56^{b}	-0.724 ± 1.491^{bc}	227.18 ± 16.81^{b}	-0.106 ± 1.009^{b}
3200-3900	97.88 ± 44.58^{a}	-0.583 ± 1.412^{ab}	226.20 ± 17.97^{bc}	-0.192 ± 1.115^{bc}
3200-4100	105.62 ± 39.36^{a}	-0.316 ± 1.316^{a}	232.59 ± 13.32^{a}	0.249 ± 0.946^{a}
3375-3375	39.41 ± 22.55^{kl}	-2.051 ± 0.762^{jlm}	195.34 ± 11.00^{fg}	-2.057 ± 0.580^{f}
3375-3550	46.98 ± 18.00^{j}	-1.807 ± 0.62^{hj}	185.15 ± 12.52^{ij}	-2.670 ± 0.618^{j}
3375-3725	49.31 ± 19.73^{ij}	-1.749 ± 0.592^{hi}	183.43 ± 13.65^{j}	-2.532 ± 0.591^{ij}
3375-3900	62.12 ± 17.29^{eg}	-1.556 ± 0.492^{g}	187.32 ± 15.42^{hj}	-2.339 ± 0.611^{gh}
3375-4100	71.34 ± 22.01^{c}	-1.349 ± 0.669^{df}	201.90 ± 13.83^{e}	-1.778 ± 0.770^{e}
3550-3550	25.50 ± 9.13^{m}	-2.487 ± 0.361^{o}	169.55 ± 9.40^{k}	-3.654 ± 0.403^{l}
3550-3725	32.83 ± 11.14^{l}	-2.241 ± 0.370^{ln}	166.24 ± 11.02^{kl}	-3.520 ± 0.381^{l}
3550-3900	38.20 ± 10.14^{k}	-2.274 ± 0.246^{n}	170.45 ± 14.76^{k}	-3.337 ± 0.485^{k}
3550-4100	52.62 ± 18.38^{hi}	-1.958 ± 0.582^{jk}	190.36 ± 14.39^{gh}	-2.591 ± 0.818^{ij}
3725-3725	22.21 ± 9.42^{m}	-2.514 ± 0.303^{o}	161.85 ± 12.34^{m}	-3.454 ± 0.387^{kl}
3725-3900	31.26 ± 8.18^{l}	-2.451 ± 0.243^{o}	165.90 ± 15.82^{klm}	-3.297 ± 0.475^{k}
3725-4100	54.25 ± 16.06^{h}	-1.890 ± 0.422^{ij}	188.05 ± 15.92^{hi}	-2.475 ± 0.767^{hi}
3900-3900	12.58 ± 6.85^{n}	-3.155 ± 0.194^{q}	163.28 ± 14.50^{lm}	-3.529 ± 0.359^{l}
3900-4100	54.71 ± 15.59^{fh}	-2.101 ± 0.426^{km}	189.81 ± 15.63^{h}	-2.430 ± 0.732^{hi}
4100-4100	34.56 ± 15.04^{l}	-2.865 ± 0.523^{p}	199.33 ± 11.78^{ef}	-2.179 ± 0.699^{fg}

DISCUSSION

We analyze the taxonomic and phylogenetic diversity of an altitudinal gradient in a tropical alpine ecosystem (*páramo*) in northeastern Colombia. Overall, we observe that taxonomic diversity decreases with increasing altitude from 3,200 m to 4,100 m above sea level and that alpha and beta phylogenetic diversity decrease with decreasing soil depth and increasing altitude. These results are consistent with the general expectation that assemblage attributes should be more similar as stressful environmental conditions increase up a gradient; that is, the environmental filtering promoted by the decrease in soil productivity and the increase in altitude has negative effects on species richness and phylogenetic diversity. This pattern has been observed in temperate and tropical alpine grasslands (Galván-Cisneros et al., 2023; Li et al., 2014; Marx et al., 2017; Ndiribe et al., 2013; Xu et al., 2017; Zhao et al., 2017).

Environmental filtering to the mountaintop leads to a decrease in lineage representation in these stressful habitats of low temperatures, high 24-hour temperature variability, high winds, lower atmospheric pressure and radiant energy. Species of Asteraceae and graminoids are among the few phylogenetic branches that have successfully adapted to higher altitudes in alpine environments (Ndiribe et al., 2013; Schubert et al., 2020; Sklenář et al., 2011; Zhao et al., 2017). Other orders, such as Rosales and Ericales also are important in the *páramos*, for example, Ericaceae can form belts of vegetation dominated by their species above the tree line, known as the "ericaceous belt" (Luteyn, 1989; Wesche et al., 2000). The strip of vegetation above the tree line in the Andean *páramos* is called lower *páramo* or *subpáramo* and is characterized by the presence of sclerophyllous shrubs, tussock grasses, forbs and caulescent rosettes. This is the strip vegetation of *páramo* with the greatest heterogeneity of habitats and species richness (Díaz-Granados Ortiz et al., 2005; Rangel-Ch, 2000).

All three taxonomic metrics are consistent with the explanation that increased altitude (and decreased soil depth and temperature) cause decreased taxonomic diversity (Chawla et al., 2008; Galván-Cisneros et al., 2023; Sánchez-González & López-Mata, 2005). The species composition changes as the altitude increases; higher altitudes tend to have a homogeneous composition dominated by a few species due to site-specific environmental conditions favorable to only a few adaptable species (Pescador et al., 2015; Wani et al., 2022). The Shannon diversity index and the inverse Simpson's index showed a different behavior for the highest altitudinal level, at 4100 m; it is more diverse than the levels at 3900, 3725 or 3550 m. This may be due to the fact that, unlike the other five sampling points, this point was located on the mountain's top, where the slope, drainage and exposure characteristics are different. The montaintop is more heterogeneous, with a greater variety of microhabitats; where despite the decrease in species richness, the heterogeneity of microhabitats promotes greater equitability between species. In addition, the increase in the global mean surface temperature promotes the ascent of species towards the top of the mountains (J. T. Anderson & Wadgymar, 2020; Feeley et al., 2011; Zu et al., 2021), and this creates an increase in the density of species at the top, since they have nowhere else to ascend.

Concerning the first question, if increasing altitude continues to cause increasing environmental filtering in a vegetation type adapted to high altitudes, the overall response is yes. We consider the question answered. However, the decreasing of taxonomic diversity is clear from 3220 m up to 3900 m of altitude, but it is not that clear in between 3900 m and 4100 m of altitude. Despite the interpretation of this species richness increasing on the last 200 m of the studied sites, we think that communities' assembly is influenced by other important rules beyond environmental filtering (see previous paragraph). Considering that environmental filtering of increasing altitudes has been detected causing a linear decreasing taxonomic diversities and clustering phylogenetic distances in habitats of tropical mountains of different continents and island (Galván-Cisneros et al., 2023), it is also important to consider that this effect was detected in a wider range of altitudes from below 1000 m up to

4000 m. In the narrower range of high altitudes of the studied samples, the effect was similar, but with samples of highest altitudes showing intermediate species densities. Although the effect is not as expected at the very mountaintop samples, the general effect of environmental filtering of increasing altitude is associated with decreasing taxonomic diversities and clustering phylogenetic structures.

Our results show that in these *páramo* communities, as soil depth decreases with increasing altitude, the phylogenetic distance between species decreases clustering phylogenetic structures. Although studies under the niche conservatism hypothesis show that alpine plant communities in temperate and, mainly, tropical zones fall within the range of phylogenetic clustering expectations (Qian et al., 2021), correlations from our standardized effect size (ses) metrics show that, at the beginning of the gradient, the *páramo* community is phylogenetically overdispersed where soils are deepest, that is at the first altitudinal level (3200 m), moving subsequently to a phylogenetic clustering pattern as soil depth decreases and altitude increases. This high diversity at the lowest altitudes of the gradient may be related to the fact that the Andes are the most biodiverse region on Earth (Rahbek et al., 2019; Sklenář et al., 2014), being able to maintain communities of *páramo* plants with high taxonomic and phylogenetic diversity in the vegetation strip close the tree line (lowest *páramo* strip). This also is congruent with the fact that the vegetation formations towards the top of the mountain are dominated by grasslands of graminoids and Asteraceae species, while in the formations adjacent to the tree line the lineages of Eudicotyledons begin to stand out much more.

Altitude, as an aggregator variable of environmental variables, proved to be a relatively strong explanatory variable. But soil depth, a direct environmental variable, was shown to be a much more powerful explanatory variable. This suggests that decreasing soil depth (with increasing altitude) is primarily responsible for patterns of diversity in these plant communities. These results suggest that our second working hypothesis can be rejected.

The spatial turnover observed in the phylogenetic beta diversity metrics indicates that, as the difference in altitude between the sampling stations (altitude levels) increases, the phylogenetic relationships between the species of the plant communities of the studied *páramo* increase. And, like alpha phylogenetic diversity, the phylogenetic beta diversity decreases with increasing altitude (and with the decrease of the soil depth), that is, the spatial distance was directly correlated with the environmental distance and with the phylogenetic distance in this study. This result is similar to patterns found in China, where beta phylogenetic diversity was positively correlated with edaphic distances between plots along the altitudinal gradient (Qian et al., 2014). This suggests that environmental filtering caused by the decrease in soil depth with increasing altitude is partially responsible for the structuring processes of these plant communities, adapted to these severe environmental conditions. These results suggest that our third working hypothesis was confirmed.

The *páramos* are very important in the Andean region, since they function as a great sponge, which absorbs water that falls in the form of rain or mist, and releases it slowly, so that the biological communities continue to function (Cleef, 2013; Molina & Little, 1981); in the northern Andes they provide water and generate hydroelectric power for the majority of the population. Climate change is occurring rapidly in the tropical Andes, projections suggest that it is expected to reach an additional 1°C to 4°C by the end of the century (Pabón-Caicedo et al., 2020). The *páramo* species face a series of challenges to cope these temperature changes, among these are: geographical isolation, the disconnection of the populations of the species due to anthropic activities, the high altitude, the specialization of many species and the endemism limit the "adaptive capacity" of many species to migrate uphill (Cuesta et al., 2020; Peyre et al., 2020; Valencia et al., 2020); leaving *páramo* species with no time to readapt to the new scenarios generated by global temperature increases (Valencia et al., 2020). Therefore, some threats may not be overcome by ecological and evolutionary processes alone, and the scenario is that tropical montane grasslands could be greatly affected by loss of lineages in phylogeny (Galván-Cisneros et al., 2023). Research and long-term monitoring of plant communities and changes in land use can provide information to help conserve the biodiversity and ecosystem services provided by the *Páramo* in the face of continuing pressures from current climatic alterations.

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Supplementary data

S1. Effects of elevation and soil depth on species richness using a general linear model (GLM).

```
mode <- glm(scale (richness) ~ scale(Soil) + scale (Altitude), data = dato, na.action=na.fail)

summary(mode)

summ(modelo1, confint = TRUE, digits = 3)
```

```
MODEL INFO:
Observations: 60
Dependent Variable: scale(richness)
Type: Linear regression

MODEL FIT:
χ²(2) = 23.268, p = 0.000
Pseudo-R² (Cragg-Uhler) = 0.419
Pseudo-R² (McFadden) = 0.178
AIC = 147.174, BIC = 155.552


Standard errors: MLE
----------------------------------------------------------------
                          Est.     2.5%   97.5%   t val.       p
--------------------- -------- -------- ------- -------- -------
(Intercept)              0.000   -0.200   0.200    0.000   1.000
scale(Soil)              0.494    0.049   0.939    2.176   0.034
scale(Altitude)         -0.146   -0.591   0.298   -0.645   0.521
----------------------------------------------------------------

Estimated dispersion parameter = 0.627

(Dispersion parameter for gaussian family taken to be 0.6268732)

    Null deviance: 59.000  on 59  degrees of freedom
Residual deviance: 35.732  on 57  degrees of freedom
AIC: 147.17
```

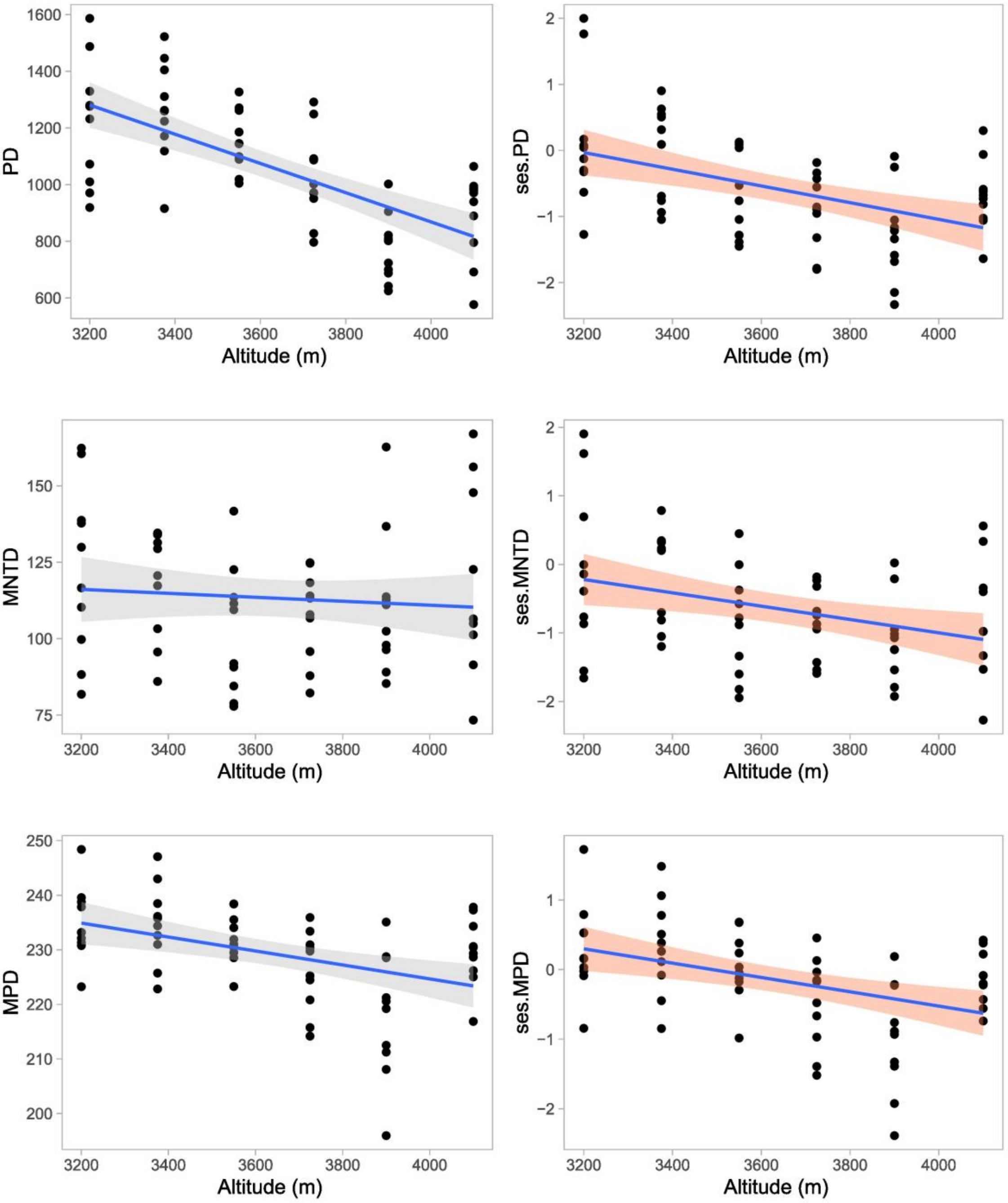

Figure S1. Relationships between altitude and (A) Phylogenetic diversity, (B) standardized effect size of phylogenetic distance - ses.PD, (C) phylogenetic distance of the nearest taxon, (D) standardized effect size of mean nearest taxon distance - ses.MNTD, (E) mean pairwise phylogenetic distance and (F) standardized effect size of mean pairwise phylogenetic distance - ses.MPD. Solid lines represent fitted (predicted) model's values, and the shaded polygons are the 95% confidence interval associated with the modeled predictions.

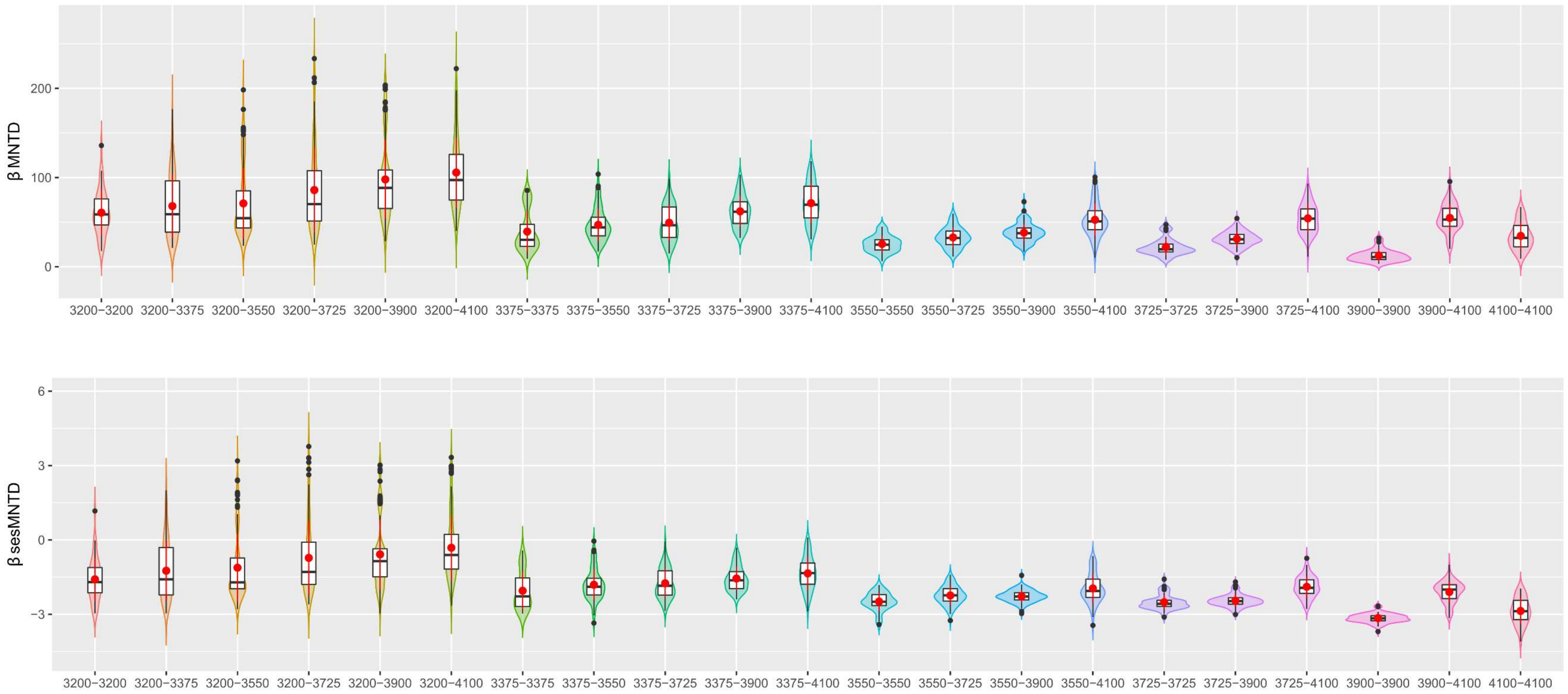

Figure S2. Patterns the ses.MNTD and β ses.MNTD between pairs of surveys from six altitudinal levels in the *páramo* of Santurbán in the tropical Andes.

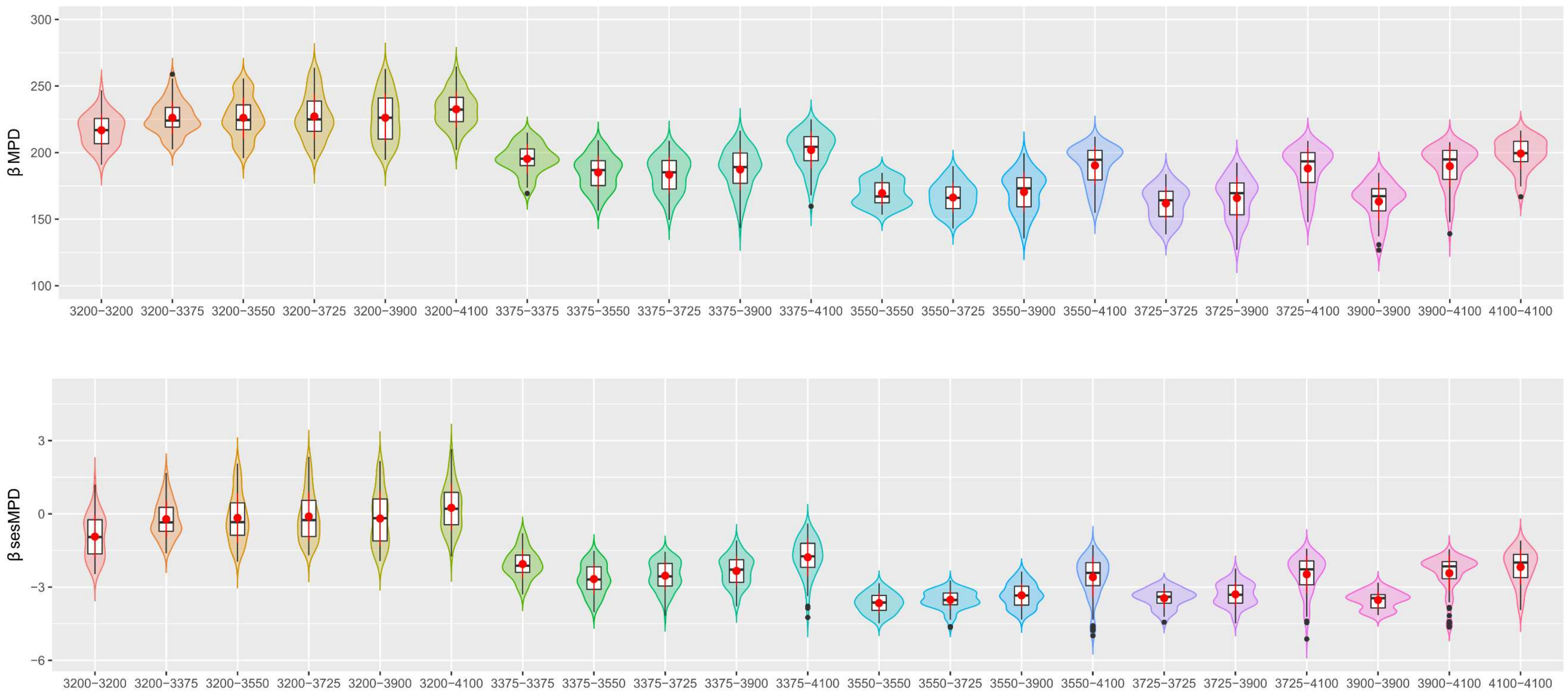

Figure S3. Patterns the ses.MPD and β ses.MPD between pairs of surveys from six altitudinal levels in the *páramo* of Santurbán in the tropical Andes.

CHAPTER 3: Trait-based community assembly along an elevational gradient in Andean *Páramo*

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Abstract

Altitudinal gradients offer special opportunities to discover the role of interspecific trait variations in relation to stress gradients. In tropical mountain ecosystems, environmental characteristics can change, even within small temporal and spatial scales, notably affecting functional diversity. We used an altitudinal gradient in the *páramos* de Santurbán complex (Eastern mountain range, Colombia) to study how community-weighted means (CWM) and Functional diversity (FD) vary with elevation (and soil depth) for maximum plant height, leaf length, leaf area, leaf dry matter content, and leaf thickness. We tested i) if the functional traits related to leaf size and plant size tended to decrease with increasing altitude (and the decrease in the depth of the soil), which is also reflected in a decreasing CWM of these traits; ii) the reduction of functional diversity as altitude increases (and the decrease in the depth of the soil) as a result of environmental filtering, and iii) the relationship between phylogenetic diversity/structure and functional diversity is based on the fact that evolutionary diversification has generated diversification of functional traits; thus, under the assumption of niche conservation, it is expected that the metrics of functional diversity and phylogenetic diversity are positively related along the elevation gradient. Across all communities, LDMC and leaf thickness increased with elevation (and decreased with soil depth), whereas plant height decreased, which is in line with H1. FDis and FRic decreased with increasing elevation and decreasing soil depth, consistently with H2. Our results indicate a convergence of plant traits towards an intensification of the resource conservation strategy with increasing altitude in Andean *páramos*.

Key words: Colombia, *páramos* Santurbán complex, functional traits, stress gradient, functional diversity

Introduction

In most ecosystems, the environment can act as a selective filter on the functional traits of plants along environmental gradients. This process, often known as abiotic filtering, mediates the assembly of plant communities such that species with similar functions tend to co-occur more frequently than would be expected by chance (Pescador et al., 2015a; Read et al., 2014; Swenson & Enquist, 2009). Following the concept of environmental filtering, it can be expected that, at higher elevations, the trait range of a plant community is narrower under more severe environmental conditions (Ohdo & Takahashi, 2020). Variations in plant functional traits along altitudinal gradients, whether caused by phenotypic plasticity or phylogenetic divergence, can influence how ecosystems respond to global change (Read et al., 2014). Thus, along an altitudinal gradient, a complex relationship can be detected indicating a trade-off in plant function between growth rate and efficient nutrient conservation (Garnier et al., 2001; Liu et al., 2017; Read et al., 2014). Therefore, altitudinal gradients offer ideal opportunities to discover how plant communities might respond to environmental pressures because in mountain ecosystems, environmental characteristics can change even within small temporal and spatial scales, notably affecting functional diversity (Di Biase et al., 2021; Körner, 2007).

Functional traits are attributes of the phenotypes of organisms and are the products of evolution in branches of phylogenies (Díaz et al., 2013). So, the relationship between phylogenetics and functional diversity is based on the assumption that evolution along the branches of phylogenetic trees has generated diversification of functional traits (Cavender-Bares et al., 2009; Díaz et al., 2013; Flynn et al., 2011). Niche conservatism can explain why related species retain a high degree of ecological similarity, and it is expected that new habitats will generally be occupied by species that are already well adapted to similar conditions (Harvey & Pagel, 1991). Whether phylogenetically related species tend to have similar functional traits, in environments with high climatic stress is expected co-occurrence of close related species (X.-H. Li et al., 2014; Pellissier et al., 2013). This and other processes that relate functional traits to phylogeny can be used to investigate how community assembly processes occur (D. Li et al., 2017).

Common adjustments to the functional traits of plants at higher altitudes include, for example, specific leaf area (SLA) reduction (Xu et al., 2017) and increase in leaf dry matter content (LDMC) (Kichenin et al., 2013), which are adaptations to increasing stressful conditions with increasing altitude. Several studies have described how species characteristics have important effects on alpine environments properties. Leaf area (LA) and leaf width (LW) are related to light-energy acquisition and water balance (Pérez-Harguindeguy et al., 2013), and several studies have shown that the LA decreases with altitude (Guo et al., 2016; Milla & Reich, 2011; Pfennigwerth et al., 2017). Leaf thickness (TL) is a trait related to the physical resistance of leaves (Luo et al., 2016; Pérez-Harguindeguy et al., 2013), which has been observed to increase with increasing altitude (Pescador et al., 2015); SLA is related to potential relative growth or relative photosynthetic rates and is expected to decrease with altitude (Scheepens et al., 2010; Xu et al., 2017); LDMC is related to hardness and resistance to physical hazards, and several studies have shown that it tends to increase with increasing altitude (Cruz-Maldonado et al., 2021; Guo et al., 2016); plant height (Hmax) is related to competitive vigor and stress tolerance (Pescador et al., 2015), and generally decreases with increasing altitude (2013; Cruz-Maldonado et al., 2021; De Bello et al., 2013).

Plant functional traits have the potential to explain how the composition of communities responds to environmental gradients and provide a strong link between communities, functioning and services provided by the ecosystem (Bu et al., 2019; Díaz & Cabido, 2001). Two measures are primarily used in trait-based ecology: the Community Weighted Mean (CWM) (Garnier et al., 2004), which is the average of the trait values for plants at each site weighted by species abundance (Miller et al., 2019) and refers to the degree of communities dominated by a single plant strategy (Ali et al., 2017); and Functional Diversity (FD) (Villéger et al., 2008), which is a measure of diversity used to estimate how ecosystems function (Díaz & Cabido, 2001; Laureto et al., 2015) and can also be a tool to predict the functional consequences of biotic change caused by human actions (Petchey & Gaston, 2006). In environmental gradients, as stress conditions increase (e.g., temperature decrease), it is expected that the prevailing climatic conditions should exert an environmental filter, mainly affecting the CWM (De Bello et al., 2013; Di Biase et al., 2021). For example, Guittar et al., (2016) showed that LA and SLA tend to decrease with decreasing temperature in most species along spatial temperature gradients, which is reflected in decreasing CWM values. According to the productivity hypothesis, the number of available niches should increase toward the benign part of a gradient, suggesting that functional diversity should also increase; therefore functional diversity should decline toward environmental extremes due to stronger abiotic filtering (Schellenberger Costa et al., 2017). Several studies on elevation gradients have shown that functional diversity decreases with increasing elevation (Thakur & Chawla, 2019; Zhang et al., 2017).

Páramo is a biome that occurs above the tree line of the forest, with altitudes between 3,000 and 4,700 m, with an area of approximately 35,000 km², occurring in Venezuela, Colombia, Ecuador, and northern Peru in South America, and in the Talamanca mountain range in Costa Rica and Panama in Central America (Cleef, 1978; Llambí & Cuesta, 2014; Rangel-Ch, 2001). Physiognomically, *páramo* is characterized by the predominance of open tropalpine vegetation, which extends above the upper limit of the equatorial Andean forests (Cleef, 2013). These areas are characterized by highly endemic vegetation (Rangel-Ch, 2000; Sklenář et al., 2014), composed of plants of various forms of life, including sclerophyllous shrubs, rosettes, cushion-type plants, bambusoids, grasses (in tussock), and non-graminoid herbs (Cleef, 2013; Llambí & Cuesta, 2014; Rada et al., 2019). The characteristics of vegetation, soil, and climate make *páramo* an important regulator of the water cycle (Buytaert et al., 2006; Correa et al., 2020; Lazo et al., 2019). Due to these characteristics, the *páramo* plays a fundamental ecological and socioeconomic role in the tropical Andes (Berdugo-Lattke et al., 2016; Llambí et al., 2020); and given current environmental changes, it is essential to make efforts to understand how the functional diversity of *páramo* plants can influence the properties of ecosystems, mainly related to climate and land use (Rada et al., 2019).

Along altitudinal gradients, the environment rapidly changes over short distances (Pan et al., 2013). In Andean *páramos*, plants are subjected to stressors such as low temperatures, rapid temperature changes, greater solar irradiance, lower atmospheric pressure, high soil acidity, and strong winds. Accordingly, the following hypothesis were established: in an elevation gradient, the increase in altitude is an environmental filter that acts on the functional structure of plant communities in the Andean *páramos*. It is expected that i) the functional traits related to leaf size and plant size tend to decrease with increasing altitude (and the decrease in the depth of the soil), which also is reflected in a decreasing Community Weighted Mean (CWM) of these traits, ii) the reduction of functional diversity as altitude increases (and the decrease in the depth of the soil) as a result of environmental filtering, and iii) the relationship between phylogenetic diversity/structure and functional diversity is based on the fact that evolutionary diversification has generated diversification of functional traits; thus, under the assumption of niche conservation, it is expected that the metrics of functional diversity and phylogenetic diversity are positively related along the elevation gradient.

Materials and methods

Study area

The study area is located on the eastern slope of the Eastern mountain range of Colombia, in the *páramos* Santurbán complex, between the coordinates 7°20'41.36"N, 72°48'36.36"W and 7°18'12.92"N, 72°49'35.07"W, in the department of Norte de Santander. The study elevation gradient ranged from 3200 to 4100 m above sea level. This *Páramo* complex shows that precipitation has a bimodal regime, with high periods between April and May and between September and November, and with average rainfall values that vary between 600 and 2,500 mm. The multiannual minimum average temperature values are between 0.3 and 4.6 °C, and the multiannual average values vary between 6 and 12 °C. The soils are very shallow, bounded by rocks, moderately deep to deep, and have a clay loam texture. In addition, they are excessively drained, with a very strong acid reaction (pH 4.5 to 5.0) and very low-to-moderate natural fertility. The main taxonomic classes of soils are Udorthents, Dystrudepts, Fluvaquents, and Udifolists (Morales et al., 2007).

Sampling

For this study, six sampling stations (altitude levels) were established at elevation gradient 3200 m, 3375 m, 3500 m, 3725 m, 3900, and 4100 m. At each station, 10 plots of 2.5 m x 4 m were established, spaced every 40 m (N = 60 plots).

Functional traits were measured only for the dominant species (in terms of coverage). Among the ten plots at each altitudinal level, the most abundant species were identified, representing more than 80% of the total coverage.

Small branches with multiple leaves were collected and stored in dark plastic bags to avoid dehydration of the tissue, which was sealed and labeled for later rehydration in the laboratory (Garnier et al., 2001). In the laboratory, five individuals per species and five leaves per individual were selected, which were fully expanded and healthy.

Table 1. Functional traits

Number	Trait	Unity
1	*Leaf area* (LA)	mm^2
2	*Leaf length* (LL)	mm
3	*leaf thickness,* LT;	mm
4	*Leaf dry matter content* (LDMC)	$mg\ g^{-1}$
5	*Maximum plant height* (H_{max})	cm

Five functional traits were measured, four leaf traits: *leaf area* (LA)*, leaf length* (LL), *leaf thickness* (LT), and l*eaf dry matter content* (LDMC). LA was measured using ImageJ software, LL were measured with a ruler on a flat surface, LT was calculated using a thickness gauge (caliper), and LDMC was calculated as dry leaf weight divided by fresh leaf weight. Finally, a growth trait was selected: *the maximum plant height* (H_{max}), which was calculated as the distance from the soil to the highest photosynthetic tissues. These traits were chosen because they are known to be sensitive to climate and soil variables and to variations in resource availability (Luo et al., 2016; Pinho et al., 2018).

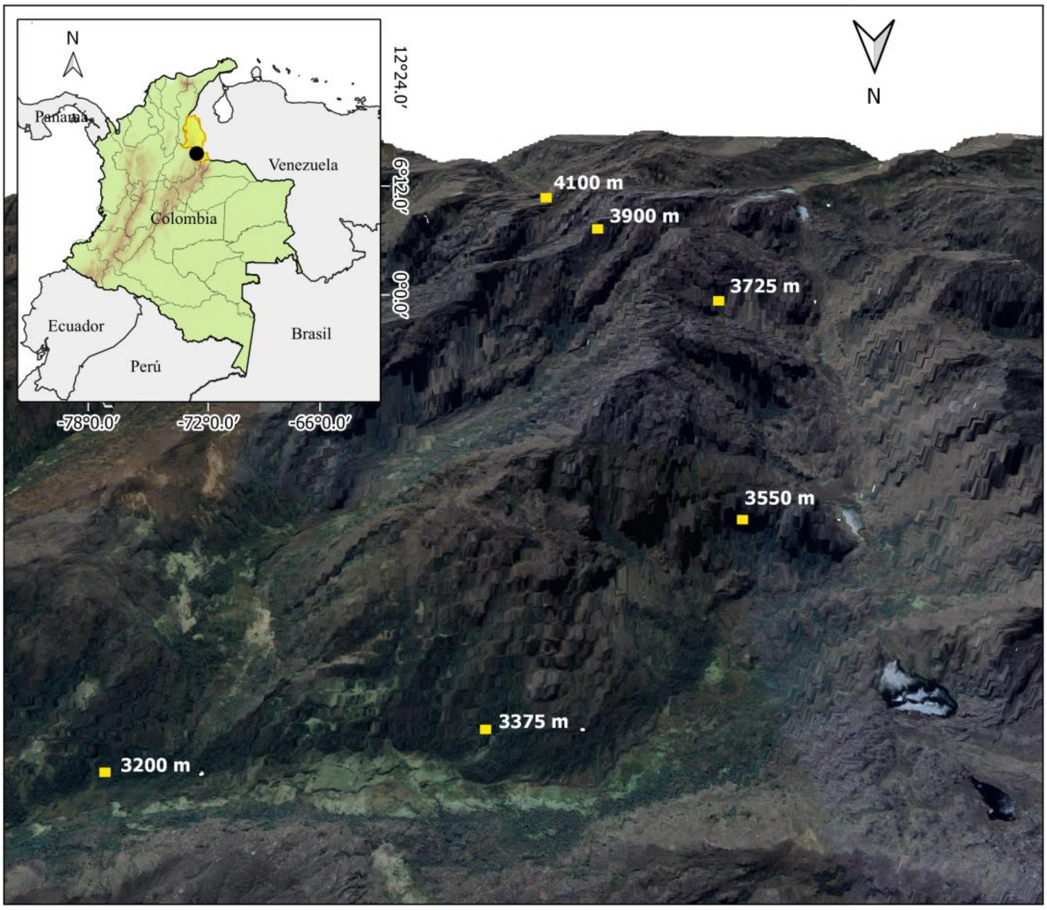

Fig. 1 Study area indicating the location of sampling elevation levels along an elevational gradient on Santurbán *páramos* complex, Norte de Santander department, Colombia (Modified from Galván-Cisneros et al. IN PRESS).

Soil depth

At each altitudinal level, soil depth was measured using a sharp metal rod, and one measurement was made for each plot (N = 60 measurements).

Functional analysis

To determine the functional responses that drive community assembly along the elevation gradient, four functional metrics were estimated. First, the CWM of each functional trait (Eq. 1) was calculated as the mean value of the trait in the community weighted by the coverage (%) of the species (Pescador et al., 2015).

$$CWM_x = \sum_{i=1}^{s} c_i t_i \tag{1}$$

where CWM_x is the CWM for trait x, s is the number of species in the community, C_i is the relative coverage of the i-th species in the community, and t_i is the trait value for the i-th species.

The second index was Functional Dispersion (FDis), which represents the variation in the values of the traits weighted by the abundance (in this case, by coverage) of each species in the community (Mason et al., 2005). FDis is a measure of functional divergence that is unaffected by the number of species present in a community (Schellenberger Costa et al., 2017). The third calculated index was functional richness (FRic), which estimates the dispersion of species in the functional trait space (Villéger et al., 2008). The fourth index to be calculated was Functional Evenness (FEve), which describes the degree to which a community's abundance is evenly distributed in the functional trait space (Mason et al., 2005; Villéger et al., 2008).

The CWM was calculated using function *functcomp* and diversity functional indices were calculated using function *db*FD, both on the FDiversity package (Casanoves et al., 2011), in R 4.0.4 (R Development Core Team, 2021).

Phylogenetic metrics

For each altitudinal level (each plant community), the following phylogenetic metrics were calculated based on abundance: (i) phylogenetic distance (PD); (ii) Mean Nearest Taxon Distance (MNTD); (iii) Mean Phylogenetic Distance (MPD); (iv) standardized effect size of PD (ses.PD); (v) standardized effect size of MNTD (ses.MNTD); and (vi) standardized effect size of MPD (ses.MPD). For standardized effect size calculations, our phylogeny was compared with 10,000 null model randomizations using the algorithm '*phylogeny pool*' of the '*picante*' package.

Statistical analysis

The univariate relationships between each trait and each metric of functional diversity (CWM and FD) with elevation and soil depth were explored. To test the two predictions, simple linear models were explored using plant traits (CWM) and functional diversity metrics (FD) as a dependent factor, "elevation" and "soil depth" as predictor variable. For a better model fit, we used a log-scale with the functional diversity metrics (FDis, Fric, and FEv) on the y-axis, with elevation as a predictor variable. In the models with metrics of functional diversity versus soil depth, we used a log-scale for both axes. Normality of standardized residuals was assessed using the Shapiro-Wilk goodness-of-fit test and the Q-Q plot.

Generalized Linear Models (GLMs) were generated in the R statistical environment (R Development Core Team, 2021) using the lme4 package with the *glm* function. The response variables were logarithmically transformed to reduce skewness. The global models were:

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glm(FDis_log ~ sesPD + sesMNTD + MNTD +  sesMPD + MPD)

glm(FRic_log ~ sesPD + sesMNTD + MNTD +  sesMPD + MPD)

glm(FEve_log ~ sesPD + sesMNTD + MNTD +  sesMPD + MPD)
```

Model selection was performed using the *dredge* function of the MuMIn package (R Development Core Team, 2021) to test all combinations of FDis, Fric, and FEve with the phylogenetic metrics of the global models. To select the model that best explained the variation in FDis, Fric, and FEve the value of Δ of the Akaike information criterion (ΔAIC) was used, with the best model being the one with the lowest Δ value; all models with $\Delta \leq 2$ are included in the supplementary material.

For all graphics and statistical analysis, was used the statistical software R version 4.0.4 (R Core Team 2021), using the packages nlme, lme4, MuMIn and ggplot2.

Results

Variation of traits with elevation

Our results showed that three of the five traits were significantly correlated with the altitude. CWM Plant height decreased (LM: $p < 0.000$, $R^2 = 0.80$), whereas CWM LDMC (LM: $p < 0.000$, $R^2 = 0.446$), and CWM LT (LM: $p < 0.045$, $R^2 = 0.067$) increased (Figure 2a, 2d, and 2e). The CWM LL and CWM LA did not display a significant relationship with altitude (Figure 2b and 2c).

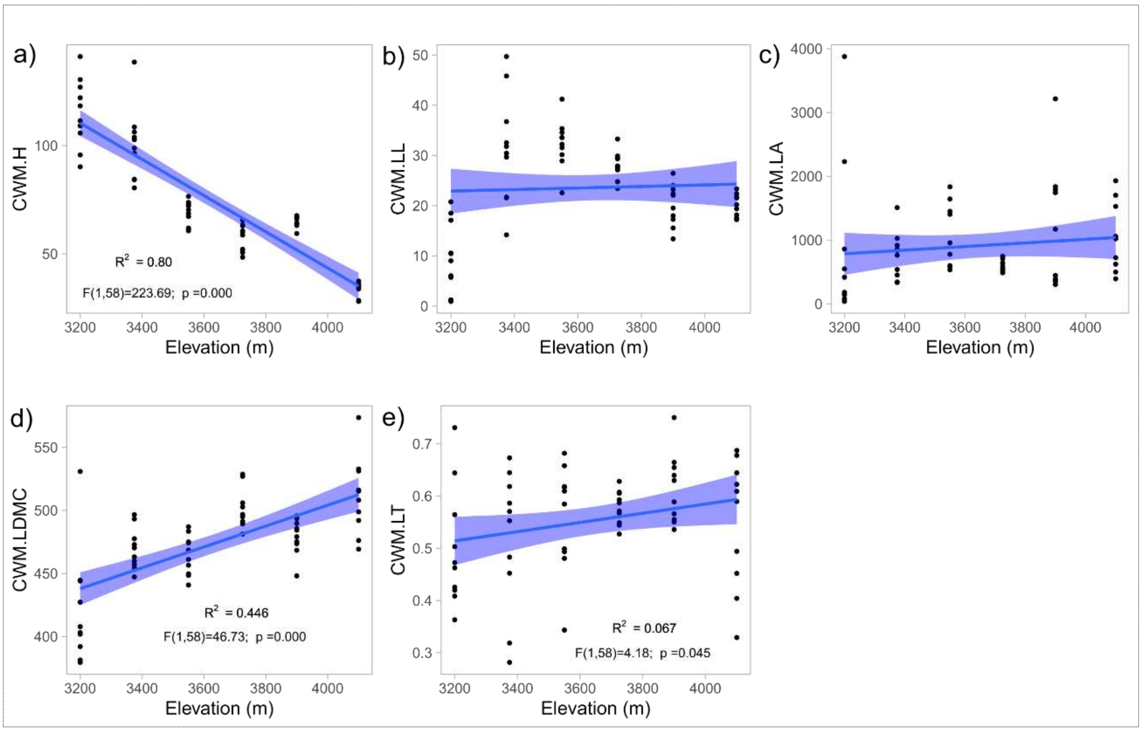

Figure 2. Variation in five plant traits along the elevation gradient: a) plant height (cm), b) leaf length (mm), c) leaf area (mm^2), d) leaf dry-matter content (LDMC, mg/g) and e) leaf thickness (mm).

The functional indices FDis and FRic were significantly correlated with elevation. As elevation increased, functional dispersion (LM: $p < 0.012$, $R^2 = 0.104$) and functional richness (LM: $p < 0.001$, $R^2 = 0.163$) decreased (Figure 3a and 3b). Functional evenness was not significantly correlated (Figure 3c).

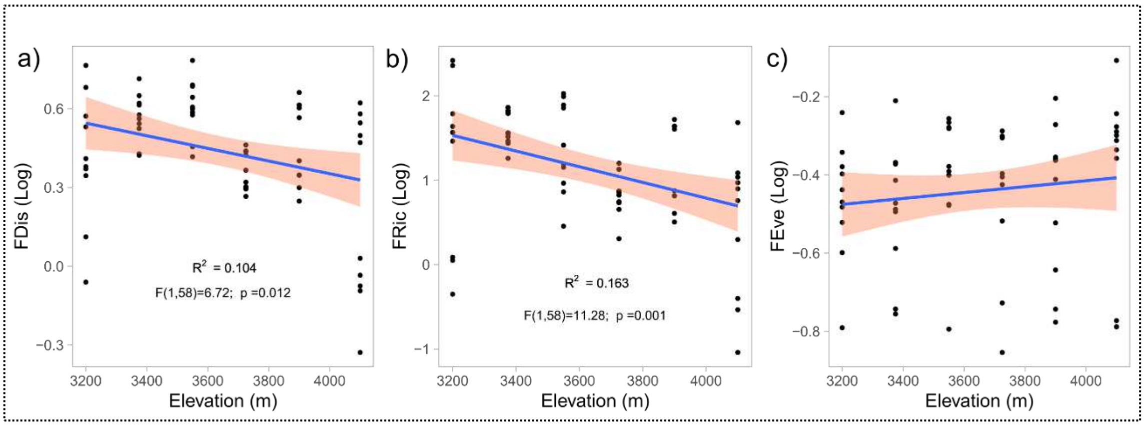

Figure 3. Variation along the elevation gradient for functional diversity indices: a) FDis functional dispersion, b) FRic functional richness and c) FEve functional evenness.

Variation of traits with soil depth

Our results showed that soil depth and altitude have an opposite relationship. Three of the five traits were significantly correlated with soil depth. As the soil depth increased, the CWM

Plant height increased (LM: $p < 0.000$, $R^2 = 0.61$), whereas CWM LDMC (LM: $p < 0.000$, $R^2 = 0.26$) and CWM LT (LM: $p < 0.007$, $R^2 = 0.12$) decreased (Figure 4a, 4d, and 4e). CWM LL and CWM LA did not display a significant relationship with soil depth (Figure 4b and 4c).

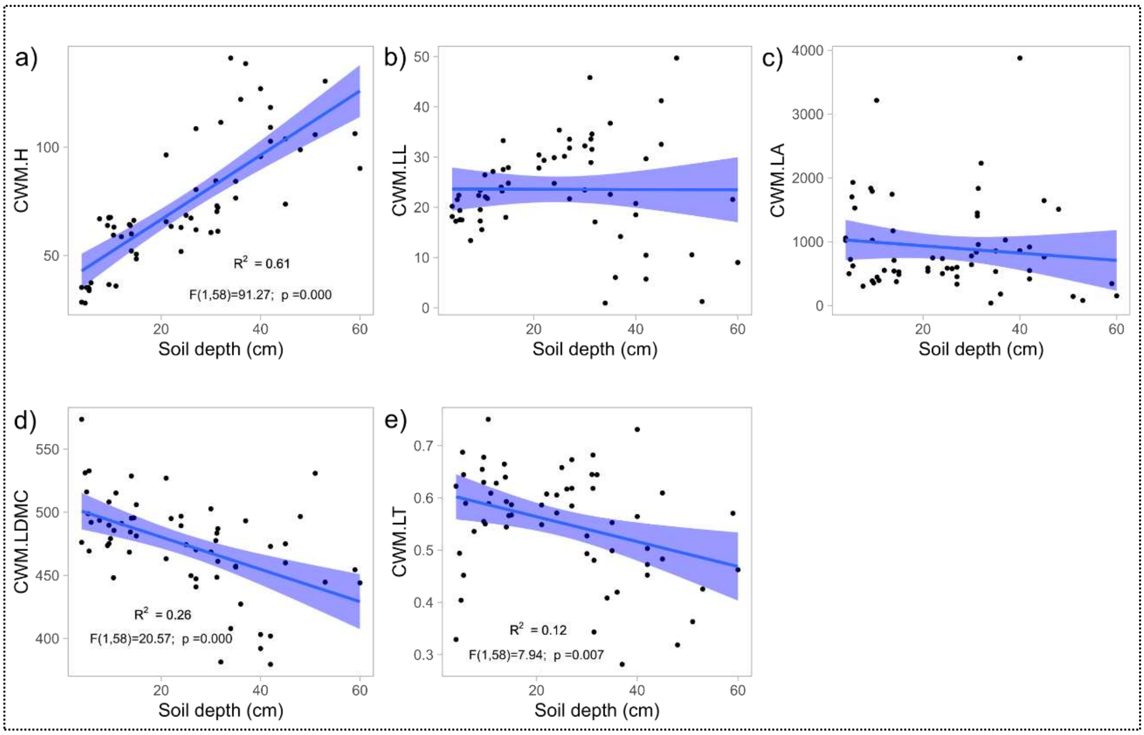

Figure 4. Relation of traits with soil depth: a) plant height (cm), b) leaf length (mm), c) leaf area (mm^2), d) leaf dry-matter content (LDMC, mg/g) and e) leaf thickness (mm).

In addition to the weighted mean of the community (CWM), soil depth showed an inverse relationship with altitude for the functional indices. The functional indices FDis and FRic showed a significant correlation with soil depth. As the soil depth increased, functional dispersion (LM: $p < 0.002$, $R^2 = 0.15$) and functional richness (LM: $p < 0.001$, $R^2 = 0.18$) decreased (Figure 5a and 5b). Functional evenness was not significantly correlated (Figure 5c).

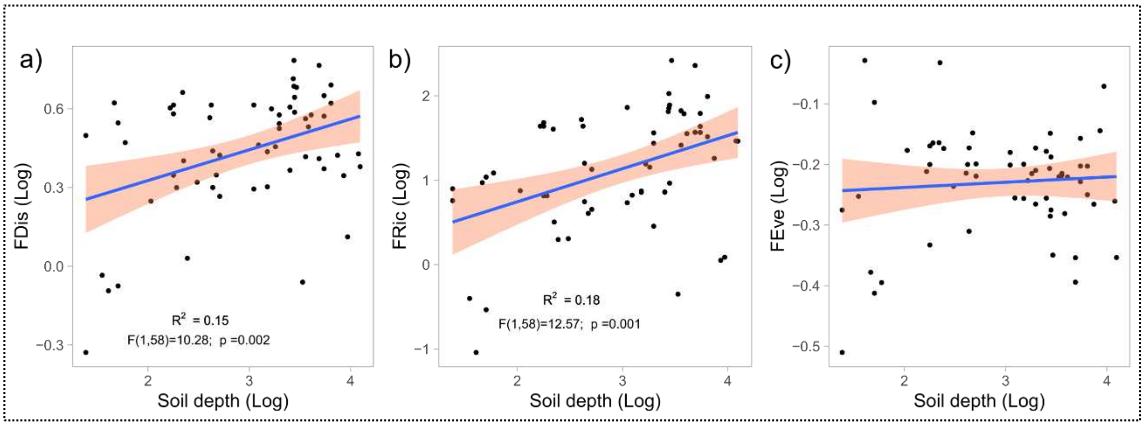

Figure 5. Relation of functional diversity indices with soil depth: a) FDis functional dispersion, b) FRic functional richness and c) FEve functional evenness.

Generalized linear models

The Two GLM global models selected with FDis as the response variable ($\triangle AIC \leq 2$) had weights varying from 0.273 to 0.101 (Table S1). After the model selection, only the MNTD explanatory variable was significant ($p \leq 0.028$) (Table 2).

Using FRic as the response variable, seven global models were selected with $\triangle AIC < 2$ and weights varying from 0.181 to 0.067 (Table S2). After the model selection, only the MNTD explanatory variable was significant ($p \leq 0.00759$) (Table 2).

Using FEve as the response variable, eight global models were selected with $\triangle AIC < 2$ and weights varying from 0.118 to 0.043 (Table S3). After the model selection, no explanatory variable was significant (Table 2).

Table 2. Model-conditional averaged coefficients for the impacts of phylogenetic metrics on Functional and Richness dispersion. Coefficient values are significant at $p < 0.05$

Response	Parameters	Estimate	Std. Error	Adjusted SE	Z value	Pr(>|z|)
FDis	Intercept	0.7091	0.8236	0.8352	0.849	0.396
	MNTD	-0.0038	0.0017	0.0017	2.198	0.028 *
	ses.MNTD	0.3973	0.2554	0.2577	1.542	0.123
	ses.MPD	0.3052	0.2005	0.2039	1.497	0.134
	ses.PD	-0.5878	0.3862	0.3908	1.504	0.133
	MPD	0.0034	0.0071	0.0072	0.471	0.638
FRic	Intercept	2.4498	2.3241	2.362	1.037	0.2997
	MNTD	-0.0135	0.005	0.005	2.67	0.0076 **
	ses.MNTD	0.9204	0.6099	0.6161	1.494	0.1352
	ses.MPD	0.3477	0.6406	0.6482	0.536	0.5916
	ses.PD	-1.089	0.9959	1.0081	1.08	0.28
	MPD	0.0067	0.0192	0.0195	0.342	0.732
FEve	Intercept	-0.3281	0.2420	0.2455	1.337	0.181
	MNTD	0.0008	0.0006	0.0006	1.334	0.182
	sesMNTD	-0.0179	0.0342	0.0348	0.516	0.606
	sesPD	-0.0131	0.0436	0.0444	0.294	0.768
	sesMPD	-0.0153	0.0407	0.0413	0.37	0.711
	MPD	0.0007	0.0020	0.0020	0.329	0.742

Discussion

The results showed that several functional traits (CWM) and several functional diversity indices varied significantly along the elevation and soil gradients in the studied *páramo* in the Colombian Andes. Three out of five functional traits showed how functional composition of *páramo* communities responded to the increasing environmental severity along these environmental gradients. Two functional diversity indices, FDis and FRic, decreased significantly with increasing elevation and decreasing soil depth. Functional evenness did not show a significant relationship with altitude or soil depth. These results agree with the increase in environmental filtering at high altitudes, as shown in other studies in temperate and tropical environments (Cruz-Maldonado et al., 2021; De Bello et al., 2013; Gazol et al., 2017; Thakur & Chawla, 2019).

Three out of five traits showed significant relationships with elevation and soil depth. Plant height decreases with increasing altitude, a trait that is related to total plant size as well as to competitive interactions for light (Pescador et al., 2015; Spasojevic et al., 2014). LDMC and LT increase with increasing altitude, traits related to hardiness and resistance to physical hazards (Luo et al., 2016; Pérez-Harguindeguy et al., 2013). LDMC and LT are associated with stress factors at higher altitudes in tropical mountains, such as low temperatures, high solar irradiation, and strong winds (Cruz-Maldonado et al., 2021; Guo et al., 2016). These results are consistent with the strategy of resource conservation, which becomes more pronounced towards the top of the mountain. This is congruent with the fact that in Andean *páramos* climatic conditions become more severe as the altitude increases. For example, when the transition occurs from the grass strip of *parámo* dominated by tussocks and *frailejones* (*Espeletia* spp. and relatives) to the *superpáramo* strip characterized by scattered vegetation with an average temperature of 2 °C strong winds and bare rocky soil (Hofstede, 2003; Sklenář & Ramsay, 2001), plant survival becomes critical and a few lineages with certain conserved traits can withstand these harsh environment. The strategy of conserving resources becomes dominant in such environments. Among the lineages that have successfully adapted to alpine mountain tops, both temperate and tropical Asteraceae and graminoids stand out (Galván-Cisneros et al., 2023; Ndiribe et al., 2013; Schubert et al., 2020), which were well represented in our work, as well as other groups characteristic of pantropical alpine ecosystems, such as Ericaceae and Rosaceae. Our results confirm our first hypothesis that functional traits related to leaf and plant size tend to decrease with increasing altitude (and decreasing soil depth), and this is reflected in a decrease in the Community Weighted Mean of these traits.

The patterns observed for FDis and FRic indicated less niche diversification as altitude increased (and soil depth decreased); that is, species at higher altitudes are functionally more similar to each other, and this manifested itself in less functional diversity. It can also be said that as environmental severity increases with increasing altitude, resource use becomes less efficient for species in *páramo* communities. This decrease in functional diversity is probably associated with the exclusion by environmental filtering of certain life forms and species as altitude increases, moving from larger life forms such as large shrubs and climbers to smaller life forms such as erect herbs, prostrate herbs, and tussocks at higher altitudes. This trend of functional diversity along elevational gradients has already been reported in other studies (De Bello et al., 2013; Gazol et al., 2017; Thakur & Chawla, 2019). However, few studies with contrasting results have been reported. For example, Liu et al. (2022) reported a decrease in FRic and an increase in FDiv with increasing altitude in the Qinghai-Tibet Plateau in China. Our results confirmed the second hypothesis that functional diversity decreases with increasing altitude (and decreasing soil depth) as a result of environmental filtering.

Altitude is a variable that aggregates environmental variables, such as temperature, soil depth, soil fertility and water availability, but it has commonly been questioned whether altitude should be used as explanatory variable in ecological studies across elevation gradients. Despite the reasoning that altitude is a proxy of temperature and other abiotic variables, several studies have reported robust conclusions that altitude can be used as the explanatory variable (Cuesta et al., 2017; Galván-Cisneros et al., 2023; R. Li et al., 2015; Qian et al., 2019; Worthy et al., 2019; Xu et al., 2019). In this study, we used two explanatory variables to test our hypotheses: altitude and soil depth. With each variable and using functional traits and indices as response variables, we obtained similar significant results since altitude and soil depth were inversely and significantly related. Based on these results, we conclude that altitude is a good explanatory variable as an abiotic variable and that it can be used as a tested proxy of soil depth in *páramos* vegetation.

MNTD had a significant negative relationship with FDis and FRic. In the case of FDis, it indicates that as the average distance in the space of the multidimensional traits of the individual species moves away from the centroid, the species that are closest to each other at the poles of the functional envelope and drive that envelope are phylogenetically closer. This same pattern explains the inverse relationship between MNTD and FRic, that is, the groups of species located at the extremes of the functional space that drive its expansion are phylogenetically closer. This is because the MNTD is a metric that measures the average distance to the nearest taxon. These results reject our third hypothesis because we did not find a positive relationship between phylogenetic metrics and functional metrics, although they do not reject the assumption of niche conservatism. The importance of the MNTD in functional diversity can be explained by the fact that the *páramo* biome is geologically recent, so the phylogenetic distance between species is quite close. This is confirmed by the fact that there are few endemics at the genus level and many at the species level in *páramos* (Rangel-Ch, 2000; Sklenář et al., 2014). More studies are needed to investigate the mechanisms of community assembly with a phylogenetic and functional approach, and the relationship between these two dimensions of biodiversity, along environmental gradients in tropical ecosystems.

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Supplementary data

Appendix S1. Coefficients estimated from the Generalized Linear Models for all 32 possible combinations of explanatory variables. Dependent variable: Functional dispersion (FDis). Models are arranged by AICc values.

```
modelo1 <- glm(formula=FDis_log ~ sesPD + sesMNTD + sesMPD + MPD, data = dato, na.action = "na.fail" )
```

Model selection table

	(Intrc)	MNTD	MPD	sesMNTD	sesMPD	sesPD	df	logLik	AIC	delta	weight
30	0.958	-0.00392		0.5607	0.3399	-0.7618	6	10.034	-8.1	0	0.273
32	0.8912	-0.00397	0.000342	0.5599	0.3316	-0.7575	7	10.035	-6.1	2	0.101
24	-0.6383	-0.00499	0.00814	0.3762		-0.3721	6	8.965	-5.9	2.14	0.094
6	0.9182	-0.00359		0.09504			4	6.851	-5.7	2.36	0.084
22	0.939	-0.00376		0.1706		-0.07947	5	7.488	-5	3.09	0.058
2	0.6308	-0.00156					3	5.43	-4.9	3.21	0.055
14	0.9281	-0.00367		0.111	-0.02101		5	7.038	-4.1	3.99	0.037
8	1.069	-0.00354	-0.00074	0.1017			5	6.934	-3.9	4.2	0.033
18	0.7017	-0.00206				0.02708	4	5.602	-3.2	4.86	0.024
1	0.439						2	3.596	-3.2	4.88	0.024
10	0.6408	-0.00163			0.005419		4	5.444	-2.9	5.18	0.021
4	0.6032	-0.0016	0.000157				4	5.434	-2.9	5.2	0.02
31	2.421		-0.00932	0.4705	0.5507	-0.8369	6	7.353	-2.7	5.36	0.019
16	-0.05376	-0.00439	0.005045	0.1359	-0.1129		6	7.294	-2.6	5.48	0.018
29	0.4262			0.3904	0.3176	-0.6977	5	6.151	-2.3	5.77	0.015
17	0.4274					-0.03206	3	4.079	-2.2	5.91	0.014
3	0.7373		-0.00143				3	4.004	-2	6.06	0.013
26	0.785	-0.00265			-0.05413	0.09696	5	5.904	-1.8	6.26	0.012
9	0.4333				-0.02061		3	3.844	-1.7	6.38	0.011
5	0.4303			-0.02226			3	3.835	-1.7	6.4	0.011
20	1.096	-0.00223	-0.00172			0.06187	5	5.782	-1.6	6.5	0.011
12	0.9884	-0.00154	-0.00168		0.03399		5	5.479	-1	7.11	0.008
11	1.548		-0.00521		0.07253		4	4.213	-0.4	7.64	0.006
21	0.4293			0.03146		-0.06074	4	4.173	-0.3	7.72	0.006
25	0.4259				0.01892	-0.05052	4	4.129	-0.3	7.81	0.006
19	0.5202		-0.00043			-0.02462	4	4.09	-0.2	7.89	0.005
7	0.6839		-0.00119	-0.00864			4	4.029	-0.1	8.01	0.005
28	0.3402	-0.00298	0.002289		-0.1055	0.117	6	5.951	0.1	8.17	0.005
13	0.43			-0.01368	-0.01334		4	3.903	0.2	8.26	0.004
27	1.606		-0.00551		0.1205	-0.0543	5	4.546	0.9	8.98	0.003
15	1.549		-0.00523	-0.01396	0.08027		5	4.276	1.4	9.51	0.002
23	0.1473		0.001316	0.05733		-0.1071	5	4.215	1.6	9.64	0.002

Appendix S2. Coefficients estimated from the Generalized Linear Models for all 32 possible combinations of explanatory variables. Dependent variable: Richness dispersion (FRic). Models are arranged by AICc values.

modelo2 <- glm(formula=Fric_log ~ sesPD + sesMNTD + MNTD+ sesMPD + MPD, data = dato, na.action = "na.fail")

Model selection table

Code	Intrc	MNTD	MPD	sesMNTD	sesMPD	sesPD	df	logLik	AIC	delta	weight
30	2.974	-0.01383		1.518	0.6906	-1.745	6	-57.28	126.6	0	0.181
22	2.936	-0.0135		0.7257		-0.358	5	-58.421	126.8	0.28	0.157
24	-0.2796	-0.01601	0.01659	1.145		-0.9545	6	-57.748	127.5	0.94	0.114
6	2.842	-0.01277		0.3852			4	-59.838	127.7	1.12	0.104
14	2.906	-0.01326		0.4887	-0.1358		5	-58.982	128	1.41	0.09
8	4.1	-0.01229	-0.00619	0.4406			5	-59.208	128.4	1.86	0.072
32	2.815	-0.01395	0.000814	1.516	0.6709	-1.734	7	-57.279	128.6	2	0.067
16	0.6518	-0.01492	0.01158	0.5458	-0.3467		6	-58.833	129.7	3.11	0.038
2	1.677	-0.00452					3	-62.322	130.6	4.09	0.024
26	2.506	-0.01039			-0.3763	0.581	5	-60.539	131.1	4.52	0.019
20	4.998	-0.00762	-0.01342			0.3661	5	-60.937	131.9	5.31	0.013
1	1.121						2	-63.941	131.9	5.32	0.013
18	1.926	-0.00627				0.09523	4	-62.1	132.2	5.64	0.011
3	2.408		-0.00615				3	-63.136	132.3	5.71	0.01
4	2.081	-0.0039	-0.00229				4	-62.237	132.5	5.91	0.009
10	1.641	-0.00427			-0.01947		4	-62.303	132.6	6.05	0.009
9	1.096				-0.08785		3	-63.466	132.9	6.37	0.007
28	1.323	-0.01127	0.006087		-0.5128	0.6344	6	-60.503	133	6.45	0.007
17	1.09					-0.08515	3	-63.583	133.2	6.61	0.007
11	6.096		-0.02335		0.3298		4	-62.672	133.3	6.78	0.006
31	8.194		-0.03316	1.202	1.441	-2.014	6	-60.748	133.5	6.94	0.006
5	1.108			-0.03162			3	-63.891	133.8	7.22	0.005
12	4.837	-0.00346	-0.01541		0.2431		5	-61.99	134	7.42	0.004
7	2.761		-0.00774	0.05718			4	-63.02	134	7.48	0.004
19	3.029		-0.009			0.07046	4	-63.06	134.1	7.56	0.004
21	1.103			0.2254		-0.2906	4	-63.075	134.2	7.59	0.004
29	1.098			0.9172	0.6122	-1.518	5	-62.31	134.6	8.06	0.003
13	1.106			0.03792	-0.108		4	-63.417	134.8	8.27	0.003
25	1.097				-0.08963	0.002275	4	-63.466	134.9	8.37	0.003
15	6.095		-0.0233	0.03668	0.3094		5	-62.625	135.3	8.69	0.002
27	6.11		-0.02342		0.3419	-0.01377	5	-62.669	135.3	8.78	0.002
23	2.243		-0.00532	0.1209		-0.1034	5	-63.001	136	9.44	0.002

Appendix S3. Coefficients estimated from the Generalized Linear Models for all 32 possible combinations of explanatory variables. Dependent variable: Evenness dispersion (Eve). Models are arranged by AICc values.

```
modelo3 <- glm(formula=FEve_log ~ sesPD + sesMNTD + MNTD+ sesMPD + MPD, data = dato, na.action = "na.fail" )
```

Model selection table

Code	Intrc	MNTD	MPD	sesMNTD	sesMPD	sesPD	df	logLik	AIC	delta	weight
1	-0.2297						2	61.318	-118.6	0	0.118
2	-0.2747	0.000366					3	61.998	-118	0.64	0.086
6	-0.3685	0.00103		-0.03101			4	62.989	-118	0.66	0.085
18	-0.332	0.000767				-0.0219	4	62.748	-117.5	1.14	0.067
10	-0.2938	0.000497			-0.01035		4	62.348	-116.7	1.94	0.045
9	-0.2303				-0.00239		3	61.341	-116.7	1.95	0.044
5	-0.2287			0.002613			3	61.341	-116.7	1.96	0.044
3	-0.2406		5.19E-05				3	61.322	-116.6	1.99	0.044
17	-0.2296					0.00019	3	61.319	-116.6	2	0.043
4	-0.2004	0.00048	-4.22E-04				4	62.182	-116.4	2.27	0.038
14	-0.3668	0.001017		-0.02825	-0.00363		5	63.025	-116	2.59	0.032
22	-0.3669	0.001017		-0.02507		-0.00625	5	63.014	-116	2.61	0.032
8	-0.3359	0.001042	-1.61E-04	-0.02957			5	63.014	-116	2.61	0.032
11	-0.7913		2.62E-03		-0.04926		4	61.98	-116	2.68	0.031
20	-0.4761	0.000831	6.29E-04			-0.0346	5	62.909	-115.8	2.82	0.029
26	-0.3551	0.000931			0.01497	-0.04123	5	62.903	-115.8	2.83	0.029
12	-0.6427	0.000409	1.68E-03		-0.03903		5	62.586	-115.2	3.47	0.021
13	-0.2288			0.006316	-0.00575		4	61.428	-114.9	3.78	0.018
25	-0.2288				-0.01072	0.01065	4	61.427	-114.9	3.78	0.018
21	-0.2289			0.01263		-0.01132	4	61.42	-114.8	3.8	0.018
7	-0.2223		-2.98E-05	0.002955			4	61.342	-114.7	3.95	0.016
19	-0.2614		1.47E-04			-0.00236	4	61.327	-114.7	3.98	0.016
27	-0.8046		2.69E-03		-0.06029	0.01249	5	62.1	-114.2	4.44	0.013
15	-0.7915		2.63E-03	0.006456	-0.05284		5	62.073	-114.1	4.49	0.012
30	-0.3677	0.001024		-0.04073	-0.01365	0.02115	6	63.039	-114.1	4.56	0.012
16	-0.4404	0.000963	3.78E-04	-0.02638	-0.01052		6	63.034	-114.1	4.57	0.012
24	-0.3508	0.00103	-8.29E-05	-0.02716		-0.00327	6	63.015	-114	4.61	0.012
28	-0.4341	0.000872	4.06E-04		0.00586	-0.03767	6	62.913	-113.8	4.81	0.011
23	-0.5131		1.33E-03	0.0387		-0.05802	5	61.713	-113.4	5.21	0.009
29	-0.2288			0.003763	-0.00785	0.00441	5	61.428	-112.9	5.78	0.007
31	-0.8406		2.86E-03	-0.02082	-0.07932	0.04711	6	62.136	-112.3	6.36	0.005
32	-0.4755	0.000947	5.53E-04	-0.04214	-0.02704	0.02815	7	63.057	-112.1	6.52	0.005

CHAPTER 4: Importance of caulescent rosettes in facilitating plant communities in the Colombian *páramos*

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Abstract

Facilitation has long been recognized as an assembly rule for communities and is one of the most important positive interactions in plant communities, playing a key role in maintaining biodiversity in adverse climate environments. Rosette caulescents are one of the most common growth-forms in Andean *páramos*. The aim of this study was to estimate whether a caulescent rosette acts as a facilitator, causing an increase in taxonomic and phylogenetic diversity at the community level in Andean *páramos*. In this study, 28 *Espeletia lopezii* nurse plants and 28 control plots were selected in the *superpáramo* belt of the El Cocuy *páramo* complex in Colombia. Understory vegetation abundance (e.g., cover) was measured using a metal ring around the nurse trees and control areas. We found that vegetation under the canopy of nurse plants (*E. Lopezii*) had a positive impact on taxonomic diversity compared with the control areas. Regarding phylogenetic diversity, we observed that the dominant pattern was mainly random, these results suggest that, at these altitudes, the metacommunity is strongly filtered by climate and soil factors, and despite the benefits of the facilitation exerted by nurse plants, it is difficult to detect a phylogenetic overdispersion pattern, as expected in our second hypothesis.

Key words: Andean *páramos* ecosystems, abiotic stress, rosette caulescent, positive interactions, phylogenetic diversity.

INTRODUCTION

Plant-plant interactions directly influence the dynamics of community structure and can be responsible for the presence or absence of species (Brooker et al., 2007; O'Brien et al., 2017; Padilla & Pugnaire, 2006). Plant-to-plant facilitation occurs when the presence of neighboring plants improves the survival, recruitment, or growth of the target plant by modifying environmental conditions or mitigating the negative effects of herbivores (García & Obeso, 2003; Zhang & Shao, 2013). Beneficial species, also known as nurses or facilitators, generally exhibit adaptations that enable them to establish themselves in highly stressful environments. As these species grow, they modify their microhabitat, increasing humidity, providing shade, and fertilizing the soil with leaves and root exudates (Holmgren et al., 1997; Pugnaire et al., 2011). Facilitation has long been recognized as an assembly rule of communities and is one of the most important positive interactions in plant communities (Brooker & Callaway, 2009; Callaway, 1997; Dalotto et al., 2018). Facilitation is especially common in stressful environments such as deserts, arid regions, Mediterranean ecosystems, and alpine fields (Al-Namazi, 2019; Anthelme et al., 2017; Carrión et al., 2017; García-Cervigón et al., 2016; Klanderud & Totland, 2004; Llambí et al., 2020; Mora et al., 2019; Ramírez et al., 2015), and its intensity increases with the stress gradient (Al-Namazi, 2019).

Facilitative interactions between plants form the basis of numerous ecosystem functions that drive plant community assembly (Carrión et al., 2017; Navarro-Cano et al., 2019). An example of facilitation between plants is the facilitating plant effect, which refers to the positive influence of adult plants on the establishment of germination and/or recruitment of seedlings under their canopy, an effect that occurs because of the improvement in extreme environmental conditions (Padilla & Pugnaire, 2006; Ren et al., 2008). Other benefits observed in facilitation are the attraction of fruit and seed-dispersing animals (Carlo, 2005; Duncan & Chapman, 1999), reducing temporal stochasticity in the local supply of seeds, increasing the retention of frugivores at the site, and promoting the fitness of individuals and the coexistence of different species (Carlo, 2005). Another characteristic of facilitation between plants is that facilitators diversify the establishment niche of their beneficiaries and increase the diversity of plant communities (Carrión et al., 2017; Valiente-Banuet & Verdú, 2007). Due to the way in which facilitation between plants operates in nature, the increase in plant diversity occurs not only in terms of taxonomic diversity, but also functional and phylogenetic diversity (Carrión et al., 2017; Navarro-Cano et al., 2019; Valiente-Banuet & Verdú, 2007).

In alpine meadows, positive interactions between plants tend to increase with elevation because of the increase in environmental severity with altitude, where facilitator plants modify the environment, thereby reducing physical stress and allowing less-tolerant plant species to survive (Anthelme et al., 2014; Molenda et al., 2012). This suggests that the main mechanism behind the facilitator process in alpine environments is thermal improvement and protection from strong desiccating winds provided by neighbors, which are crucial for survival in cold environments (Cavieres et al., 2006). *Páramos* are tropical alpine ecosystems characterized by a range of various life forms, including sclerophyllous shrubs, rosettes, cushion plants, bambusoids, and tussocks (Cleef, 2013; Rada et al., 2019). They have the potential to facilitate plants (Rada et al., 2019), modify the availability of water and nutrients, and reduce frost (Anthelme & Dangles, 2012).

In alpine ecosystems, stem rosettes can act as facilitators in stressful environments because of their ability to mitigate extreme environmental conditions, which favors the establishment and survival of other species growing under their canopies compared to open microsites (Ballantyne & Pickering, 2015; Bueno & Llambí, 2015; Gómez-Aparicio et al., 2004; Liu et al., 2020; Mora et al., 2019). Rosettes produce a large amount of humus, which improves soil conditions and the abiotic environment, thereby increasing the richness and abundance of species compared with areas outside their immediate influence (Mizuno, 1998; Mora et al., 2019). Stem rosettes are one of the most common life forms in Andean páramos (Llambí & Cuesta, 2014; Rangel-Ch, 2000). Studies in Andean *páramos* have shown the positive influence of large stem rosettes on maintaining the diversity of plant communities (Mora et al., 2019), and the eventual local extinction of these life forms could have negative effects on many other species in these diverse tropical alpine communities (Mora et al., 2019).

There is a need to improve the understanding of facilitation between plants under a changing climate as part of assessing the impacts of climate change on plant communities and ecosystems (Anthelme et al., 2014). This study investigated how plant-plant interactions play a role in the structure of the plant community under a caulescent rosette species, *Espeletia lopezii* Cuatrec. (Asteraceae). The following hypotheses were proposed: (1) The rosette acts as nurse plants improving local microhabitat conditions and increasing plant abundance and species richness (i.e., alpha taxonomic diversity) compared to open areas (control) without focal species. (2) Plant communities under the rosette canopy are phylogenetically overdispersed, assuming niche conservatism in the phylogenetic lineages of the plant species sampled as an effect of niche diversification promoted by facilitation. These hypotheses were addressed by focusing on the influence of facilitating plant species on the taxonomic and phylogenetic diversity of the local *páramo* species.

MATERIALS AND METHODS

Study area

This study was conducted on the western slope of El Cocuy National Natural Park, in the El Cocuy *Páramos* complex. The sampling points were located in the *Superpáramo* vegetation belt at 4,550 AMSL in the jurisdiction of the municipality of Guicán in the department (state) of Boyacá, Colombia. This *páramos* complex has an average multi-year temperature of 6.4 ºC and a bimodal rainfall regime with two wet and two dry periods, with minimum values in

January and maximum values in April. Soils vary according to their position on the terrain. On steep slopes and escarpments, they are shallow to very shallow, with little or no erosion, low fertility, well-to excessively drained, and acidic. In areas with fewer slopes, valleys, or depressions, the soils are poorly drained, shallow to moderately deep depending on the water table, rich in organic matter, low fertility, and moderately acidic (Morales et al., 2007).

Data collection

A 200-meter transect was established at the study site, where 28 isolated *Espeletia lopezii* individuals with crown diameters between 50 and 110 cm were selected. A 70 cm diameter metal ring was centered on each stem rosette, delimiting the area under the canopy. To compare the structure of the community under the direct influence of the rosette with the local community outside the influence of the focal species, 28 control rings (plots) were established in open areas with the same dimensions as the plots of the focal species and the same information was obtained. The minimum distance between focal species was 2-4 m. A total of 56 plots were established.

In each plot, the number of individuals and percentage cover per vascular plant species were counted. Species that could not be individualized were calculated as percentages of cover. Conspecifics (generally smaller individuals below the crown of the focal species) were also counted.

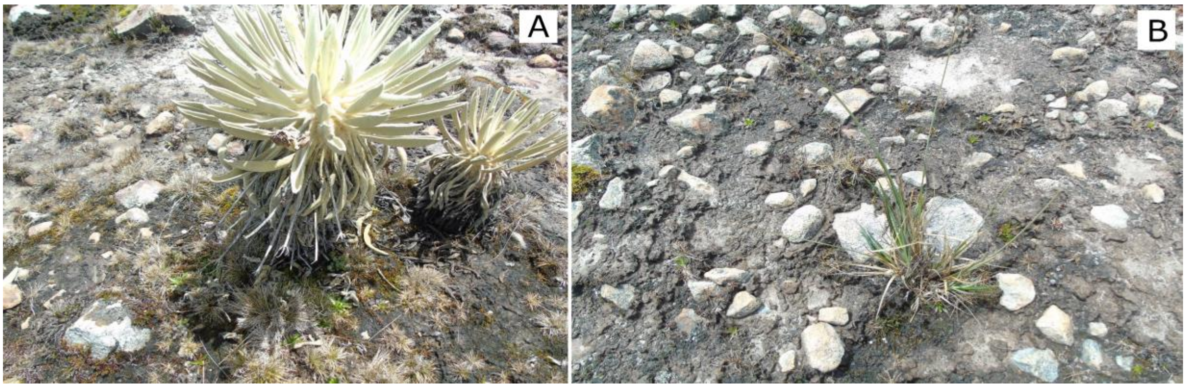

Figure 1. *Espeletia lopezii*, a caulescent rosette showing a conspicuous community under the canopy (a) and an adjacent open area (b) in the study area.

Focal facilitator plant

Espeletia lopezii is a caulescent rosette up to 5 m high; leaves in a terminal rosette; blade up to 40 cm long and 6.5 cm wide; inflorescence with branches 50-60 cm long, with three chapters per inflorescence; chapters 40-50 mm in diameter; ray flowers 4-5 rows, corolla 21 mm long; disk flowers 11.5 mm long; mature achene 5 mm long (Cuatrecasas, 1940). This species is endemic to El Cocuy *páramo* in the eastern mountain range of Colombia between 3100-4550 m (Avila et al., 2022; Diazgranados & Castellanos-Castro, 2021). Hereafter, plants of this species is assumed as nurse plants for the hypothesis's tests.

Taxonomic diversity

To gain insight into the differences in the alpha taxonomic diversity of the community between the areas located under and outside the canopies of the focal species, the database was assembled based on cover data from which the Hill numbers were calculated: ^{0}D (species richness), ^{1}D (Shannon exponential), and ^{2}D (Simpson inverse) curves. For the comparison of taxonomic diversity, the values estimated by rarefaction curves and confidence intervals were used.

Phylogenetic diversity

To prepare the phylogenetic tree, a list of species, genera, and families was constructed according to the APG IV (2016). The list of all species in the study sample was added to the *GBOTB.extended.TPL.tre* phylogenetic tree and inserted into the 'V.PhyloMaker2' package (Jin & Qian, 2022) in the R statistical environment (R Development Core Team, 2021).

To gain insight into the differences in the community's alpha phylogenetic diversity between the areas located under the canopies of the focal species and outside them, the following phylogenetic metrics were calculated based on the coverage data: (i) phylogenetic diversity (PD), (ii) mean nearest taxon distance (MNTD), and (iii) mean pairwise phylogenetic distance (MPD) (Webb et al., 2002). To remove the influence of richness, the standardized effect size (ses) was calculated based on a null model for each community (Swenson, 2014). These standardizations were performed by randomly drawing the same number of species from the phylogeny present in the community, repeated 10,000 times, calculating the PD, MPD, and MNTD for each randomization, taking the difference between the observed values of PD, MPD, and MNTD and the mean of the random values, and dividing these differences by the standard deviation between the randomizations.

Statistical analysis

The distribution of diversity and phylogenetic structure data to determine normality were assessed using the Shapiro-Wilk test. Differences in phylogenetic structure between plant communities under the rosette canopy and outside the rosette canopy were checked using a t-test, subsequent to the normality check. All metrics were calculated using the species cover. All analyses were performed in the R environment (R Development Core Team, 2021).

RESULTS

Composition

A total of 26 angiosperm species belonging to 22 genera, 12 families, and 9 orders were compiled across all vegetation surveys. The two most diverse families were Asteraceae and Poaceae, each with seven species (figure 2). The 4 species with the highest frequency and percentage of coverage were, in descending order were *Poa orthophylla* Pilg. (Poaceae), *Werneria pumila* Kunth (Asteraceae), *Lachemilla nivalis* (Kunth) Rothm. (Rosaceae) and *Carex bonplandii* Kunth (Cyperaceae). All species that occurred in the control plots also occurred in nurse plant plots.

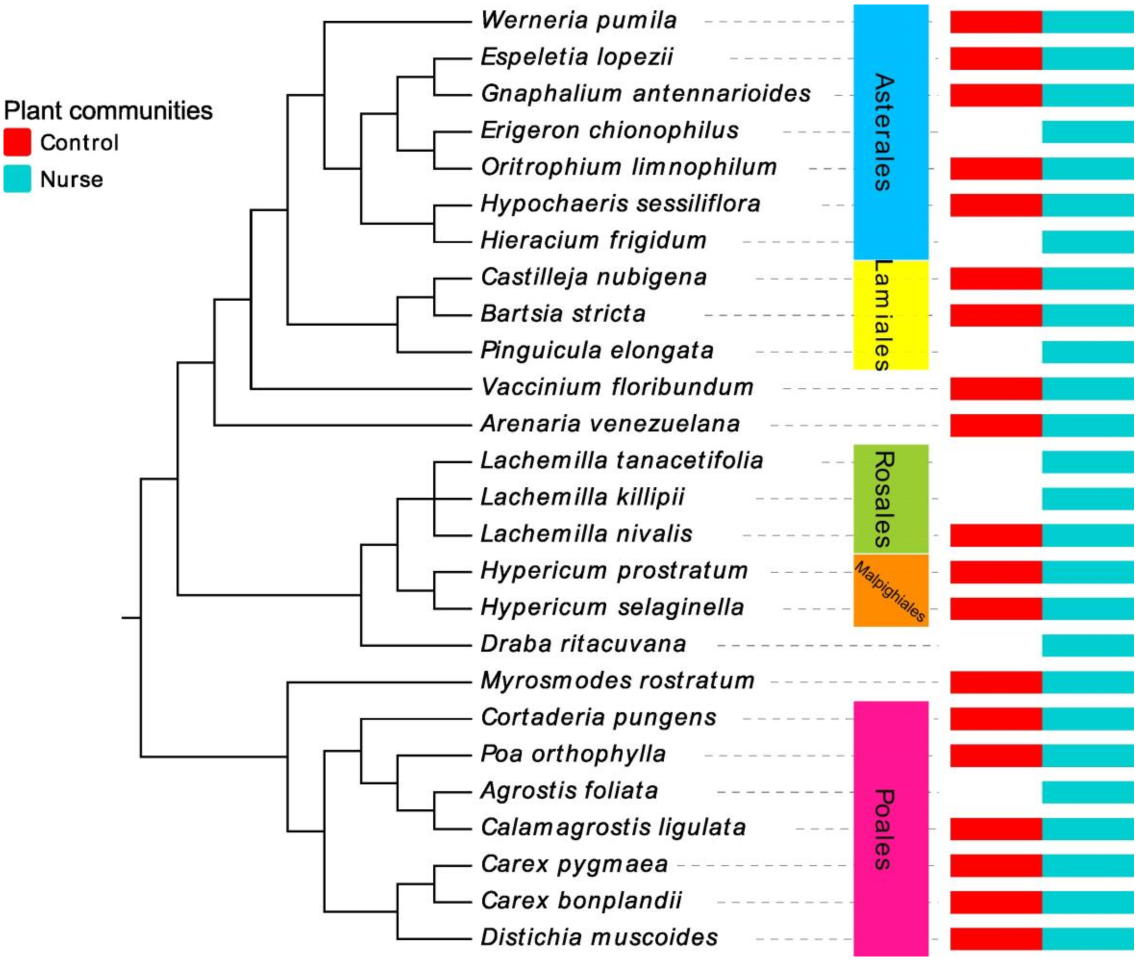

Figure 2. Phylogenetic tree of plant communities of the *páramo* of El Cocuy, Colombia. The main orders are highlighted in the tree.

Taxonomic diversity

The Nurse plots presented 26 species in total compared to 19 species in the Control plots (q = 0); all species that occurred in the control plots also occurred in the nurse plots. The measure of "typical" diversity (q = 1) found that nurse plots had a greater diversity (15.2) than the control plots (9.3), which means that the control plots had 61.2% of the diversity of the nurse plots. Finally, the measure of diversity of order 2 (q = 2) confirmed the same trend, with a smaller number of effective species in the control plots, as this measure mainly considers abundance (in this study, the plant cover). For all three metrics, there were significant differences between the two groups (Figure 3).

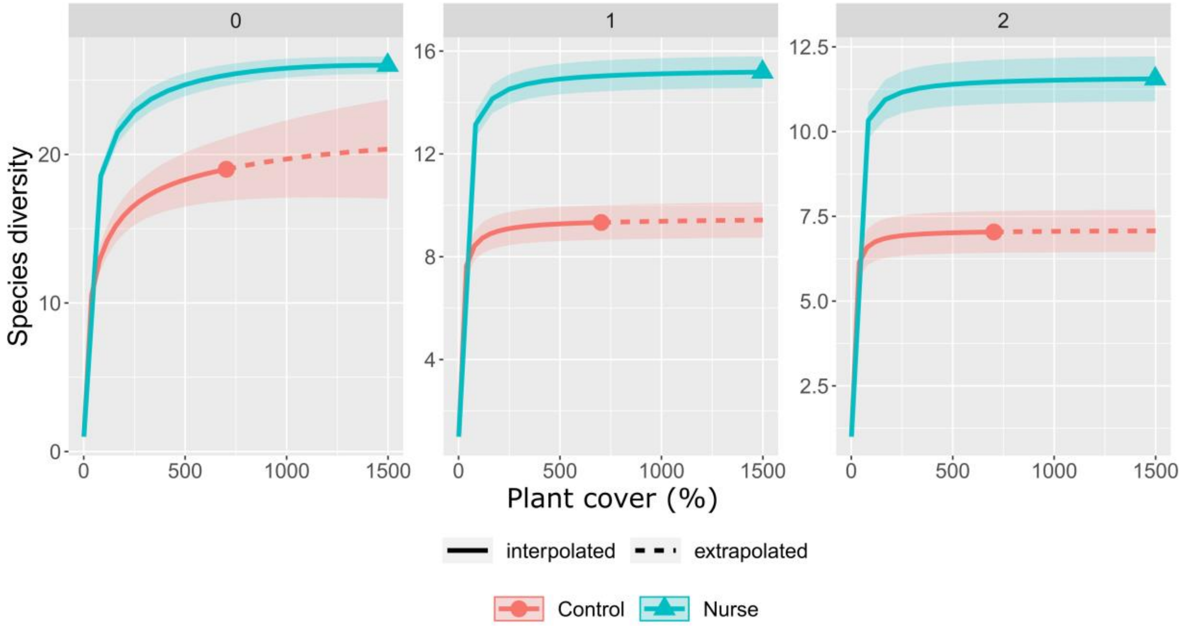

Figure 3. Diversity of plant species of plant communities of the *páramo* of Cocuy in Colombia. 0- q0 diversity (Species Richness), 1- q1 diversity (Shannon's diversity index), 2- q2 diversity (inverse Simpson's index).

Phylogenetic structure

The PD and MNTD results showed significant differences between the groups (Fig. 4A, 4C). Nurse plots showed a significantly higher PD than control plots. Control plots showed significantly higher MNTD than nurse plots. The MPD showed no significant differences. In contrast, the standardized indices (ses.PD, ses.MNTD, and ses.MPD) did not show significant differences. Furthermore, the standardized indices fluctuated within the range of random expectations.

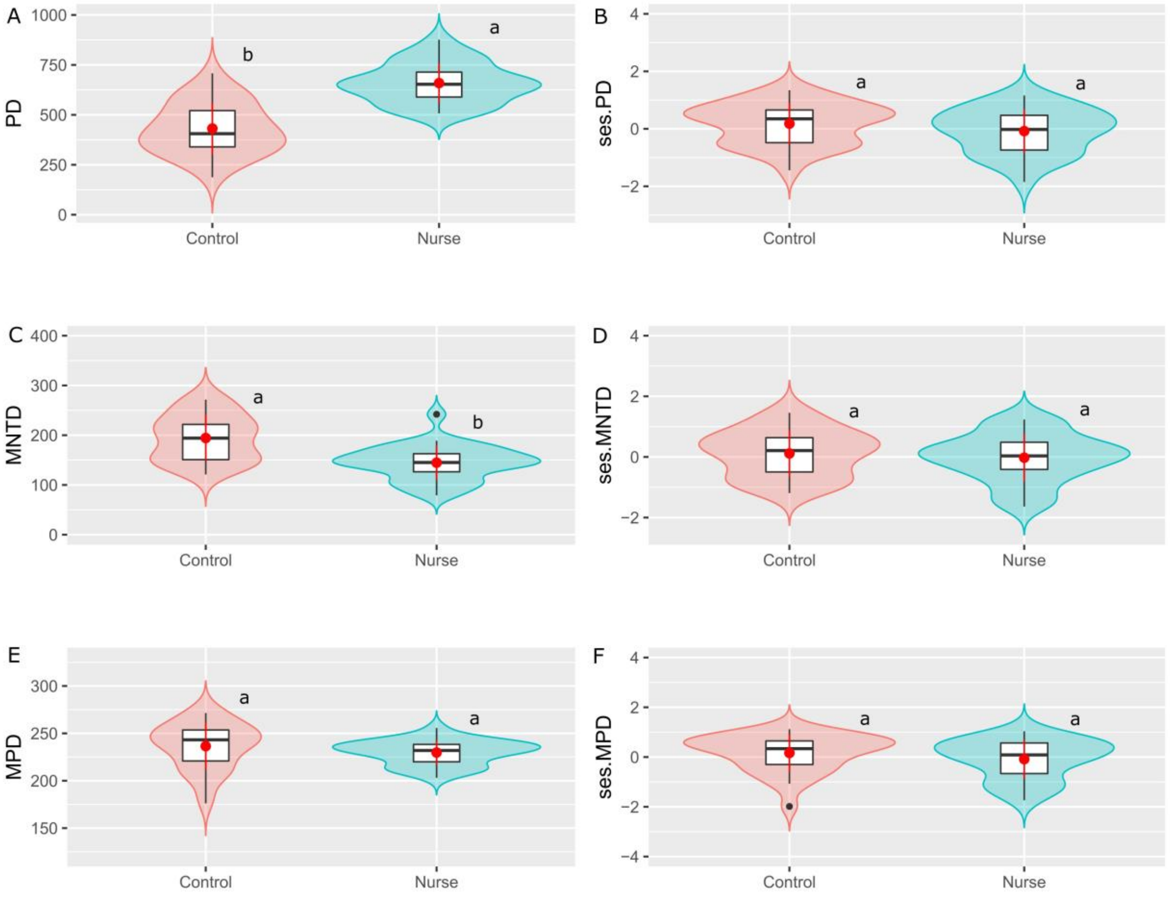

Figure 4. Patterns of the (A) phylogenetic diversity (PD), (B) standardized effect size of phylogenetic diversity (ses.PD), (C) mean nearest taxon distance (MNDT), (D) standardized effect size of mean nearest taxon (ses.MNTD), (E) Mean Phylogenetic Distance (MPD) and (F) standardized effect size of mean pairwise phylogenetic distance (ses.MPD), of two plant communities of the *páramo* of Cocuy in Colombia. The letters indicate that there are no significant differences according to a t-test and a Mann–Whitney U test ($p < 0.05$) between communities.

DISCUSSION

Nurse plants modify their conditions in stressful environments by generating a microclimate under their canopy. Therefore they can increase species richness, phylogenetic diversity, water and nutrient availability, and protection against herbivory (Carrión et al., 2017; Filazzola & Lortie, 2014; Padilla & Pugnaire, 2006). In this study conducted in a *páramo* region in Colombia, we observed a positive effect on the taxonomic diversity of a caulescent rosette species on the plant community under its canopy. We found that the *Espeletia lopezii* plant had higher species richness and taxonomic diversity than the adjacent control vegetation. This study showed that many species are more abundant under or near the canopy of *Espeletia lopezii*, most notably *Poa orthophylla*, *Lachemilla nivalis*, *Carex pygmaea* and, *Werneria pumila*. A similar study in the *páramos* of Venezuela found a positive impact of culescent rosettes of the species *Coespeletia timotensis*, which had strong positive effects on local plant species richness, vegetation cover, and abundance of many plants in the community, including herbs, cushions, and grasses (Mora et al., 2019).

Our results support the first hypothesis that the caulescent rosette acts as an ecosystem engineer, improving local microhabitat conditions and increasing plant abundance and taxonomic diversity compared with open areas.

The metrics ses.PD, ses.MPD, ses.MNTD, and MPD did not indicate differences in the phylogenetic structure between nurse plants and control plots. Therefore, no clear conclusion can be drawn from these metrics regarding the influence of facilitation processes on the phylogenetic structure of plant communities in the *superpáramo* belt of the Colombian Andes. In contrast, a higher MNTD could indicate a slight phylogenetic overdispersion in the control plots and a slight phylogenetic clustering in the nurse plots. The observed MNTD patterns may have resulted from differences in species richness between the control and nurse plant plots, as has been reported in other studies (Honorio Coronado et al., 2015; Villa et al., 2018).

Although facilitation predicts that facilitating plants should preferentially promote the coexistence of ecologically different species with little niche overlap, if ecological characteristics are conserved within evolutionary lineages, this should result in a pattern of phylogenetic overdispersion (Carrión et al., 2017; Valiente-Banuet & Verdú, 2007). In our study, we observed that the dominant phylogenetic pattern was mainly random, we speculate that the environmental conditions of the *superpáramo* belt of frost occurrence during all nights of the year, rocky surfaces, mean temperature fluctuations between 0 and 6°C, and strong thermal oscillations have allowed the evolution of few plant lineages to survive in these climatic conditions; therefore, it is expected that the metacommunity in this vegetation belt is strongly filtered; consequently, despite the benefits of facilitation exerted by nurse plant with different growth habits, it would be difficult to find a clear pattern of phylogenetic overdispersion. Other authors posit that the benefits of facilitation in stressful environments increase as phylogenetic relatedness is reduced, as plants not only compete less but can also cooperate more (Duarte et al., 2021); in this case, under the canopy of nurse plants, we would expect a pattern closer to phylogenetic clustering. Although this pattern has not been found in other studies (Gavini et al., 2019).

The Asterales and Poales orders were the most species-rich. The family Asteraceae is well represented in alpine ecosystems worldwide (Galván-Cisneros et al., 2023; Pegoraro et al., 2020; Körner, 1995) and is represented by seven species. The considered graminoids. That means Poaceae, Cyperaceae, and Juncaceae also stood out. This group is well adapted to a range of environmental conditions (Dolezal et al., 2019; Venn et al., 2014; Zedek et al., 2021). Many grasses and sedges can rapidly increase in abundance following sufficient rainfall and improved abiotic conditions (Venn et al., 2014). *Poa orthophylla*, *Carex pygmaea*, and *Carex bonplandii* were common in the study area. Asterales and Poales are the two main lineages that explain the phylogenetic patterns in alpine summits, with phylogenetic clustering being the most common pattern (Galván-Cisneros et al., 2023; Li et al., 2014; Marx et al., 2017).

In conclusion, our results do not support our second hypothesis that plant communities under the rosette canopy are phylogenetically overdispersed as an effect of niche diversification promoted by facilitation. Our results suggest that, at these altitudes, the metacommunity is strongly filtered by climate and soil factors, and despite the benefits of the facilitation exerted by nurse plants, it is difficult to observe phylogenetic overdispersion pattern.

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CHAPTER 5. Structures of tropical dry forests in the Andes: forest conservation, composition and the role of Fabaceae and Myrtaceae*

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ABSTRACT

Background:

Tropical Dry Forests (TDFs) are repositories of biodiversity, ecosystem services and carbon that are threatened by fragmentation and climate change. Floristic and phytosociological studies are fundamental database for many studies of conservation and sustainability, but there is a knowledge gap concerning TDFs, especially in the Andes valleys. The aim of this study was to determine the phytosociological structure and composition of woody vegetation of seven TDFs in the Colombian Andes, and because the flora associated with this type of forest has a geographical distribution restricted to each locality where this biome exists, provide information on the main species, genera and families for conservation and restoration actions as well as for future meta-analyses. We sampled seven TDFs with 20 plots of 25 m × 4 m.

Results:

In the 1.88 hectares of samples, 8422 individuals were surveyed, distributed in 170 species, 120 genera and 50 botanical families. Of these species, 78.82% were identified at the species level, 17.05% at the genus level, and 4.11% at the family level. The most important families were Fabaceae and Myrtaceae. Nitrogen-fixing Fabaceae species were prominent amongst the important species, especially in low altitude and more stressing sites.

Conclusion:

The structure, composition and ecological importance of these forests must be considered for conservation and ecological restoration plans, in particular the habitat preference of species along the topographic gradient. Particularly noteworthy for conservation are the Myrtaceae species because promote connectivity and regeneration by providing resources for the fauna, a driver of dispersal, as well as nitrogen-fixing Fabaceae species, because promote the resilience and natural regeneration of TDFs in the Andes, a key feature of stability.

Key words**:** Tropical Dry Forest; phytosociology; Fabaceae; nitrogen-fixing; conservation.

HIGHLIGHTS

The TDF is the most threatened biome in Colombia.

A prominent characteristic of the composition and structure of TDFs is the importance of species of the Fabaceae family.

Species with highest VIs: *Machaerium arboreum*, *Platymiscium pinnatum* and *Handroanthus ochraceus*.

Myrtaceae and Fabaceae species are promising for the conservation of TDFs in the Andes.

INTRODUCTION

Floristic and phytosociological surveys in the Neotropics have generated, over more than 40 years, an extensive database that today allows us to understand how landscape, climate, altitude, soils and history affect phytogeography, diversity, evolution and ecology, from populations and communities to entire biomes (e.g., Bueno et al., 2016; Gastauer et al., 2015; Lima et al., 2020; Neves et al., 2020; A. T. Oliveira-Filho & Fontes, 2000). Tropical Dry Forests (TDFs) have less than 1000 mm of rainfall in tropical and equatorial latitudes (see Oliveira-Filho et al. 2015) and are less studied by floristic and phytosociological studies than other large biomes with woody vegetation (Andrade et al., 2011), but the absence of this type of study is especially worrying with the climate change predicted for the coming decades (IPCC,

2021) in mountains such as the Andes where isolated fragments of TDFs will have their climates altered in heavily anthropized landscapes (Galván-Cisneros et al., 2021).

The knowledge about neotropical biomes was greatly benefited by the extensive database of phytosociological studies set over the years (Oliveira-Filho, 2017; Oliveira-Filho & Fontes, 2000), but the TDFs in the Andes Mountains are still a gap in phytosociological data, which makes them necessary and important for many studies that need meta-analyses (Medina-García et al., 2020) such as conservation studies and sustainability diagnostic studies of human activities (Zerwes et al., 2018). In Colombia, more than 90% of the TDFs have been cleared, with only 5% of their original coverage remaining, with more than 70% of the transformed areas having soils with degradation and erosion, and more than 65% are in the process of desertification caused by continuous human activities (García et al., 2014).

The TDF biodiversity, its potential in carbon sequestration and its role in the provision of ecosystem services are important justifications for proposing changes in land use regulations and for promoting TDF conservation programs (Portillo-Quintero et al., 2015). In this context, compositional and phytosociological data are important to generate knowledge about the status of TDFs, their plant populations, their functioning and their responses to global changes (Siyum, 2020).

The most prominent characteristic of the TDFs' composition and structure is the importance of Fabaceae species, especially the nitrogen-fixers (Bhaskar et al., 2016; Vargas G. et al., 2015). The nitrogen-fixing Fabaceae species are abundant in neotropical forests in general and in TDFs in particular (Gei et al., 2018), especially at the very early regeneration (Avendaño-Yáñez et al., 2018) promoting resilience and shifts in succession in a forest type almost without pioneer species (Lebrija-

Trejos et al., 2008). However, there is still knowledge gaps of composition and structure of TDFs concerning other important plant families and concerning some regions as Andes mountains, especially in Colombia.

In the Neotropics, the main areas with tropical dry forests are found in the northeast of Brazil (the 'Caatinga'), on the Caribbean coasts of Colombia and Venezuela. Other areas of tropical dry forests are found in the dry valleys of the Andes in Bolivia, Peru, Ecuador and Colombia, the coast of Ecuador and northern Peru (Tumbesina region). In Central America, dry forests are concentrated along the Pacific coast from Guanacaste in northern Costa Rica to the Mexican state of Sonora. Throughout the Antilles, there are areas with dry forests (Banda et al., 2016; Pennington et al., 2000). The original distribution of TDFs in Colombia covered regions of the Caribbean plain and the Andean slopes and valleys (IAvH, 1998) with some small enclaves (IAvH, 1998; González-M et al., 2018; Pizano & García, 2014). The Colombian North-Andean TDF region is formed by three nuclei: the Chicamocha river canyon, in the province of Santander (Albesiano & Fernández-Alonso, 2006), the Ocaña-Convencion nucleus (IAvH, 1998), and the nucleus of Cúcuta and its surroundings, in the province of Norte de Santander (Galván-Cisneros et al., 2021; Hernández et al., 1992). The Cúcuta nucleus forms a continuum with the dry enclave of Tachira in Venezuela (Hernández et al., 1992). It is estimated that less than 50% of the original coverage persists in this region (Hernández et al., 1992). In Colombia, most studies of TDFs on floristics and phytosociology have taken place in the Caribbean region and in the Magdalena River valley. Most floristic studies that have been carried out in the North-Andean region of Colombia have focused in the Chicachocha River canyon and its areas of influence (Albesiano et al., 2003; Albesiano & Fernández-Alonso, 2006; Albesiano & Rangel-Ch, 2006; Díaz-Pérez, 2012; Fajardo-Gutiérrez et al., 2018; Valencia-Duarte et al., 2012). In the nucleus of Cúcuta and surroundings there is an evident information gap in the literature with very few publications in which the work of Carrillo-Fajardo et al., (2007) stands out, who performed floristic and structural characterization of a TDF in Cerro Tasajero.

The information gap increases the problem that TDFs are one of the most threatened biomes in Colombia (Pizano et al., 2014) with urgent need for phytosociological data (Banda et al., 2016). Therefore, the aim of this study was to determine the phytosociological structure and composition of woody vegetation of seven TDFs along a topographic gradient in the TDFs of Cucuta and surrounding, in the eastern range of the Colombian Andes, and provide information on the main species, genera and families for conservation and restoration actions as well as for future meta-analyses.

Material and methods

Study area

The study was carried out in the region of Cúcuta and its surroundings. All forests studied are on a south-north oriented slope that forms part of the eastern slope of the Cordillera Oriental de Colombia (Fig. 1). The altitude range between the studied TDFs was from 282 m to 799 m ASL (Table 1). This slope still conserves TDFs remnants in a semi-arid corridor in the middle and lower part of the microbasins of the Zulia and Pamplonita rivers, within the Catatumbo river basin.

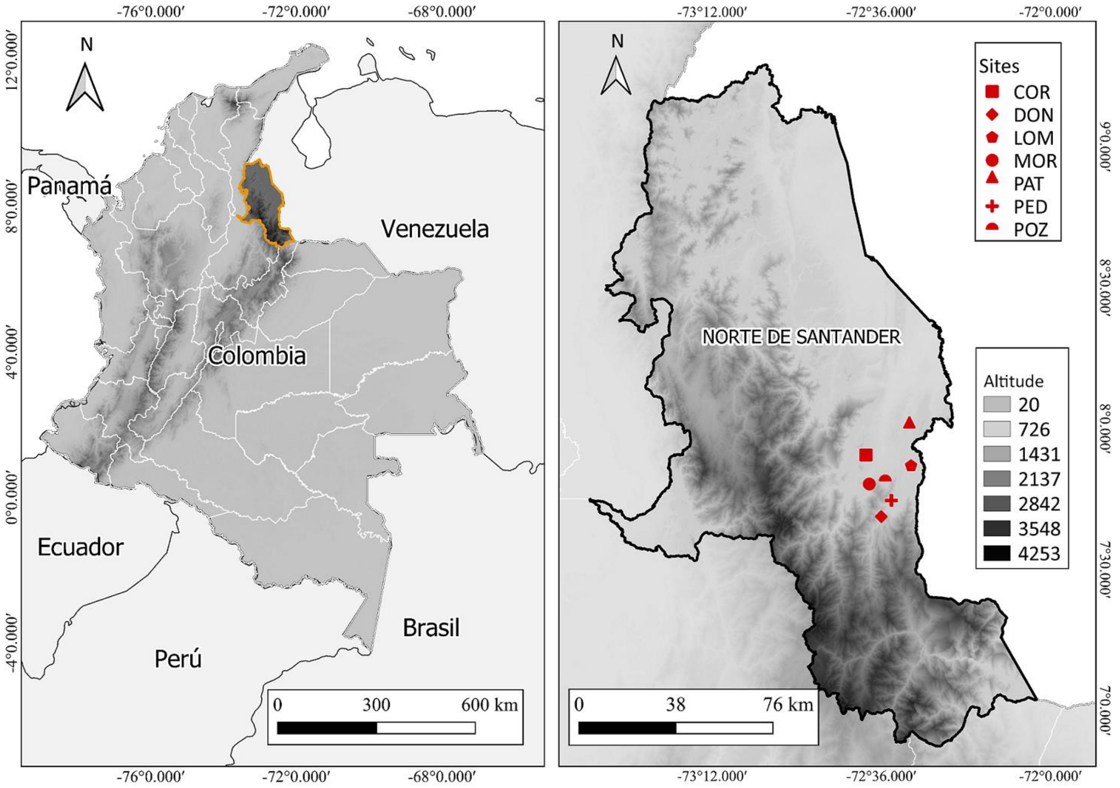

Fig. 1 Sites of Tropical Dry Forest surveyed in Cúcuta and neighboring municipalities, province of Norte de Santander, Colombia.

Tab 1. Geographical information of sampled sites of Tropical Dry Forests surveyed in Cúcuta and neighboring municipalities, province of Norte de Santander, Colombia.

Site code	Site	Municipality	Coordinates	Altitude (m.a.s.l.)
PAT	Patillales	Cúcuta	7° 59' 57,4" N 72° 29' 58,1" w	282
LOM	Las Lomas	Cúcuta	7° 52' 03,6" N 72° 29' 36,6" w	389
POZ	Pozo Azul	San Cayetano	7° 48' 50,2" N 72° 35' 7,2" w	505
DON	La Don Juana	Bochalema/Chinacota	7° 41' 14,4" N 72° 35' 57,1" w	799
PED	San Pedro	Cúcuta/Los Patios	7° 44' 39,9" N 72° 33' 47,7" w	656
COR	Cornejo	San Cayetano	7° 54' 20,5" N 72° 39' 13" w	393
MOR	Morretón Bajo	Durania	7° 48' 10,3" N 72° 38' 30,6" w	528

Sampling

We sampled seven sites. For each site, 20 plots of 25 m × 4 m were established, except for the locality of Patillales (PAT) where 68 plots were established, totaling 188 plots throughout the study area (Table 1). In each plot, all individuals with a diameter at breast height (DBH) of at least 1 cm were measured. The botanical material collected was identified from the specialized literature or by comparison in the HECASA Herbarium of the University of Pamplona, Colombia. Botanical identification followed APG IV (The Angiosperm Phylogeny Group, 2016).

Horizontal structure

To determine the horizontal structure of the communities, the phytosociological parameters of absolute density, absolute dominance, absolute frequency, relative density, relative dominance and relative frequency were used, as well as the importance value (VI) according to Curtis & McIntosh, (1950) and calculated with formulas described by Mueller-Dombois & Ellenberg, (1974). These calculations were carried out with basic functions in R statistical environment (R Development Core Team, 2021).

Species Density

To compare sites of different area sizes, it is advantageous to use species density using the following equation (Vetaas & Grytnes, 2002):

$SD = S/\ln(A)$

where S is the number of species in each location and A is the area (m^2) of each location.

Floristic composition

We ordered the plots using non-metric multidimensional scale ordination (NMDS), with Bray-Curtis as the dissimilarity metric based on abundances, in order to assess the existence of a gradient in species composition along the topographic gradient. The NMDS was performed using the '*metaMDS*' function of the "*vegan*" package (Oksanen et al., 2018). We tested the significance of the groups generated with a permutational multivariate analysis of variance (PERMANOVA) with 999 permutations (Anderson, 2001), using the '*adonis*' function available within the "*vegan*" package (Oksanen et al., 2018). To generate the graphs for this study, we used the "ggplot2" package (Wickham, 2016).

All analyzes were performed using packages of the R software (R Development Core Team, 2021).

RESULTS

Horizontal structure

In the 1.88 hectares of samples, 8422 individuals were surveyed, distributed in 170 species, 120 genera and 50 botanical families (Table 2). Of these species, 78.82% were identified at the species level, 17.05% at the genus level, and 4.11% at the family level. The main limitation of identification was the absence of fertile botanical material during the survey period.

Tab 2. Floristic list of 1.88 hectare of Tropical Dry Forest, Cúcuta and neighboring municipalities, province of Norte de Santander, Colombia.

Family	Species
Acanthaceae	*Aphelandra macrophylla* Leonard
Achatocarpaceae	*Achatocarpus nigricans* Triana
Anacardiaceae	*Astronium graveolens* Jacq.
	Spondias mombin L.
Annonaceae	*Duguetia lucida* Urb.
	Guatteria cargadero Triana & Planch.
	Guatteria sp
	Oxandra venezuelana R.E. Fr.
	Xylopia frutescens Aubl.
Apocynaceae	*Aspidosperma cuspa* (Kunth) S.F. Blake ex Pittier
	Aspidosperma darienense Woodson ex Dwyer
	Aspidosperma megalocarpon Müll. Arg
	Tabernaemontana grandiflora Jacq
Araliaceae	*Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin
Asteraceae	Asteraceae NI
	Chromolaena sp
	Piptocoma discolor (Kunth) Pruski
Bignoniaceae	*Crescentia cujete* L.
	Handroanthus ochraceus (Cham.) Mattos
	Jacaranda caucana Pittier

Boraginaceae	*Cordia alliodora* (Ruiz & Pav.) Oken
	Cordia bicolor A. DC
	Varronia curassavica Jacq.
Burseraceae	*Protium heptaphyllum* (Aubl.) Marchand
	Protium laxiflorum Engl.
Cactaceae	*Acanthocereus tetragonus* (L.) Hummelinck
	Cereus hexagonus (L.) Mill.
	Opuntia caracassana Salm-Dyck
	Pilosocereus lanuginosus (L.) Byles & G.D. Rowley
	Praecereus euchlorus (F.A.C. Weber ex K. Schum.) N.P. Taylor
Cannabaceae	*Celtis iguanaea* (Jacq.) Sarg.
Capparaceae	*Capparidastrum frondosum* (Jacq.) Cornejo & Iltis
	Crateva tapia L.
	Cynophalla polyantha (Triana & Planch.) Cornejo & Iltis
	Cynophalla verrucosa (Jacq.) J. Presl
	Monilicarpa tenuisiliqua (Jacq.) Cornejo & Iltis
	Morisonia americana L.
	Neocapparis pachaca (Kunth) Cornejo
	Quadrella indica (L.) Iltis & Cornejo
Celastraceae	*Monteverdia sieberiana* (Krug & Urb.) Biral
	Schaefferia frutescens Jacq.
Chrysobalanaceae	*Leptobalanus apetalus* (E. Mey.) Sothers & Prance
	Licania cf. *hypoleuca* Benth.
	Licania sp
	Parinari pachyphylla Rusby
Clusiaceae	*Garcinia madruno* (Kunth) Hammel
Combretaceae	*Terminalia amazonia* (J.F. Gmel.) Exell
Erythroxylaceae	*Erythroxylum macrophyllum* Cav.
	Erythroxylum novogranatense (D. Morris) Hieron.
	Erythroxylum sp.1
	Erythroxylum sp.2
Euphorbiaceae	*Adelia ricinella* L.
	Cnidoscolus urens (L.) Arthur
	Croton argyrophyllus Kunth
	Croton caracasanus Pittier
	Croton micans Sw.
	Croton sp
	Jatropha gossypiifolia L.
	Mabea nitida Spruce ex Benth.
Fabaceae	*Albizia guachapele* (Kunth) Dugand
	Albizia niopoides (Spruce ex Benth.) Burkart
	Apuleia leiocarpa (Vogel) J.F. Macbr.
	Bauhinia aculeata L.
	Bauhinia sp
	Brownea ariza Benth.
	Brownea sp
	Calliandra riparia Pittier
	Calliandra sp
	Clitoria arborescens R. Br.
	Crudia sp
	Cynometra cf. *fissicuspis* (Pittier) Pittier
	Fabaceae NI.1

	Fabaceae NI.2
	Fabaceae NI.3
	Fabaceae NI.4
	Hymenaea courbaril L.
	Inga marginata Willd.
	Lonchocarpus velutinus Benth. ex Seem.
	Machaerium arboreum (Jacq.) Benth.
	Machaerium biovulatum Micheli
	Ormosia sp
	Peltogyne paniculata Benth.
	Piptadenia flava (DC.) Benth.
	Pithecellobium dulce (Roxb.) Benth.
	Platymiscium pinnatum (Jacq.) Dugand
	Platypodium elegans Vogel
	Prosopis juliflora (Sw.) DC.
	Pterocarpus acapulcensis Rose
	Samanea saman (Jacq.) Merr.
	Senegalia riparia (Kunth) Britton
	Senna fruticosa (Mill.) H.S. Irwin & Barneby
	Senna robiniifolia (Benth.) H.S. Irwin & Barneby
	Swartzia pinnata (Vahl) Willd.
	Swartzia sp
Lauraceae	*Aiouea* sp
	Nectandra sp.1
	Nectandra sp.2
Lecythidaceae	*Gustavia poeppigiana* O. Berg
Malpighiaceae	*Malpighia glabra* L.
Malvaceae	*Guazuma ulmifolia* Lam.
	Helicteres baruensis Jacq.
	Luehea speciosa Willd.
Melastomataceae	*Miconia prasina* (Sw.) DC.
	Miconia stenostachya DC.
Meliaceae	*Trichilia hirta* L.
Menispermaceae	*Sciadotenia* sp
Moraceae	*Brosimum alicastrum* Sw.
	Brosimum sp
	Maclura tinctoria (L.) D. Don ex Steud.
	Sorocea affinis Hemsl.
	Sorocea sp
	Sorocea sprucei (Baill.) J.F. Macbr.
Myrtaceae	*Calyptranthes* sp
	Eugenia biflora (L.) DC.
	Eugenia punicifolia (Kunth) DC.
	Eugenia sp.1
	Eugenia sp.2
	Eugenia sp.3
	Myrcia sp
	Myrcia tomentosa
	Myrtaceae NI.1
	Myrtaceae NI.2
	Myrtaceae NI.3
	Psidium friedrichsthalianum (O. Berg) Nied.
Nyctaginaceae	*Guapira costaricana* (Standl.) Woodson
	Guapira sp
	Neea sp.1
	Neea sp.2

Ochnaceae	*Ouratea angulata* Tiegh.
Opiliaceae	*Agonandra brasiliensis* Miers ex Benth. & Hook. f.
Peraceae	*Pera arborea* Mutis
	Pera colombiana Cardiel
Petiveriaceae	*Seguieria americana* L.
Picramniaceae	*Picramnia latifolia* Tul.
Picrodendraceae	*Piranhea longipedunculata* Jabl.
Piperaceae	*Piper amalago* L.
Polygalaceae	*Bredemeyera floribunda* Willd.
	Bredemeyera lucida (Benth.) Klotzsch ex Hassk.
Polygonaceae	*Coccoloba padiformis* Meisn.
	Ruprechtia costata Meisn.
	Ruprechtia ramiflora (Jacq.) C.A. Mey.
	Triplaris americana L.
Primulaceae	*Clavija latifolia* (Willd. ex Roem. & Schult.) K. Koch
Proteaceae	*Roupala montana* Aubl.
Rubiaceae	*Amaioua corymbosa* Kunth
	Chomelia cf. *spinosa* Jacq.
	Randia armata (Sw.) DC.
	Rudgea marginata Standl.
	Warszewiczia coccinea (Vahl) Klotzsch
Rutaceae	*Amyris sylvatica* Jacq.
	Helietta plaeana Tul.
	Zanthoxylum fagara (L.) Sarg.
	Zanthoxylum cf. *lenticulare* Reynel
	Zanthoxylum sp
Salicaceae	*Banara ulmifolia* (Kunth) Benth.
	Casearia grandiflora Cambess.
	Casearia javitensis Kunth
	Casearia sp.1
	Casearia sp.2
	Casearia sylvestris Sw.
Sapindaceae	*Cupania latifolia* Kunth
	Melicoccus bijugatus Jacq.
Sapotaceae	*Chrysophyllum argenteum* Jacq.
	Pouteria caimito (Ruiz & Pav.) Radlk.
Solanaceae	*Solanum hazenii* Britton
Verbenaceae	*Lippia origanoides* Kunth
	Petrea cf. *rugosa* Kunth
	Petrea volubilis L.
Violaceae	*Pombalia phyllanthoides* (Planch. & Linden ex Triana & Planch.) Paula-Souza
Vochysiaceae	*Vochysia lehmannii* Hieron.

The families with the highest number of species in the total survey were Fabaceae with 35 species (20.59% of the total number of species), 19 of which are nitrogen fixing, Myrtaceae with 12 species (7.06%), Capparaceae and Euphorbiaceae with 8 (4.71%) each, Moraceae and Salicaceae with 6 (3.53%) each, Annonaceae, Cactaceae, Rubiaceae and Rutaceae with 5 each (2.94%). These ten families represent 55.88% of the total species found in the floristic survey. The richest genera were: *Casearia* and *Eugenia* with 5 species each, followed by *Croton* and *Erythroxylum* with 4 species each. The species with the highest number of individuals were *Machaerium arboreum* (1011), *Platymiscium pinnatum* (714), *Guapira costaricana* (577), *Handroanthus ochraceus* (573), *Croton micans* (489) and *Aspidosperma cuspa* (314).

Considering the seven TDFs studied, six species had the highest VIs: *Machaerium arboreum, Platymiscium pinnatum, Handroanthus ochraceus, Guapira costaricana, Croton micans* and *Machaerium biovulatum* with values of 9.71; 6.6; 5.63; 4.52; 3.82 and 3.03, respectively. Of these, three are nitrogen-fixing Fabaceae species and accounted for about 20% of the total VI. Another nine species had an importance value between 2.34 and 1.69. These fifteen species accounted for just over 50% VI of the seven TDFs (Fig. 2).

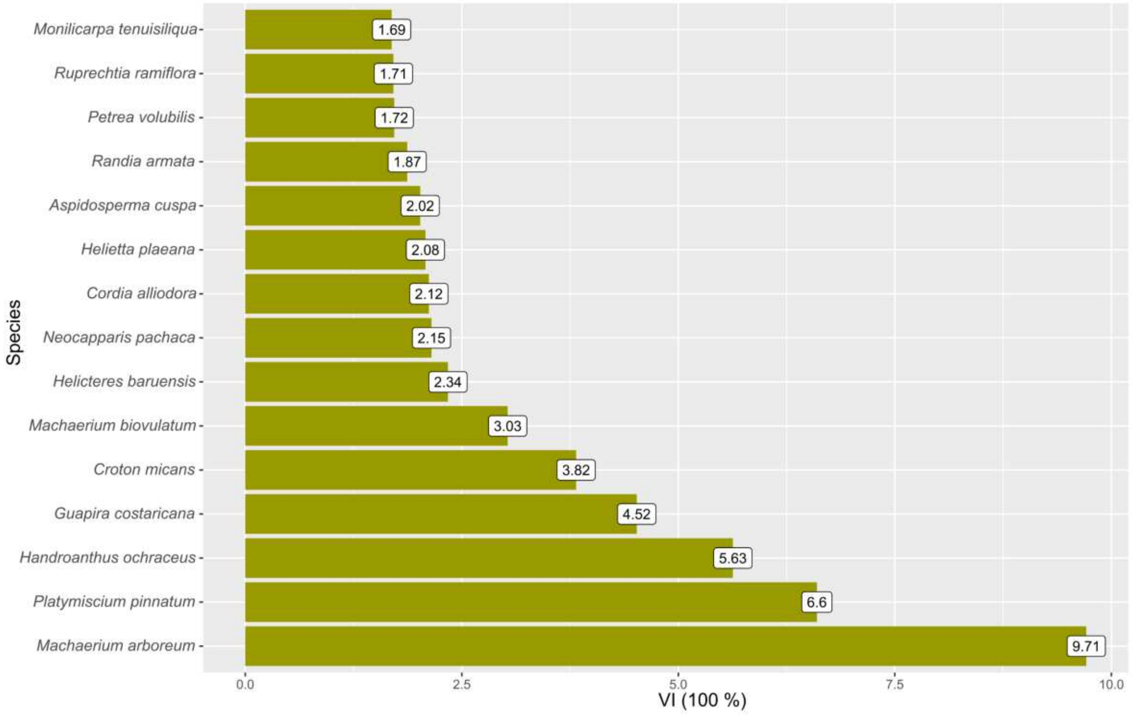

Fig. 2 - Percentages of species with the highest importance values (VI 100%) for the total of sampled forests.

Of the six species with VI above 3.0 in the TDFs studied, three are nitrogen-fixing Fabaceae species. Of the 170 surveyed species, one appears on the Red List of Endangered Species of Colombian Flora: *Parinari pachyphylla* Rusby, Endangered (EN). It also appears in the same category in Resolution No. 1912 of 2017, from the Colombian Ministry of Environment and Sustainable Development's list of threatened species in Colombia. However, the vast majority of species sampled have a low number of individuals and a small basal area, as shown in the phytosociological tables (See tables for supplementary material).

In Patillales, the species with the highest VI were *Machaerium arboreum* (13.6), *Platymiscium pinnatum* (9.9), *Guapira costaricana* (9.31) and *Croton micans* (7.2). These four species represented 40.19% of the total VI, with the two most important species being nitrogen-fixing Fabaceae species. An additional 21.95% of the VI is from another five species: *Neocapparis pachaca* (6.1), *Handroanthus ochraceus* (6.1), *Helietta plaeana* (5.8) and *Ruprechtia ramiflora* (3.8) (Table 3).

Tab 3. Phytossociological parameters of species sampled in 1.88 hectare of Tropical Dry Forest, Cúcuta and neighboring municipalities, province of Norte de Santander, Colombia. Ordered in decreasing value of importance, where DoA= absolute dominance (m^2 /ha), DoR = relative dominance (%), FA = absolute frequency, FR = relative frequency (%), DA = absolute density (number of individuals/ha), DR = relative density (%), VI 300 % = importance value (%) and VI 100 % = importance value (%).

Patillales (PAT), 282 m.a.s.l.								
Species	DoA	DoR	FA	FR	DA	DR	VI 300	VI 100

Machaerium arboreum	6.05	17.71	67.65	7.07	833.82	16.14	40.92	13.64
Platymiscium pinnatum	4.32	12.64	70.59	7.37	507.35	9.82	29.84	9.95
Guapira costaricana	2.43	7.12	66.18	6.91	719.12	13.92	27.96	9.32
Croton micans	0.92	2.69	82.35	8.60	545.59	10.56	21.85	7.28
Neocapparis pachaca	3.62	10.58	45.59	4.76	158.82	3.08	18.42	6.14
Handroanthus ochraceus	2.32	6.80	60.29	6.30	269.12	5.21	18.30	6.10
Helietta plaeana	3.02	8.83	41.18	4.30	232.35	4.50	17.63	5.88
Ruprechtia ramiflora	1.81	5.29	39.71	4.15	105.88	2.05	11.49	3.83
Helicteres baruensis	0.34	0.99	54.41	5.68	244.12	4.73	11.40	3.80
Monilicarpa tenuisiliqua	0.36	1.06	51.47	5.38	252.94	4.90	11.34	3.78
Praecereus euchlorus	0.71	2.07	50.00	5.22	179.41	3.47	10.77	3.59
Prosopis juliflora	1.73	5.05	22.06	2.30	125.00	2.42	9.77	3.26
Rest of species	6.55	19.17	305.88	31.95	991.18	19.19	70.31	23.44
Total	34.17	100	957.35	100	5164.71	100	300	100

Las Lomas (LOM), 389 m.a.s.l.

Species	DoA	DoR	FA	FR	DA	DR	VI 300	VI 100
Platymiscium pinnatum	13.96	41.44	100.00	17.54	1740.00	45.19	104.17	34.72
Pilosocereus lanuginosus	7.34	21.78	60.00	10.53	445.00	11.56	43.87	14.62
Handroanthus ochraceus	2.74	8.12	70.00	12.28	635.00	16.49	36.90	12.30
Helicteres baruensis	0.45	1.35	50.00	8.77	240.00	6.23	16.36	5.45
Prosopis juliflora	2.98	8.83	30.00	5.26	80.00	2.08	16.17	5.39
Cynophalla polyantha	1.12	3.33	45.00	7.89	60.00	1.56	12.79	4.26
Randia armata	0.47	1.40	50.00	8.77	90.00	2.34	12.51	4.17
Acanthocereus tetragonus	0.21	0.63	25.00	4.39	80.00	2.08	7.10	2.37
Aspidosperma cuspa	0.34	1.00	15.00	2.63	125.00	3.25	6.87	2.29
Neea sp.1	1.49	4.42	5.00	0.88	55.00	1.43	6.72	2.24
Pithecellobium dulce	1.06	3.16	10.00	1.75	20.00	0.52	5.43	1.81
Lippia origanoides	0.03	0.09	10.00	1.75	80.00	2.08	3.93	1.31
Rest of species	1.50	4.45	100.00	17.54	200.00	5.19	27.18	9.06
Total	33.69	100	570.00	100	3850.00	100	300	100

Cornejo (COR), 393 m.a.s.l.

Species	DoA	DoR	FA	FR	DA	DR	VI 300	VI 100
Handroanthus ochraceus	3.72	7.26	90.00	7.76	775.00	17.71	32.74	10.91
Cordia alliodora	5.08	9.90	75.00	6.47	385.00	8.80	25.17	8.39
Calliandra riparia	6.21	12.12	55.00	4.74	230.00	5.26	22.12	7.37
Machaerium arboreum	1.68	3.27	70.00	6.03	240.00	5.49	14.79	4.93
Aspidosperma cuspa	0.68	1.33	55.00	4.74	355.00	8.11	14.19	4.73
Petrea volubilis	0.77	1.49	60.00	5.17	245.00	5.60	12.27	4.09
Croton micans	0.93	1.82	65.00	5.60	195.00	4.46	11.88	3.96
Samanea saman	5.53	10.79	5.00	0.43	5.00	0.11	11.34	3.78
Cynophalla verrucosa	0.47	0.92	65.00	5.60	195.00	4.46	10.98	3.66
Randia armata	1.13	2.21	40.00	3.45	185.00	4.23	9.89	3.30
Ormosia sp	3.92	7.64	10.00	0.86	55.00	1.26	9.76	3.25
Guapira costaricana	1.04	2.03	55.00	4.74	130.00	2.97	9.74	3.25
Rest of species	20.10	39.21	515.00	44.40	1380.00	31.54	115.15	38.38
Total	51.27	100	1160.00	100	4375.00	100	300	100

Pozo Azul (POZ), 505 m.a.s.l.

Species	DoA	DoR	FA	FR	DA	DR	VI 300	VI 100
Machaerium arboreum	5.80	13.01	95.00	6.69	640.00	14.88	34.58	11.53
Pterocarpus acapulcensis	6.98	15.64	60.00	4.23	200.00	4.65	24.51	8.17
Machaerium biovulatum	4.11	9.21	65.00	4.58	180.00	4.19	17.97	5.99
Handroanthus ochraceus	2.15	4.81	80.00	5.63	300.00	6.98	17.43	5.81
Fabaceae NI.1	5.14	11.53	10.00	0.70	40.00	0.93	13.16	4.39
Calliandra riparia	1.57	3.52	40.00	2.82	225.00	5.23	11.57	3.86
Petrea volubilis	1.03	2.31	65.00	4.58	200.00	4.65	11.54	3.85
Luehea speciosa	3.14	7.04	25.00	1.76	55.00	1.28	10.08	3.36
Piptocoma discolor	1.32	2.95	30.00	2.11	205.00	4.77	9.83	3.28
Eugenia biflora	0.49	1.10	55.00	3.87	155.00	3.60	8.58	2.86
Astronium graveolens	0.66	1.48	50.00	3.52	85.00	1.98	6.97	2.32
Erythroxylum novogranatense	0.32	0.71	45.00	3.17	125.00	2.91	6.79	2.26
Rest of species	11.91	26.69	800.00	56.34	1890.00	43.95	126.99	42.33
Total	44.61	100	1420.00	100	4300.00	100	300	100

Morretón Bajo (MOR), 528 m.a.s.l.

Species	DoA	DoR	FA	FR	DA	DR	VI 300	VI 100
Apuleia leiocarpa	8.54	13.21	60.00	3.61	115.00	2.98	19.80	6.60
Protium heptaphyllum	3.14	4.86	70.00	4.22	355.00	9.20	18.27	6.09
Brosimum alicastrum	4.36	6.75	20.00	1.20	130.00	3.37	11.32	3.77
Xylopia frutescens	1.17	1.80	50.00	3.01	220.00	5.70	10.52	3.51
Platypodium elegans	4.63	7.16	30.00	1.81	45.00	1.17	10.13	3.38
Hymenaea courbaril	4.06	6.28	30.00	1.81	55.00	1.42	9.51	3.17
Petrea volubilis	0.83	1.28	50.00	3.01	190.00	4.92	9.22	3.07
Myrcia sp	1.71	2.64	45.00	2.71	95.00	2.46	7.82	2.61
Oxandra venezuelana	1.43	2.21	40.00	2.41	95.00	2.46	7.08	2.36
Warszewiczia coccinea	0.33	0.50	40.00	2.41	150.00	3.89	6.80	2.27
Pterocarpus acapulcensis	3.03	4.69	20.00	1.20	35.00	0.91	6.80	2.27
Cupania latifolia	0.67	1.04	45.00	2.71	115.00	2.98	6.73	2.24
Rest of species	30.75	47.58	1160.00	69.88	2260.00	58.55	176.01	58.67
Total	64.62	100	1660.00	100	3860.00	100	300	100

San Pedro (PED), 656 m.a.s.l.

Species	DoA	DoR	FA	FR	DA	DR	VI 300	VI 100
Machaerium arboreum	13.31	29.88	60.00	5.06	520.00	12.61	47.55	15.85
Randia armata	2.14	4.80	80.00	6.75	280.00	6.79	18.34	6.11
Machaerium biovulatum	3.81	8.55	55.00	4.64	165.00	4.00	17.19	5.73
Piptocoma discolor	1.81	4.07	40.00	3.38	330.00	8.00	15.44	5.15
Croton micans	1.01	2.26	60.00	5.06	330.00	8.00	15.33	5.11
Handroanthus ochraceus	2.25	5.05	45.00	3.80	170.00	4.12	12.97	4.32
Guapira costaricana	1.39	3.13	55.00	4.64	180.00	4.36	12.14	4.05
Cynophalla polyantha	1.14	2.56	60.00	5.06	185.00	4.48	12.10	4.03
Erythroxylum sp.2	1.43	3.21	30.00	2.53	205.00	4.97	10.72	3.57
Cordia alliodora	1.96	4.41	30.00	2.53	105.00	2.55	9.49	3.16
Helicteres baruensis	0.49	1.11	50.00	4.22	110.00	2.67	7.99	2.66

Chomelia spinosa	1.14	2.55	25.00	2.11	115.00	2.79	7.45	2.48
Erythroxylum sp.1	1.53	3.44	20.00	1.69	95.00	2.30	7.43	2.48
Rest of species	11.13	24.98	575.00	48.52	1335.00	32.36	105.87	35.29
Total	44.53	100	1185.00	100	4125.00	100	300	100

La Don Juana (DON), 799 m.a.s.l.

Species	DoA	DoR	FA	FR	DA	DR	VI 300	VI 100
Machaerium arboreum	5.49	13.45	65.00	5.86	780.00	19.31	38.62	12.87
Machaerium biovulatum	6.15	15.07	95.00	8.56	255.00	6.31	29.94	9.98
Guazuma ulmifolia	5.35	13.11	45.00	4.05	110.00	2.72	19.88	6.63
Swartzia sp	4.06	9.93	30.00	2.70	270.00	6.68	19.32	6.44
Picramnia latifolia	2.22	5.44	45.00	4.05	325.00	8.04	17.54	5.85
Piper amalago	1.46	3.58	50.00	4.50	330.00	8.17	16.25	5.42
Casearia sp.1	0.66	1.63	70.00	6.31	240.00	5.94	13.87	4.62
Casearia sylvestris	2.72	6.66	30.00	2.70	135.00	3.34	12.70	4.23
Astronium graveolens	0.90	2.22	70.00	6.31	160.00	3.96	12.48	4.16
Cordia alliodora	1.90	4.65	25.00	2.25	160.00	3.96	10.86	3.62
Adelia ricinella	2.55	6.24	15.00	1.35	80.00	1.98	9.57	3.19
Zanthoxylum sp	0.88	2.15	40.00	3.60	100.00	2.48	8.23	2.74
Rest of species	6.48	15.88	530.00	47.75	1095.00	27.10	90.73	30.24
Total	40.83	100	1110.00	100	4040.00	100	300	100

The phytosociological structure of Las Lomas was mainly characterized by the dominance of the species *Platymiscium pinnatum* (VI = 34.7%), a nitrogen-fixing species belonging to the Fabaceae family, a family commonly prominent in tropical dry forests. Other important species were *Pilosocereus lanuginosus* (14.6) and *Handroanthus ochraceus* (12.3). These three species represented 61.64% of the total VI. This was the location that showed the lowest species richness.

In Cornejo, the species with the highest VI were *Handroanthus ochraceus* (10.9), *Cordia alliodora* (8.39), *Calliandra riparia* (7.3) and *Machaerium arboreum* (4.9). These four species represented 31.6% of the total VI. Another 17.27% corresponded to five other species: *Aspidosperma cuspa* (4.7), *Petrea volubilis* (4.09), *Croton micans* (3.9) and *Samanea saman* (3.7). Among these eight species, three are nitrogen-fixing Fabaceae species.

In Pozo Azul, three Fabaceae species stood out: *Machaerium arboreum* (11.5), *Pterocarpus acapulcensis* (8.1) and *Machaerium biovulatum* (5.9). These three species represented 25.69% of the total VI. Other important species were *Handroanthus ochraceus* (10.9), an unidentified Fabaceae (4.3) and *Calliandra riparia* (7.3). Among the six identified species, four are nitrogen-fixing Fabaceae species.

Morretón Bajo stood out for its high number of species (89), and none of them surpassed 7% of the total VI. The species with the highest VI were *Apuleia leiocarpa*, *Protium heptaphyllum*, *Brosimum alicastrum*, *Xylopia frutescens*, *Platypodium elegans* and *Hymenaea courbaril*. Only *Platypodium elegans* is a nitrogen fixer.

In San Pedro, the species with the highest VI were *Machaerium arboreum* (15.8), *Randia armata* (6.1), *Machaerium biovulatum* (5.7) and *Piptocoma discolor* (5.1). These four species represented 33.44% of the total VI. Other highlighted species were *Handroanthus ochraceus, Guapira costaricana, Cynophalla polyantha* and *Erythroxylum* sp.2. The two mentioned species of the genus *Machaerium* are nitrogen fixing.

In La Don Juana, the species with the highest VI were *Machaerium arboreum* (12.8), *Machaerium biovulatum* (9.9), *Guazuma ulmifolia* (6.6) and *Swartzia* sp (6.4). These four species represented 35.92% of the total VI and only *Guazuma ulmifolia* is not a nitrogen-fixing Fabaceae species. An additional 24.28% correspond to five highlighted species: *Picramnia latifolia* (5.8), *Piper amalago* (5.4), *Casearia* sp.1 (4.6), *Casearia sylvestris* (4.2) and *Astronium graveolens* (4.1).

Richness, density and composition of species

The highest species richness was found in Morretón Bajo and Pozo Azul, while the lowest was recorded in Las Lomas. A similar pattern was found for species density, which tended to be higher in locations at higher altitudes (MOR, DON, POZ, PED), while locations at lower altitudes had the lowest values (LOM, PAT and COR). The locations with the highest values were Pozo Azul and Morretón Bajo, the location with the lowest value was Las Lomas (Table 4).

Tab 4. Richness and Species density (SD) of seven the sites of Tropical Dry Forest, Cúcuta and neighboring municipalities, province of Norte de Santander, Colombia.

Sites code	Sites	Richness	SD	Altitude
LOM	Las Lomas	22	2.89	389
PAT	Patillales	58	6.57	282
COR	Cornejo	48	6.32	393
POZ	Pozo Azul	72	9.47	505
PED	San Pedro	51	6.71	656
DON	La Don Juana	57	7.5	799
MOR	Morretón Bajo	89	11.71	528

The NMDS of species composition showed significant differences. The groups formed in this analysis were considered consistent, according to the PERMANOVA results (F6.139 = 10.56; p <0.001). The variables generated by NMDS describe the variation in plant community composition along a topographic gradient (Figure 3), from sites at lower altitudes and less species richness to places at higher altitudes and greater species richness (Table 1). The wider dispersion of the plots in the Morretón Bajo (MOR) location in comparison with the other locations indicates that the forest in this location has a composition more variable than others.

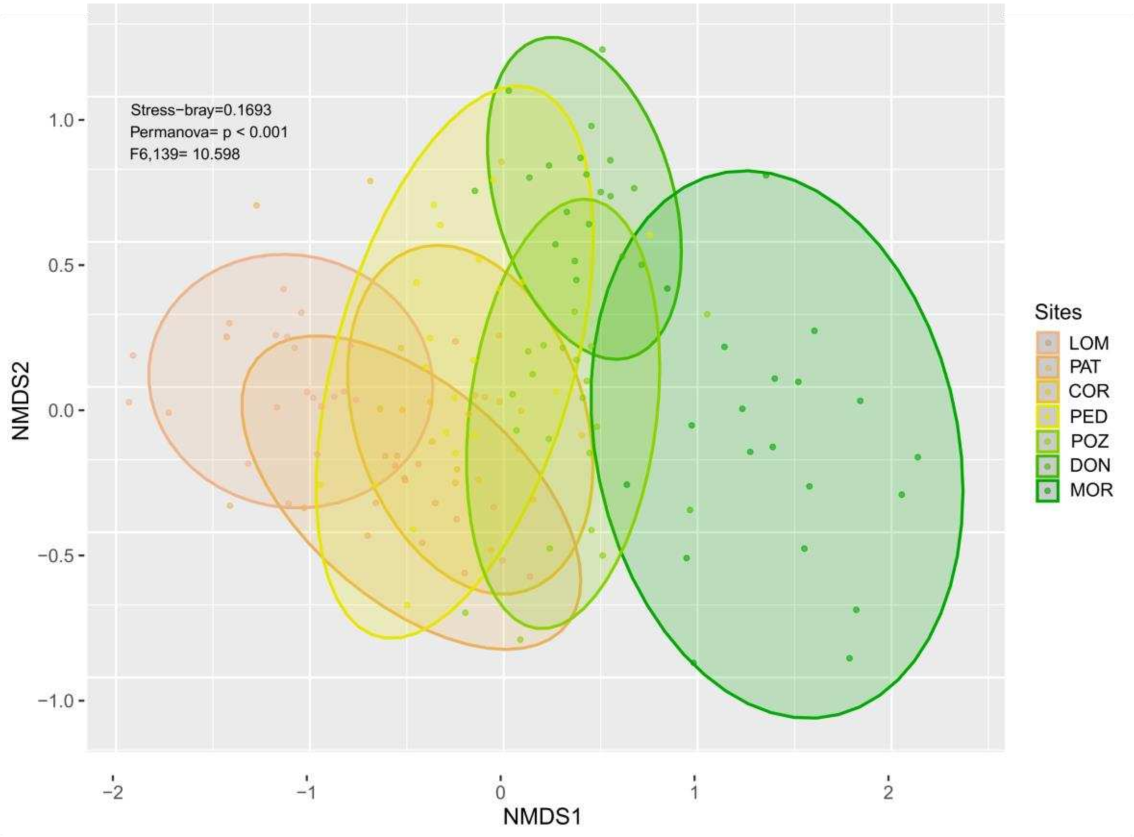

Fig. 3 Non-metric multidimensional scaling (NMDS) plot based on a Bray-Curtis abundance matrix, showing patterns of community composition among all seven sites of Tropical Dry Forest, Cúcuta and neighboring municipalities, province of Norte de Santander, Colombia.

DISCUSSION

In our study, the Fabaceae family was dominant, followed by Myrtaceae, Capparaceae, Euphorbiaceae, Moraceae and Salicaceae. Fabaceae had the highest VI in six of the seven localities always with prominent nitrogen-fixing species importance. In general, the floristic composition of these tropical dry forests maintains a trend similar to those reported by Albesiano & Rangel-Ch, (2006) e Albesiano & Fernández-Alonso, (2006) for Chicamocha Canyon, in the department of Santander, that the families with the most important woody species were Fabaceae, Bignoniaceae, Euphorbiaceae, Cactaceae and Rubiaceae. These families are among the most representative in phytosociological surveys in the arboreal-shrubby layer of the dry tropical forests of the Neotropics (Gentry, 1995; Rodríguez et al., 2012).

Fabaceae was the family with the greatest representation in species richness of these TDFs, with 35 species, just over 20% of all species sampled. This high representation may be related to the ability to fix atmospheric nitrogen by symbiotic association with bacteria, which is capable of occurring in harsh environments (da Silva et al., 2017). Despite TDFs present low species richness of pioneers comparatively to wetter tropical forests (Chazdon et al., 2011; Lebrija-Trejos et al., 2008), TDFs recover structure and biodiversity readily through succession (Ruiz et al., 2005; Vieira & Scariot, 2006). Much of this resilience can be because nitrogen-fixing Fabaceae species are drivers of early ecological succession in TDFs by making nitrogen available in their plants and in the soil and, since nitrogen is available, these nitrogen-fixing plants can allocate it to seeds and leaves, improving germination performance and deterring herbivory (Dovrat et al., 2020). Regardless of whether Fabaceae species are nitrogen fixing or not, they have seed germination twice as fast as the germination of seeds from species of other families in TDFs, which gives an adaptive advantage in environments with long droughts by increasing seedling growth rates, increasing fecundity and avoiding seed predators (Vargas G. et al., 2015). Therefore, Fabaceae species in TDFs are drivers of resilience and stability. Among the 35 Fabaceae species, 19 species are of known nitrogen-fixing genera (Sprent, 2009). *Machaerium, Platymiscium, Calliandra, Pterocarpus* and *Prosopis*, were the genera that presented the highest IV in the Fabaceae family, and all of them are nitrogen-fixing (Sprent, 2009).

The high importance of Myrtaceae in these TDFs is not as common in other TDFs in Colombia, a result also obtained by Carrillo-Fajardo et al., (2007) in the area known as Cerro Tasajero, near the Patillales, a site of our study, which denotes a particularity of the studied region. According to Rocha & Silva, (2002), the Myrtaceae family is important because it has many vertebrate-dispersed species that are fundamental to natural regeneration and connectivity. Thus, is fundamental the importance of the prominent Myrtaceae species for the maintenance of these remaining TDFs, for regeneration processes and associated fauna that promote connectivity.

The species with the highest VI among all sites was *Machaerium arboreum*, a dominant nitrogen-fixing Fabaceae species in five out seven localities; this is the first work where this species appears as dominant in an TDF in Colombia. Other works in TDFs have shown the dominance of other species of the genus *Machaerium* in Colombia, such as in the Magdalena river valley and in the Caribbean region (Mendoza-C, 1999; Romero-Duque et al., 2019). *Platymiscium pinnatum*, was the second most important species in the VI general, and was very common in localities located at lower altitudes and more severe environments (Galván-Cisneros et al., 2021). This species is also prominent in the Neguanje TDF, within the Tayrona National Natural Park in the Colombian Caribbean, a zone with stressing bioclimatic characteristics similar to the areas where the species was recorded in our study (Carbonó-Delahoz & García-Q, 2010). *Handroanthus ochraceus, Guapira costaricana* and *Croton micans* are the third, fourth and fifth species with the highest overall VI, respectively; this result is quite similar to the finding in the Tayrona National Natural Park where species of the genus *Handroanthus, Platymiscium, Guapira* and *Croton*, were among the five highest VI (Carbonó-Delahoz & García-Q, 2010).

Morretón Bajo was the location that presented the most different and heterogeneous floristic composition of all, which can be observed in the floristic composition ordination (NMDS). Also, in this forest, the largest DAP was registered. The five species with the highest VI in this locality were *Apuleia leiocarpa, Protium heptaphyllum, Brosimum alicastrum, Xylopia frutescens* and *Platypodium elegans*. *A. leiocarpa* is a Fabaceae species but it is not nitrogen-fixing species (Sprent, 2009). *A. leiocarpa* was also found to be prominent in several Atlantic Forest forests in Brazil (Carvalho et al., 2007; Ruschel et al., 2009). *P. heptaphyllum, B. alicastrum, X. frutescens* and *P. elegans* are very common species, occurring widely in almost all lowland forests in the Neotropics (Dionisio et al., 2016; Gardner et al., 2021; Hufford & Hamrick, 2003). Due to the greater richness, trees with greater DAP and for having only one nitrogen-fixing Fabaceae species among the prominent species, this forest seems to be the most advanced in the successional process among the TDFs in our study.

Parinari pachyphylla, was the only species registered in an IUCN-Colombia threat category; in this study, the species was found only in a portion of the Morretón Bajo locality, the locality with the greatest floristic heterogeneity. The species was prioritized within the National Plant Conservation Strategy of Colombia (ENCP) (Pizano et al., 2014), and Program for the Integral Conservation of Ten Priority Plant Species of the TDF (Sofrony-Esmeral et al., 2020). The main cause of its threat is the drastic transformation of forest areas into areas of intensive agriculture (Calderón et al., 2002). In Colombia, this species is distributed in the Caribbean region, in the lower valley of the Magdalena River, in the Zulia region, in the Serranía de Perijá borders with Venezuela (Norte de Santander province), in the Urabá de Antioquia and Orinoquia (Calderón et al., 2002; Pizano & García, 2014); and it is estimated that the provinces of Norte de Santander and Vichada are home to the best preserved populations (Calderón et al., 2002). However, it is very likely that several other species will be threatened in the near future due to climate changes in fragmented landscapes that make connectivity difficult. (Galván-Cisneros et al., 2021; IPCC, 2021) because most species sampled has a low number of individuals and a small basal area. It is possible that a significant number of species will be at risk of extinction in the near future, which shows a clear need to protect these forests through public policies.

As a general trend, a greater number of species was found in locations at higher altitudes, decreasing in locations at lower altitudes and where climatic seasonality is more marked and filters out species from lineages that are less tolerant to stressful environments (Galván-Cisneros et al., 2021). The species richness of these TDFs in lower altitude is small, which contrasts with the species richness of humid tropical forests in low altitude (Janzen, 1988; Van Bloem et al., 2004).

In TDFs the number of species varies in response to altitudinal variation (Galván-Cisneros et al., 2021). Therefore, the variable species composition is a response to higher temperature and greater drought intensity at lower altitudes and contrasts with mild temperatures and less intense droughts at higher altitudes. Also, as altitude decreases and environmental stress increases, nitrogen-fixing Fabaceae species become more important. These environments reveal differences that must be observed in the elaboration of actions for the conservation and sustainability of human activities. A similar floristic gradient was found for eight TDF fragments at the confluence of Caatinga, Cerrado and Atlantic Forest in Brazil, where climatic seasonality was the main factor of floristic differentiation (Fagundes et al., 2020).

CONCLUSION

Fabaceae and Myrtaceae were consistent important families with high species richness in the studied TDFs in the Andes. The two species of greatest ecological importance in the region were *M. arboreum* and *P. pinnatum*, species belonging to the Fabaceae family, both nitrogen fixing species and easily found in most localities; *H. ochraceus* and *G. costaricana*, one Bignoniaceae and one Nyctaginaceae, respectively, also stood out. Las Lomas was characterized by its low number of species and the ecological dominance of *P. pinnatum*. In contrast, Morretón Bajo was characterized by its high number of species and its high variability. The locations (or fragments) of FTS's sampled in this study present a topographic gradient that influences species richness, floristic and structural composition driven by climatic factors (climate seasonality) and altitude. The structure, composition and ecological importance of these forests must be considered for conservation and ecological restoration plans, in particular the habitat preference of species along the topographic gradient. However, it is essential to consider the prominence of Myrtaceae species that promote connectivity and regeneration as they provide resources for fauna as well as the prominence of Fabaceae species, especially nitrogen-fixing ones, which promote resilience and natural regeneration of TDFs in the Andes.

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