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Campo de altitude: diversity patterns and assembly mechanisms of plant communities across multiple dimensions

Miguel Ângelo Teixeira da Silva
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Assent:

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This thesis is dedicated to my parents, Marlúcia (in memoriam) and José Ferreira (in memoriam), who so greatly encouraged me to seek in studies the source of freedom and the fulfillment of dreams.

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ABSTRACT

SILVA, Miguel Ângelo Teixeira da, D.Sc., Universidade Federal de Viçosa, March, 2026. **Campo de altitude: diversity patterns and assembly mechanisms of plant communities across multiple dimensions**. Adviser: Andreza Viana Neri.

Campos-de-altitude are unique ecosystems occurring above 1,500–1,800 m elevation in the mountains of south and southeastern Brazil, characterized by high ecological diversity and plant endemism. Despite their ecological importance and vulnerability to climate change, the mechanisms that structure these communities remain poorly understood. This thesis investigated patterns of taxonomic, phylogenetic, and functional diversity in 11 sites of high-altitude grassland (campo-de-altitude) in the Caparaó and Brigadeiro mountain ranges, along gradients of altitude (1,665-2,892 m) and soil depth (0-60.0 cm). In the first chapter, we demonstrated that community assembly is governed by hierarchical environmental filtering, in which climatic constraints override edaphic conditions in phylogenetic structuring. Although deep soils consistently promote taxonomic and phylogenetic diversity, high-altitude communities remain phylogenetically clustered independently of edaphic resources, reflecting strong selection for cold tolerance adaptations. Standardized metrics (SES_PD, SES_MPD, SES_MNTD) revealed increasing phylogenetic clustering with altitude, indicating that only closely related lineages persist in extreme environments. In the second chapter, we found that soil depth strongly modulates plant trait responses to elevational gradients. While deep soils function as hydraulic refugia (favoring conservative woody species) and act as an edaphic buffer against the climatic stress of high elevations, shallow soils filter for acquisitive leaf traits and short-cycle plant life forms. Ultimately, the synthesis of these chapters reveals a distinct decoupling between evolutionary history and ecological strategy: while macroclimatic stress (elevation) strictly filters closely related lineages (phylogenetic clustering), microhabitat heterogeneity (soil depth) drives substantial functional divergence within these surviving clades. By integrating these approaches, we demonstrate that environmental gradients act more strongly on evolutionary relationships and functional traits than on species richness per se. These results have direct implications for conservation: high-elevation communities harbor evolutionarily unique and functionally specialized lineages, making them particularly vulnerable to climate change. We recommend prioritizing the protection of high-elevation sites that maintain distinctive phylogenetic diversity, as well as patches of deep soil that function as diversity hotspots

along the elevational gradient.

Keywords: Plant Ecology; Community phylogeny; Functional traits; Environmental gradients; Community assembly; Rocky grasslands; Atlantic Forest; Brazilian Páramos

RESUMO

SILVA, Miguel Ângelo Teixeira da, D.Sc., Universidade Federal de Viçosa, março de 2026. **Campos de altitude: padrões de diversidade e mecanismos de montagem de comunidades vegetais em múltiplas dimensões**. Orientadora: Andreza Viana Neri.

Os campos de altitude são ecossistemas singulares que ocorrem acima de 1.500–1.800 m de elevação nas montanhas do sul e sudeste brasileiros, caracterizados por alta diversidade ecológica e endemismo vegetal. Apesar de sua importância ecológica e vulnerabilidade às mudanças climáticas, os mecanismos que estruturam essas comunidades permanecem pouco compreendidos. Esta tese investigou padrões de diversidade taxonômica, filogenética e funcional em 11 áreas de campos de altitude nas Serras do Caparaó e do Brigadeiro, ao longo de gradientes de altitude (1.560-2.892 m) e profundidade de solo (0-60,0 cm). No primeiro capítulo, demonstramos que a montagem de comunidades é governada por filtragem ambiental hierárquica, onde restrições climáticas sobrepõem-se às condições edáficas na estruturação filogenética. Embora solos profundos promovam consistentemente a diversidade taxonômica e filogenética, comunidades de alta altitude permanecem filogeneticamente agrupadas independentemente dos recursos edáficos, refletindo forte seleção para adaptações de tolerância ao frio. Métricas padronizadas (SES_PD, SES_MPD, SES_MNTD) revelaram agrupamento filogenético crescente com a altitude, indicando que linhagens estreitamente relacionadas persistem em ambientes extremos. No segundo capítulo, descobrimos que a profundidade do solo modula fortemente as respostas das características das plantas aos gradientes altitudinais. Enquanto solos profundos funcionam como refúgios hídricos, favorecendo espécies lenhosas conservadoras e atuando como uma barreira edáfica contra o estresse climático de altitudes elevadas, solos rasos filtram características foliares aquisitivas e formas de vida de plantas de ciclo curto. Em última análise, a síntese desses capítulos revela uma provável dissociação entre história evolutiva e estratégia ecológica: enquanto o estresse macroclimático (altitude) filtra estritamente linhagens intimamente relacionadas (agrupamento filogenético), a heterogeneidade do micro-habitat (profundidade do solo) impulsiona uma imensa divergência funcional dentro desses clados sobreviventes. Integrando essas abordagens, demonstramos que os gradientes ambientais atuam mais fortemente sobre as relações evolutivas e as características funcionais do que sobre a riqueza de espécies em si. Esses resultados têm implicações diretas para a conservação: comunidades de alta altitude abrigam

linhagens evolutivamente únicas e funcionalmente especializadas, tornando-as particularmente vulneráveis às mudanças climáticas. Recomendamos priorizar a proteção de zonas de elevada altitude que mantêm diversidade filogenética singular, bem como áreas de solo profundo que funcionam como pontos de alta diversidade ao longo do gradiente de elevação.

Palavras-chave: Ecologia de comunidades; Filogenia de comunidades; Traços funcionais; Gradientes ambientais; Páramos brasileiros; Montagem de comunidades; Campos rupestres; Mata Atlântica

SUMMARY

INTRODUCTION

NEOTROPICAL MONTANE ECOSYSTEMS AND THREATS TO PLANT COMMUNITIES

Neotropical montane ecosystems are recognized worldwide as biodiversity hotspots (Antonelli, 2015; Leitão et al., 2020; Rahbek et al., 2019) and species endemism centers (Colli-Silva et al., 2019; Guedes et al., 2020; Overbeck et al., 2022). Despite recent advances in the knowledge of tropical and subtropical mountain biodiversity, threats to these ecosystems are continually increasing. Montane communities are particularly vulnerable to climate change, as cold-adapted species tend to migrate toward the upper altitudes as optimal temperature ranges shift up the altitudinal gradient (Rahbek et al., 2019; Hoffmann et al., 2020; Zu et al., 2021). The phenomenon of upward migration has already been documented in several natural ecosystems (Steinbauer et al., 2018; Zu et al., 2021), and projections indicate an intensification of this process due to global warming (Ribeiro et al., 2023).

HIGH-ALTITUDE GRASSLANDS: ISLANDS OF BIODIVERSITY THREATENED

In the south and southeast of Brazil, landscapes above approximately 1,500-1,800 m of altitude are dominated by grassland and shrub formations known as "high-elevation tropical grasslands" (Vasconcelos, 2011; Safford, 1999; Figures 1 and 2). These ecosystems are part of the Atlantic Forest domain, a severely degraded and threatened global biodiversity hotspot (Rezende et al., 2018). Despite being home to remarkably diverse plant communities and being equally vulnerable to climate change and anthropogenic impacts, high-altitude grasslands remain poorly known by the scientific community (Bitencourt et al., 2016; Christmann et al., 2021).

The vegetation of high-altitude grasslands develops on rocky substrates consisting of intrusive igneous rocks (granites, syenites) or high-grade metamorphic rocks (gneisses, migmatites) (Benites et al., 2007; Safford, 1999). These formations exhibit floristic and structural affinities with the higher altitude vegetation of the Andes (Campos et al., 2018; Overbeck et al., 2022; Safford, 2007). Considered relicts of once more extensive montane ecosystems during glacial periods of the Pleistocene, highland grasslands were progressively reduced by the expansion of the surrounding forest matrix into warmer and wetter interglacial periods (Safford, 2007). Currently, these formations are home to a large number of endemic and micro-endemic species

(Fiaschi & Pirani, 2009; Safford, 2007; Veríssimo et al., 2012), many of which are restricted to a few mountains or even to a single massif.

ECOLOGICAL IMPORTANCE AND THREATS TO CONSERVATION

Although part of the territories of high-altitude grasslands is protected by conservation units, the biodiversity of these ecosystems remains highly vulnerable to anthropogenic disturbances and climate change (Bitencourt et al., 2016; Leão et al., 2014). In addition to their intrinsic value for biodiversity conservation, vegetated mountainous areas play a crucial role in maintaining essential ecosystem services, such as regulating the local climate and the hydrological cycle, since they intercept winds and clouds and function as springs for watersheds (Fernandes et al., 2020; Ribeiro & Freitas, 2010). This environmental and social importance is particularly relevant in densely populated regions of Brazil, reinforcing the urgency of their conservation (Assis & de Mattos, 2016; Gastauer et al., 2020).

COMMUNITY STRUCTURE AND ENVIRONMENTAL GRADIENTS

In high-altitude grasslands, plant communities are characterized by a dynamic arrangement of herbaceous and shrubby components, forming complex mosaics influenced by multiple environmental gradients on a reduced spatial scale (Campos et al., 2018; Cordeiro & Neri, 2019). These gradients include variations in altitude, topography, and edaphic features (Benites et al., 2007; Campos et al., 2018; Neri et al., 2017). The combined effects of substrate limitations, low temperatures, and intense solar radiation act as potent environmental filters, shaping the physiological, phenological, and morphological adaptations of the plant species that thrive in these high-altitude tropical grasslands and shrubs (Aparecido et al., 2018; Camerik & Werger, 1981; Neri et al., 2017; Vitarelli et al., 2016).

The vegetation is dominated by families such as Asteraceae, with characteristic genera such as *Baccharis*, *Vernonanthura*, *Senecio* and *Chionolaena*, and by graminoid families (Poaceae, Cyperaceae, Juncaceae), and the conspicuous presence of other families of the order Poales, especially Bromeliaceae, which form dense fields of clumps adapted to a wide range of daily thermal variation, high exposure to wind and water stress seasonal (Safford, 2007; Vasconcelos, 2011). These plant communities have high richness and endemism, with estimates indicating that endemism in highland grasslands can reach 60% in certain lineages, evidencing the role of these ecosystems as centers of diversification and isolation (Safford, 2007).

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Despite the intrinsic relevance of high-altitude grasslands, research focused on ecological patterns, processes, and the influence of environmental factors on community structuring is still relatively scarce (Campos et al., 2020, 2018; Christmann et al., 2021; Cordeiro & Neri, 2019; Gastauer et al., 2020). Approaches integrating multiple dimensions of diversity—taxonomic, phylogenetic, and functional—are particularly rare, limiting our understanding of the mechanisms of community assembly and the responses of these formations to environmental changes.

Figure 1- Serra do Brigadeiro, Minas Gerais, Brazil, protected by a State Park, presents a significant area of primary and regenerating Atlantic Forest (A, B), and at the tops of the mountain we find vast areas of rocky outcrops with native vegetation in pockets of soil (C), as well as continuous herbaceous-shrub fields (D), the typical 'highland fields'. The highest altitudes reach almost 2000 m above sea level.

This thesis aimed to fill this gap by investigating patterns of plant diversity in highland grasslands of southeastern Brazil along altitude gradients and soil depth, integrating taxonomic, phylogenetic and functional approaches. In **Chapter 1**, we examine how hierarchical environmental filters (climate and soil) structure taxonomic and phylogenetic diversity, testing whether phylogenetic clustering increases with altitude due to phylogenetic conservation of stress tolerance traits. In **Chapter 2**, we investigate patterns of functional diversity and their relationship with phylogenetic structure, evaluating whether convergence or divergence of traits

predominate in different environmental conditions. The findings of this thesis offer new perspectives to the theory of community assembly in tropical high mountain ecosystems and provide subsidies for the conservation of these unique and threatened ecosystems.

Figure 2. Serra do Caparaó, ES/MG, Brazil, protected by the National Park, has an extensive area of Atlantic Forest, and near the tops of the mountain there are vast areas with typical high-altitude grasslands (A, B, C) and rocky outcrops with native vegetation in soil pockets (D), as such. The highest altitude is found at Pico da Bandeira (A), 2892 m of altitude; (B) Pico do Cristal with 2770 m, is the highest in the state of Minas Gerais.

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CHAPTER 1

SOIL DEPTH PROMOTES DIVERSITY BUT CANNOT OVERCOME ENVIRONMENTAL FILTERING IN TROPICAL MONTANE GRASSLANDS

To be submitted to the Journal of Tropical Ecology

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ABSTRACT

Questions: How do elevation and soil depth shape taxonomic and phylogenetic diversity in tropical high-altitude grasslands? Does environmental filtering intensify at higher elevations, and can soil depth mitigate climatic constraints on community assembly?

Location: Eleven high-altitude grasslands sites in Southeastern Brazil spanning 1,500–2,892 m elevation.

Methods: We sampled plant community composition and coverage across gradients of elevation (1,665–2,890 m) and soil depth. We constructed a phylogenetic tree using V.PhyloMaker2 and calculated taxonomic diversity metrics using the complete species list, and phylogenetic metrics (phylogenetic diversity [PD], mean pairwise distance [MPD], mean nearest taxon distance [MNTD]). We computed standardized effect sizes (SES) for

phylogenetic metrics through null model randomizations to detect phylogenetic clustering or overdispersion. Linear mixed-effects models evaluated effects of elevation and soil depth (standardized) and their interaction on diversity metrics, with sampling sites as a random effect.

Results: Species richness and Shannon diversity increased significantly with soil depth ($t = 7.82$ and 7.65, $p < 0.001$) but showed no elevation effect. Phylogenetic diversity (PD) followed similar patterns. However, standardized phylogenetic metrics revealed contrasting patterns: SES.PD, SES.MPD, and SES.MNTD all decreased significantly with elevation ($t = -4.14$ to -5.48, $p < 0.01$), indicating stronger phylogenetic clustering at high elevations. Significant negative interactions between elevation and soil depth for SES.MNTD ($t = -3.24$, $p = 0.001$) demonstrated that deep soils promote diversity at lower elevations but cannot overcome climatic filtering at high elevations. Phylogenetic models explained more variance (R^2 marginal = 0.12–0.18) than taxonomic models (R^2marginal = 0.05–0.09).

Conclusions: Environmental filtering intensifies with elevation in tropical montane grasslands, producing phylogenetically clustered communities as only closely related lineages with cold-tolerance adaptations persist at high altitudes. Soil depth promotes both taxonomic and phylogenetic diversity but operates as a secondary filter subordinate to climatic constraints. This hierarchical filtering - where climate overrides edaphic conditions - has important implications for predicting community responses to climate change.

INTRODUCTION

Understanding the mechanisms that structure plant communities along environmental gradients is a central question in ecology (Körner 2007, Sundqvist et al. 2013). Elevation gradients provide natural laboratories for testing ecological and evolutionary hypotheses, as they encompass steep changes in temperature, precipitation, solar radiation, and soil conditions over short geographic distances (McCain & Grytnes 2010). These gradients generate predictable patterns in species diversity and composition, making them ideal systems to investigate how environmental factors filter species from regional pools and shape local community assembly (Bryant et al., 2008). A phylogenetic perspective is essential for unraveling the mechanisms of community assembly and species coexistence within the unique constraints of high-altitude tropical systems (Muellner-Riehl 2019, Long et al. 2025). By integrating evolutionary history, we can better understand the links between biodiversity patterns and ecosystem functioning (Cheng et al. 2023). This is particularly relevant in tropical mountains, where pronounced topographic heterogeneity creates a complex mosaic of microhabitats that act as distinct selective pressures on plant lineages (Vanneste et al. 2024).

Community assembly theory posits that local communities are structured by the interplay between environmental filtering and biotic interactions (Weiher & Keddy 1995, HilleRisLambers et al. 2012). Environmental filtering selects species with similar functional traits and evolutionary adaptations to local conditions, while competitive exclusion may prevent coexistence of ecologically similar species (Kraft et al. 2015). Phylogenetic approaches provide a powerful framework to infer these processes, as closely related species often share similar ecological traits due to phylogenetic niche conservatism (Webb et al. 2002, Wiens et al. 2010). When environmental filtering dominates, communities exhibit phylogenetic clustering, species are more closely related than expected by chance, reflecting shared adaptations to environmental stress (Cavender-Bares et al. 2009). Conversely, competitive exclusion may promote phylogenetic overdispersion, where co-occurring species are less related than expected (Webb et al. 2002). Beyond these niche-based mechanisms, neutral theory suggests that community assembly arises from stochastic processes, such as dispersal limitation and speciation, resulting in a phylogenetic structure indistinguishable from random null expectations (Webb et al. 2002, Hubbell 2005). However, interpreting such patterns requires caution; deterministic forces can operate simultaneously and in opposition, such as the

counterbalancing effects of filtering and competition, potentially yielding a random phylogenetic signal that mimics neutral dynamics (Cavender-Bares et al., 2009).

Along elevation gradients, environmental filtering is expected to intensify at higher altitudes due to increasingly harsh conditions such as low temperatures, high wind exposure, and intense solar radiation (Körner 2003, Machac et al. 2011). These stressors should favor phylogenetically clustered communities, as only lineages with appropriate cold-tolerance and stress-adaptation traits can persist (Cavender-Bares et al. 2004, Ackerly 2009). Additionally, soil depth represents a critical but often overlooked resource gradient in montane ecosystems, particularly in rocky grasslands where shallow soils limit water retention, nutrient availability, and root space (Jenny 1980, Benites et al. 2007). Deeper soils may relax environmental filtering by providing more heterogeneous microhabitats and resources, potentially supporting higher species richness and phylogenetic diversity through niche partitioning (Silvertown 2004, Kraft et al. 2008).

High-altitude grasslands in the Brazilian Atlantic Forest (*campo de altitude*) represent island-like ecosystems on mountain summits above 1,500-1,800 m elevation, forming natural laboratories for studying community assembly along steep environmental gradients. These ecosystems are characterized by harsh abiotic conditions including frequent frost events, high solar radiation, strong winds, and shallow nutrient-poor soils developed over plutonic substrates such as granite, gneiss, and syenite (Safford 1999, Benites et al. 2007). The vegetation consists of rocky outcrops interspersed with grassy and shrubby communities dominated by herbaceous species, dwarf shrubs, and scattered trees adapted to cold and drought stress (Safford 2007). Floristically, *campo de altitude* shares affinities with other Neotropical mountain systems including Andean páramos and Venezuelan tepuis yet harbor distinct assemblages with high endemism rates reaching 60% in some taxa (Safford 2007, Campos et al. 2018, Kessous et al. 2024).

These formations are considered relicts of more extensive montane ecosystems that occurred during Pleistocene glacial periods, subsequently fragmented by warmer interglacial climates, erosional processes, and forest expansion (Safford 1999). This paleoclimatic legacy, combined with current steep environmental gradients and geographic isolation among mountain ranges, makes campos de altitude particularly valuable for testing community assembly theory. Despite

their ecological importance as biodiversity hotspots and vulnerability to ongoing climate change (Martinelli 2007, Coelho et al. 2016, Scarano et al. 2016), few studies have examined how phylogenetic and functional community structure respond to environmental gradients in these systems (Gastauer et al. 2020, Massante et al. 2023). Understanding assembly mechanisms in *campo de altitude* thus contributes both to global montane ecology and to conservation of these threatened ecosystems.

Here, we investigate patterns of taxonomic and phylogenetic diversity across elevation and soil depth gradients in eleven high-elevation *campo de altitude* sites in southeastern Brazil. We use phylogenetic metrics to test whether environmental filtering or competitive interactions shape community assembly, and how these processes vary along environmental gradients. Based on community assembly theory and the environmental characteristics of high-altitude grasslands, we tested the following hypotheses: (i) Environmental filtering increases with altitude: We predict that species richness and phylogenetic diversity (PD) will decrease with elevation, as harsher conditions (lower temperatures, increased wind exposure) filter out lineages lacking cold-tolerance adaptations. Standardized phylogenetic metrics (SES-PD, SES-MPD, SES-MNTD) should exhibit negative values at higher elevations, indicating phylogenetic clustering driven by environmental filtering; (ii) Soil depth promotes diversity and relaxes environmental filtering: Deeper soils provide greater resource availability (water, nutrients, rooting space), supporting higher species richness and phylogenetic diversity. We predict positive relationships between soil depth and both taxonomic and phylogenetic diversity metrics. Additionally, phylogenetic clustering should be weaker (less negative SES values) in deeper soils, as increased resource availability allows coexistence of more distantly related lineages; (iii) Altitude and soil depth interact to shape community structure: the positive effect of soil depth on diversity will be stronger at lower elevations, where climatic conditions are less limiting. At high elevations, extreme environmental filters may override the benefits of deeper soils, resulting in persistent phylogenetic clustering regardless of soil depth.

MATERIAL AND METHODS

Study area and data collection

We conducted this study in eleven high-altitude grassland sites (*campos de altitude*) within the Atlantic Forest biogeographic province in southeastern Brazil (Figure 1). Sampling sites were

distributed across two mountain ranges: Serra do Caparaó (20°19'–20°37'S, 41°43'–41°53'W), reaching 2,892 m elevation and protected by Caparaó National Park; and Serra do Brigadeiro, with peaks up to 1,985 m elevation and protected by Serra do Brigadeiro State Park (Table 1). Both regions feature highland temperate climate (Cwb, Köppen classification), with mean annual temperatures of 9.4°C and 18°C, respectively, and mean annual precipitation around 1,300–1,400 mm (Alvares et al. 2013). The vegetation consists of rocky outcrops interspersed with grassy and shrubby communities occurring from 1,500 m elevation (Brade 1942, Veríssimo et al. 2012).

At each plot, we recorded elevation using a GPS device and measured soil depth at the plot center using a sharp metal rod. Plant cover was visually estimated for each species using the Braun-Blanquet cover-abundance scale. These environmental variables (elevation and soil depth) were used to investigate drivers of phylogenetic and taxonomic diversity patterns across the altitudinal gradient.

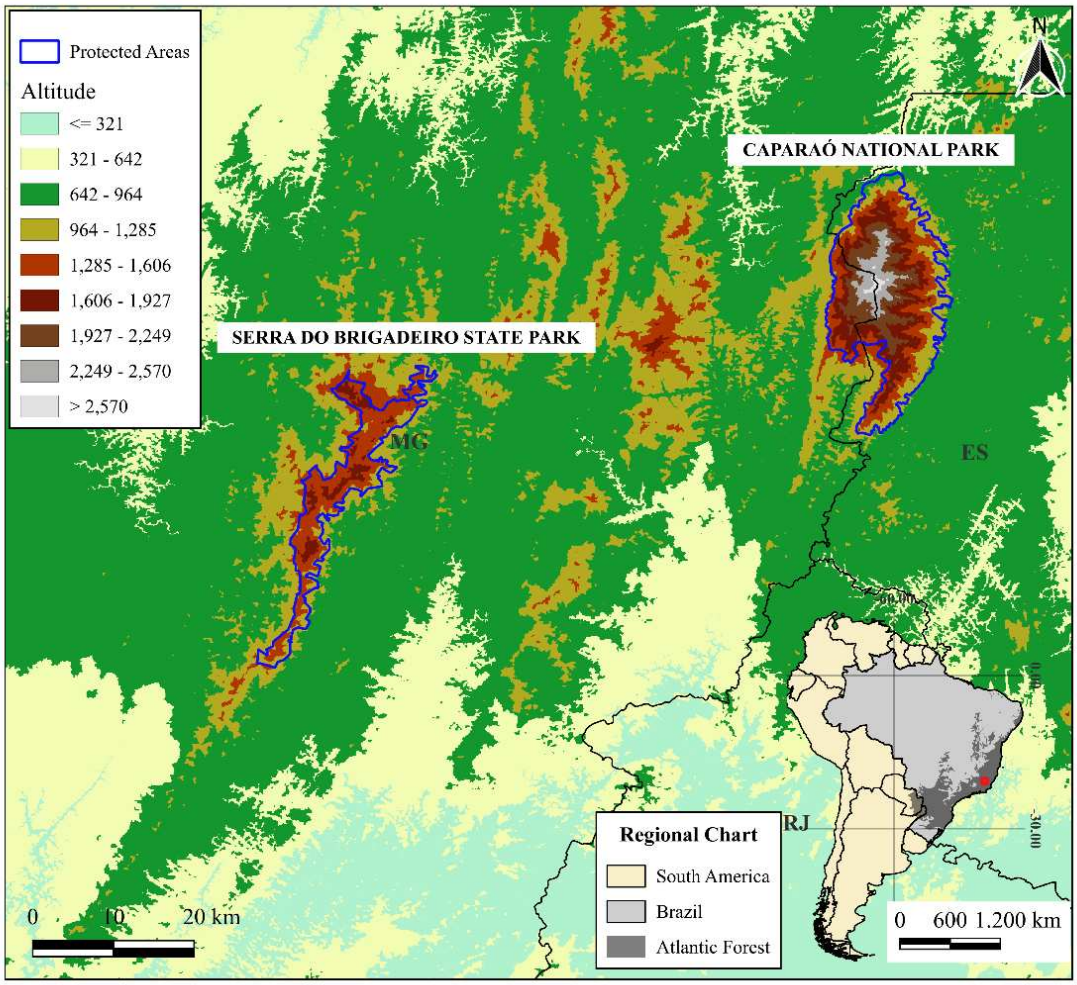

Figure 1. Regional context and geographic location of the two study areas within the Atlantic Forest biome, southeastern Brazil. The regional chart situates the study area (red dot) within the extent of the Brazilian Atlantic Forest. The main map displays the regional topography using a color scale for elevation (m a.s.l.), state borders (MG, ES, RJ), and the boundaries of the protected areas: Serra do Brigadeiro State Park and Caparaó National Park (blue lines).

Taxonomic standardization

The study was conducted using 1025 plots of 1 ×1 m, randomly distributed across eleven mountain summits and sampling sites (Table 1). Within each plot, all angiosperm species were inventoried, and their percentage of canopy cover was recorded. To ensure taxonomic consistency, all species names were standardized according to the Brazilian Flora 2020 database using the *florabr* package in R (Trindade 2024).

Table 1. Sampled sites with respective elevation range, number of plots set, and mountain range in Brazil they belong to (CNP: Caparaó National Park; SBSP: Serra do Brigadeiro State Park).

Sampled areas	Elevation range (m)	N° of plots (1x1m)	Mountain Range
***Cristal* Peak**	2229-2769	100	CNP
***Calçado* Peak**	2774-2841	100	CNP
***Bandeira* Peak**	2841-2890	100	CNP
Trail-2100	2100-2150	71	CNP
Trail-2300	2300-2350	72	CNP
Trail-2500	2500-2550	73	CNP
Trail-2700	2700-2750	74	CNP
***Pedra do Pato* Peak**	1687-1897	135	SBSP
***Elefante* Peak**	1687-1791	100	SBSP
***Mamute* Peak**	1813-1857	100	SBSP
***Totem-Deitado* Peak**	1665-1725	100	SBSP

Taxonomic and phylogenetic diversity metrics

To characterize taxonomic diversity, we compiled a comprehensive species list from all sampled plots. Species richness was quantified as the total number of species per plot. Additionally, we calculated Shannon diversity (H') and Simpson diversity using the *vegan* package in R (Oksanen et al. 2026). To ensure that differences in species richness were not an artifact of varying sampling intensities of individual densities across the elevational gradient, we generated individual-based rarefaction and extrapolation curves using the iNEXT package (Chao et al. 2021). This approach standardizes diversity estimates through the framework of Hill numbers based on sample coverage. To perform this rarefaction analysis across the elevation range, elevation was categorized into three distinct zones: low, medium and high. These boundaries were established based on the 10th, 50th, and 90th statistical percentiles of the elevation distribution across all plots, ensuring that the categories accurately reflected the empirical distribution of our sampling effort rather than arbitrary thresholds.

To explore the phylogenetic dimension of these plant communities, we first constructed a phylogenetic tree with 193 species identified (Figure 2) to serve as backbone. This was achieved

using the V.PhyloMaker2 package (Jin & Qian 2022) under Scenario 3, which generates phylogenies based on the mega-tree GBOTB.extended. The resulting tree was aligned with our community matrix using the 'match.phylo.comm' function from the *picante* package (Kembel et al. 2022), retaining only species present in both datasets.

We then calculated the following phylogenetic diversity metrics: (1) Faith's phylogenetic diversity (PD), representing the total branch length spanning all species in a community; (2) mean pairwise distance (MPD), the average phylogenetic distance between all species pairs; and (3) mean nearest taxon distance (MNTD), the average phylogenetic distance to the nearest heterospecific neighbor for each species.

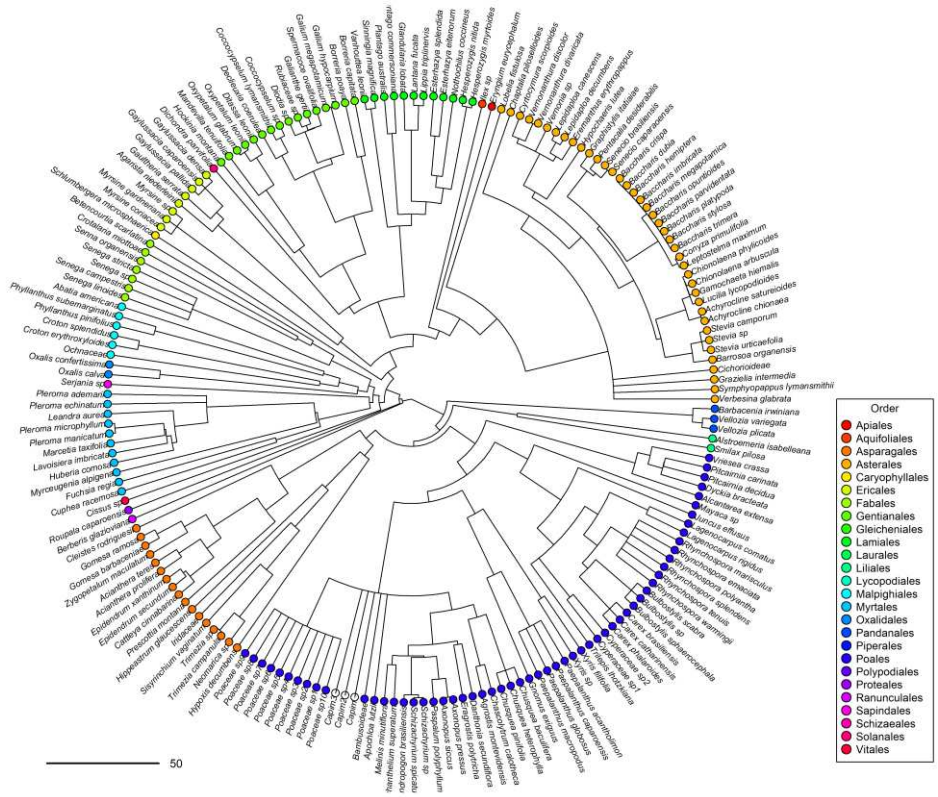

Figure 2. Phylogenetic tree of plant species sampled in campos de altitude of southeastern Brazil. The tree was constructed using V.PhyloMaker2 based on the GBOTB mega-tree. Colored circles at branch tips indicate botanical orders. Scale bar represents millions of years of evolutionary divergence. The tree includes 193 species from 54 families used in phylogenetic diversity analyses.

To assess phylogenetic community structure, we calculated standardized effect sizes (SES) for PD, MPD, and MNTD by comparing observed values against null distributions generated

through 999 randomizations using the "taxa.labels" null model. Negative SES values indicate phylogenetic clustering (species more related than expected by chance), while positive values indicate overdispersion (species less related than expected). All phylogenetic analyses were conducted using the *picante* package. The *SES* metrics were calculated using the following equation:

$$SES = \frac{\text{Metric}_{observed} - Mean(\text{Metric}_{\text{null}})}{\text{SD}(\text{Metric}_{null})}$$

Where $\text{Metric}_{observed}$ is the observed phylogenetic metric (PD, MPD, or MNTD), $\text{Mean}(\text{Metric}_{null})$ is the mean of the metric across the 999 null communities, and $\text{SD}(\text{Metric}_{null})$ is the standard deviation of the null communities.

Statistical analysis

We used linear mixed-effects models (LMMs) to evaluate the effects of elevation and soil depth on diversity metrics. Each diversity metric was modeled as a response variable, with altitude and soil depth (both standardized) as fixed effects, including their interaction. 'Sampling-site' was included as a random effect to account for spatial non-independence. Models were fitted using restricted maximum likelihood (REML) in the *lme4* package (Bates et al. 2026), with p-values calculated using Satterthwaite's approximation using *lmerTest* package (Kuznetsova et al., 2026). Model fit was assessed using marginal R^2 (variance explained by fixed effects) and conditional R^2 (variance explained by fixed and random effects combined) from the *performance* package (Lüdecke et al. 2021).

RESULTS

Floristic composition

We recorded a total of 5797 angiosperm plant occurrences (individual plants or clumps), belonging to 209 species, 132 genera, and 45 families. Of these species, 77.03% were identified at the species level, 7.21% at the genus level, and 7.76% at the family level. A small fraction (6.30%) remained indeterminate due to the absence of diagnostic reproductive material or insufficient taxonomic resolution.

Species accumulation and sampling effort

Rarefaction and extrapolation curves revealed distinct diversity patterns across elevational zones (Figure 3). Medium-elevation sites exhibited substantially higher species diversity (~130 species at standardized sampling effort) compared to both low (~85 species) and high-elevation sites (~75 species), demonstrating a mid-elevation diversity peak. All three elevational zones showed asymptotic rarefaction curves, indicating adequate sampling coverage, though extrapolation curves suggest medium-elevation communities harbor additional undetected species. The steeper initial slope of medium-elevation curves indicates higher species encounter rates and communities more even compared to the extremes of the gradient. High-elevation sites reached asymptotes earliest, consistent with smaller species pools filtered by harsh environmental conditions. These patterns confirm that the lower species richness observed at high elevations in our models reflects genuine ecological filtering rather than sampling artifacts.

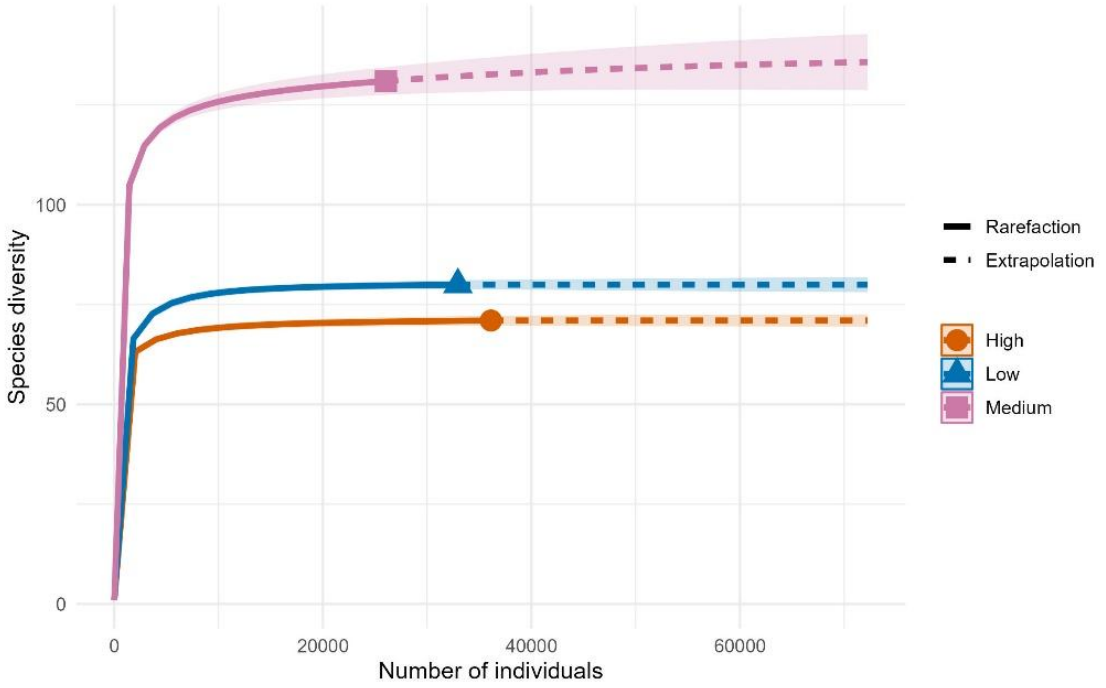

Figure 3. Individual-based rarefaction (solid lines) and extrapolation (dashed lines) curves for species diversity across three elevational zones in campo de altitude (Low, Medium, and High). Solid geometric shapes (triangle, square, and circle) represent the observed number of individuals (reference samples) for each elevational band. Curves were calculated using iNEXT with 95% confidence intervals (shaded areas). Medium-elevation sites exhibit substantially higher diversity than low and high elevations, demonstrating a mid-elevation diversity peak. Asymptotic curves indicate adequate sampling coverage across all zones.

Drivers of absolute taxonomic and phylogenetic diversity

Soil depth was the primary driver of absolute diversity metrics across the mountain ranges studied (Table 0). Species richness showed a strong positive response to soil depth ($t = 7.82$, $p < 0.001$) but no effect of elevation ($t = 0.17$, $p = 0.87$; Figure 0.4A). The interaction between elevation and soil depth was not significant ($t = 1.14$, $p = 0.26$), indicating that the positive effect of soil depth on richness was consistent across the elevational gradient. Both Shannon and Simpson diversity indices exhibited similar patterns, with significant positive effects of soil depth (Shannon: $t = 7.65$, $p < 0.001$; Simpson: $t = 7.34$, $p < 0.001$, Figure 0.4 B-C) and significant interactions with elevation (Shannon: $t = 2.05$, $p = 0.04$; Simpson: $t = 2.51$, $p = 0.01$). This suggests that the positive effect of soil depth on evenness-weighted diversity strengthens at lower elevations. Fixed effects explained 5.2-8.6 % of the variance in taxonomic metrics, while sampling site accounted for an additional 14-19 % of the variance. We observed a strong, positive, and highly significant effect of soil depth on total Phylogenetic Diversity (PD) ($t = 5.624$, $p < 0.001$; Figure 0.4D), but elevation alone did not significantly affect this unstandardized metric ($p > 0.15$). Models for these four absolute metrics explained a substantial portion of the variance, with marginal R^2 ranging from 0.020 to 0.168.

Table 0. Linear mixed-effects model results for diversity metrics. Alt = altitude; Soil = soil depth; Int = interaction; R^2_marg = variance explained by fixed effects; R^2_cond = variance explained by fixed and random effects. SES = standardized effect size; MPD = mean pairwise distance; MNTD = mean nearest taxon distance; PD = phylogenetic diversity. Sampling site was included as random effect. Bold values indicate $p < 0.05$.

Metric	*Alt_t*	*Alt_p*	*Soil_t*	*Soil_p*	*Int_t*	*Int_p*	*R2_marg*	*R2_cond*
Richness	0.174	0.864	7.815	1.32e-14	1.139	0.255	0.052	0.190
Shannon	1.502	0.158	7.652	4.44e-14	2.051	0.040	0.086	0.278
Simpson	1.686	0.117	7.344	4.17e-13	2.508	0.012	0.093	0.295
PD	0.720	0.485	7.171	1.40e-12	0.465	0.642	0.051	0.211
SES.PD	-3.948	0.002	-3.992	6.98e-05	0.247	0.805	0.168	0.267
MPD	-2.443	0.039	-0.096	0.923	-1.267	0.205	0.020	0.043

SES.MPD	-3.168	0.012	1.169	0.242	-2.085	0.037	0.039	0.066
MNTD	-5.477	0.0004	-3.117	1.87e-03	-3.085	0.002	0.120	0.147
SES.MNTD	-3.497	0.006	-0.270	0.787	-3.141	0.002	0.087	0.150

Shifts in phylogenetic community structure

While absolute lineage richness (PD) was driven by soil resources, the standardized phylogenetic structure and mean evolutionary distances were strongly constrained by elevation (Figure 0.4 E-I). Elevation had a significant negative effect on MPD ($t = -2.443$, $p = 0.039$), MNTD ($t = -5.477$, $p < 0.001$), and SES.PD ($t = -4.141$, $p = 0.002$). Furthermore, soil depth negatively affected MNTD ($t = -3.117$, $p = 0.002$) and SES.PD ($t = -3.698$, $p < 0.001$). Crucially, the standardized effect sizes of the phylogenetic distances (SES.MPD and SES.MNTD), which account for variations in species richness, revealed strong interactive effects of the environment. Elevation consistently drove SES.MPD ($t = -3.527$, $p = 0.007$) and SES.MNTD ($t = -3.483$, $p = 0.006$) towards more negative values, indicating a shift towards phylogenetic clustering at higher altitudes. This clustering effect was further modulated by the interaction between elevation and soil depth, which was significantly negative for both SES.MPD ($t = -2.149$, $p = 0.032$) and SES.MNTD ($t = -3.236$, $p = 0.001$). The variance explained by the fixed effects (R^2_m) for these structural metrics ranged from 0.046 to 0.120, with the full models (R^2_c) explaining up to 0.150 of the variance.

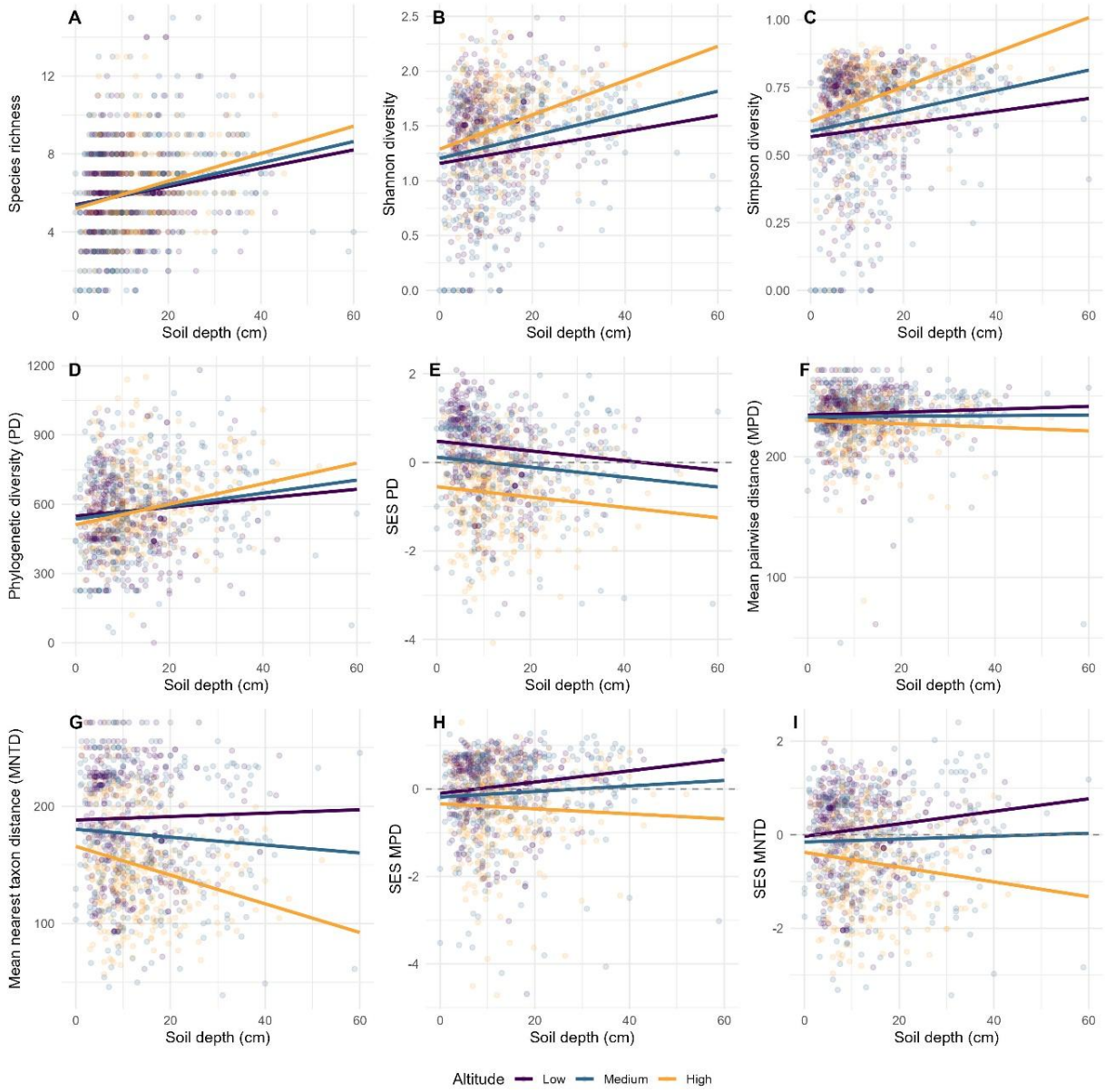

Figure 0.4. Effects of soil depth and elevation on diversity metrics in campos de altitude. Lines show model predictions at low (purple), medium (blue), and high (orange) elevations for: (A) species richness, (B) Shannon diversity, (C) Simpson diversity, (D) phylogenetic diversity (PD), (E) SES PD, (F) mean pairwise distance (MPD), (G) mean nearest taxon distance (MNTD), (H) SES MPD, and (I) SES MNTD. Dashed lines in panels E, H, and I indicate null expectation (SES = 0). See Table 1 for statistics.

DISCUSSION

Mid-elevation diversity peak and sampling adequacy

The pronounced mid-elevation diversity peak revealed by rarefaction analysis aligns with global patterns observed in montane systems worldwide (McCain & Grytnes 2010, Rahbek et al. 2019). This pattern likely reflects the interplay between climatic harshness at high elevations and competitive or resource limitations at low elevations (the "optimal conditions hypothesis"; (Colwell & Lees 2000). Medium elevations in *campos de altitude* may represent transitional zones where climatic stress is relaxed relative to summits, yet environmental filtering remains strong enough to prevent dominance by a few competitive species, maximizing species coexistence (Körner 2007). Additionally, mid-elevation sites in our study exhibited intermediate soil depths, potentially offering the greatest habitat heterogeneity and niche diversity. The asymptotic rarefaction curves across all elevational zones confirm that our diversity estimates are robust and not driven by differential sampling effort, strengthening conclusions about environmental filtering processes on phylogenetic lineages. The earlier asymptote at high elevations further supports the interpretation that these communities are genuinely species-poor due to environmental filtering, not under-sampling.

Environmental filtering drives phylogenetic clustering at high elevations

Our results provide strong evidence for environmental filtering as the primary mechanism structuring plant communities in high-altitude grasslands. The significant negative relationship between altitude and standardized phylogenetic metrics (SES.MPD and SES.MNTD) demonstrates that communities at higher elevations are phylogenetically clustered-composed of more closely related species than expected by chance. This pattern indicates that harsh environmental conditions at mountain summits, including low temperatures, high wind exposure, and intense solar radiation (Safford 1999, Körner 2003, Larcher et al. 2010), impose strong selection pressures that only certain evolutionary lineages can tolerate.

The phylogenetic clustering observed at fine evolutionary scales (SES.MNTD) is particularly revealing. While broad-scale clustering (SES.MPD) may reflect filtering of entire clades, clustering at the tips of the phylogeny suggests that even recently diverged species require similar adaptations to persist in extreme high-altitude environments (Cavender-Bares et al. 2009). This pattern is consistent with phylogenetic niche conservatism, where closely related species retain similar physiological tolerances and ecological requirements (Wiens et al. 2010). In *campos de altitude*, the dominance of certain lineages at high elevations provides clear evidence of this filtering process. Asteraceae emerged as the most species-rich family across

the elevational gradient, with peak diversity at high altitudes where genera such as *Baccharis*, *Chionolaena* and *Senecio*, dominate the shrubby component. Lineages within the order Poales, specifically graminoid families such as Poaceae, Cyperaceae, and Juncaceae, alongside Bromeliaceae show pronounced clustering at mountain summits, forming dense tussock and rosettes grasslands adapted to cold temperatures, high wind exposure, and seasonal water stress. Within Poaceae, genera like *Chusquea* and *Danthonia* are characteristic of the highest elevations, while Cyperaceae (*Trilepis*, *Bulbostylis*) and Bromeliaceae (*Dyckia*, *Pitcairnia*) occupy rocky outcrops with shallow soils. This taxonomic concentration reflects phylogenetic conservatism of key functional traits such as cold tolerance, drought resistance during dry seasons, C4 photosynthesis in grasses, CAM metabolism in bromeliads, and ability to withstand high UV radiation, adaptations that appear phylogenetically conserved and limit which lineages can colonize and persist at the highest elevations (Safford 2007, Zorger et al. 2025).

Interestingly, while phylogenetic diversity (PD) and species richness increased with soil depth, these metrics showed no direct relationship with elevation. This pattern likely reflects the relatively narrow elevational range of campos de altitude (~700–1,600 m in our study), where vegetation is primarily controlled by local edaphic heterogeneity rather than broad climatic zonation (Safford 1999, Christmann & Oliveras 2020). Unlike continental mountain systems with elevational gradients spanning 3,000–4,000 m where distinct vegetation belts emerge, the compressed elevational range in southeastern Brazilian mountains creates a mosaic landscape where soil depth, rockiness, and drainage patterns exert stronger local control on species distributions than elevation per se. This apparent contradiction - the phylogenetic structure shaped by environmental filters in the high mountains, but not the overall diversity - can be explained by considering absolute versus standardized metrics. Raw PD reflects both the number of species and their evolutionary relationships, whereas SES metrics explicitly account for richness differences through randomization procedures (Webb et al. 2002). Our results suggest that high-altitude communities may maintain moderate species richness across elevations through recruitment from different microhabitats (deep soils, rock crevices, waterlogged depressions; see Benites et al. 2007), but these species are drawn from a phylogenetically restricted subset of the regional pool, concentrated within lineages possessing critical stress-tolerance adaptations. Thus, while soil depth determines how many species can coexist locally via resource availability, elevation determines which lineages can persist via physiological filtering.

Soil depth promotes diversity but cannot overcome climatic constraints

Soil depth emerged as a consistent and strong predictor of both taxonomic and phylogenetic diversity. Deeper soils supported significantly higher species richness, Shannon diversity, and phylogenetic diversity, confirming that edaphic conditions play a crucial role in shaping plant communities in rocky grasslands (Benites et al. 2007, Schaefer et al. 2016). This pattern likely reflects multiple mechanisms: deeper soils retain more water during dry periods, accumulate greater nutrient pools, and provide more rooting space for diverse plant growth forms (Jenny 1980, Silvertown 2004). The positive effect of soil depth on diversity suggests that resource availability can partially relax environmental filtering, allowing coexistence of species with different resource acquisition strategies.

However, the significant interactions between altitude and soil depth in several phylogenetic structure metrics (SES.MNTD, SES.MPD) reveal a critical nuance: the benefits of deeper soils are context-dependent and diminish under extreme climatic stress. At high elevations, even plots with deep soils exhibited phylogenetic clustering, indicating that climatic filtering overrides edaphic benefits. This hierarchical filtering process, where climate (elevation) acts as a primary filter and soil as a secondary modulator, is consistent with niche theory predictions that fundamental physiological tolerances (e.g., cold tolerance) constrain species distributions more strongly than resource competition (Weiher & Keddy 1995, HilleRisLambers et al. 2012).

The negative interaction effects in SES models indicate that the positive relationship between soil depth and phylogenetic diversity weakens at higher elevations. In other words, while deep soils at lower elevations can support phylogenetically diverse assemblages through niche partitioning, the same deep soils at high elevations still harbor phylogenetically clustered communities. This suggests that soil depth cannot "rescue" communities from climatic filtering - no amount of soil resources can compensate for lack of cold tolerance or other high-altitude adaptations (Körner 2003). This finding has important implications for predicting community responses to global change: even if soil conditions remain favorable, warming-driven upward migration of species will be constrained by their phylogenetic legacy of physiological tolerances.

Taxonomic versus phylogenetic diversity: different responses to environmental gradients

A notable finding is the decoupling between taxonomic and phylogenetic diversity patterns. While species richness and abundance-weighted diversity indices (Shannon and Simpson) showed strong positive responses to soil depth with minimal altitude effects, phylogenetic structure metrics (SES.PD, SES.MPD, SES.MNTD) exhibited pronounced altitude effects and complex interactions. The congruent results between Shannon and Simpson indices confirm that these patterns are robust regardless of whether diversity is measured emphasizing richness or evenness (Magurran 2004), strengthening confidence in our taxonomic diversity findings. This divergence between taxonomic and phylogenetic patterns underscores the value of integrating both approaches: taxonomic metrics reveal how many species coexist and their relative abundances, while phylogenetic metrics reveal which lineages coexist and whether their evolutionary relationships deviate from random assembly (Cadotte et al. 2010, Morris et al. 2014).

The stronger explanatory power of phylogenetic models (R^2 marginal = 0.12-0.18 for MNTD and SES.PD) compared to taxonomic models (R^2 marginal = 0.05-0.09) suggests that environmental gradients act more strongly on evolutionary relatedness than on species counts. This pattern implies that environmental filtering operates primarily through selection on phylogenetically conserved traits rather than through stochastic reduction of species numbers. Communities at different elevations may harbor similar numbers of species, but these species represent fundamentally different evolutionary lineages with distinct adaptive capabilities (Ackerly 2009).

Implications for conservation and global change

Our findings have direct implications for conservation and management of campos de altitude ecosystems. The strong phylogenetic clustering at high elevations indicates that these communities are composed of evolutionarily unique lineages with specialized adaptations, making them particularly vulnerable to environmental change (Thuiller et al. 2011). Climate warming may disrupt these filtered assemblages by favoring upward migration of lowland species, potentially homogenizing the distinct phylogenetic structure of high-altitude communities (Pauli et al. 2012).

The critical role of soil depth in maintaining diversity highlights the importance of protecting the physical integrity of these rocky grasslands. Soil formation is extremely slow in high-

altitude environments, and disturbances that reduce soil depth, such as erosion from trampling, fire, or infrastructure development, may cause irreversible diversity losses (Benites et al. 2007, Fernandes 2016). Conservation strategies should prioritize areas with deeper soils as hotspots of diversity while recognizing that even deep-soil patches at high elevations harbor phylogenetically specialized communities requiring protection.

CONCLUSIONS

Environmental filtering operates hierarchically in *campos de altitude*, with climate overriding edaphic conditions to shape phylogenetic community structure along elevational gradients. While deeper soils consistently promote taxonomic diversity, communities at high elevations remain phylogenetically clustered regardless of soil resources, reflecting strong selection for cold-tolerance adaptations concentrated in specific lineages such as Asteraceae, Iridaceae and Poales families (Poaceae, Cyperaceae, Juncaceae, Bromeliaceae). The mid-elevation diversity peak and decoupling between taxonomic and phylogenetic patterns demonstrate that environmental gradients act more strongly on evolutionary relatedness than species richness, with medium elevations offering optimal conditions for phylogenetically diverse assemblages. These findings advance understanding of tropical montane community assembly and highlight urgent conservation needs: high-altitude communities harbor phylogenetically unique lineages particularly vulnerable to climate warming, while deep-soil patches across the gradient function as diversity hotspots requiring protection from anthropogenic disturbances. Integrating phylogenetic approaches with traditional diversity metrics thus provides crucial insights for both ecological theory and conservation prioritization in threatened mountaintop ecosystems.

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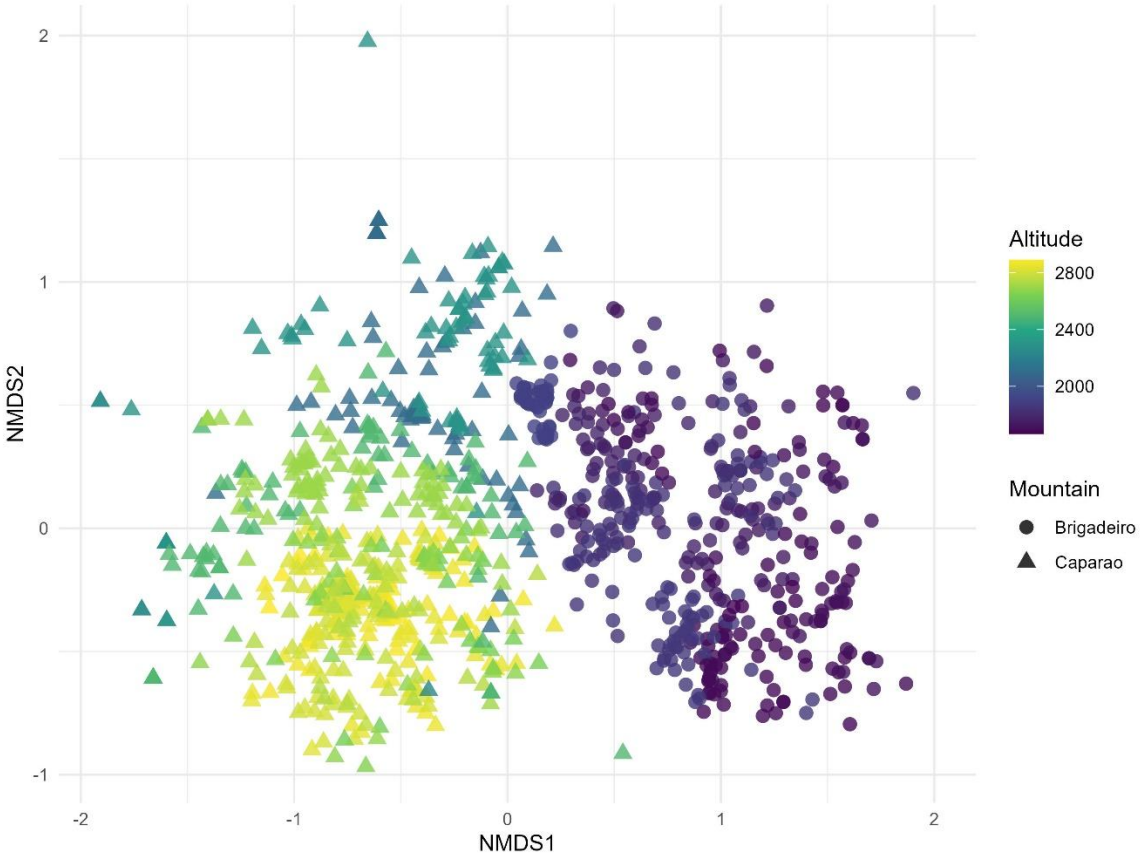
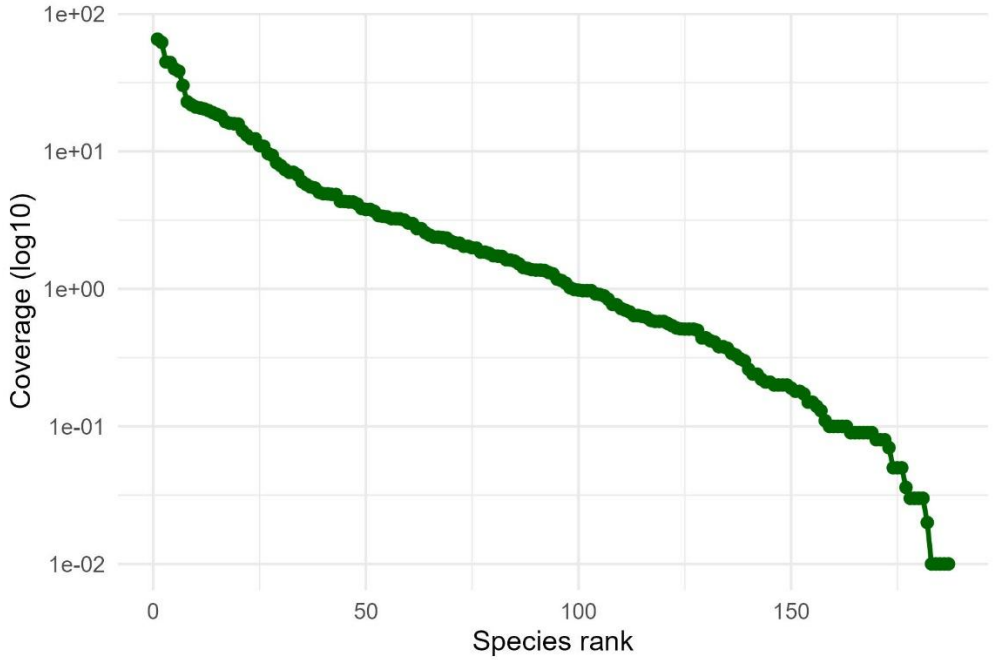
SUPPLEMENTARY MATERIAL



Suppl. Figure 1 Non-metric multidimensional scaling (NMDS) ordination based on plant species composition across 1 m² sampling plots in campos de altitude. Each point represents a plot, and distances among points reflect compositional dissimilarity, with closer points indicating more similar species assemblages. Point colors represent plot elevation, showing how floristic composition varies along the elevational gradient.



Suppl. Figure 2. Rank-abundance curve (Whittaker plot) for the angiosperm community sampled across the elevational gradient in the Campos de Altitude. Species are ranked on the x-axis from the most abundant to the least abundant, with their respective total canopy coverage (used as a proxy for abundance, log10-transformed) on the y-axis. The steep initial decline followed by a long tail illustrates a community structured by a few highly dominant species and a large pool of rare taxa.

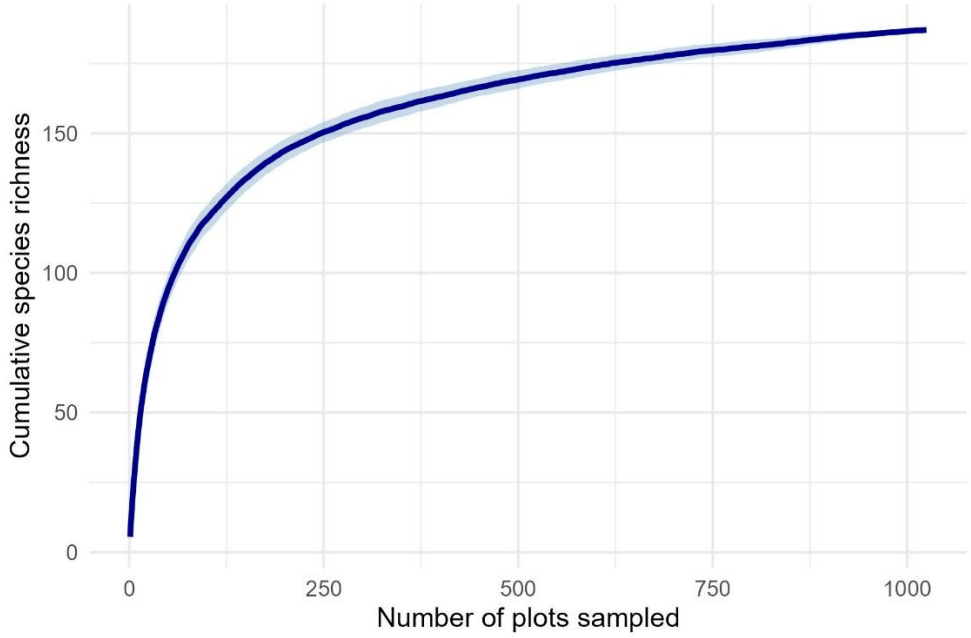


Figure 5. Plot-based species accumulation curve for the entire study area. The solid blue line represents the expected cumulative species richness as a function of the number of sampled plots (total $n = 1025$). The light blue shaded area indicates the 95% confidence intervals based on random permutations. The clear asymptotic trend of the curve demonstrates that the sampling effort was robust and sufficient to capture the vast majority of the regional species pool.

CHAPTER 2

THE EDAPHIC BUFFER: SOIL DEPTH DECOUPLES PLANT FUNCTIONAL TRAITS FROM ELEVATIONAL GRADIENTS IN TROPICAL HIGH-ALTITUDE GRASSLANDS AND ROCK OUTCROPS

To be submitted to the journal '*Ecosystems'*.

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HIGHLIGHTS

- Soil depth strongly modulates plant trait responses to elevational gradients.
- Deep soils function as an edaphic buffer against the climatic stress of high altitudes.
- Shallow soils filter for acquisitive traits and short-cycle plant life forms.
- Deep soil pockets serve as hydraulic refugia, favoring conservative woody species.

ABSTRACT

Aim/Questions: In tropical mountain ecosystems, climatic gradients are traditionally viewed as the primary drivers of plant community assembly. However, in mountain grasslands with rocky outcrops, fine-scale soil heterogeneity may override climatic constraints. Here, we investigated how elevation and soil depth interact to shape the functional structure and life-form composition of plant communities in a Brazilian high-altitude rocky complex.

Location: Eleven sampling sites in high-altitude grasslands. across two mountain ridges in Brazilian Atlantic Forest.

Methods: We established 1025 1.0 m² plots along an elevational gradient from 1650 m to 2892 m, recorded all vascular plants and measured functional traits and soil depth in each plot. The patterns of abiotic variables, functional diversity, and community-weighted mean (CWM) of functional traits were explored along the elevational gradient by using regression linear mixed models.

Results: Contrary to classical expectations, elevation was not the main predictor of functional variation. Instead, we identified a critical "Edaphic Buffering Effect" where soil depth modulated plant responses to the climatic gradient. While shallow soils at high elevations tend to select stress-avoidance strategies, deep soil pockets acted as hydraulic refugia. These deeper microhabitats supported conservative strategies (low SLA, high LDMC) and woody life forms (nanophanerophytes), effectively buffering the reduction in leaf and fruit dimensions typically induced by high altitude.

Conclusions: Our results demonstrate that edaphic filters can decouple functional traits from atmospheric forcing, creating a mosaic of "acquisitive" and "conservative" strategies within the same climatic envelope. These findings challenge the assumption of uniform functional responses to elevation and highlight the importance of soil depth in maintaining the functional diversity and resilience of tropical montane floras.

Keywords: Environmental filtering; community-weighted mean; leaf economics spectrum; campo de altitude; microrefugia; natural grassland.

INTRODUCTION

Tropical mountain ecosystems are globally recognized as biodiversity hotspots (Antonelli 2015; Rahbek and others 2019) and as centers of species endemism (Colli-Silva and others 2019; Guedes and others 2020). However, these ecosystems are particularly vulnerable to habitat changes, especially as current climate change progresses and optimal temperature ranges shift upwards, mountain species – generally less resilient to such fluctuations – are expected to face significant habitat reduction (Hoffmann and others 2020; Zu and others 2021). Upslope species migration in natural mountain systems has already been documented by

scientific literature (Lenoir and Svenning 2013; Steinbauer and others 2018), and current models predict a contraction of suitable areas for species in tropical mountaintop grasslands due to warming (Ribeiro and others 2023). While elevational gradient studies are widely used as proxies to predict climate change responses (Körner 2007), these macroclimatic models often overlook the critical role of edaphic heterogeneity. In tropical high-altitude grasslands and rock outcrops, fine-scale variations in soil depth create distinct microhabitats that may buffer or exacerbate climatic stress (Schaefer and others 2016). Therefore, to accurately predict plant community shifts, it is essential to understand how multiple interacting filters, specifically elevation and soil characteristics, jointly shape plant functional strategies. Assessing the variation in functional traits across these combined gradients offers a mechanistic understanding of species' responsiveness and their true adaptive potential under future climate scenarios (Heilmeier 2019; Ahrens and others 2020).

In the Atlantic Forest of southern and southeastern Brazil, a highly threatened global biodiversity hotspot, landscapes above 1500 m are often dominated by high-elevation grasslands and shrublands known as *campos de altitude* (Safford 1999; Rezende and others 2018). Established on crystalline basements (e.g., granite, syenite, gneiss), this vegetation shares floristic and structural affinities with other Neotropical mountain systems (Safford 2007; Campos and others 2018; Costa and others 2018; Kessous and others 2024). Considered relicts of a once more extensive montane ecosystem during last glacial ages, these formations have been progressively reduced by the erosional process, the warmer and wetter climate of interglacial periods, and forest expansion (Safford 2007). Nevertheless, they continue to sustain a remarkable diversity of species, several endemic or even micro-endemic (Fiaschi and Pirani 2009; Tinti and others 2015). Despite their recognized importance for water provision, tourism, and climate regulation (Christmann and Oliveras 2020; Fernandes and others 2020), c*ampos de altitude* are continuously threatened by changes in Brazilian environmental legislation, which historically prioritize forest biomes while leaving non-forest open ecosystems legally unprotected (Ribeiro and Freitas 2010; Overbeck and others 2024; Bencke and others 2025; Kessous 2026). While several protected areas have been established (Azevedo and others 2024), these environments remain highly vulnerable to specific anthropogenic disturbances. Unregulated tourism, historical overgrazing, and human-induced frequent fires cause severe physical degradation to the already shallow edaphic layer, accelerating soil erosion and facilitating the establishment of aggressive invasive exotic species (e.g., African grasses, trees

like *Pinus* and *Eucalyptus/Corymbia*). Compounded by the shrinking of the alpine climatic envelope due to climate change (Christmann and others 2021), the rapid degradation of these microhabitats highlights the urgent need for a deeper understanding of their ecological dynamics to support effective conservation strategies (Assis and de Mattos 2016; Gastauer and others 2020).

Plant communities in *campos de altitude* are characterized by a dynamic mosaic of herbaceous and shrubby components, driven by complex environmental gradients at short spatial scales (Campos and others 2018; Cordeiro and Neri 2019). Variations in elevation, topography, and particularly soil depth create formidable environmental filters (Benites and others 2007; Neri and others 2016). The combination of substrate limitations, low temperatures, and intense solar radiation shapes the assembly of these communities, selecting flora with specific functional traits associated with stress tolerance and avoidance (Vitarelli and others 2016; Aparecido and others 2018). Common adaptations to the harsh conditions of these tropical mountain environments include sclerophyllous leaves and pubescence, which provide protection against radiation and enhance water retention, as well as rosette architectures that minimize wind exposure. Low-growing shrubs, forbs, graminoids (many forming tussocks), herbaceous perennials, and geophytes are also prominent. Notably, the presence of belowground storage organs (e.g., bulbs, tubers, *xylopodia*) confers resilience to both natural environmental harshness and anthropogenic physical disturbances, representing a key adaptive strategy in these ecosystems (Lopes-Mattos and others 2013; Ott and others 2019). However, research mechanistically linking these specific environmental drivers, especially edaphic constraints, to functional community assembly rules is still scarce (Campos and others 2020; Zorger and others 2025b). As a result, there is a pressing need to expand our understanding of how these unique ecosystems function and unravel the intricacies of their trait-environment dynamics.

To bridge this knowledge gap, it is essential to look beyond taxonomic diversity, which focuses solely on species identity, and incorporate a multidimensional functional perspective (Cadotte and others 2015). Functional ecology provides a powerful framework by focusing on traits that influence species' performance and their response to environmental conditions (Violle and others 2007; Cadotte and others 2015). By analyzing functional diversity and community-weighted means (Laliberte and Legendre 2010), researchers can better disentangle the mechanisms governing community assembly. While studies frequently show a change in

resource-use strategy along elevational gradients, with plants at higher elevations typically exhibiting conservative traits (Ding and others 2019; Schroeder and others 2024), these macroclimatic models often overlook local edaphic heterogeneity. In highly restrictive environments, variations in soil depth dictate root space, nutrient availability, and water retention capacity. Thus, deeper soils might act as crucial microrefugia, potentially buffering the climatic stress of high altitudes and altering the expected fast-slow-plant economic spectrum (Reich 2014).

In this study, we aimed to assess how functional strategies in Campos de Altitude respond to fine-scale environmental gradients. Specifically, we tested the following hypotheses: (i) Along the climatic gradient, increasing elevation will generally filter for resource-conserving strategies and reduced plant dimensions due to thermal and exposure stress; (ii) Along the edaphic gradient, shallow soils will impose severe resource limitations, selecting for stress-avoidance strategies (e.g., short life cycles, acquisitive leaf traits) or extreme stress-tolerance, shifting the dominant life forms to hemicryptophytes and therophytes; and crucially, (iii) The Edaphic Buffer Hypothesis: Soil depth will interact with elevation, effectively decoupling functional traits from the climatic-altitudinal gradient. We predict that deep soil pockets will mitigate the harshness of high altitudes, buffering the expected reduction in plant size and sustaining conservative woody strategies even at the uppermost limits of the gradient.

MATERIAL AND METHODS

Study area and vegetation data

The study was conducted across 11 high-altitude rocky grasslands (hereafter, refered as sampling sites; Table 1) distributed along an elevational gradient in the Atlantic Forest biome, southeastern Brazil (Figure 1). These discrete mountain peaks and *campo de altitude* spots are located within two adjacent mountain ranges – Serra do Caparaó (up to 2892 m a.s.l.) and Serra do Brigadeiro (up to 1985 m a.s.l.) – situated approximately 80 km apart. Both ranges share a similar geological history, established on Precambrian crystalline substrates (primarily high-grade gneisses and migmatites) (Safford 1999, Benites et al. 2007). The regional climate transitions from subtropical highland (Cwb, Köppen classification) in the lower outcrops to cold subtropical highland (Cwc) at the highest summits, with mean annual temperatures ranging from 18°C to 9.4°C, and a relatively evenly distributed annual precipitation of 1300–1400 mm

(Alvares et al. 2013). Rather than comparing the two mountain ranges, our sampling design utilized the individual sampling sites as independent units to capture a continuous environmental gradient. The selected sites encompass an elevational range from 1665 m to 2890 m. This design encapsulates the high environmental heterogeneity characteristic of *campos de altitude*, allowing us to assess how fine-scale variations in soil depth interact with the broader elevational gradient across multiple distinct microhabitats.

Table 1 - Characteristics of the 11 sampling sites located in the Campos de Altitude ecosystems of Caparaó National Park (CNP) and Serra do Brigadeiro State Park (SBSP), including elevation (m a.s.l.) and the number of sampled plots per site.

Sampling sites	**Elevation (m a.s.l.)**	**Number of plots**	**Mountain Range**
Cristal Peak	2229-2769	100	CNP
Calçado Peak	2774-2841	100	CNP
Bandeira Peak	2841-2890	100	CNP
Trail-2100	2100-2150	71	CNP
Trail-2300	2300-2350	72	CNP
Trail-2500	2500-2550	73	CNP
Trail-2700	2700-2750	74	CNP
Pedra do Pato Peak	1687-1897	135	SBSP
Elefante Peak	1687-1791	100	SBSP
Mamute Peak	1813-1857	100	SBSP
Totem-Deitado Peak	1665-1725	100	SBSP

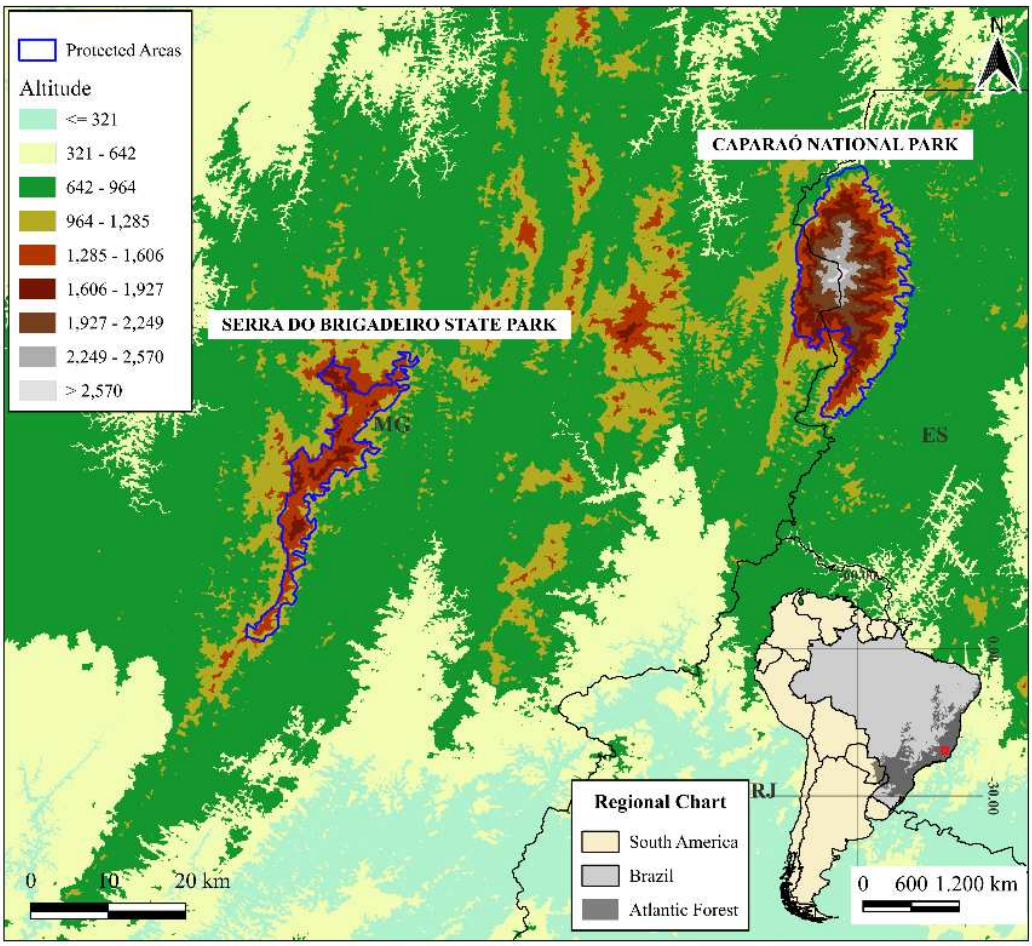

Figure 1. Regional context and geographic location of the two study areas within the Atlantic Forest biome, southeastern Brazil. The regional chart situates the study area (red dot) within the extent of the Brazilian Atlantic Forest. The main map displays the regional topography using a color scale for elevation (m a.s.l.), state borders (MG, ES, RJ), and the boundaries of the protected areas: Serra do Brigadeiro State Park and Caparaó National Park (blue lines).

Data collection, trait gap-filling, and phylogenetic imputation

We sampled 1025 plots of 1.0×1.0 m, randomly distributed across eleven sites, primarily on seven summits of the mountains studied (**Erro! Fonte de referência não encontrada.**) (Campos et al., 2018; Cordeiro et al., 2023; Cordeiro & Neri, 2019; Neri et al., 2016). Bare rock outcrops lacking vascular plants were not included in sampling. Within each plot, all vascular plant species were inventoried, and the percentage of canopy cover of all species was recorded. Taxonomic classification followed Brazilian Flora (2026) and APG IV (Angiosperm Phylogeny

Group 2016). In each plot, elevation information was collected using a GPS device; a sharp metal rod and a metric ruler were used to measure the depth of the soil at the center of the plot.

Functional traits were selected aiming to reflect the ecological strategies of plants in tropical highland grasslands, under an evolutionary scenario of environmental conditions of stress and resource limitation (Rosado and others 2013; Negreiros and others 2014; Neri and others 2016; Pérez-Harguindeguy and others 2016), including traits connected to plant growth, light interception and protection from environmental stress (Table 2). Following standard protocols for functional community ecology (Pérez-Harguindeguy and others 2016), our trait collection strategy was abundance-driven. We prioritized in situ measurements for the dominant species, ensuring that functional data captured at least 80% of the cumulative relative cover at each of the 11 sampling sites. This approach aligns with the mass ratio hypothesis (Grime 1998), which posits that ecosystem functioning is primarily determined by the traits of the most abundant species.

The collected species were initially classified according to a modified version of Raunkiaer's life-form system (Braun-Blanquet 1979). This categorical classification is based on the position of the plant's perennating tissues relative to the soil surface, which dictates plant strategies during unfavorable growth periods (Pérez-Harguindeguy and others 2016). The maximum height of each species was primarily sourced from published literature and flora databases, reflecting measurements of either vegetative or reproductive structures. When in the field, we carefully selected at least three representative adult individuals from each species, collected leaves, branches or even whole plants, when necessary. After collecting, the material was brought to the laboratory where its traits were measured and categorized following Pérez-Harguindeguy et al. (2016). For continuous traits, when in situ measurement was not possible, we gap-filled our matrix using secondary data extracted from global and regional databases (e.g., Flora e Funga do Brasil, TRY, BIEN, GBIF) and relevant literature (Mariano and others 2021; Ordóñez-Parra and others 2023b). By combining field and database sources, we achieved a high data completeness rate: functional information was available for species representing over 75% of the total community cover across all evaluated traits.

To prevent the exclusion of subordinate and rare species from the community-level analyses and to fill the remaining minor gaps, we performed phylogenetic data imputation (Gorné and

others 2025). We constructed a phylogenetic tree for our complete species pool using the R packages *V.PhyloMaker2* and *ape*. Subsequently, we applied the *Rphylopars* package, which uses evolutionary models to estimate missing trait values based on the phylogenetic covariance among related taxa. Because our imputation was restricted to a small fraction of the community biomass (mostly subordinate species representing the remaining < 20% of cover), the imputed values did not artificially drive the Community-Weighted Means (CWM) but allowed for a complete representation of the taxonomic pool in the models.

To assess the functional responses underlying community assembly along the environmental gradient, we calculated the CWM for each functional trait. This metric represents the average trait value in the community, weighted by the relative coverage (%) of each species (Violle and others 2007; Pescador and others 2015), according to the following equation:

$$CWM_x = \sum_{i=1}^{S} c_i \cdot t_i$$

Where S is the total number of species in the community; c_i is the relative coverage of the i-th species, and t_i is the trait value of the i-th species.

Table 2- Plant functional traits evaluated in this study, including their abbreviations, units of measurement, and primary ecological functions. The table also details the sampling coverage, indicating the total number of species measured, and the percentage of community abundance represented by the dominant species for each trait.

Functional traits	Abbreviation	Unit	Leading function	Total number of species	% of data dominant species
Plant maximum height	Hmax	cm	Light interception (competition fitness)	176	98
Leaf blade area	LA	cm²		120	76.6
Leaf blade length	LL	cm	Plant economics (Light capture versus overheating, fixation of carbon)	158	93.8
Leaf blade width	LW	cm		158	93.8
Leaf thickness	LTh	mm		86	56.3
Leaf dry matter content	LDMC	mg/g		101	78.1
Leaf area per leaf dry mass	SLA	mm2/mg		123	96.9
Fruit mean length	FL	cm	Plant reproductive economics	113	70.3

Life forms	LiFor	classes	Level of protection of vital tissues in the unfavorable season	195	98.4

Data analysis - Life forms

We used Generalized Linear Mixed Models (GLMMs) to assess the effects of elevation and soil depth on the relative coverage of Raunkiaer's life forms. Because the response variable is a continuous proportion (0–1), we fitted Beta GLMMs with a logit link function. To account for the nested sampling design, sampling site was included as a random intercept (1|sampling_site). Continuous predictors were Z-transformed to enable direct comparison of effect sizes. The model evaluated the main effects of elevation, soil depth, and life form, alongside their interactions. Overall significance was tested using Type III Analysis of Deviance (Wald chi-square tests). For significant interactions, we conducted post-hoc trend analyses using the *emmeans* package (*emtrends* function) to calculate the response slopes of each life form along both gradients. Slopes were considered statistically significant ($p < 0.05$) if their 95% confidence intervals did not overlap zero.

Data analysis and assessment of functional traits

Linear mixed models with the 11 sampling sites as random effects (*lmer*, lme4 package) were used to assess the relationship between functional traits and environmental variables. Due to the asymmetric distribution of trait values, we applied logarithmic transformation of the response variable (functional traits), to fit the assumptions of normality and homoscedasticity of the residuals. The fixed predictors (elevation, soil depth, and the interaction) were standardized. We compared those models with generalized linear mixed models (*glmer*) with a Gamma (link = log) distribution to check whether the latter would provide a better fit. However, based on the inspection of the scaled residuals, the log-normal model showed a better fit to the extreme values (max. residual < 4) compared to the Gamma model (max. residual > 5), maintaining consistency in the direction and magnitude of the estimated coefficients, correcting for heteroscedasticity and the presence of outliers observed in the original distributions. (Table S2). All analyses were conducted in the R (v. 4.5.2) using RStudio (v. 2025.09.2+418) and Quarto (v. 1.8.26).

RESULTS

Floristic composition and family-level responses to environmental gradients

In our sampling, we recorded a total of 6264 vascular plant occurrences (individual plants or clumps), belonging to 222 species, 132 genera, and 54 families. Of these species, 77.03% were identified at the species level, 7.21% at the genus level, and 7.76% at the family level. A small fraction (6.30%) remained indeterminate due to the absence of diagnostic reproductive material or insufficient taxonomic resolution.

Analysis of the most representative families revealed distinct response patterns to elevation and soil depth. Apiaceae was the only family driven exclusively by edaphic conditions, showing a positive association with soil depth (β = 0.043, P = 0.002). In contrast, Bromeliaceae and Euphorbiaceae responded primarily to the elevation gradient, exhibiting a significant increase in dominance with increasing elevation (β = 0.078, P = 0.004 and β = 0.043, P = 0.012, respectively), independent of soil depth. The dominance of the three most species-rich families (Asteraceae, Poaceae, and Cyperaceae) was governed by significant interactions between elevation and soil depth. Poaceae and Cyperaceae (typical graminoids) showed a positive interaction (β = 0.039 and β = 0.027, respectively). Conversely, Asteraceae exhibited a significant negative interaction (β = -0.040, $P < 0.001$). Apiaceae was the only family driven exclusively by edaphic conditions, showing a positive association with soil depth (β = 0.043, P = 0.002). In contrast, Bromeliaceae and Euphorbiaceae responded primarily to the elevation gradient, exhibiting a significant increase in dominance with increasing elevation (β = 0.078, P = 0.004 and β = 0.043, P = 0.012, respectively), independent of soil depth.

Raunkiaer life forms and functional groups

We found that soil depth and elevation strongly influence the distribution of plant life forms (Figure 2). Across all the altitudinal range, hemicryptophytes are the dominant life form, followed by chamaephytes and nanophanerophytes. Our Beta GLMM model revealed that environmental gradients do not uniformly affect the relative dominance of all life forms. The deviance analysis (Type III ANOVA) confirmed that the response of dominance depended significantly on the interactions between life form and environmental predictors (elevation interaction: $\chi^2 = 25.22$, $p < 0.001$; Soil depth Interaction: $\chi^2 = 61.55$, $p < 0.001$) and the *post-hoc* analysis of the slopes provided a clear view of those interactions (based on 95% Confidence Level).

Soil depth proved to be a stronger factor in community structuring, inducing significant and divergent responses (**Erro! Fonte de referência não encontrada.**A). Nanophanerophytes were the only group to clearly benefit from deeper soils, significantly increasing their dominance (Slope = 0.086, 95% CI [0.014, 0.157]). On the other hand, three groups showed a significant reduction in deep soils: the strongest negative response was observed in hemicryptophytes (Slope = -0.300, 95% CI [-0.369, -0.231]), followed by therophytes (Slope = -0.153, 95% CI [-0.301, -0.005]) and chamaephytes (Slope = -0.090, 95% CI [-0.163, -0.017]). Geophytes and phanerophytes appeared indifferent to this gradient.

Elevation functioned as a selective environmental filter along the gradient (**Erro! Fonte de referência não encontrada.**B). Among the evaluated life forms, only chamaephytes exhibited a statistically significant increase in relative dominance with rising elevation (slope = 0.132; 95% CI [0.038, 0.227]). In contrast, none of the remaining life forms showed a significant response to elevation, as evidenced by confidence intervals that consistently encompassed zero.

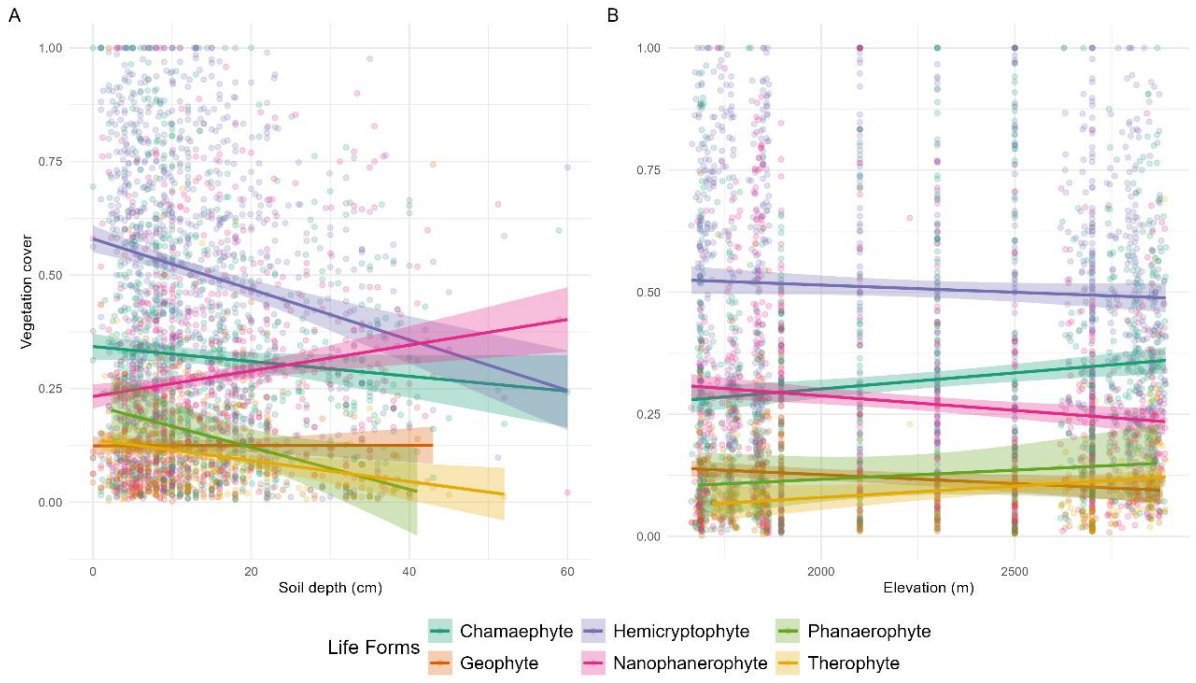

Figure 2. Shifts in the functional structure of plant communities based on Raunkiaer's life form spectra along environmental gradients: soil depth (A) and elevation (B). Data points represent Community-Weighted Means of relative vegetation cover. Solid lines represent linear regression fits, illustrating that soil depth (A) is a stronger

driver of functional assembly than elevation (B). Shaded regions denote the 95% confidence intervals around the regression lines.

Influence of soil depth and elevation on functional traits

Overall, soil depth and elevation acted as interacting drivers of functional trait variation in the plant community (Table 3). For all traits, the interaction term (Elevation x Soil Depth) was consistently significant, indicating that the effect of elevation on plant functional traits is strongly modulated by soil depth (Figure 3). In shallow soils, the vegetation response to increasing elevation was accentuated, resulting in a rapid reduction in organ dimensions (smaller/thinner leaves and shorter fruits). In contrast, in deep soil this reduction was significantly attenuated (buffered), indicating that the availability of edaphic resources partially disconnects the community from the climatic pressures of altitude in tropical mountains (Figure 4).

Plant maximum height

Community-weighted mean of maximum plant height (Hmax) was positively associated with soil depth (β = 0.176, P < 0.001). Elevation had a marginally positive effect on height (β = 0.156, P = 0.061), contrary to the expected reduction in stature typically associated with high altitudes. However, a significant negative interaction (β = -0.091, P < 0.001) revealed that the positive effect of soil depth on plant height is more pronounced at lower elevations. In higher elevations, the difference in height between shallow and deep soil communities becomes less distinct, suggesting a homogenization of plant stature towards the mountain top.

Leaf dimensions: area, length, width, thickness

All dimensional leaf traits exhibited a consistent response pattern to the environmental gradients (B, E, F, G). Leaf Area (LA), Leaf Length (LL), and Leaf Thickness (LTh) showed significant decreases with both increasing soil depth (β_{LA} = -0.10, P < 0.001; β_{LL} = -0.11, P = 3.2e-11; β_{LTh} = -0.08, P = 4.01e-09) and increasing elevation (β_{LA} = -0.35, P < 0.01; β_{LL} = -0.24, P = 0.009; β_{LTh} = -0.75, P = 3.44e-06). In contrast, Leaf Width (LW) exhibited a significant negative relationship only with soil depth (β_{LW} = -0.053, P = 0.001), showing no significant response to elevation as a main effect. Crucially, a significant positive interaction was detected for all dimensional traits (Table 3), including LW, which did not respond to elevation alone. This

positive interaction indicates an edaphic buffering effect: in shallow soil, leaf dimensions decrease sharply as elevation increases (e.g., steep reduction in Leaf Thickness and Area). However, in deep soil, this reduction is significantly attenuated, allowing plant communities to maintain larger and thicker leaves even at higher altitudes (**Erro! Fonte de referência não encontrada.**B-E).

Leaf economics: SLA and LDMC

The two traits related to the leaf economics spectrum showed opposing but highly complementary trends (Table 3). Notably, neither Specific Leaf Area (SLA) nor Leaf Dry Matter Content (LDMC) were significantly affected by elevation as a main factor (β_{SLA} = 0.085, P = 0.410; β_{LDMC} = 0.029, P = 0.163; **Erro! Fonte de referência não encontrada.**C-D). Instead, both traits were primarily governed by soil depth and its interaction with the elevational gradient. SLA exhibited a positive response to soil depth (β_{SLA} = 0.05, P = 0.002) but a strong negative interaction with elevation (β_{SLA} = -0.110, P < 0.001). This interaction reveals that the expected increase in SLA with the decrease of elevation is restricted to shallow soils. In deep soils, this trend is effectively buffered, and SLA values remain stable.

Mirroring this pattern, LDMC showed a negative response to soil depth (β_{LDMC} = -0.015*;* P = 0.041) and a significant positive interaction (β_{LDMC} = 0.059*;* P < 0.001; **Erro! Fonte de referência não encontrada.**D). This inverse symmetry between the negative interaction for SLA and the positive interaction for LDMC confirms that deep soils decouple the conservative-acquisitive trade-off from the strict control of the altitudinal gradient, favoring intermediate values of tissue density even at higher elevations.

Reproduction trait: fruit length

Similar to vegetative traits, the reproductive trait analyzed here was shaped by the interplay between soil and elevation. Fruit length decreased with soil depth (β_{FL} = -0.132, P = 7.15e-15) and elevation gradients (β_{FL} = -0.26, P = 0.002). However, these effects were strongly interdependent, as evidenced by the significant positive interaction (β_{FL} = 0.06, P = 0.002). In shallow soils, fruit size was severely reduced at high elevations, whereas deep soils supported communities with larger fruits, buffering the limiting effect of the elevation (**Erro! Fonte de referência não encontrada.** H).

Table 3 Results of regression models of logarithmic values of functional traits (CWM) and environmental variables.

Responsible variable	Predictor variable	*Estimate*	Std error	*t value*	*p value*
H.max	Elevation	0.156	0.071	2.265	0.0621 ·
	Soil depth	0.176	0.016	10.968	**< 2e-16*** **
	Interaction	-0.091	0.017	-5.16	**< 0.001** ***
Leaf length	Elevation	-0.236	0.071	-3.309	**0.009** **
	Soil depth	-0.110	0.016	-6.710	**3.2e-11** ***
	Interaction	0.080	0.018	4.405	**1.17e-05** ***
Leaf width	Elevation	-0.152	0.096	-1.579	0.158
	Soil depth	-0.053	0.016	-3.257	**0.001** **
	Interaction	0.055	0.018	3.105	**0.002** **
LA	Elevation	-0.352	0.099	-3.554	**0.005****
	Soil depth	-0.106	0.285	-3.745	**<0.001*****
	Interaction	0.287	0.031	9.176	**<2e-16*****
Leaf thickness	Elevation	-0.751	0.119	-6.328	**3.44e-06** ***
	Soil depth	-0.082	0.014	-5.936	**4.01e-09** ***
	Interaction	0.136	0.015	8.893	**<2e-16** ***
SLA	Elevation	0.085	0.102	0.840	0.410
	Soil depth	0.050	0.016	3.095	**0.002** **
	Interaction	-0.112	0.018	-6.293	**4.61e-10** ***
LDMC	Elevation	0.029	0.019	1.508	0.163
	Soil depth	-0.015	7.4e-03	-2.051	**0.041***
	Interaction	0.059	8.1e-03	6.823	**<0.001*****
Fruit Length	Elevation	-0.266	0.063	-4.220	**0.002** **
	Soil depth	-0.132	0.017	-7.901	**7.15e-15** ***
	Interaction	0.057	0.018	3.096	**0.002** **

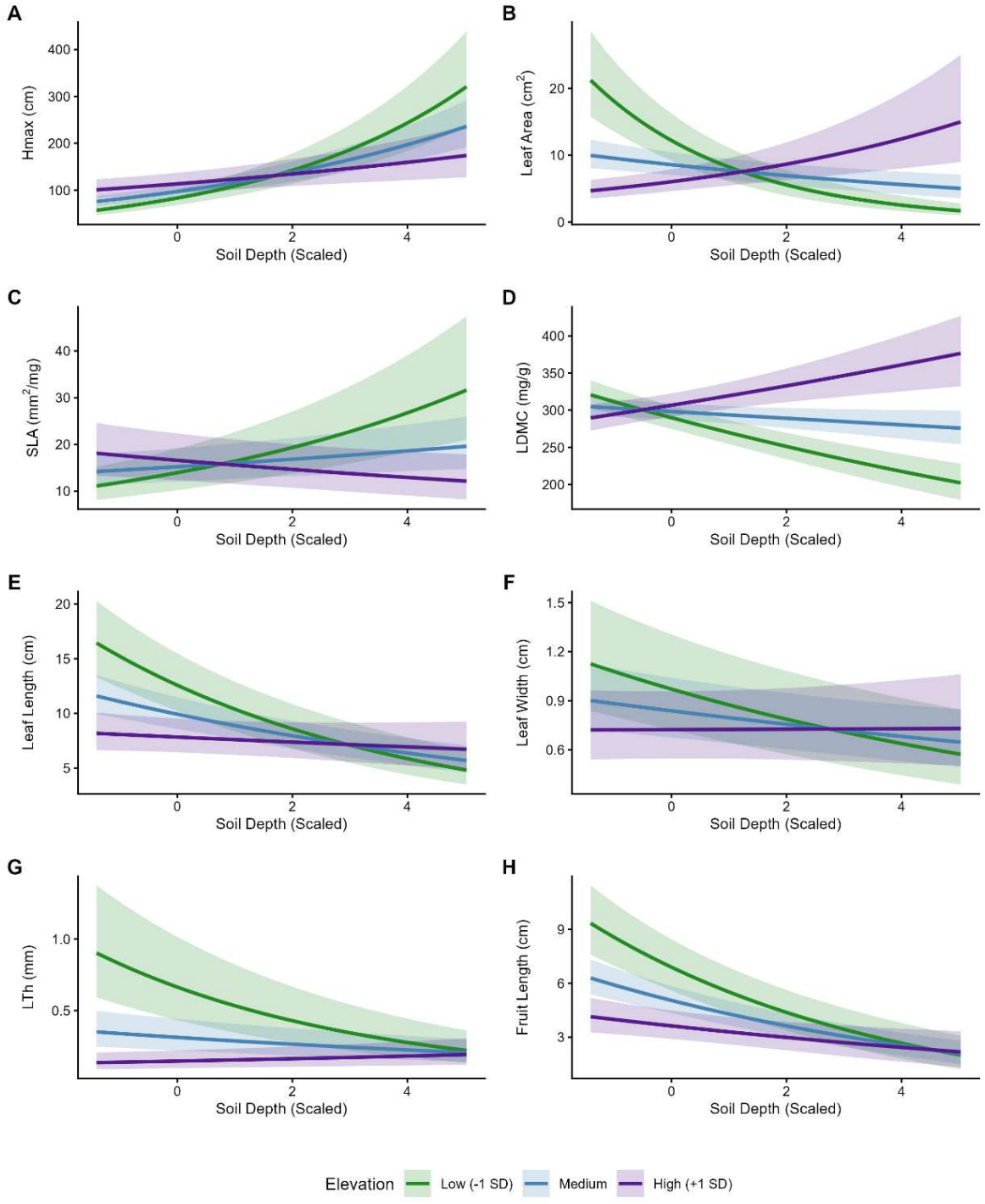

Figure 0.1 - Predicted response of functional traits (CWM) to soil depth across three elevation levels. Trends are based on linear mixed models with log-transformed response variables. Shaded areas represent 95% confidence intervals. The interaction of environmental variables is significant for all traits.

DISCUSSION

Taxonomic drivers of functional patterns

The functional shifts observed in the plant community are underpinned by distinct taxonomic responses, validating the role of environmental filters on phylogenetic lineages. The positive response of Bromeliaceae and Euphorbiaceae dominance to elevation aligns with the high diversity of these families in Brazilian Inselbergs and high-altitude grasslands (*campo de altitude*), where they evolved specialized physiological traits (e.g., CAM photosynthesis, tank structures, succulent leaves, trichome-like emergences, latex etc.) to cope with high irradiance and water intermittency on rock outcrops and shallow soils (Safford and Martinelli 2000; de Paula and others 2016; Vitarelli and others 2016).

The interactive effects observed for the dominant herbaceous families highlight a clear trade-off between stress tolerance and competition (Negreiros et al. 2014), as these graminoids thrive under combined abiotic stress but expand competitively in resource-enriched microsites (Cordeiro and Neri 2019; Campos and others 2020). In the ‘grassland matrix’ (Poaceae and Cyperaceae), the positive interaction for these graminoid families indicates that they are the primary beneficiaries of high-altitude soil pockets, where canopy openness is greater (Schroeder and others 2024). While they are often shaded out by forests at lower elevations, deeper soils at high altitudes allow these families to form dense turfs and tussocks, thereby explaining the persistent dominance of hemicryptophytes in the matrix despite nanophanerophytes prevailing in the deepest patches Shaheen et al., 2023). This indicates that while their dominance may be limited in low-elevation deep soils (due to forest competition), their abundance is maximized in high-elevation sites with localized soil accumulation.

Conversely, the "stress specialist family" Asteraceae shows a negative interaction which is particularly revealing. This family is a classic dominant of tropical high-altitude environments (Safford 2007; de Deus Vidal and Clark 2020; Galván-Cisneros and others 2025), often characterized by rosette herbs, erect herbs, and small shrubs (chamaephytes). The negative interaction suggests that Asteraceae thrives precisely under the most adverse conditions, specifically, at high elevations with shallow and poorly developed soils. When soil depth increases at these altitudes, it creates an "edaphic buffering" effect that facilitates the establishment of larger woody species, likely belonging to families such as Melastomataceae, Myrtaceae, or Fabaceae. These taller, competitively superior species probably outcompete the light-demanding Asteraceae, restricting them to the most exposed and resource-limited

microsites (Kraft and Ackerly 2010; Kraft and others 2015b). Thus, shallow soils at high elevations function as a refuge for Asteraceae, preventing their competitive exclusion. The positive dependence of Apiaceae on soil depth may reflect the prevalence of geophytes or robust hemicryptophytes within this family (e.g., Eryngium spp.), which require a minimum soil volume to develop taproots or rhizomes, restricting them to crevices and deeper depressions (Cianfrani and others 2019).

Soil depth as the primary filter for life forms and competition

Our results identify soil depth, more than elevation, as the primary environmental filter structuring the high elevation plant communities studied here. This supports the hypothesis that edaphic conditions in localized mountain rock outcrops function as fine-scale determinants of vegetation structure and functioning, often overriding macro-climatic gradients (Safford 1999; Rafiee and others 2022; Pierick and others 2024). The strong segregation of life forms along the soil depth gradient aligns with Grime's CSR theory (Grime 1977). Shallow soils, characterized by low water retention and root space, act as environmental filters that tend to select stress-tolerant strategies (Castro and others 2018). This explains the dominance of hemicryptophytes and chamaephytes in these microsites; their ability to maintain buds close to the ground protects them from thermal amplitude and desiccation (Braun-Blanquet 1979; Körner 2003; Testolin and others 2021).

Conversely, the shift toward nanophanerophytes in deeper soils suggests a release from edaphic stress, shifting the community driver from abiotic filtering to biotic competition (Bertness and Callaway 1994; Kraft and others 2015a). Deeper soil provides the water and nutrient resources necessary to support woody biomass. Under these favorable conditions, nanophanerophytes (mostly shrubs) likely outcompete smaller life forms for light, reducing the cover of hemicryptophytes. This pattern corroborates previous regional studies in the *campo de altitude* and *campo rupestre* (Campos and others 2018; Silva Mota and others 2018; Cordeiro and Neri 2019; Gastauer and others 2020), where soil pockets act as "islands of resources" allowing woody encroachment into the grassland matrix.

Elevation appears to act as a selective filter that positively favors a single specialist group. The increased dominance of chamaephytes at higher elevation is ecologically consistent, given that their morphology (low-growing buds, but above the soil surface) represents a classic adaptation

to exposed, cold, and water-stressed environments (Cordeiro and Neri 2019). The fact that other groups appear indifferent suggests a greater generality with respect to this specific gradient. This predominance of soil depth over elevation as a determinant of mean functional trait values, occasionally reversing expected altitudinal trends, agrees with previously documented studies of tropical montane vegetation like those examined here (Bernard-Verdier et al., 2012; Galván-Cisneros et al., 2023 Ottaviani et al., 2016). As stated by Christmann and Oliveras (2020), in *campos de altitude* elevational ranges are likely too short (about 700 m) to form vegetation belts easily distinguishable. And so, local topography, distribution of soil types and drainage network are the most significant controlling factors of vegetation structure.

Rethinking altitudinal trends: The edaphic decoupling of maximum plant height

Contrary to global alpine patterns where plant height universally decreases with elevation due to temperature and wind stress (Moles et al., 2009; Zorger et al., 2025a), our models reveal a more complex dynamic governed by fine-scale edaphic conditions. Rather than a simple positive or negative main effect of elevation ($p = 0.062$), we found a highly significant interaction between elevation and soil depth driving maximum plant height (*Hmax*). Deeper soils consistently supported taller plant communities (e.g., nanophanerophytes), but crucially, they acted as an edaphic buffer against macroclimatic constraints. In shallow, restrictive soils, plant height is highly sensitive to environmental fluctuations. However, in deep soil pockets, *Hmax* is effectively decoupled from the elevational gradient. This buffering effect allows taller woody vegetation to persist at higher elevations than climatic models would typically predict, utilizing these deeper substrate patches as structural refugia against the severe alpine atmospheric filtering.

Furthermore, the lack of a sharp decline in plant height at higher elevations - even in shallower areas - can be attributed to specific adaptations of the regional flora. In environments subject to frequent fog (the "nebulosity hypothesis"), plants may adopt light-acquisition strategies, elongating stems to maximize photon capture (Krömer et al., 2013; Zorger et al., 2025a). Additionally, the "rosette" architecture common in dominant high-elevation families (e.g., Asteraceae, Bromeliaceae, Eriocaulaceae) often involves elongated inflorescence stalks for anemochoric dispersal. This reproductive strategy increases the community-weighted maximum height even if the vegetative body remains prostrate (Safford, 2007; Neri et al., 2016). Ultimately, in these tropical highlands, the combination of deep soil refugia and

specialized reproductive architectures effectively dampens the classical thermal limitations on plant height.

The "Edaphic Buffer": Interaction between soil and climate

A key finding of this study is the significant interaction between soil depth and altitude across morphological traits (Leaf Area, Thickness, Length, and Fruit Length). While elevation imposes a general constraint, reducing leaf and fruit sizes in shallow soils, deep soils consistently buffer this effect. This "Edaphic Buffer Hypothesis" suggests that resource availability (water and nutrients) in deep soil pockets decouples plant functional traits from the atmospheric stress of the elevational gradient (Joswig and others 2022; Galván-Cisneros and others 2025). For instance, in leaf morphology, we observed that in shallow soils, the sharp reduction in leaf area and thickness with altitude reflects a classic stress-avoidance strategy to minimize transpiration and embolism risk (Wright and others 2017; Sun and others 2025).

On the other hand, the maintenance of larger leaves in deep soils at high altitudes indicates that when root water access is secured, plants can maintain more acquisitive leaf phenotypes even in colder and windy environments (Wright and others 2017; Eller and others 2020). Similarly, in fruit size, the reduction of fruit length with elevation was evident in shallow soils but mitigated in deep soils. This may relate to the energetic cost of producing large fleshy fruits (dispersed by vertebrates), which is only sustainable at high altitudes if edaphic resources are abundant (Galetti and others 2013; Lyu and others 2021).

Linking life forms and functional strategies

The functional signature of the community, specifically the predominance of acquisitive traits (high SLA, low LDMC) in shallow soils, is intrinsically linked to the shift in biological life forms driven by edaphic filtering. The sharp reduction of nanophanerophytes and the concurrent dominance of hemicryptophytes and therophytes in shallow soils (slope = -0.300 and -0.153, respectively) explains the functional patterns observed. Nanophanerophytes, dominant in deep soils, typically invest in lignified, long-lived tissues (high LDMC) to ensure survival across seasons, characterizing a conservative strategy. In contrast, the assemblage of hemicryptophytes and therophytes that colonize shallow soils relies on a strategy of stress avoidance rather than stress tolerance (Negreiros and others 2014; Volaire and others 2020). Therophytes must complete their life cycle rapidly, taking advantage of short and often

unpredictable periods of water availability. To achieve this, they produce "cheap", distinctively thin leaves with high SLA to maximize photosynthetic gain and growth rates before the onset of edaphic drought (Gonzalez-Paleo and Ravetta 2018; Poorter et al., 2009). Similarly, many hemicryptophytes in these outcrops possess deciduous aerial biomass or graminoid architectures that favor high SLA during the vegetative season (Biedinger and others; Schweingruber and Poschlod 2005; Jakob and others 2022).

Therefore, the "acquisitive" functional profile observed in the shallowest, high-elevation soils is not a sign of resource abundance, but rather a successful adaptation of short-cycle and ephemeral life forms (Castro and others 2018). These organisms exploit the shallow substrate through rapid resource acquisition, contrasting with the "slow and persistent" strategy of woody nanophanerophytes which are restricted to the hydraulic refuge of deep soils (Poot and others 2012; Aparecido and others 2018).

This decoupling of functional dimensions supports the view that environmental filtering is multidimensional (Laughlin, 2014). While altitude drives a thermal filter, soil depth creates a hydraulic and nutritional filter that can override or reverse climatic trends. The intersection of these gradients creates a mosaic of micro-habitats where "conservative" (deep soil) and "acquisitive/opportunistic" (shallow soil) strategies coexist in proximity, providing a functional explanation for the high beta-diversity and endemism often reported for these tropical mountain tops (Rapini and others 2008; Hopper 2009).

CONCLUSIONS

These findings demonstrated that the functional responses of plant communities to environmental gradients critically depend on interactions between multiple environmental filters. Soil depth modulates the ability of communities to respond functionally to altitudinal gradients, with likely implications for predicting responses to climate change in heterogeneous landscapes. Deep soil consistently acts as an environmental buffer. In shallow soils, vegetation responds drastically to the altitude gradient (rapidly changing strategy). In deep soil, the availability of underground resources partially disconnects vegetation from the climate and other altitude effects, allowing for more stable and acquisitive phenotypes along the mountain.

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SUPPLEMENTARY MATERIAL

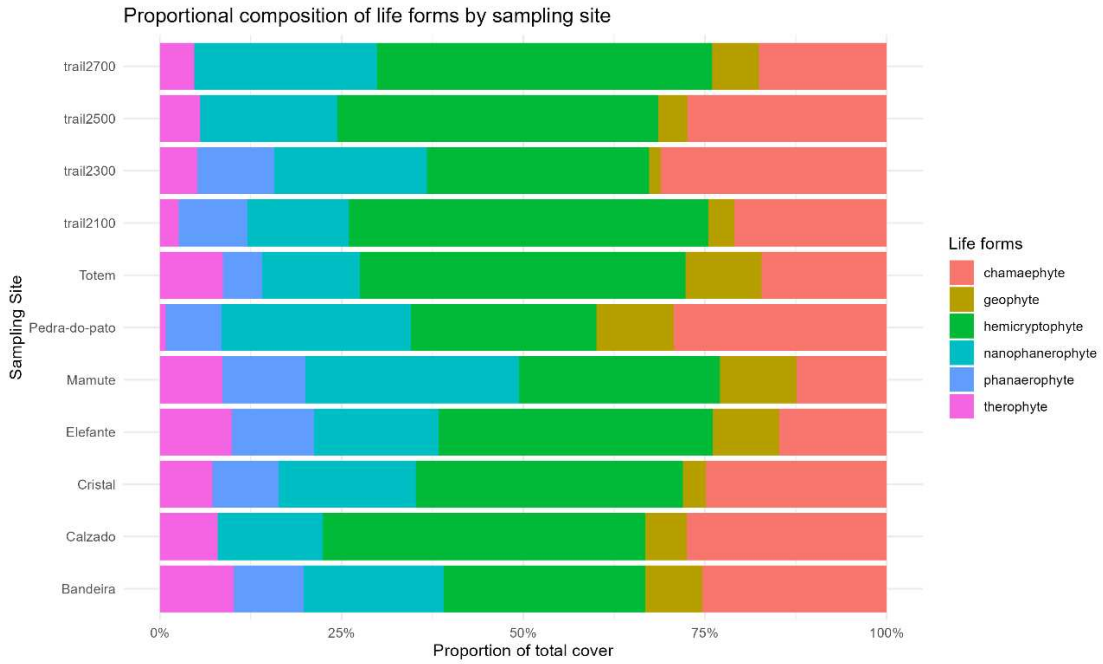

Figure S1. Proportional composition of plant life forms across the sampled mountain summits and trails. Bars represent the relative contribution of each Raunkiær life form to the total canopy cover (0-100%) within each sampling site. This visual breakdown demonstrates the spatial heterogeneity in functional community structure and the overall dominance of hemicryptophytes and nanophanerophytes across the highland landscape.

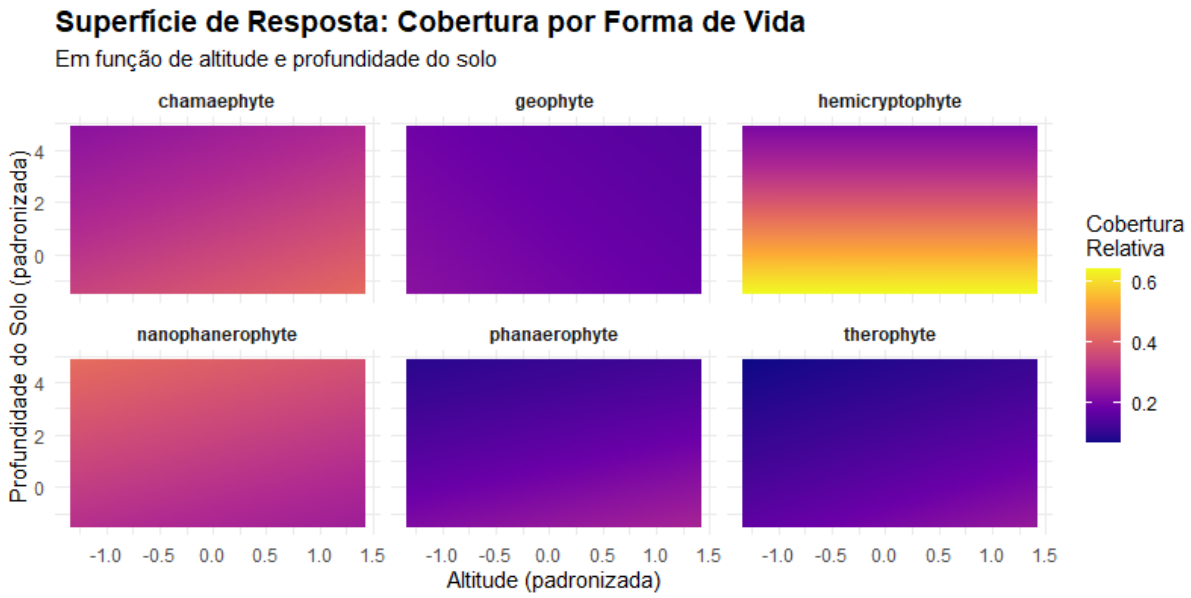

Figure S2. Response surface heatmaps illustrating the predicted relative cover of distinct plant life forms across the interacting gradients of elevation (x-axis) and soil depth (y-axis). Both environmental predictors were

standardized. The color gradient, ranging from dark purple to yellow, indicates the relative canopy cover of each life form, highlighting how structural dominance shifts under varying environmental conditions.

GENERAL CONCLUSIONS

This thesis demonstrates that the formation of plant communities in high-altitude tropical ecosystems is not dictated by a single environmental factor, but rather by a complex and hierarchical filtering process. By integrating taxonomic, phylogenetic, and functional perspectives, we reveal a fundamental disconnect between evolutionary history and ecological strategy in the high-altitude field. While macroclimatic stress associated with increasing altitude acts as a rigorous evolutionary filter, restricting survival to phylogenetically grouped and cold-tolerant lineages, it is the heterogeneity of the small-scale micro-habitat that dictates the functional structure of these communities. Ultimately, within the rigorous climatic envelope of mountain peaks, soil depth emerges as the main factor of functional divergence, shifting communities between stress avoidance and tolerance strategies.

A central theoretical advance of this research is the proposition of the "Edaphic Buffer Hypothesis". Classic alpine models often assume a linear response to altitude, predicting uniform changes toward conservative traits and reduced plant height at higher altitudes. Our findings fundamentally challenge this understanding, proving that deep soil pockets can overcome macroclimatic constraints. We demonstrate that deep soils function as vital hydraulic and nutritional refuges, effectively buffering the climatic severity of high altitudes and allowing the persistence of woody and conservative life forms (such as nanophanerophytes) where classical theory would predict their exclusion. Conversely, shallow soils act as an extreme environmental sieve, filtering out short-cycle life forms and acquisitive leaf traits, regardless of altitude.

These ecological mechanisms translate into urgent conservation priorities for the highly threatened high-altitude grasslands of southeastern Brazil. Our results indicate that conservation strategies based solely on altitudinal zoning are insufficient; instead, policies should prioritize the protection of edaphic heterogeneity. Since deep soils act as a critical buffer against climate extremes, physical disturbances that cause soil erosion—such as unregulated tourism, historical overgrazing, and man-made fires—do more than destroy local vegetation; they actively dismantle the ecosystem's inherent capacity to withstand climate change. Protecting these mountain ecosystems requires safeguarding the physical integrity of the soil layer, which

sustains both the unique phylogenetic diversity and the functionally specialized lineages described in this study.

Finally, while this thesis provides a fundamental understanding of the decoupling between traits and environment, it opens critical avenues for future research. To fully capture the mechanisms of edaphic buffering, future studies should incorporate subterranean functional traits (e.g., root economy, presence of xylopodia), as our results highlight the substrate as the primary environmental filter. In addition, deploying in situ microclimate sensors to continuously monitor soil temperature and moisture along these gradients will be essential to physically quantify the buffering capacity identified here. By advancing these lines of research, we can refine predictive models of ecosystem responses, ensuring the long-term conservation of high-altitude Neotropical biodiversity in the context of rapid global change.