Title: Environmental heterogeneity mediates plant diversity and ecosystem stability in mountain ecosystems of the Mediterranean Andes

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Author contributions

LPG, JL, and DC conceptualized the idea. LPG and JCP data curation. LPG led the writing, with support from DC, JL and JCP. JL secured the funding. LPG, JL, JCP collected data. All authors contributed to and revised the manuscript.

Data availability statement

Data and code to support the results are available in the following GitHub repository: https://github.com/LAURACPEREZ/Mapocho_diversity/tree/main.

Conflict of interest statement

The authors have no conflicts of interest to declare.

Abstract

1. Globally, mountains are highly diverse ecosystems that serve as natural laboratories for testing fundamental ecological theories, while also providing vital ecosystem services. The biodiversity of these ecosystems is largely attributed to their complex topography, which creates gradients of elevation and environmental heterogeneity. These gradients in turn influence the maintenance of ecosystem functions, such as vegetation productivity, over time. However, how topography influences ecosystem stability and its relation with different facets of biodiversity in mountain ecosystems remains relatively unexplored. Here, we evaluated the impacts of environmental heterogeneity and spatial autocorrelation on taxonomic and phylogenetic diversity, and the extent to which they mediate ecosystem stability in a mountain ecosystem.

2. Using a highly-replicated fractal sampling design, we estimated plant taxonomic and phylogenetic diversity locally and across space. We estimated the temporal stability of vegetation productivity with a high-resolution, remotely-sensed time series of vegetation productivity in the Mediterranean Andes of central Chile. We assessed the effects of topographic gradients as proxies for environmental heterogeneity and local phylogenetic and taxonomic diversity and turnover on ecosystem stability using generalized linear and structural equation models that account for spatial autocorrelation.

3. We found that environmental heterogeneity associated with topographic ruggedness and elevation and spatial processes play a key role in shaping plant diversity and ecosystem stability. While increasing topographic ruggedness and elevation increased taxonomic turnover, it decreased taxonomic and phylogenetic α diversity. Yet, we found that plant diversity did not stabilize vegetation productivity, indicating that the diversity-stability relationship is highly spatially structured.

4. *Synthesis:* Our results highlight the context dependency of diversity-stability relationships in naturally assembled ecological communities and that environmental heterogeneity has a stronger influence on ecosystem stability than plant diversity in mountain ecosystems. We provide empirical evidence that areas of high topographic complexity should be prioritised for biodiversity conservation and maintenance of ecosystem functioning in mountain ecosystems.

Keywords: Mediterranean vegetation; Phylogenetic diversity; Mountain biodiversity; Ecosystem stability.

Introduction

Mountain ecosystems cover 24% of the Earth's surface and play a fundamental role in human well-being, and their characteristics influence the structure, functioning, and stability of ecosystems (Yu et al., 2021). These ecosystems provide essential ecosystem services to sustain human livelihoods and directly benefit about half of the world's population (Viviroli et al., 2020). Moreover, their topographic complexity results in a mosaic of spatially heterogeneous landscapes that regulate the evolution and diversification of plant species (Körner et al., 2017; Gomes et al., 2020; Rahbek et al., 2019). These gradients occur over relatively short geographical distances in mountain ecosystems and, crucially, underpin spatial variation in plant diversity and ecosystem functioning (Woldu et al., 2020; Deák et al., 2021; Heydari et al., 2023).

Patterns of plant species diversity along topographic gradients often vary in important ways for ecosystem stability, i.e., the invariability of ecosystem functioning over time (Oliver et al., 2010; Vetaas, 2021). For many taxonomic groups, diversity usually declines markedly with increasing elevation and aspect (McCain and Grytnes, 2010; Bañares-de-Dios et al., 2024), as decreasing temperatures often lower diversity via multiple mechanisms (e.g., energy; McCain & Grytnes, 2010, Vetaas et al., 2019) and steeper slopes often have lower diversity due to higher erosion and greater exposure to wind and solar radiation (Körner et al., 2017).

While environmental heterogeneity - created by small-scale topographic variation - often enhances species coexistence (MacArthur and MacArthur 1961, Steinbauer et al., 2016, Deák et al., 2024), endemism generally increases with elevation, reflecting how topography-driven isolation may accelerate speciation rates (Steinbauer et al., 2016). Independent of the effects of environmental heterogeneity, changes in diversity in mountain ecosystems may also be driven by distance-related declines in similarity ('distance-decay relationships'), highlighting the importance of dispersal processes (Morlon et al., 2008). The underlying drivers of diversity patterns in mountain ecosystems likely have cascading effects on ecosystem functioning, which may or may not be mediated by diversity (Maestre et al., 2012; García-Palacios et al., 2018; Wang et al., 2023). In areas with greater diversity, a decline in the productivity of one species is likely to be offset by an increase in the productivity of other species, thus maintaining overall ecosystem functioning (Bai et al., 2004; Tilman et al., 2006). However, the relationship between plant diversity and ecosystem stability in naturally-assembled communities is not as straightforward as in experimental communities, as it can exhibit spatial autocorrelation (Wardle 2016), and abiotic conditions and species composition can be stronger drivers of stability than diversity alone (van der Plas, 2019; Wang et al., 2023). Therefore, examining how topography - which drives the variation in gradients in species diversity and composition and many abiotic variables - may affect the diversity-ecosystem stability relationship is particularly critical for mountain ecosystems, whose biodiversity and ecosystem services are increasingly threatened by increasing temperatures (IPCC, 2019). However, diversity-stability relationships in mountain ecosystems have not been fully explored.

The stabilizing effects of diversity and associated ecological mechanisms, such as species asynchrony and population stability, on ecosystem functioning have typically been investigated at local spatial scales, i.e., α or local diversity, (van der Plas, 2019; de Bello et al., 2021). This is despite a large body of evidence showing that other components of diversity, such as β diversity, vary systematically along environmental gradients; β diversity, i.e, variation in α diversity or species composition across local sites, tends to decline as environmental conditions become less favorable, such as extremely high or low temperatures and high aridity, which are often captured along latitudinal or altitudinal gradients (e.g., Qian et al., 2012, Soininen et al., 2017, Cao et al., 2021, Tolmos et al., 2022). The decline of β diversity along environmental gradients can have negative consequences for ecosystem functioning, although the direction and magnitude of the relationship likely shifts across contexts (van der Plas et al., 2023). The relatively recent development of a cross-scale theoretical framework for assessing ecosystem stability (Wang and Loreau, 2014) has clarified the ecological mechanisms through which β diversity may affect stability at local and regional scales, revealing that β diversity contributes to stabilizing ecosystem functioning at larger spatial scales via its effects on local ecosystem stability or spatial asynchrony, i.e. spatial variation in local ecosystem stability (e.g., Wilcox et al., 2017, Wang et al., 2021, Liang et al., 2022, Qiao et al., 2023). Together, these results suggest that spatially heterogeneous landscapes, such as those of mountain ecosystems, likely stabilize ecosystem functioning over time via statistical mechanisms such as species asynchrony and population stability (Thibaut and Connolly, 2012), although the relative importance of proximate ecological causes, such as temperature and water availability gradients, remain relatively unexplored (García-Palacios et al., 2018).

Integrating other facets of biodiversity, such as phylogenetic and functional diversity, in addition to taxonomic diversity, may further enhance current understanding of the evolutionary and ecological processes that determine ecosystem stability (Cadotte, 2013; Craven et al., 2018; de Bello et al., 2021). Phylogenetic diversity, which represents the diversity of phylogenetically conserved functional traits and is a useful proxy for high-dimensional functional diversity (Tucker et al., 2018), can therefore provide clear mechanistic links to ecological processes, such as compensatory dynamics and insurance effects (de Bello et al., 2021), that have been shown to stabilize ecosystem functioning in experimental and naturally-assembled communities (e.g., Flynn et al., 2011, Cadotte, 2013, Craven et al., 2018, Dolezal et al., 2020). For example, if phylogenetic diversity stabilizes ecosystem functioning, this would suggest that compensatory dynamics underlie the relationship between diversity and ecosystem stability, as phylogenetically dissimilar species respond differently to similar environmental conditions or facilitate phylogenetically distinct species, particularly under environmentally stressful conditions (de Bello et al., 2021). Alternatively, if phylogenetic diversity exhibits a negative relationship with ecosystem stability, this would suggest that the insurance effect determines ecosystem stability, whereby phylogenetically similar (or redundant) species have similar effects on ecosystem functioning (de Bello et al., 2021).

In mountain ecosystems globally, ecological and evolutionary processes such as environmental filtering and in-situ speciation have created unique plant assemblages with high levels of endemism, which usually increases with elevation (Steinbauer et al, 2016), and consequently may have unexpected effects on ecosystem stability. Particularly at higher elevations, mountain flora may be more closely related than expected by chance (Li et al., 2017; Bañares-de-Dios et al., 2024), and are dominated by a few families that have evolved tolerance to low temperatures (Qian et al., 2021; Qian et al., 2017). In the harsh environments of high-elevation mountain ecosystems, communities with low phylogenetic diversity - due to phylogenetic clustering - would be expected to have low ecosystem stability (Cadotte et al., 2012). However, if closely related species in these communities occupy different ecological niches due to the unique dispersal, environmental, and biotic filters present in mountain ecosystems, it is possible that communities with low phylogenetic diversity may stabilize ecosystem functioning.

Here, we examined how gradients in environmental heterogeneity, the spatial autocorrelation and plant taxonomic and phylogenetic diversity generated by the complex topography of mountain ecosystems impacts ecosystem stability in the Mediterranean Andes of central Chile. Because of its high levels of plant diversity and remarkable climatic and topographic variation (Rahbek et al., 2019; Bañares-de-Dios et al., 2024), this is an ideal system in which to assess the extent to which plant diversity mediates the effects of environmental heterogeneity on ecosystem stability across spatial and ecological scales. We therefore *i*) evaluated shifts in α and β taxonomic and phylogenetic plant diversity along gradients of elevation and environmental heterogeneity once accounting for spatial autocorrelation and *ii*) evaluated the direct and indirect effects of environmental heterogeneity, spatial autocorrelation, and taxonomic and phylogenetic diversity on ecosystem stability. We expected that both α and β taxonomic and phylogenetic plant diversity to decline with increasing elevation and decreasing environmental heterogeneity, and β taxonomic and phylogenetic plant diversity to decrease with increasing of spatial autocorrelation. We therefore expected that, once accounting for the effects of environmental heterogeneity and spatial autocorrelation, α and β taxonomic and phylogenetic plant diversity would enhance ecosystem stability overall, implying that the stabilizing effects of diversity may be reduced in plant communities at higher elevations.

Materials and methods

Study sites

We performed this study in the Mapocho River basin in the Mediterranean Andes Mountains of central Chile (Figure 1). Specifically, the study area was located within Estero Covarrubias, with an elevation spanning from 1200 to 2400 m a.s.l. The study area has a semi-arid Mediterranean climate with a mean annual temperature of 14°C and rainfall of 360 mm year-1 (Cavieres et al., 2007). The dominant ecosystem in the study area is the Andean Sclerophyllous Forest and Scrubland (Gajardo, 1994; Luebert and Pliscoff, 2018), which is dominated by the following tree and shrub species: *Lithraea caustica* (Anacardiaceae), *Quillaja saponaria* (Quillajaceae), *Kageneckia oblonga* (Rosaceae), *Kageneckia angustifolia* (Rosaceae), *Guindilia trinervis* (Sapindaceae), *Colliguaja integerrima* (Euphorbiaceae), *Nardophyllum lanatum* (Asteraceae), and *Euphorbia collina* (Euphorbiaceae) (Luebert and

Pliscoff, 2018)

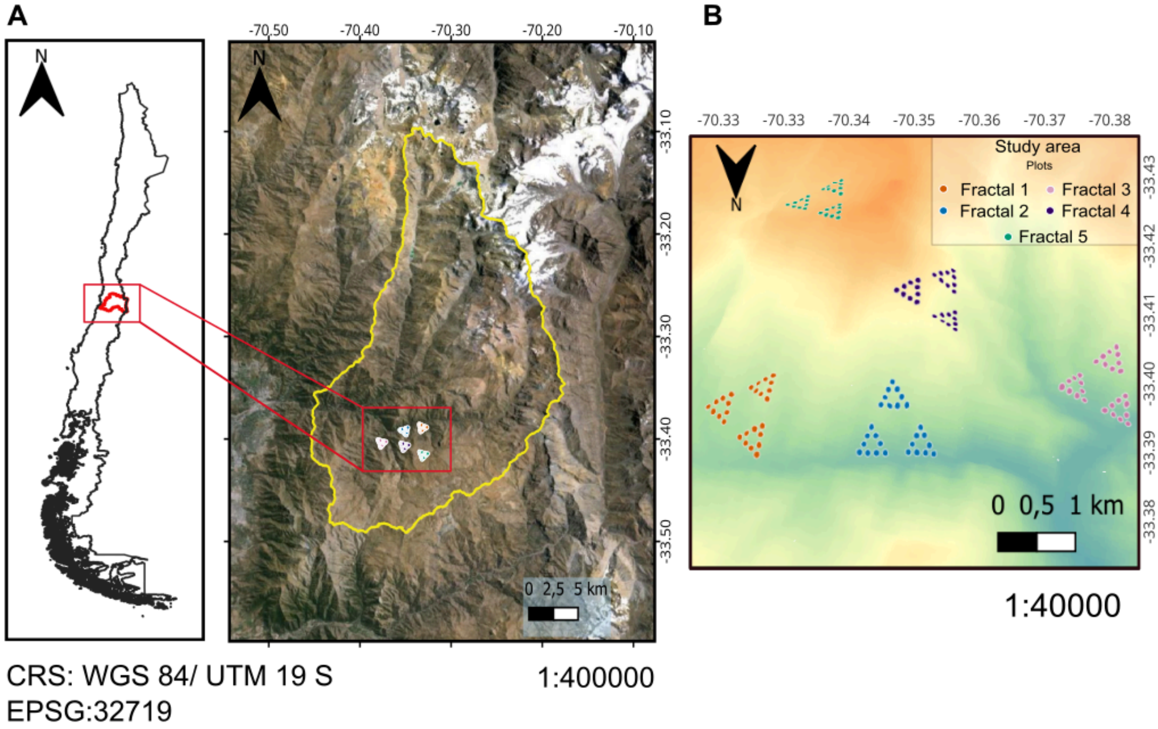

Figure 1*. Study area in the Mapocho River basin in the Mediterranean Andes Mountains of central Chile (****A****) and fractal study design used to examine patterns of plant diversity, ecosystem stability, topography, and spatial autocorrelation (****B****). Blue areas indicate low elevations and red areas high elevation.*

Field sampling

We conducted a vegetation survey using a fractal design to characterize plant communities across the elevation gradient (Marsh and Ewers, 2012). A fractal design offers distinct advantages over random sampling approaches (Simpson and Pearse, 2021); by concentrating comparisons of distances by pairs of plots within specific spatial scales, a fractal design maximizes information content across all spatial scales. In contrast, random sampling designs dilute these comparisons, concentrating information primarily at median spatial distances.

The fractals consist of an equilateral triangle with a side length of 900 m. Within each fractal, three sub-triangles are located at $1/3$ of the length of the primary triangle. Each sub-triangle consists of nine circular plots, each with a radius of 6 m and an area of 113.1 m^2 that are separated by 100 m, resulting in a total of 27 plots per fractal (Simpson and Pearse, 2021).

We established five fractals along the elevation gradient of the Mapocho River basin, from 1280 to 2362 m a.s.l. We established a total of 129 plots, as six plots could not be sampled due to the presence of steep cliffs or roads. In each plot, we identified and measured the diameter at 1.3 m height (DBH) of all tree and shrub individuals with a DBH >1 cm. We identified all individuals to species using local herbarium resources, local botanical experts, and field guides.

Environmental heterogeneity

We used the Advanced Array Type L-Band Synthetic Aperture Radar Instrument Earth Observation Satellite (ALOS-PALSAR) digital elevation model (DEM; 30 m resolution) to calculate environmental heterogeneity using topographic characteristics. We calculated a total of 25 characteristics, e.g., elevation, slope, aspect, curvature, flow accumulation, and the topographic wetness index (TWI; see Supplementary Material for the complete list) using SAGA GIS (Conrad et al., 2015). We estimated Pearson pairwise correlations between topographic features and discarded 9 variables with correlations $r \geq 0.7$ (Figure S7). We then used principal component analysis (PCA) to reduce the dimensionality of the selected topographic characteristics (Pearson, 1901). We used the first two principal components in subsequent analyses, which explained 29.7% and 25.9% of total variation in topographic characteristics. The first principal component (PC1) was positively associated with elevation, flat terrain, and terrain features enhancing soil moisture retention, and negatively associated with topographic features indicating terrain heterogeneity or roughness. We thus interpret this first component as an elevation-ruggedness gradient (Figure S8). The second component (PC2) is mainly related to topographic characteristics indicating water availability.

Positive values in PC2 are associated with areas of higher water flow and erosion, suggesting more dynamic and disturbed conditions and higher water availability. Conversely, negative values indicate areas with lower water flow and erosion and lower water availability (Table S3 and Figure S8). We interpret this second axis as a water availability gradient.

Taxonomic diversity

For each plot, we calculated Hill diversity indices (Chao et al., 2014; Ellison, 2010) to assess plant taxonomic and phylogenetic diversity for Hill numbers 0 and 2 using the R package *iNEXT* (Hsieh et al., 2016). Species diversity with Hill number 0 is equivalent to species richness ('Hill–Richness'), which gives equal weight to common and rare species, while species diversity with Hill number 2 is similar to Simpson diversity ('Hill-Simpson') and gives greater weight to more common species (Hsieh and Chao, 2016; Roswell et al., 2021). We used rarefaction and extrapolation to estimate diversity at the same level of sample coverage (sample coverage = 0.925; Chao et al., 2014). We present results for Hill number 0 in the main text and for Hill number 2 in Supplementary Information (Figure S1).

To quantify changes in community composition, i.e. species turnover, across plots, we calculated β diversity using the Sorensen index with the '*beta.div.comp*'. We then calculated the local contribution of each plot to total β diversity (LCBD), which is a measure of the uniqueness of communities in a region in terms of composition (Legendre and De Cáceres, 2013; Lozada Piña et al., 2023) using the R package *adespatial* (Dray et al., 2023).

Phylogenetic diversity

We constructed a species-level phylogenetic tree (Figure S3) using the R package *V.PhyloMaker* (Jin and Qian, 2019) based on the mega-phylogeny of Smith and Brown (2018) and Zanne et al. (2013). However, including *Ephedra chilensis,* a gymnosperm, could disproportionately influence phylogenetic diversity estimates given its longer evolutionary distance from other species in our study. We therefore performed a square root transformation of the phylogenetic distance matrix (Letten and Cornwell, 2015) prior to calculating phylogenetic diversity. Similar to taxonomic diversity, we calculated phylogenetic diversity with a standardized sample coverage for Hill numbers 0 and 2 (sample coverage = 0.925; (Chao et al., 2014)) using the R package *iNEXT-PD* (Chao et al., 2014; Hsieh and Chao, 2016).

To quantify phylogenetic turnover, we calculated phylogenetic dissimilarity distance matrices using the Sorensen index (Nogueira et al., 2019) with the *phylo.beta.pair* function in the R package *betapart* (Baselga and Orme, 2012). This index can be used to test whether two communities are more or less phylogenetically similar than expected given the similarity of their taxa, and is an index that has low sensitivity to species richness (Bryant et al., 2008). Finally, we estimated the local contribution of each community to phylogenetic β diversity (LCBD) with the *LCBD.comp* function in the R package *adespatial* (Dray et al., 2023).

Temporal stability of vegetation productivity

To calculate vegetation productivity over time, we used all available Sentinel-2' surface reflectance data (L2) (Sen2Cor; Main-Knorn et al., 2017) from January 2017 to December 2022 (n = 464) to calculate a six-year time series of the kernel Normalised Difference Vegetation Index (kNDVI). kNDVI, a nonlinear variant of NDVI, is more resistant to saturation and noise, making it a more robust tool for estimating and monitoring primary productivity of plant communities (Wang et al., 2023). Similar to NDVI, kNDVI quickly captures changes in vegetation greenness or cover, but is less prone to saturation over highly vegetated areas (Wang et al., 2023) . Consequently, kNDVI can also be used to assess ecosystem responses to environmental change and ecosystem stability (Engel et al., 2023). We used Level-2 (L2) . Data was collected and processed through Data Cube Chile (https://datacubechile.cl/).To quantify the temporal variability of kNDVI, we used the Consecutive Disparity Index (D; Fernández-Martínez et al., 2018). Unlike the coefficient of variation (CV), which measures the dispersion of data around the mean and is frequently used to quantify temporal variability of ecosystem functioning (e.g., Tilman et al., 2006), the

D index captures the degree of change between consecutive values in a time series. This means that D is more sensitive to patterns of variability over time and is less affected by outliers. The D index is calculated as the mean rate of change of the log ratios between consecutive values; high values of the D index indicate greater temporal variation in kNDVI, while low values of the D index indicate the opposite. As low values of D indicate high temporal stability, we use the inverse of the D index (1/D) in all our analyses. To validate the use of kNDVI for estimating ecosystem stability, we correlated ecosystem stability, i.e., temporal variation in kNDVI, with field data that are often correlated with vegetation productivity, i.e., total tree cover, aboveground biomass, plant herbaceous cover, and tree density.

Data analysis

We evaluated the bivariate relationships of environmental heterogeneity on taxonomic and phylogenetic diversity and turnover, and ecosystem stability using GLMs regressions with Gaussian or Gamma error distributions. We used the first two components of the PCA (i.e., Elevation-Roughness and Water Availability) as explanatory variables (Paradis and Schliep, 2019). Additionally, we applied a distance-decay model using the *decay.model* function of the *betapart* package in R to assess changes in taxonomic or phylogenetic composition across spatial gradients (supplementary material, Table S5). For this analysis, we calculated dissimilarity in taxonomic or phylogenetic composition using the Bray index.

Finally, we used piecewise structural equation models (SEMs; Lefcheck, 2015) to assess the direct and indirect relationships between ecosystem stability, α diversity, species turnover (LCBD), spatial autocorrelation, and topographic features. Prior to fitting the SEMs, we first built a hypothetical causal model of our initial hypothesis that α diversity, species turnover, topography (represented by elevation-ruggedness and water availability), and spatial autocorrelation all directly affect ecosystem stability, and that the effects of topography on ecosystem stability are mediated by taxonomic (or phylogenetic) α diversity and turnover

(Figure S5). First, we built generalized linear models (GLMs) with a Gaussian distribution using the *glm* function in the R package *ape* (Paradis and Schliep, 2019) to estimate autocovariate terms accounting for the residuals of spatial autocorrelation (RAC) between α diversity and species turnover (LCBD) with topography (i.e., α diversity ~ Topography; LCBD ~ Topography) and ecosystem stability (Stability ~ Topography + α diversity + LCBD) (Bardos et al., 2015). We calculated the spatial autocovariate term ('Spatial autocorrelation') using the *spdep* package in R (Bivand et al., 2011). In the SEMs, we interpret spatial autocorrelation as indicating the extent to which nearby communities have similar values of plant diversity or ecosystem stability. .

We fitted two different SEMs, one for taxonomic diversity and one for phylogenetic diversity, using GLMs including previously estimated autovariates ('Spatial autocorrelation') to account for spatial autocorrelation. For each SEM, we assessed overall model fit using Shipley's *d* separation test (Shipley, 2013), which identifies missing paths in hypothesized relationships. If there were no missing paths and the *d* separation test was still not significant, we calculated the AIC value based on Fisher's C statistic (Shipley, 2013); a lower AIC indicates a better model fit. We removed a path if it improved the fit by ΔAIC ≥ 2. However, if the removed path violated any condition, such as creating missing paths or increasing the AIC, the path was retained. We performed this iterative process until the most parsimonious model was reached. We assessed overall model fit using Fisher's C statistic and a p-value greater than 0.05 (Grace and Irvine, 2020). SEM analyses were performed using the *piecewiseSEM* R-package (Lefcheck, 2016). We performed all analyses and most visualizations with R v. 4.3.2 (R Core Team, 2024).

Results

Taxonomic and phylogenetic diversity patterns across elevation gradient

We observed a total of 2135 individuals of 40 plant species (Table S1). In all fractals, taxonomic diversity and phylogenetic diversity showed a non-saturating relationship with the number of individuals, with the exception of phylogenetic diversity in Fractal 5 (Figure 2). In contrast, taxonomic and phylogenetic Hill-Simpson diversity (Hill number 2) saturated rapidly with the number of individuals (Figure S1). Average taxonomic α diversity did not vary systematically with elevation, while average phylogenetic α diversity decreased non-linearly with elevation (95% confidence do not overlap with zero; Figure 2A & B, insets). For Hill-Simpson diversity, we observed a hump-shaped pattern with elevation for average taxonomic α diversity and an increasing non-linear relationship with elevation for average phylogenetic α diversity (Figure S1A & B).

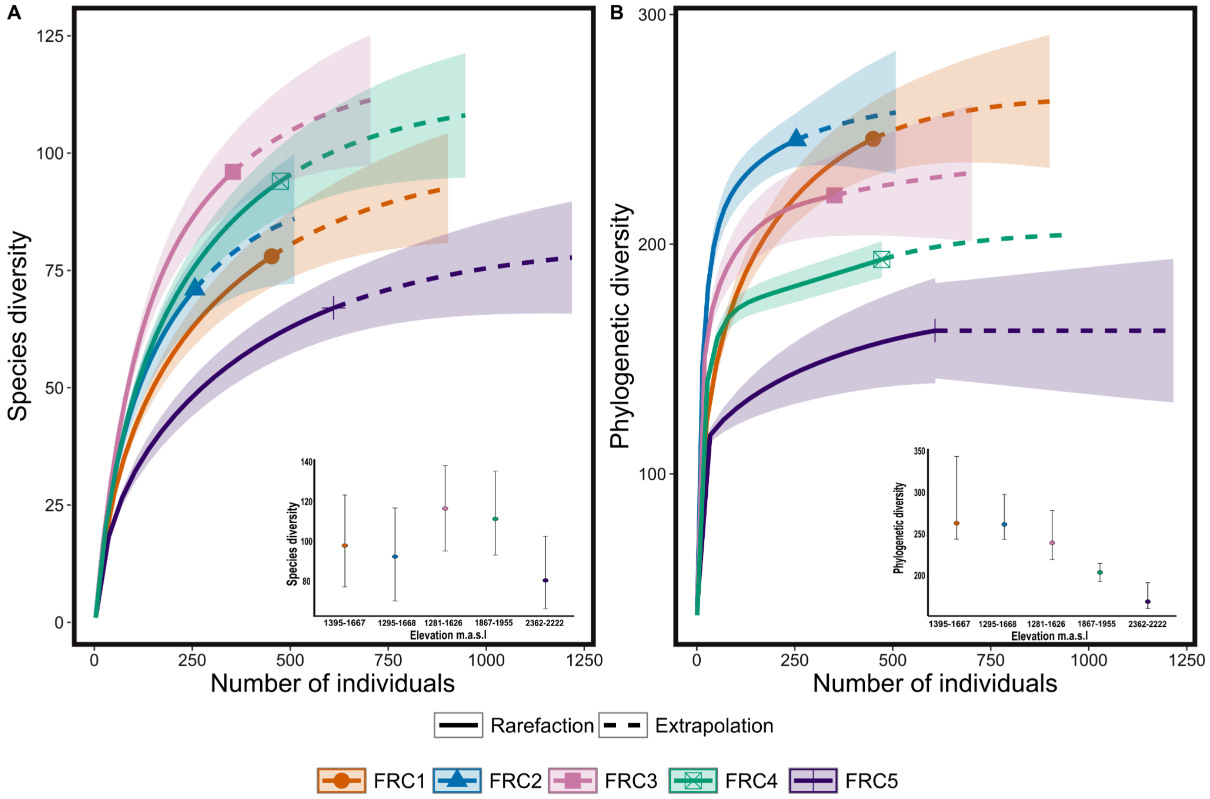

Figure 2. *Species (**A**) and lineage (**B**) accumulation curves across an elevational gradient in the Mediterranean Andes of central Chile. Taxonomic and phylogenetic diversity were estimated with interpolation and extrapolation for Hill number 0, which gives equal weight to rare and abundant species. FRC1 is located at 1519 m a.s.l., FRC2 at 1410 m a.s.l., FRC3 at 1414 m a.s.l., FRC4 at 1955 m a.s.l. and FRC5 at 2281 m a.s.l. Solid lines represent species and phylogenetic diversity estimated with individual-based rarefaction, dashed lines*

represent taxonomic and phylogenetic diversity estimated with individual-based extrapolation, and shaded regions are with 95% confidence intervals. Solid symbols represent observed taxonomic and phylogenetic diversity. In the insets, we estimated average taxonomic and phylogenetic α *diversity for each fractal, which are ordered by elevation.*

Effects of plant diversity and topography on ecosystem stability

Consistent with our expectations, we found that taxonomic dissimilarity increased significantly with spatial autocorrelation (Figure 3A; Table S5). We also found that species turnover increased significantly with elevation (Figure 3B & S2; Table S5) indicating that high-elevation communities contributed the most to species turnover across the elevation gradient. In contrast, species turnover, species richness, nor ecosystem stability exhibited a statistically significant relationship with water availability (Figure 3C; Table S5). Yet, we observed a statistically significant negative relationship between species turnover and ecosystem stability (Figure 3D; Table S4), which did not vary significantly in response to species richness (Figure 3D; Table S5).

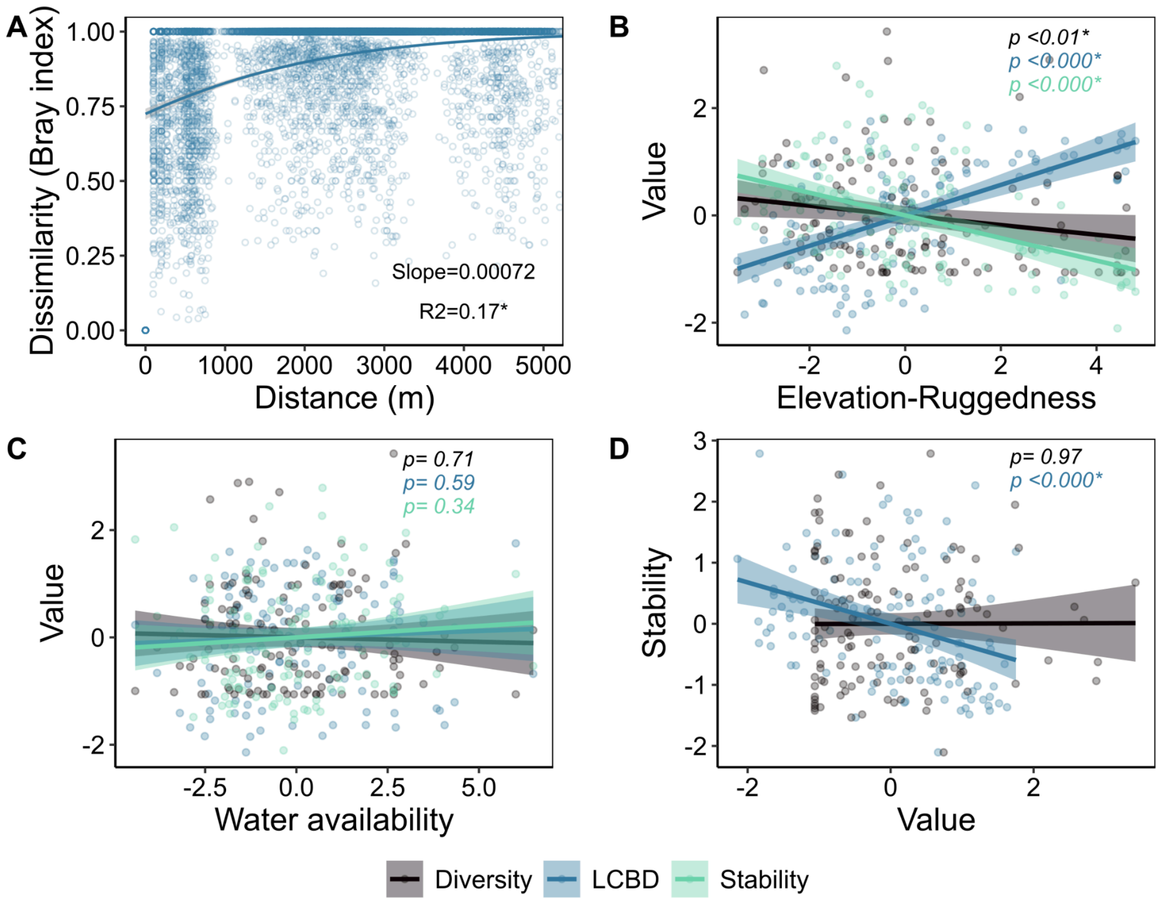

***Figure 3**. Relationships between taxonomic diversity, spatial autocorrelation, environmental heterogeneity, and ecosystem stability in the Mediterranean Andes of central Chile. (A) Distance decay of species composition, (B) shifts in taxonomic richness, taxonomic turnover (LCBD), and* ecosystem *stability in a gradient of Elevation-ruggedness (PC1), (C) relationships between water availability (PC2) and taxonomic richness, taxonomic turnover (LCBD), and ecosystem stability, and (D) the effects of plant species richness and species turnover (LCBD) on ecosystem stability. The fitted lines and R2 values were estimated using generalized linear models (GLMs). In A, the * indicates p < 0.01. Plant species richness was estimated with Hill number 0 and species turnover as local contributions to β diversity (LCBD).*

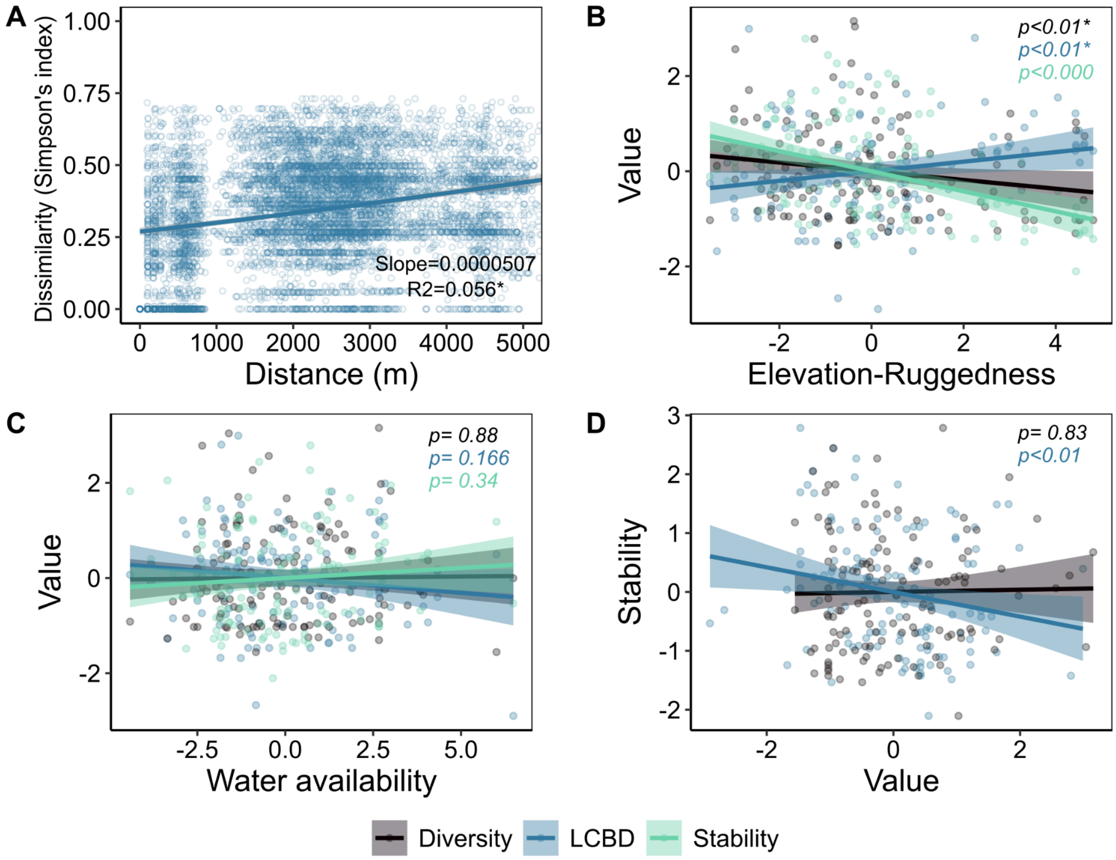

Figure 4. *Relationships between phylogenetic diversity, spatial autocorrelation, environmental heterogeneity, and ecosystem stability in the Mediterranean Andes of central Chile. (A) Distance decay of phylogenetic species composition, (B) shifts in phylogenetic richness, phylogenetic turnover (LCBD), and ecosystem stability in a gradient of Elevation-ruggedness (PC1), (C) relationships between water availability (PC2) and phylogenetic species richness, phylogenetic turnover (LCBD), and ecosystem stability, and (D) the effects of phylogenetic plant species richness and turnover (LCBD) on ecosystem stability. The fitted lines and R2 values were estimated using the generalized linear models (GLMs). In A, the * indicates p < 0.01. Phylogenetic plant species richness was estimated with Hill number 0 and phylogenetic turnover as local contributions to β diversity (LCBD).*

Similarly, phylogenetic diversity and turnover varied significantly along spatial or environmental gradients. Phylogenetic turnover (LCBD) varied significantly with both distance (Figure 4A), and with elevation-ruggedness (Figure 4b). Conversely, phylogenetic diversity and turnover did not vary significantly with water availability (Figure 4C) or ecosystem stability (Figure 4D; Table S5).

Our SEMs evaluating the direct and indirect effects of environmental heterogeneity on ecosystem stability fitted the data well (taxonomic diversity: Fisher’s C = 12.65, p = 0.39; phylogenetic diversity: Fisher’s C = 12.24, p = 0.58). Overall, the taxonomic piecewise SEM explained 67% of variation in ecosystem stability, 43% of variation in species turnover (LCBD), and 4% of variation in taxonomic α diversity (Figure 5A; Table S6). We found species turnover and taxonomic diversity did not have statistically significant direct effects on ecosystem stability. Yet, environmental heterogeneity, i.e, elevation-ruggedness (PC1) had statistically significantly positive effects on species turnover (Figure 5A), and spatial autocorrelation had a statistically significantly positive effect (standardized path coefficient = 0.30) on species turnover. Taxonomic diversity showed a significant negative relationship with Elevation-ruggedness had a statistically significant negative effect on taxonomic diversity (standardized path coefficient = -0.17). In terms of ecosystem stability, elevation-ruggedness had a statistically significant negative direct effect (Figure 5B), while spatial autocorrelation and water availability had statistically significantly positive direct effects (Figure 5B).

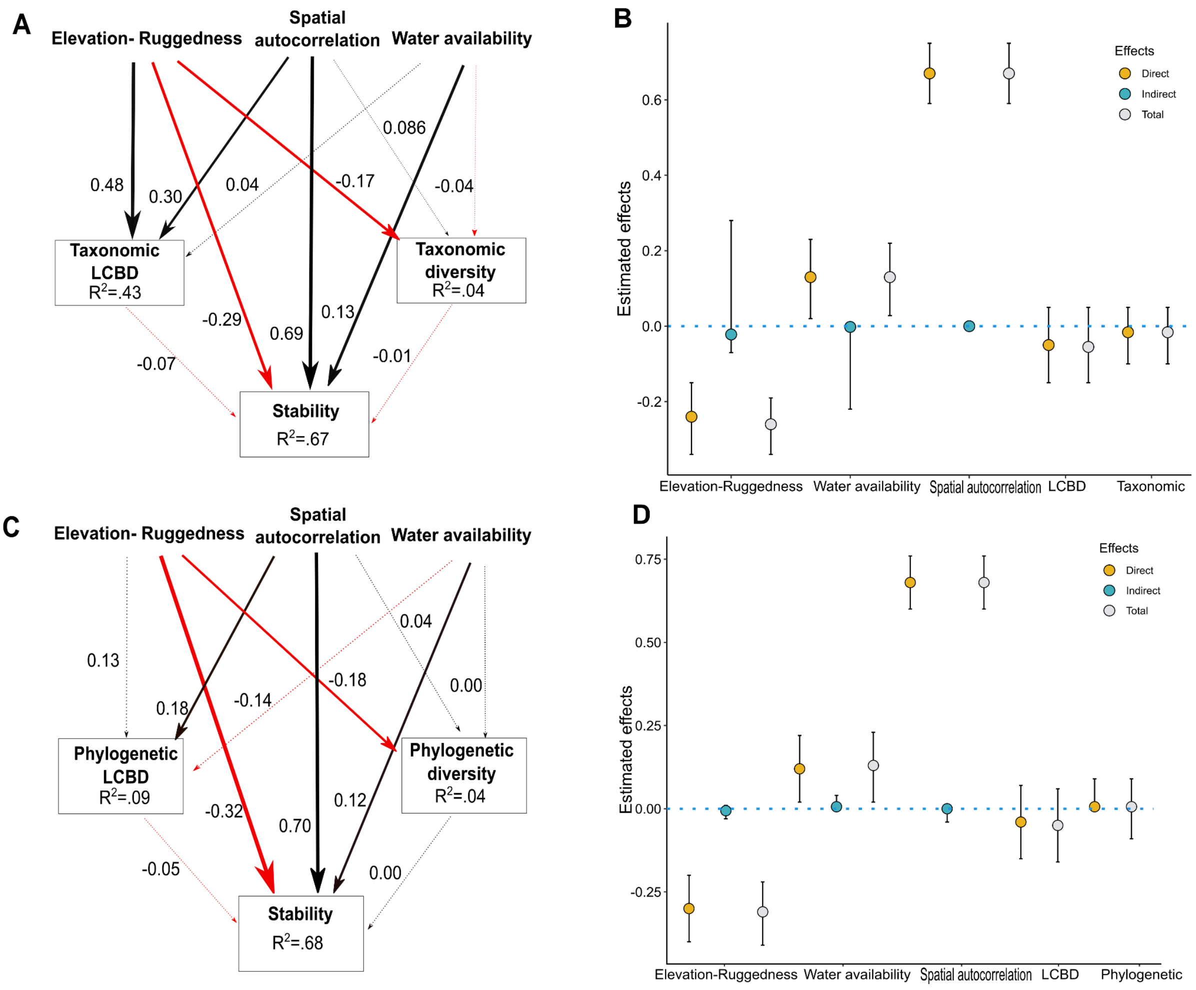

Figure 5*. Structural equation models (SEM) showing the direct and indirect effects of environmental heterogeneity, spatial autocorrelation, and taxonomic (A & B) and phylogenetic (C & D) diversity on ecosystem stability in the Mediterranean Andes of central Chile. In (A & C), solid and dashed arrows indicate statistically significant and non-significant relationships ($p < 0.05$), respectively. Red arrows indicate negative standardized path coefficients and black arrows indicate positive standardized path coefficients. In (B & D), direct, indirect, and total effects on ecosystem stability. (C) Model-fit statistics for the SEM with taxonomic diversity: Fisher's C = 12.65, p = 0.39, AIC = 893.387; Model fit statistics for the SEM with phylogenetic diversity: Fisher's C = 12.241, p = 0.58, AIC = 951.62.*

While the the phylogenetic piecewise SEM explained 68% of the variation in ecosystem stability, it only explained 9% of the variation in species turnover (LCBD) and 4% of the variation in phylogenetic α diversity (Figure 5C; Table S7). We found that ecosystem stability decreased with increasing elevation (standardized path coefficient = -0.32), and increased with increasing spatial autocorrelation (standardized path coefficient = 0.70), and water availability (standardized path coefficient = 0.12). However, neither species turnover nor phylogenetic α diversity had a statistically significant direct effect on ecosystem stability. Consequently, we found no statistically significant indirect effects on ecosystem stability (Figure 5D).

Finally, we found that ecosystem stability was positively correlated with total tree and shrub cover ($r = 0.39$, $p < 0.05$), aboveground biomass ($r = 0.25$, $p < 0.05$), and trees and shrubs density ($r = 0.40$, $p < 0.05$; Figure S4). In contrast, plant herbaceous cover showed no statistically significant relationship with ecosystem stability ($r = -0.14$, $p > 0.05$).

Discussion

Our study demonstrates that environmental heterogeneity directly influences both plant diversity and ecosystem stability, but that plant diversity does not stabilize vegetation productivity in mountain ecosystems in the Mediterranean Andes of central Chile. Although inconsistent with the predictions of diversity-stability theory (Loreau and de Mazancourt 2013), our results highlight: *i*) the context dependency of diversity-stability relationships in naturally-assembled ecological communities (Van der Plas 2019), and *ii*) that the effects of environmental heterogeneity on ecosystem stability are greater than those of plant diversity in mountain ecosystems, once accounting for spatial variation (Zhang et al., 2016, Xue et al., 2023). Our finding that environmental heterogeneity associated with elevation and topographic roughness influenced the stability of vegetation productivity more than that associated with water availability is noteworthy in light of the recent mega-drought in central Chile, which has reduced precipitation by 55 to 80% since 2010 (Garreaud et al., 2020). Taken together, our results provide evidence that environmental heterogeneity plays a crucial role in determining patterns of plant diversity and ecosystem stability in mountain ecosystems.

Spatial autocorrelation and environmental heterogeneity modulate ecosystem stability

Our SEMs revealed that spatial autocorrelation stabilized vegetation productivity to a greater extent than either environmental heterogeneity or plant diversity (Figure 5). This finding indicates that the diversity-stability relationship in mountain ecosystems in central Chile is highly spatially structured, suggesting that the temporal stability of vegetation productivity and plant diversity are predominantly shaped by mechanisms, i.e. similar environmental or soil conditions, that induce spatial homogeneity at small spatial scales, yet spatial heterogeneity at larger spatial scales (Griffith and Peres-Neto 2006). Once accounting for spatial autocorrelation in the diversity-stability relationship, our results show that plant diversity has a non-statistically significant effect on ecosystem stability. Although spatial autocorrelation is a widely-known neutral process in ecology (e.g., Koening 1999), as populations, communities, and resources occur non-randomly in patches in many natural and semi-natural ecosystems (Milne 1992, Li et al., 2024), the historical focus on studying diversity-stability relationships in experimental ecosystems - in which species diversity and composition are explicitly manipulated - likely precluded the need to consider it explicitly. However, as diversity-stability relationships are increasingly examined in non-experimental contexts (Van der Plas 2019), our results provide compelling evidence for the need to account for spatial autocorrelation when evaluating diversity-stability relationships (e.g., Qiao et al., 2023), as both diversity and stability likely share similar mechanisms that determine their spatial variation (Wardle 2016). While doing so may yield a mixture of results (e.g., positive, negative, or neutral diversity-stability relationships), likely due to potential interactions between environmental conditions and diversity-stability relationships (de Boek et al., 2018), explicitly integrating spatial autocorrelation in statistical models provides a more precise estimation of the independent effects of environmental conditions and diversity on ecosystem stability in naturally-assembled communities.

Our results therefore highlight the need to reconsider the generality of the relationship between biodiversity and ecosystem stability (e.g., Van der Plas 2019) in ecosystems characterised by high environmental heterogeneity, such as mountain ecosystems. As expected (Stein et al., 2007, Heidrich et al., 2020), we found that greater environmental heterogeneity associated with elevation and topographic roughness increased taxonomic and phylogenetic local diversity and turnover and stabilized vegetation productivity (Figures 5 and S4). Yet, we found that neither taxonomic nor phylogenetic diversity in terms of either local diversity or turnover stabilized vegetation productivity (Figures 5C and S4C). This suggests that while greater environmental heterogeneity may promote both species coexistence and ecosystem stability independently (Oommen and Shanker, 2005; Yang et al., 2015; Testolini et al., 2021), it also appears to have increased - rather than decreased, as expected (Loreau and Mazancourt, 2013; Wang et al., 2021) - spatial covariation in species responses to environmental conditions (Treddinick et al., 2017). The high synchrony in species' responses may therefore have led to the observed negative relationships between ecosystem stability and taxonomic and phylogenetic turnover (Figures 3D and 4D), a relationship that disappeared once we accounted for spatial autocorrelation in the SEM. An alternative, and perhaps, simpler explanation for the lack of a direct effect of plant diversity on ecosystem stability is that the non-random mechanisms captured by environmental heterogeneity that shape spatial variation in plant diversity and ecosystem stability are spatially structured (Wardle 2016), and once accounted for, the causal relationship between diversity and ecosystem stability cannot be detected using structural equation models (Byrnes et al., 2025). Our results therefore suggest that environmental heterogeneity, and not plant diversity, plays a predominant role in stabilizing vegetation productivity in mountain ecosystems, by spatially structuring the variation in the local microclimatic and ecological conditions that underpin ecosystem stability (Ajbilou et al., 2006; Xu et al., 2020). Our results are broadly consistent with those of recent meta-analyses showing that abiotic factors are frequently as or more important than biodiversity in explaining variation in ecosystem functioning (Duffy et al., 2017; Van der Plas 2019), and that biodiversity's relative importance for ecosystem functioning largely depends on environmental context (Ratcliffe et al., 2017; Qiao et al., 2023).

Beyond the effects of spatial autocorrelation, we found that environmental heterogeneity associated with topographic roughness and water availability had opposing effects of different magnitude on ecosystem stability. On one hand, we found that ecosystem stability was higher in areas with high topographic roughness, water flow and erosion and water availability, while on the other hand, ecosystem stability was lower in areas with high elevation, flat terrain, and low water flow, erosion, and water availability. Our results broadly support those of previous studies (e.g., Geng et al., 2019, Woldu et al., 2020, Li et al., 2024), which have found that ecosystem stability decreases with increasing elevation and varies strongly across vegetation types. In our study system, we show that ecosystem stability decreases as plant communities dominated by evergreen woody trees and shrubs are replaced by herbaceous species with increasing elevation (Luebert and Pliscoff, 2018). We extend previous findings by decomposing the effects of elevation on ecosystem stability into gradients of topographic roughness and water availability, highlighting the importance of areas with complex topography with features that enhance water availability for maintaining vegetation productivity over time (Wolf et al., 2012). The greater relative importance of topographic roughness than water availability for ecosystem stability that we found was unexpected, as our study system has experienced a mega drought since 2010 (Garreaud et al., 2017, Garreaud et al., 2020), which has dramatically increased tree mortality and reduced forest productivity in central Chile (Miranda et al., 2023). Despite differences in the magnitude of their effects on ecosystem stability, our results indicate that the dynamic interplay between both dimensions of environmental heterogeneity at relatively small spatial scales can create refugia in mountain ecosystems that are crucial for biodiversity and ecosystem processes such as vegetation productivity (Brighenti et al., 2021). However, the same topographic features that stabilise vegetation productivity over time can have a negative impact on other ecosystem services in mountain ecosystems, such as erosion resistance, which can reduce soil erosion and maintain soil fertility, complicating efforts to manage these ecosystems for multiple benefits simultaneously (Gamfeldt and Rogers 2017, Neyret et al., 2022).

Drivers of plant diversity in mountain ecosystems

Across the elevation gradient, we found contrasting non-linear shifts in taxonomic and phylogenetic diversity. While taxonomic α diversity (Hill number 0) did not vary consistently with elevation, phylogenetic α diversity (Hill number 0) decreased non-linearly. In contrast, taxonomic Hill-Simpson diversity (Hill number 2) exhibited a hump-shaped relationship with elevation, while phylogenetic Hill-Simpson diversity (Hill number 2) exhibited a high-plateau pattern with elevation. These results suggest that shifts in environmental conditions, e.g., temperature, water, and energy, along the elevation gradient differentially affected plant community structure, i.e, the diversity of common and rare species, and biodiversity facets. For instance, the mid-elevation peak of taxonomic Hill-Simpson diversity (Hill number 2) is consistent with the idea that harsh environmental conditions at low elevations, such as high temperatures and low water availability, and high elevations, such as low temperatures and low water availability, have limited the diversity of common or abundant woody plant species at these elevations (Rahbek 1995, Grytnes and Vetaas 2002, McCain & Grytnes 2010, Laiolo et al., 2018, Vetaas et al., 2019). In contrast, the non-linear decrease in phylogenetic α diversity (Hill number 0) with increasing elevation suggests that the diversity of rare lineages is likely limited by low temperatures, as has been found in the mountain ecosystems of eastern North America (Qian et al., 2020, Schroeder et al., 2023), while the diversity of common lineages remains constant at higher elevations, suggesting that common lineages at high elevations represent a mix of lineages with tropical and extratropical origins (Neves et al., 2021). Finally, the contrasting responses of taxonomic and phylogenetic diversity to the elevation gradient may reflect the high degree of endemism and evolutionary relatedness in mountain flora (Steinbauer et al., 2016, Qian et al., 2020), such that as environmental conditions becoming less limiting at lower elevations, phylogenetic diversity does not increase as rapidly as taxonomic diversity (Figure S9). Given the land-use history in central Chile (Schulz et al., 2010), it is likely that past human activity has impacted diversity-elevation relationships in our study by truncating the length of the elevation gradient (McCain and Grytnes 2010) and reducing diversity in areas with higher land-use intensity (e.g., Kessler et al., 2009, Peters et al., 2019, Monge-González et al., 2020). However, the extent of human impacts on diversity patterns in Mediterranean mountain ecosystems, such as the Andes of central Chile, remains relatively unexplored, particularly its interactions with extreme climate events such as droughts.

Our results also show that environmental heterogeneity - particularly that associated with topographic roughness and elevation - plays a critical role in structuring plant communities in mountain ecosystems. This supports the idea that complex topographic characteristics facilitate species coexistence by generating a variety of microhabitats that promote ecological niche differentiation (Zuleta et al., 2018), thereby increasing the local contribution of communities to □ diversity (Malanson et al., 2024, McNichol et al., 2024). We also found that while topographic complexity increased species and phylogenetic turnover, it negatively impacted α diversity, particularly at higher elevations. There, more extreme environmental conditions - such as lower temperatures and limited resources - are likely to limit the number of species that can coexist (Martin and Ferrer, 2015), the effects of which may be exacerbated by the high temporal variability of Mediterranean ecosystems (Shoshany, 2000, Bricca et al., 2021, Cheikh Albassatneh et al., 2021; Jourdan et al.,2020). Despite the ongoing mega-drought in central Chile (Garreaud et al., 2017, Garreaud et al., 2020) and its widespread impacts on ecosystems (Miranda et al., 2023, Venegas-González et al., 2023), we did not find a direct effect of environmental heterogeneity associated with water availability on taxonomic or phylogenetic turnover. This suggests that spatial patterns of wood plant diversity may be resilient to long periods of drought stress, possibly due to anatomical and physiological adaptations in high-elevation forests that confer greater resilience to persistent droughts (Santini et al., 2024). Taken together, our results show that plant diversity in mountain ecosystems can be efficiently conserved by prioritising areas with high topographic ruggedness and those at high altitudes, which contribute species with unique evolutionary histories despite their low diversity.

Ecosystem stability monitoring with remote sensing

Ecological stability can be assessed using remotely-sensed time series of vegetation indices, such as kernel NDVI (kNDVI), capturing temporal variation in plant photosynthetic potential and providing a synoptic view of the ecological conditions of ecosystems (Camps-Valls et al., 2021; Zhang et al., 2024). kNDVI is recognized for its sensitivity and robustness as an indicator of greenness and remains stable even in heterogeneous environments such as those present in mountain ecosystems, where factors like slope orientation have minimal impact on its variation (Gu et al., 2024). In this study, we observed that areas with greater tree cover and aboveground biomass (AGB) have higher mean kNDVI and stability values (Figure S4), indicating that ecosystems with higher gross primary productivity (GPP) tend to maintain greater ecological stability. This suggests that satellite-measured stability is generally well estimated in mountain ecosystems dominated by woody vegetation. In contrast, herbaceous cover exhibits no clear relationship with ecosystem stability or mean kNDVI (Figure S4), suggesting that kNDVI may be less well-suited for assessing mountain ecosystems dominated by herbaceous vegetation. Therefore, remotely sensed data could be used to upscale stability-diversity patterns to the landscape scale using the vegetation attributes and linkages of the SEM (e.g., Lopatin et al., 2019) or through more complex modeling. Future studies may also include stability-diversity relationships driven by trait diversity (e.g., Ma et al., 2019) and land-atmosphere feedbacks at high spatial resolution (e.g., Anderegg et al., 2019), both of which are relevant for understanding ecosystem stability using optical remote sensing data.

Conclusions

Our study highlights the crucial role of environmental heterogeneity in determining patterns of plant diversity and ecosystem stability in the Mediterranean Andes of central Chile. Counter to classical stability-diversity theory, we found that plant diversity does not directly stabilize vegetation productivity. Instead, we found that spatial autocorrelation and environmental heterogeneity associated with gradients in elevation and topographic roughness, exert a stronger influence on ecosystem stability than plant diversity. Our results underscore the need to account for spatial processes when assessing relationships between diversity and stability in naturally assembled ecological communities. Regarding plant diversity, our results support the idea that topographic complexity promotes species turnover by creating a variety of microhabitats. While topographic heterogeneity increased taxonomic and phylogenetic turnover, it had a negative effect on local alpha diversity, especially at higher elevations where environmental conditions are more limiting. Interestingly, we found no significant direct effect of water availability on taxonomic or phylogenetic turnover, suggesting that woody plant diversity in these montane ecosystems may be resilient to prolonged drought stress. Taken together, our results provide compelling evidence that environmental heterogeneity, rather than plant diversity, plays a predominant role in stabilizing vegetation productivity in montane environments. These findings have important implications for conservation, highlighting the need to prioritize areas with high topographic complexity and elevation for their contribution to maintaining biodiversity and key ecosystem functions, such as vegetation productivity. Future research should further investigate how spatial processes interact with biodiversity and a wider range of ecosystem functions, such as erosion resistance and water quality regulation, in mountain ecosystems undergoing climate change, to refine conservation and management strategies.

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Supplementary Materials for “Environmental heterogeneity mediates plant diversity and ecosystem stability in mountain ecosystems”

This file includes:

Figures S1 to S9

Table S1 to S7

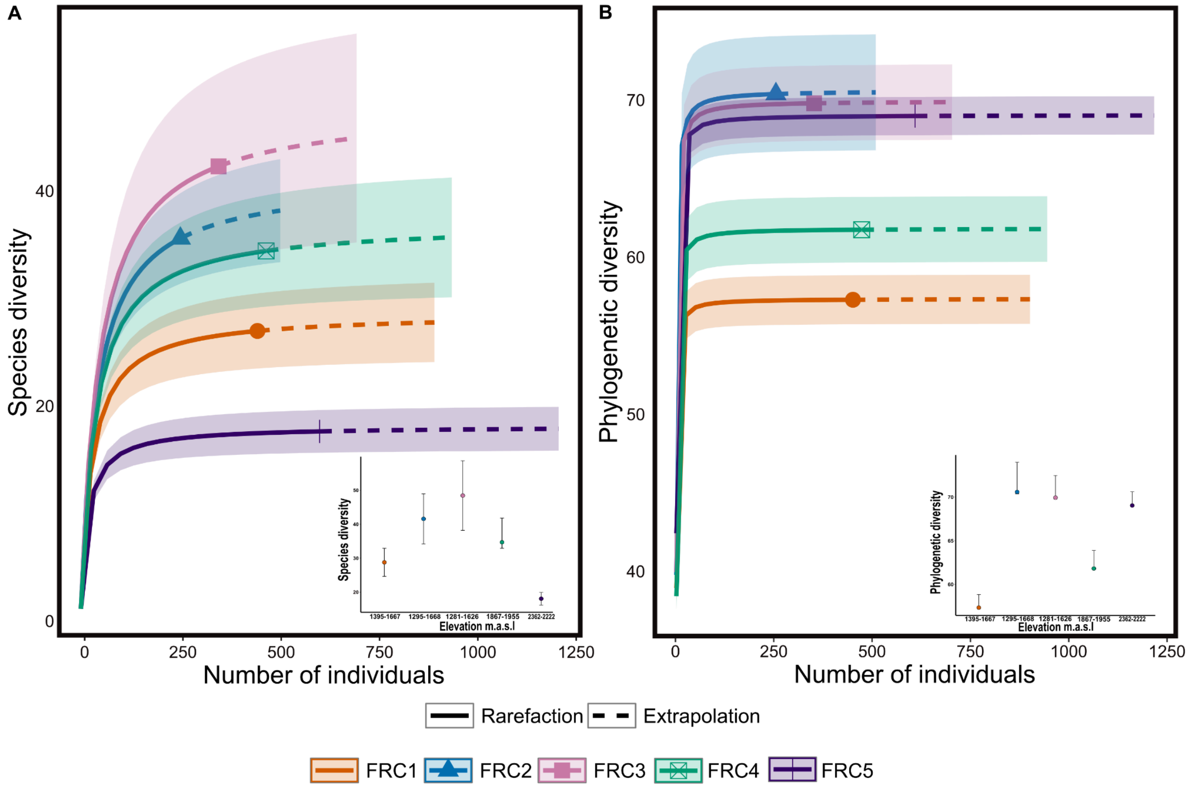

Figure S1*. Accumulation of taxonomic (****A****) and phylogenetic (****B****) Hill-Simpson diversity (Hill Number 2) with the number of individuals in the Mediterranean Andes of central Chile. Colors correspond to fractals, solid lines represent the part of diversity accumulation curves estimated with rarefaction while dashed lines represent the part of diversity accumulation curves estimated with extrapolation. Shaded bands are 95% confidence intervals. Fractals are arranged by elevation; FRC1 is located at 1519 m a.s.l., FRC2 at 1410 m a.s.l., FRC3 at 1414 m a.s.l., FRC4 at 1955 m a.s.l. and FRC5 at 2281 m a.s.l.*

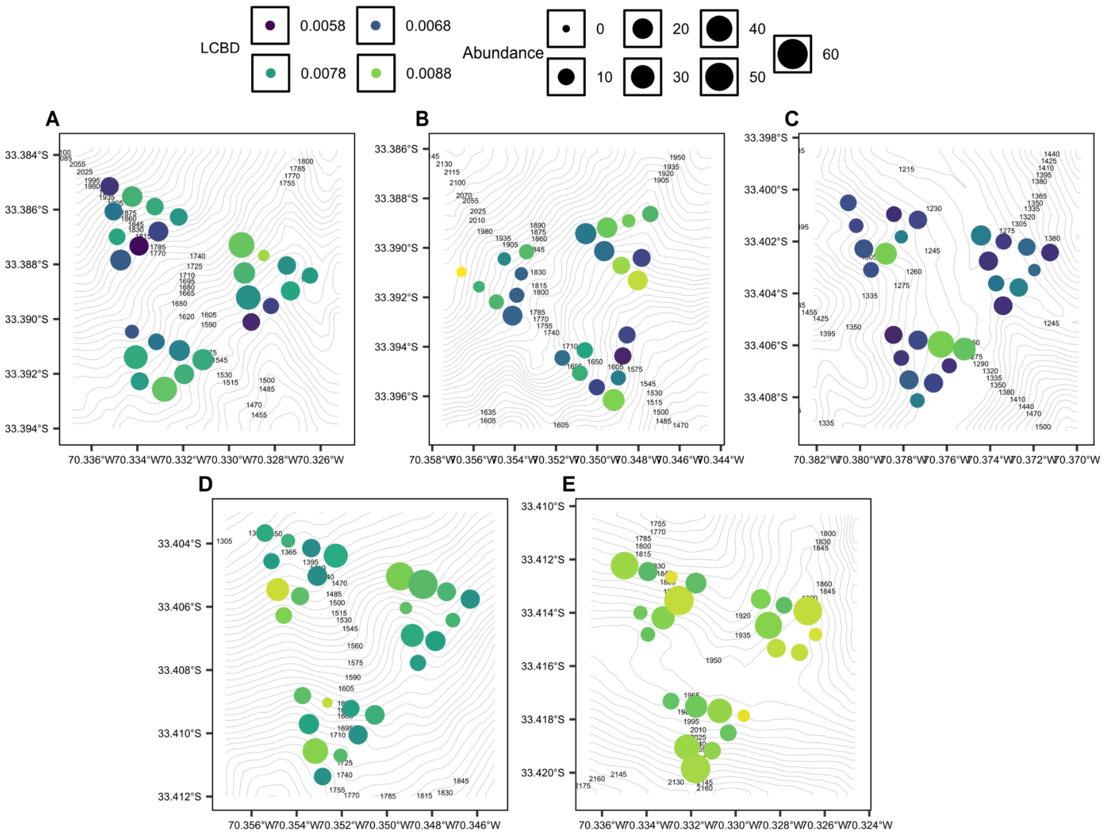

Figure S2. *Maps of local contributions to beta taxonomic diversity (LCBD) with contour lines for each fractal in the Mediterranean Andes of central Chile. (A) Fractal 1 (1519 m a.s.l.), (B) Fractal 2 (1410 m a.s.l.), (C) Fractal 3 (1414 m a.s.l.), (D) Fractal 4 (1955 m a.s.l.) and (E) Fractal 5 (2281 m a.s.l.). Each color represents the local contribution to beta diversity and each size points to the abundance of species of each plot.*

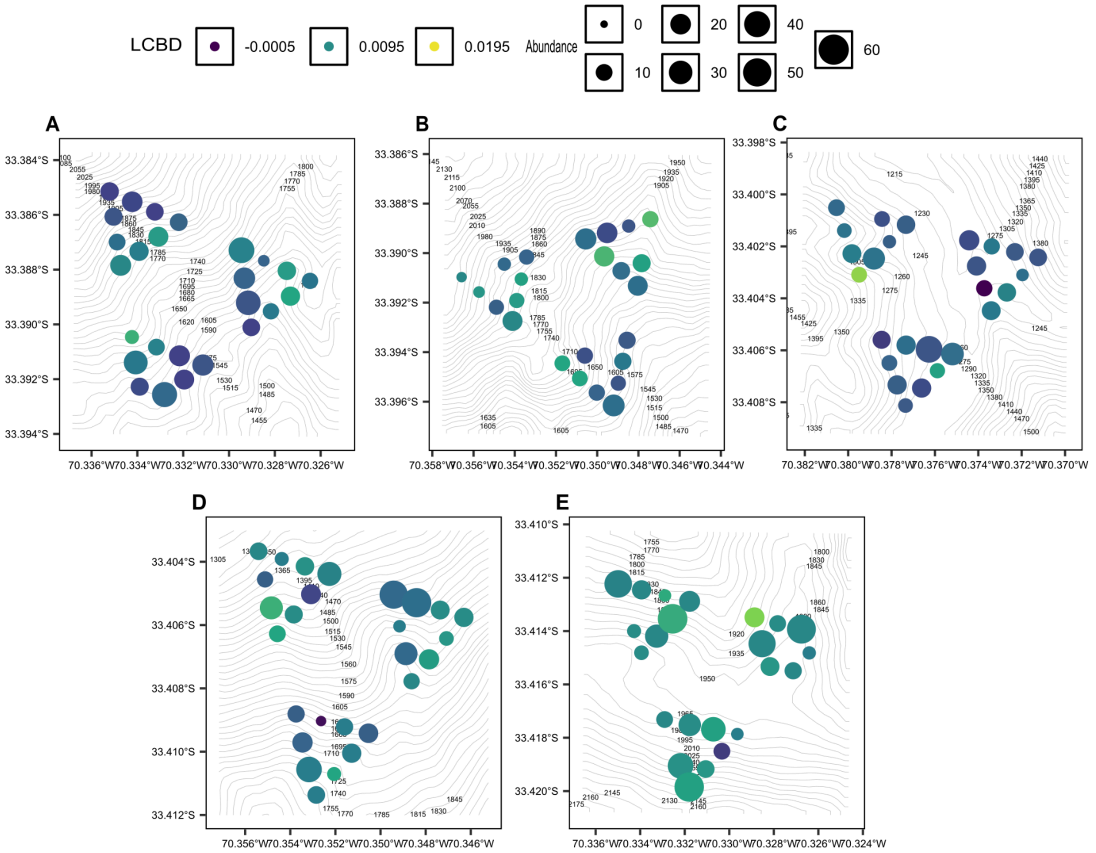

***Figure S3**. Maps of local contributions to beta phylogenetic diversity (LCBD) with contour lines for each fractal in the Mediterranean Andes of central Chile. (A) Fractal 1 (1519 m a.s.l.), (B) Fractal 2 (1410 m a.s.l.), (C) Fractal 3 (1414 m a.s.l.), (D) Fractal 4 (1955 m a.s.l.) and (E) Fractal 5 (2281 m a.s.l.). Each color represents the local contribution to beta diversity and each size points to the abundance of species of each plot.*

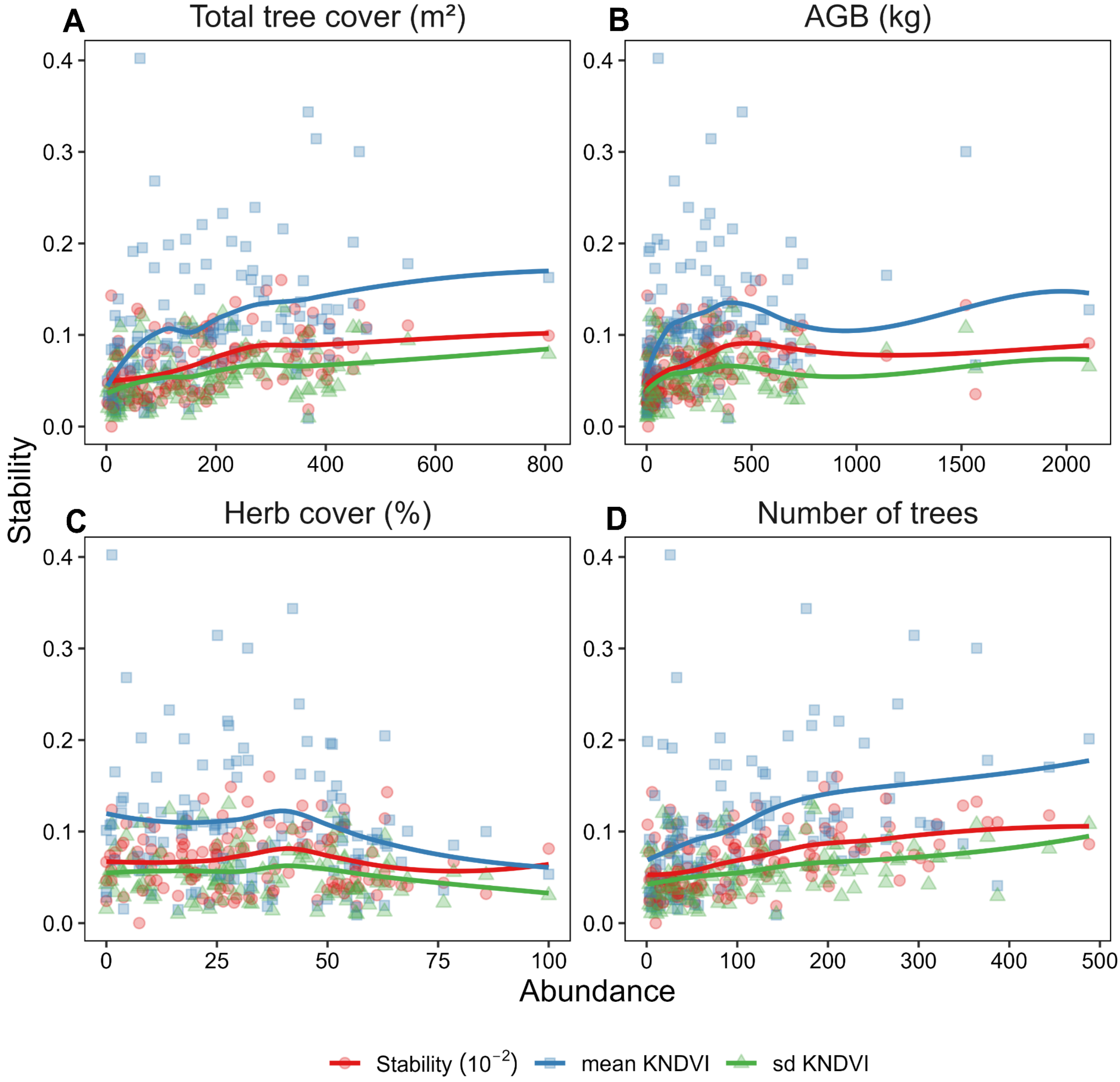

***Figure S4**. Relationship between ecosystem stability as measured by kNDVI and abundance. Each panel shows how ecological stability (red line) varies with different vegetation parameters: (A) Total tree cover (m²), (B) Aboveground biomass (AGB, kg), (C) Herbaceous cover (%), and (D) Number of trees. Mean kNDVI values (blue line) and their standard deviation (green line). The dots represent the observed data for each parameter.*

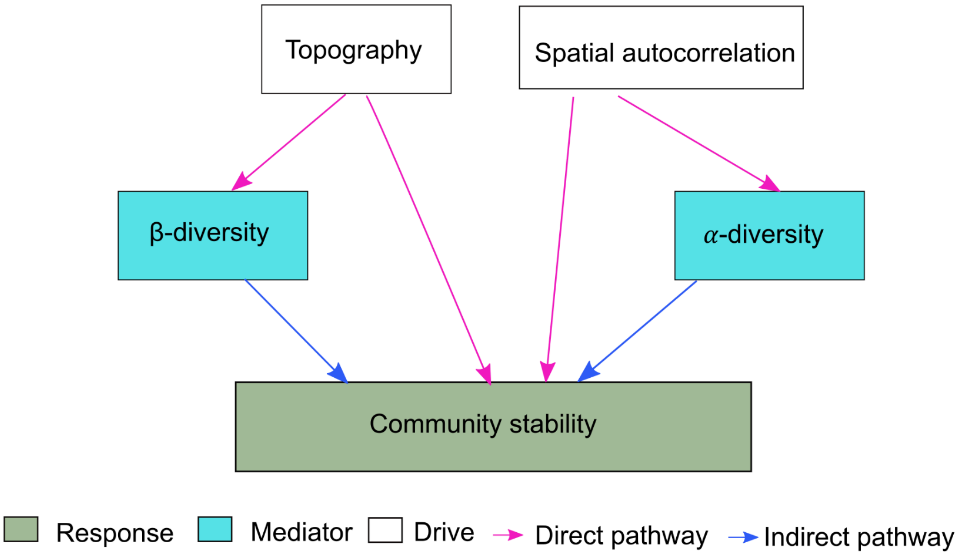

Figure S5. *Hypothetical causal model for structural equation model (SEM) investigating the effects of topography and diversity (taxonomic and phylogenetic) on vegetation stability in the Mediterranean Andes of central Chile. Pink lines are hypothesized direct paths and blue lines are hypothesized indirect path. Green box is the response variable, blue box is the mediators and white box is the drivers.*

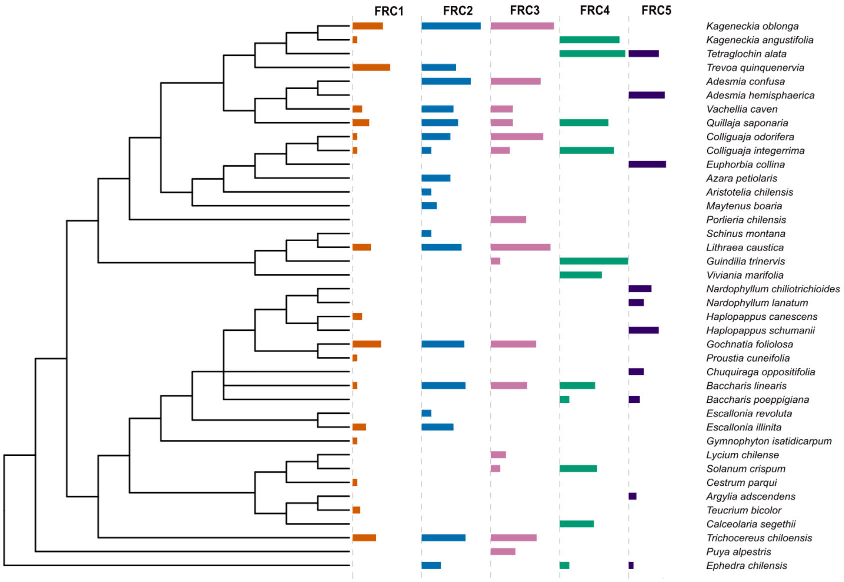

Figure S6. *Phylogenetic tree of the plant communities in the Mediterranean Andes of central Chile. The spatial arrangement and abundance of the vegetation plots is indicated by colors and bars (orange = FRC1, blue = FRC2, pink = FRC3, green = FRC4, purple = FRC5). The* *tree provides a framework for understanding the evolutionary history and relationships among the different plant species in the study area.*

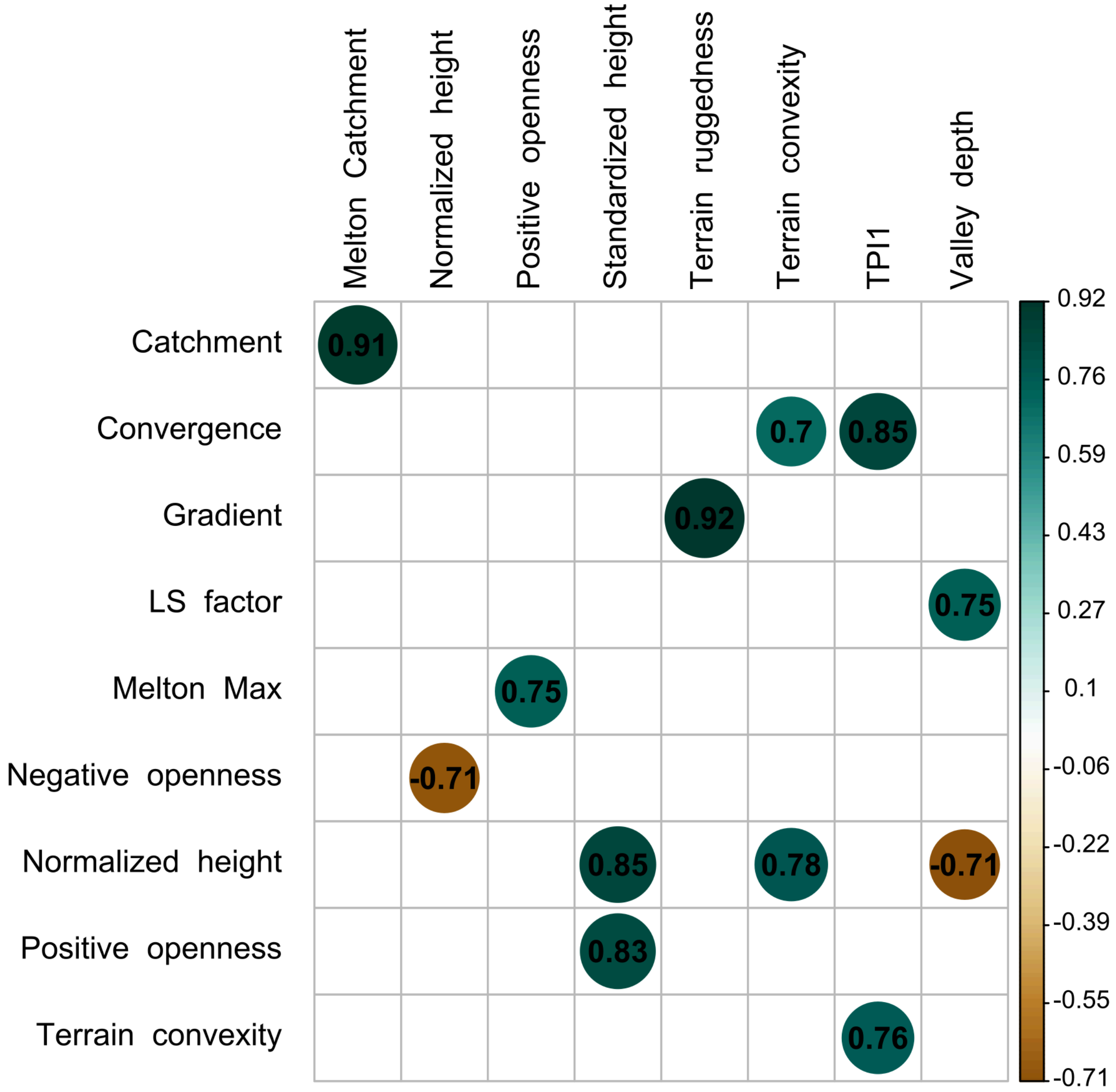

Figure S7*. Correlation matrix between 27 environmental variables, highlighting only those with absolute correlations* $r \leq 0.7$ *(positive or negative), calculated using the Pearson correlation coefficient. Positive correlations are shown in shades of green, while negative correlations are shown in shades of orange. The values inside the circles indicate the corresponding correlation coefficient.*

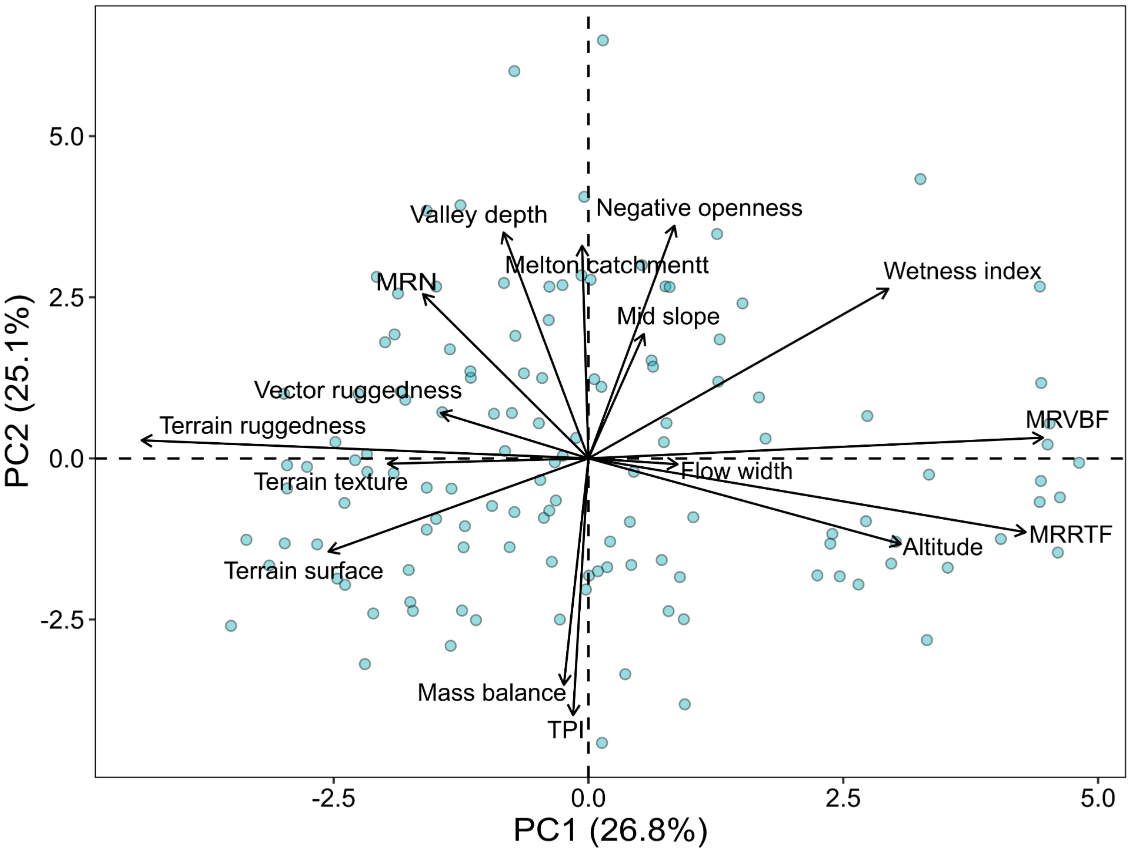

Figure S8*. Bi-plot of principal components analysis (PCA) of topographic characteristics of vegetation plots in the Mediterranean Andes of central Chile. All characteristics were calculated with SAGA GIS.*

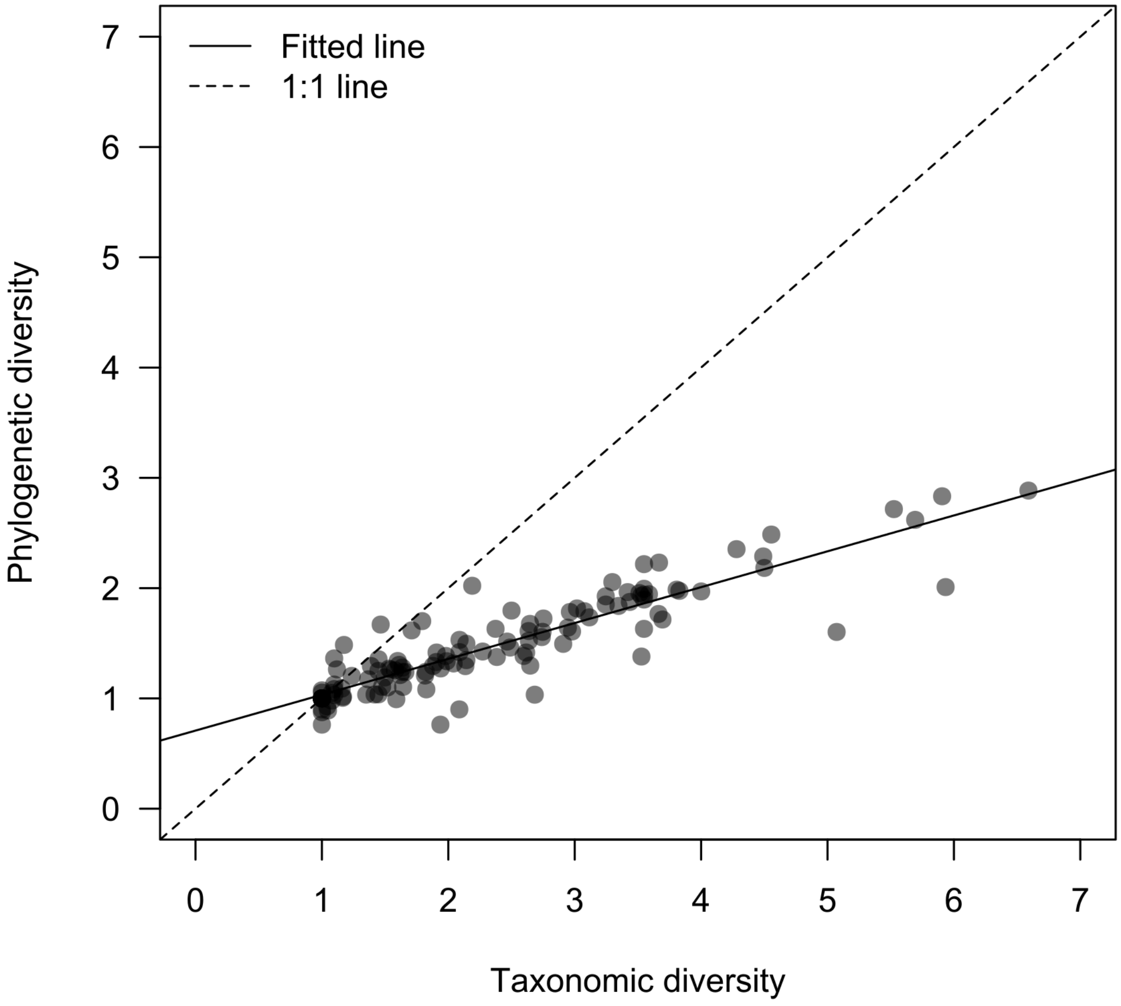

Figure S9. *Relationship between taxonomic diversity and phylogenetic diversity of all fractals in the Mediterranean Andes of central Chile. The black line represents the fitted regression, while the dashed line indicates the line of equality (1:1). The points represent the observations of each sampling plot.*

Table S1. *List of observed species, genus and family found in vegetation plots in the Mediterranean Andes of central Chile.*

Species	**Genus**	**Family**

Adesmia confusa	*Adesmia*	Fabaceae
Adesmia hemisphaerica	*Adesmia*	Fabaceae
Argylia adscendens	*Argylia*	Bignoniaceae
Aristotelia chilensis	*Aristotelia*	Elaeocarpaceae
Azara petiolaris	*Azara*	Salicaceae
Baccharis linearis	*Baccharis*	Asteraceae
Baccharis poeppigiana	*Baccharis*	Asteraceae
Cestrum parqui	*Cestrum*	Solanaceae
Chuquiraga oppositifolia	*Chuquiraga*	Asteraceae
Colliguaja integerrima	*Colliguaja*	Euphorbiaceae
Colliguaja odorifera	*Colliguaja*	Euphorbiaceae
Escallonia illinita	*Escallonia*	Escalloniaceae
Escallonia revoluta	*Escallonia*	Escalloniaceae
Euphorbia collina	*Euphorbia*	Euphorbiaceae
Gochnatia foliolosa	*Gochnatia*	Asteraceae
Guindilia trinervis	*Guindilia*	Sapindaceae
Gymnophyton isatidicarpum	*Gymnophyton*	Apiaceae
Haplopappus canescens	*Haplopappus*	Asteraceae
Haplopappus schumanii	*Haplopappus*	Asteraceae
Kageneckia angustifolia	*Kageneckia*	Rosaceae
Kageneckia oblonga	*Kageneckia*	Rosaceae
Lithraea caustica	*Lithraea*	Anacardiaceae
Lycium chilense	*Lycium*	Solanaceae
Maytenus boaria	*Maytenus*	Celastraceae
Nardophyllum chiliotrichioides	*Nardophyllum*	Asteraceae
Nardophyllum lanatum	*Nardophyllum*	Asteraceae
Porlieria chilensis	*Porlieria*	Zygophyllaceae
Proustia cuneifolia	*Proustia*	Asteraceae
Puya alpestris	*Puya*	Bromeliaceae
Quillaja saponaria	*Quillaja*	Quillajaceae
Schinus montana	*Schinus*	Anacardiaceae
Solanum crispum	*Solanum*	Solanaceae
Tetraglochin alata	*Tetraglochin*	Rosaceae
Teucrium bicolor	*Teucrium*	Lamiaceae
Trevoa quinquenervia	*Trevoa*	Rhamnaceae
Trichocereus chiloensis	*Trichocereus*	Cactaceae
Vachellia caven	*Vachellia*	Fabaceae
Ephedra chilensis	*Ephedra*	Ephedraceae

Table S2*. Definition of the topographic indices used in the analysis, generated using SAGA GIS software.*

Topographic variable	Acronyms	Definition	References

Catchment area	SCA	An area from which all cells flow into one.	Qin, C. Z., Zhu, A. X., Pei, T., Li, B. L., Scholten, T., Behrens, T. & Zhou, C. H. (2011)
Convergence index	CI	A metric that describes the arrangement of high and low points in a given area	Koethe, R. & Lehmeier, F. (1996)
Flow width	FW	Measure of water depth relative to mesh size	Gruber, S., Peckham, S. (2008)
LS factor		Determining the impact of slope and catchment area on soil erosion	Boehner, J., Selige, T. (2006)
Gradient		Index to quantify downslope controls on local drainage	Hjerdt et al., (2004)
Mass balance	MB	Quantifies the topographic factors that influence erosion and deposition processes on slopes.	Moeller, M., Volk, M., Friedrich, K., Lymburner, L. (2008)
Melton catchment area	MCA	Measure used to characterize the terrain's ruggedness.	Marchi, L. & Fontana, G.D. (2005)
Melton max height	MMH	Highest elevation within a catchment area.	Marchi, L. & Fontana, G.D. (2005)
Mid slope position	MSP	Index of location on a slope that is roughly halfway between the summit (top) and the valley bottom (bottom)	Boehner, J. & Selige, T. (2006
Melton Ruggedness Number	MRN	Index related to flow accumulation.	Marchi, L. & Fontana, G.D. (2005)
Multiresolution Index of Ruggedness Top Flatness	MRRTF	Index used to quantify the topographic roughness and flatness of a landscape at multiple spatial scales.	Gallant, J.C., Dowling, T.I. (2003)
Multiresolution Index of Valley Bottom Flatness	MRVBF	Index used to quantify the flatness of valley bottoms at multiple spatial scales.	Gallant, J.C., Dowling, T.I. (2003)

Negative openness	NO	Used to quantify the concavity of the landscape by measuring the extent to which a given cell is surrounded by lower elevations.	Anders, N. S., Seijmonsbergen, A. C., Bouten, W. (2009)
Normalized height		A measure that quantifies the relative elevation of a given point within a landscape.	Boehner, J. & Selige, T. (2006)
Positive openness	PO	Used to quantify the convexity of the landscape by measuring the extent to which a given cell is surrounded by higher elevations.	Anders, N. S., Seijmonsbergen, A. C., Bouten, W. (2009)
Wetness index	WI	Index used to identify and quantify the distribution of water accumulation in a landscape.	Boehner, J., Koethe, R. Conrad, O., Gross, J., Ringeler, A., Selige, T. (2002)
Standardized height		A measure used to express the elevation of a specific point relative to the average elevation of the surrounding area.	Boehner, J. & Selige, T. (2006)
Terrain ruggedness index	TRI	Index used to quantify the roughness or variability of the terrain by measuring the differences in elevation between a given cell and its neighboring cells.	Riley, S.J., De Gloria, S.D., Elliot, R. (1999)
Terrain surface classification	TSCL	Index to classify the surface into categories such as ridges, valleys, slopes, and flat areas.	Iwahashi, J. & Pike, R.J. (2007)
Terrain surface convexity	TSC	Index used to quantify the convexity of the landscape surface.	Iwahashi, J. & Pike, R.J. (2007)

Terrain surface texture	TST	Quantifies the micro-topography of a landscape using various texture measures.	Iwahashi, J. & Pike, R.J. (2007)
Topographic position index	TPI	Metric that measures the relative position of a point in the landscape compared to the surrounding terrain.	Wilson, J.P. & Gallant, J.C. (2000)
Valley depth	VD	Quantifies the vertical distance between a given point in a valley and the surrounding higher terrain, typically ridges or peaks.	Boehner, J. & Selige, T. (2006)
Vector ruggedness index	VRI	Measure of terrain complexity that quantifies surface roughness.	O.Conrad et al (2015)

Table S3. *Results of the principal component analysis (PCA). The table shows the values of the scores obtained for each variable.*

Variables	**PC1**	**PC2**
Flow width	-0.090531523	-0.009762907
Mass balance	0.024992983	-0.375856508
Mid slope	-0.056252098	0.206342837
MRN	0.168089354	0.272532793
Negative Openness	-0.087415637	0.386144723
Wetness index	-0.304774673	0.281476771
Terrain ruggedness	0.454097302	0.029928501
Terrain surface	0.264219106	-0.154763913
Terrain texture	0.203862606	-0.008927839

TPI	0.015602770	-0.426085093
Altitude	-0.317369734	-0.142040742
Melton catchment	0.006479904	0.352718407
MRRTF	-0.444269925	-0.122576622
MRVBF	-0.461850940	0.034367505
Valley depth	0.086322760	0.374827247
Vector ruggedness	0.150044169	0.075398274

Table S4. *Summary of observed and estimated values for taxonomic diversity and phylogenetic diversity measures for each fractal in the Mediterranean Andes of central Chile. The estimated* values are represented as mean ± 1 se and the 95% confidence intervals is a caption.

Diversity	Observed	Estimated	95% CI
Hill-Species richness			
FRC1	78	98.78	78-122
FRC2	71	93.23	71-120
FRC3	96	117.38	96-138
FRC4	94	112.18	94-134
FRC5	67	81.26	67-101
Hill-Simpson diversity			
FRC1	26.84	28.48	24-33
FRC2	35.44	41.04	34-48
FRC3	42.14	47.76	38-58
FRC4	34.28	36.89	32-41
FRC5	17.49	17.98	16-20
Hill-Faith’s PD			
FRC1	245.85	264.94	246-336
FRC2	245.36	263.53	245-304
FRC3	221.26	241.29	221-281
FRC4	193.34	205.70	195-217
FRC5	162.34	170.49	162-196
Hill-Rao’s Q			
FRC1	57.28	57.24	57-59
FRC2	70.38	70.59	70-74
FRC3	69.79	69.94	70-72
FRC4	61.74	61.82	62-64
FRC5	68.97	69.04	69-71

Table S5. *Results for the generalized linear models (GLM) of diversity taxonomic and phylogenetic, stability and environmental heterogeneity. For each model comparison (i.e., base model versus base model + added variable). AIC is the Akaike information criterion values for each model. R2 is the percentage of variance explained.*

Response	Predictor	R2	AIC	P.value
Diversity α	Elevation-Ruggedness	0.035	360.91	0.035
Diversity α	Water availability	0.001	365.27	0.71
LCBD	Elevation-Ruggedness	0.34	311.59	3.75e-13
LCBD	Water availability	0.002	365.11	0.59
Stability	Water availability	0.007	364.48	0.341
Stability	Elevation-Ruggedness	0.19	639.7	2.94e-07
Stability	LCBD	0.11	349.92	9.76e-05
Stability	Diversity α	0.00	365.4	0.97
Phylogenetic diversity α	Elevation-Ruggedness	0.036	158.29	0.032
Phylogenetic diversity α	Water availability	0.00	162.93	0.88
Phylogenetic LCBD	Elevation-Ruggedness	0.043	-1122.6	0.018
Phylogenetic LCBD	Water availability	0.015	-1118.9	0.166
Stability	Phylogenetic diversity α	0.000	365.36	0.834
Stability	Phylogenetic LCBD	0.044	359.72	0.018
Taxonomic Dissimilarity	Distance	0.17	-7070.23	0.01
Phylogenetic dissimilarity	Distance	0.05	-5714.08	0.01

Table S6. *Path coefficients taxonomic SEM between species turnover (LCBD), stability, and alpha diversity based on linear structural equation modeling (SEM).*

Response	Predictor	Estimate	SE	P value	Standardized Estimate
LCBD	Elevation-Ruggedness	0.23	0.03	0	0.48
LCBD	Water availability	0.02	0.03	0.50	0.04

LCBD	Spatial autocorrelation	1.47	0.35	0.00	0.30
Stability	Elevation-Ruggedness	-0.14	0.03	0.00	-0.29
Stability	Water availability	0.06	0.02	0.01	0.13
Stability	Spatial autocorrelation	1.68	0.12	0.00	0.69
Stability	LCBD	-0.06	0.06	0.29	-0.06
Stability	Diversity α	-0.01	0.05	0.75	-0.01
Diversity α	Elevation-Ruggedness	-0.08	0.04	0.04	-0.17
Diversity α	Water availability	-0.02	0.04	0.63	-0.04
Diversity α	Spatial autocorrelation	0.54	0.56	0.33	0.08

Table S7. *Path coefficient phylogenetic SEM between species turnover (LCBD), stability, and phyalpha diversity based on linear structural equation modeling (SEM).*

Response	**Predictor**	**Estimate**	**SE**	**P value**	**Standardized Estimate**
LCBD	Elevation-Ruggedness	0.061	0.05	0.19	0.13
LCBD	Water availability	-0.07	0.04	0.11	-0.14
LCBD	Spatial autocorrelation	1.033	0.54	0.06	0.18
Stability	Elevation-Ruggedness	-0.15	0.02	0.00	-0.32
Stability	Water availability	0.06	0.02	0.01	0.12
Stability	Spatial autocorrelation	1.69	0.12	0.00	0.70
Stability	LCBD	-0.05	0.05	0.39	-0.05
Stability	Diversity α	-0.00	0.05	0.91	0.00
Diversity α	Elevation-Ruggedness	-0.08	0.04	0.04	-0.18
Diversity α	Water availability	0.00	0.04	0.92	0.00
Diversity α	Spatial autocorrelation	0.29	0.54	0.59	0.049

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