

SOIL MICROBIAL COMMUNITIES ALONG ELEVATIONAL GRADIENTS IN THE SKY
ISLANDS

by

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ABSTRACT

The Madrean Sky Islands are mountain ranges isolated by a 'desert sea'. This area is a biodiversity hotspot currently threatened by climate change. Here, we studied soil microbial communities along elevational gradients in eight Madrean Sky Islands in southeastern Arizona (USA). Our results showed that while elevational microbial richness gradients were weak and not consistent across different mountains, the soil environment strongly influenced microbial community composition along elevation. In particular, our results suggest that warming might increase the abundance of soil-borne fungal plant pathogens that concomitantly might facilitate plants' upward elevational shifts. Furthermore, projected warming and drought in the area aggravated by anthropogenic nitrogen deposition on mountain tops might enhance a shift from ectomycorrhizal to arbuscular mycorrhizal fungi. Overall, these results indicate that climate change effects on plant-soil interactions might have profound ecosystem consequences.

1. INTRODUCTION

Mountains are biodiversity hotspots (Rahbek et al., 2019) and provide a natural space-for-time setting to study responses to environmental change (Blois et al., 2013; Dunne et al., 2004; Tito et al., 2020). The Madrean Archipelago or Madrean Sky Islands are ~55 mountains that extend from southeastern Arizona to southwestern New Mexico, and northwestern Mexico (Warshall, 1995). This region covers about 74,788 km² and is bounded by the Sonoran Desert on the west, by the Chihuahuan Desert on the east, by the Arizona/New Mexico Mountains in the north, and bridges the Sierra Madre Occidental in Mexico in the south (Sleeter et al., 2012). Mountain ranges in the Sky Islands rise to 3,000 m in elevation, with steep gradients of temperature, precipitation, and distinct biological communities (Shreve, 1922). At lower elevations drier and hotter conditions exist while higher elevations are wetter and cooler. Furthermore, lower elevation portions tend to have lower plant biomass, steeper slopes, thinner soils, and lower organic matter content than higher elevations (Badía et al., 2016; Pelletier et al., 2013). In result, mountains act like “forest islands” and low elevation desert forms a biogeographical barrier between montane biotas. Eight distinct vegetation zones (or biomes) in ascending elevation are generally recognized: desert scrub, desert grassland, oak grassland, oak woodland, pine-oak woodland, chaparral, pine forest, and mixed conifer forest (Lowe, 1967; Moore et al., 2013; Whittaker, 1967; Whittaker & Niering, 1968). However, there are three to four obvious dominant biomes: desert scrub-grassland, encinal (oak woodland or oak-grassland), forest, and a few mountains tall enough to have the uppermost pine forest or mixed conifer forest (Brusca et al., 2013). The Madrean Archipelago is the only one of the sky islands complexes to cross from temperate to subtropical latitudes and connect different floristic and faunal realms (Warshall, 1995). This convergence forms the foundation for high levels of biological diversity and unique ecological interactions (Mittermeier, 2004). Current climate change is expected to impact the Madrean Archipelago by causing species ranges to no longer contain conditions favorable for survival (Holt, 1990). This might promote upward

elevational shifts, with uppermost populations at risk of shrinking or even disappearing (Freeman et al., 2018; Morueta-Holme et al., 2015; Steinbauer et al., 2018).

Microorganisms play a vital role in all biogeochemical processes and mediate key ecosystem responses to climate change (Zhu et al., 2022). In particular, soil microbial communities control carbon and nitrogen pools, providing a mechanistic link between plant diversity and ecosystem functions (Zak et al., 2003). Thus, mountainous steep gradients of abiotic and biotic conditions provide an ideal opportunity to study soil microbial diversity, composition, and functional role (Martin & Bellingham, 2016; Wang et al., 2022). Microbial communities do not present the same diversity patterns along elevation than those observed for plants and animals that usually display mid-elevation (hump-shaped) peak in diversity (Fierer et al., 2011; Wang et al., 2011). For example, in the first study of microbial communities along a montane gradient, while soil bacterial diversity decreased monotonically with elevation, plant diversity followed a unimodal (i.e., hump-shaped) pattern (Bryant et al., 2008). In terrestrial ecosystems, microbial diversity typically decreases with increasing elevation, although increasing, hump-shaped, U-shaped or no discernible trends have been also reported (Looby & Martin, 2020; Wang et al., 2022). Understanding the potential mechanisms behind microbial biogeographical patterns along elevation and differences among microbial functional groups might help provide insights into possible responses to climate change that might cascade to other biotic levels (Bradford et al., 2016).

In this study, we sampled soils along elevational gradients in eight Sky Island mountains in southeastern Arizona (USA). Our research questions were: (1) how does different vegetation biomes along the elevation gradient influence soil microbial community diversity and composition? (2) Is the elevational gradient of soil microbial richness consistent across mountains?, and (3) What are the direct and the indirect (i.e., mediated by soil characteristics) effects of elevation on soil microbial richness and on the abundance of functional groups? We hypothesized that (i) vegetation biomes at both extremes of the elevation gradient (i.e., desert and conifer forest) would have distinct composition; (ii) richness would peak at intermediate

elevations (i.e., hump-shaped trend), and (iii) functional groups closely associated with plants such as arbuscular mycorrhizal fungi, ectomycorrhizal fungi and plant pathogens would be directly influenced by elevation, while the influence of elevation on functional groups involved in nutrient cycling such as nitrifiers and N fixers would be mostly mediated by soil properties and soil nutrient content.

2. METHODS

2.1 Study site

Eight Sky Islands peaks scattered across Southeastern Arizona were selected: Santa Catalina in the Catalinas mountain district (32°24'46"N 110°42'48"W), Mica in the Rincon (32°13'12"N 110°32'36"W), Mount Hopkins in the Santa Rita (31°43'23"N 110°52'49"W), Miller Peak in the Huachuca (31°23'34"N 110°17'34"W), Mount Glenn in the Dragoon (31°57'08"N 109°59'13"W), Chiricahua Peak in the Chiricahuas (31°50'47"N 109°17'29"W), Mount Graham in the Pinalenos (32°42'06"N 109°52'17"W) and Bassett Peak in the Galiuros (32°30'23"N 110°16'48"W) (**Fig. 1A**). Dominant vegetation was classified into biomes found across all mountain ranges: desert scrub-grassland, encinal, low forest, and high forest (see **Appendix Table 1** for details on geographic and climatic variables). In the Madrean Archipelago, the desert scrub-grassland biome is usually found at elevations ~1,000-1,500 m, and adjoins three deserts (Chihuahuan, Sonoran, and Mohave). Low precipitation mostly falling in summer favors scrub growth. Common desert vegetation are creosote (*Larrea tridentata*), yellow paloverde (*Parkinsonia microphylla*), triangle-leaf bursage (*Ambrosia deltoidea*), saddlebush (*Mortonia scabrella*), honey mesquite (*Prosopis glandulosa*), and a mixture of bunch grasses (Bennett et al., 2013). The encinal biome occurs at ~1,370-1,800 m on moderately steep slopes and is the most widespread of the Madrean woodland vegetation types (Bennett et al., 2013). This area is dominated by broadleaved evergreen oaks (< 9 m high) with an understory of a mixture of shrubs and grasses. In lower forest zones at ~1,800-2,100 m, there is a mixture of Pinyon-juniper woodlands and oak-pine forest. This biome lies on moderately steep slopes that

are deep and well-drained, usually derived from volcanic substrates (Bennett et al., 2013). Winters are mild and snowfall is light. High forest zones at ~2,100-2,600m are characterized by a mixture of conifers (Bennett et al., 2013). For this project we considered this mixture of

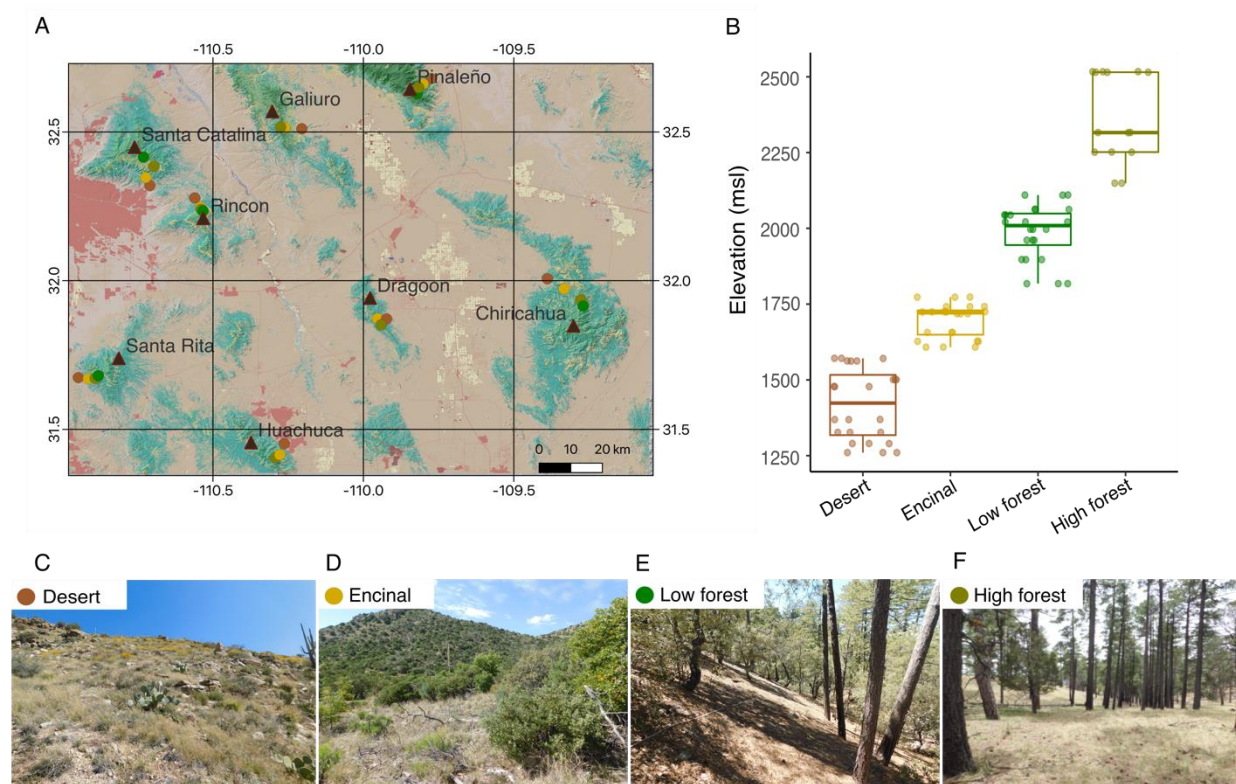


Figure 1. A) Map of the Sky Islands in Southeastern Arizona). B) Relationship between elevation and vegetation biomes. General sampling areas on the montane gradient represented by images taken from Santa Catalina: C) desert, D) encinal, E) low forest, and F) high forest.

conifer forest to be synonymous because they lie on the same elevation band and receive similar amounts of precipitation (Fig. 1B and Appendix Table 1). This zone tends to burn more periodically, killing less tolerant trees.

2.2 Soil sampling

At each vegetation biome, we collected 3 equidistant surface soil samples along a 10-m transect during April-June of 2020. To maintain a consistent procedure, we would lay the transect going from south to north. We would brush off leaf litter and other large material on the

surface, and shovel the first 10 cm of soil in a sterile Whirl-Pak bag. Soil bags were then kept on ice until they were transported to the University of Arizona where they were stored in a -80 °C freezer. The shovel was sterilized with ethanol between sampling areas to avoid cross-contamination.



Figure 2. Collecting soil samples along a transect in the Santa Catalina's encinal.

2.3 Climatic variables

Mean annual temperature (MAT) and mean annual precipitation (MAP) were obtained from PRISM Climate Group (Oregon State University) (**Appendix Table 1**). These baseline datasets describe average annual conditions over the most recent three decades (1991-2020) and are modeled with PRISM using a digital elevation model (DEM) as the predictor grid. Normalized vegetation index (NDVI) was gathered from The Terra moderate Resolution Spectroradiometer (MODIS) Vegetation Indices (MOD13Q1) Version 6 data which generates data every 16 days at 250 m spatial resolution during the time period, January 2017 to June 2020 (**Appendix Table 1**).

2.4 Soil properties

Soil subsamples were first sieved to 2 mm and air dried overnight. Soil moisture (H₂O%) was calculated by subtracting weight of soil after oven-dried from initial weight. Soil pH was measured with 1:1 (wt./vol.) soil to deionized water (ddH₂O) using a FiveEasy Plus pH meter (METTLER TOLEDO, Columbus, OH, USA). Soil electroconductivity (EC) was measured with a 1:5 (wt./vol.) soil to ddH₂O ratio using a FiveEasy Plus pH meter combined with a Cond probe LE703 (METTLER TOLEDO, Columbus, OH, USA). For total carbon (C) and nitrogen (N), samples were oven-dried at 105°C overnight, then manually grinded using a mortar, and weighed at 1 g for thermal combustion analysis (Vario MAX Cube, Elementar, Langensfeld, DE) (**Appendix Table 2**). Micronutrient concentrations of iron (Fe), copper (Cu), potassium (K), magnesium (Mg), calcium (Ca), phosphorous (P), Manganese (Mn) and sulfur (S) were measured following protocols from Amacher (1996). Samples were prepared at 3 g and mixed with 30 mL of Menlich III solution in a 50 mL polyethylene bottle. This mixture was shaken for 10 minutes on a reciprocating shaker at 180 cycles/min, then filtered through quantitative filter paper, and filtrate was analyzed for elements of interest using iCAP 7200 inductively coupled plasma-optical emission spectroscopy (ICP-OES) Duo (Thermo Scientific, Waltham, MA) (**Appendix Table 3**).

2.5 Molecular analyses

Using DNeasy PowerLyzer PowerSoil kit (Qiagen, Hilden, Germany), total genomic DNA was extracted following the manufacturer's protocols. To characterize bacteria/archaeal communities, the V4 hypervariable region of 16S RNA was PCR amplified using the primers 515-F (GTGCCAGCMGCCGCGGTAA) and the 806-R (GGACTACHVGGGTWTCTAAT) (Caporaso et al., 2012). For fungal communities, the first internal transcriber region (ITS1) was PCR amplified using the primers ITS1-F (CTTGGTCATTTAGAGGAAGTAA) and ITS2 (GCTGCGTTCTTCATCGATGC) (Schoch et al., 2012). Primers included Illumina adapters, and reverse primer pairs contained an error correcting-bp barcode specific to each sample for demultiplexing. PCR was conducted in 40 µl triplicate reactions per sample, using 3 µl of

extracted DNA, 3 μ l of each primer, 20 μ l of MyFi PCR Mix (Bioline, Taunton, MA, USA), and 11 μ l of water. PCR consisted of an initial denaturing step at 95 °C for 1 min, 35 cycles of amplification (95 °C for 15 s, 60 °C for 15 s, and 72 °C for 15 s), and a final elongation step of 72 °C for 3 min. Negative controls were included to detect potential contamination. PCR products were cleaned with an Ultra-Clean PCR Clean-Up kit (MoBio Laboratories, Carlsbad, CA, USA), and quantified with the Quant-iT PicoGreen dsDNA Assay Kit (Invitrogen, Waltham, MA USA). Purified PCR products were pooled in equimolar concentrations and sequenced on a 2x150 bp Illumina MiSeq platform. Sequencing was conducted at the Microbiome Core, Steel Children Center, University of Arizona.

2.6 Sequencing processing

Raw sequenced reads were demultiplexed using *idemp* (<https://github.com/yhwu/idemp>) and processed using the DADA2 pipeline (Callahan et al., 2016). 16S rRNA reads were trimmed to 140 base pairs (bp). Due to length variation in the ITS region, the last 20 bp were removed from reverse reads and primers were removed with *cutadapt* (Martin, 2011). Reads that exceeded a maximum error of 2 or more bp were removed. Resulting reads were used to train the error model and to infer amplicon sequence variants (ASVs). Paired-end reads were merged, and chimera sequences were removed. Using the Ribosomal Database Project (RDP) classifier (Wang et al., 2007), taxonomic identities were associated with each ASV. The SILVA nr version 132 database (Quast et al., 2013) was used to annotate 16S rRNA and the UNITE database (Nilsson et al., 2019) was used for ITS sequences. Any 16S ASVs without a bacterial or archaeal domain classification, or classified as mitochondria or chloroplasts were removed. ITS ASVs without a fungal domain assignment were removed. Samples with less than 10,000 sequences were also removed. The number of bacterial/archaeal sequences per sample ranged from 37,272 to 192,660. Fungal sequences per sample ranged from 37,156 to 378,269. Functional groups of bacteria/archaea were inferred using FAPROTAX (Louca et al., 2016) and fungal guilds were inferred using FUNGuild (Nguyen et al., 2016). Fungal ASVs with a “highly probable” or “probable” confidence ranking assigned to a single guild were retained.

2.7 Statistical analyses

All data analyses and visualizations were performed in R version 4.3.0. We explored the associations among elevation, climate (MAP, MAT) and soil properties and micronutrients (pH, EC, water content, C, N, P, K, Fe, Cu, Mg, Ca, Mn, S) using Spearman's correlations and principal component analysis (PCA). We assessed the effect of vegetation biomes along the elevation gradient using linear mixed-effects models in the lme4 package (Bates et al., 2015). All soil variables were log-transformed except for pH. We used biomes as fixed effects, and included geographic location (i.e., mountain) as random effects. While vegetation biome is a proxy for elevation and the climatic, topographical, and biotic factors that co-vary along the montane gradient (Körner, 2007), mountain accounts for the factors that co-vary across space. We assessed the explanatory power of the models using marginal R^2 (only fixed effects) and conditional R^2 (fixed and random effects) (Nakagawa & Schielzeth, 2013).

To study soil microbial diversity, we first rarefied the sequence counts to 37,000 for both Bacteria/Archaea and Fungi to control for differences in sequencing depth. We used the same linear mixed-effects model approach as described for soil variables to assess the effect of vegetation biomes on soil microbial richness (number of different ASVs) and evenness (measured using the Shannon index). We estimated the relationship between richness and elevation using linear and quadratic models, and we selected the most parsimonious model for each mountain using the Akaike Information Criterion (AIC).

To evaluate soil microbial compositional changes, we calculated Bray-Curtis dissimilarity. Differences in microbial composition were visualized using non-metric multidimensional scaling (NMDS). To assess the effect of mountain and different vegetation biomes within mountains, we used permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). Additionally, we studied microbial compositional dissimilarity changes with elevational change and geographical distance using Mantel tests. Multivariate statistics were performed using the vegan package (Okansen et al., 2018).

We evaluated the direct and the indirect (i.e., mediated by soil) effects of elevation on microbial richness and on the log-transformed abundance of functional groups using structural equation models as implemented in the package piecewiseSEM (Lefcheck, 2016). We included geographic location (i.e., mountain) as random effects. We represented ‘Soil’ as a statistical composite using all measured soil variables (pH, EC, water content, C, N, P, K, Fe, Cu, Mg, Ca, Mn, S). We calculated standardized effects with 95% confidence intervals using 1,000 bootstrapped estimates.

3. RESULTS

3.1 General environmental description

Temperature and precipitation gradients were closely associated with elevation, as expected (**Fig. 3**). In addition, soil water and iron content consistently increased along elevation (**Fig. 3**). Most soil properties and micronutrients (except for pH, P and S) were significantly different across vegetation biomes distributed along the elevation gradient, although mountain as a

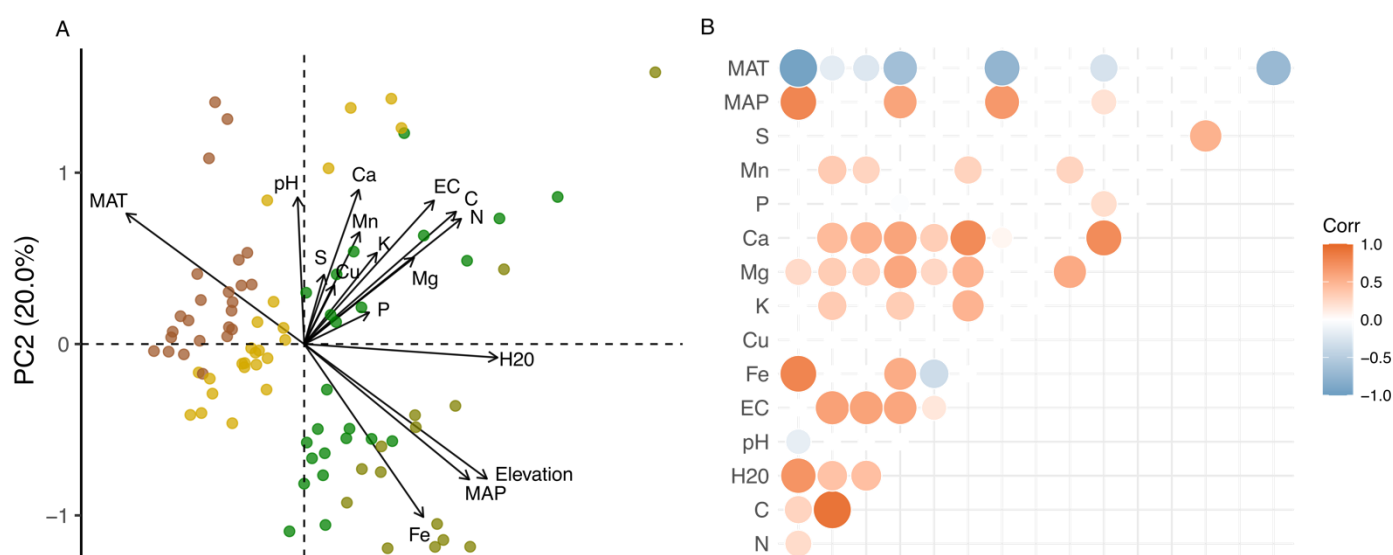


Figure 3. A) Principal component analysis (PCA) of standardized environmental variables. B) Significant Spearman's correlations ($P < 0.05$) among environmental variables. Larger circles and higher color intensity indicate stronger associations.

proxy of geographical location generally explained a larger proportion of variation than vegetation biome (**Appendix Table 4**).

3.2 Soil microbial taxonomic diversity

The total number of different bacterial/archaeal ASVs after rarefaction was 43,053. Richness per sample ranged from 681 to 2,478. The total number of different fungal ASVs was 13,966. Fungal richness per sample ranged from 121 to 604. Bacterial/archaeal richness and evenness (i.e., Shannon index) were not significantly different across vegetation biomes (**Fig. 4A, Table 1**). Although fungal richness did not vary across biomes, fungal evenness was significantly different across vegetation biomes (**Fig. 4A, Table 1**). Although the joint explanatory power of vegetation biomes along elevation and geographical location (i.e., different mountains) was low, mountain explained a larger proportion of variation than vegetation (**Table 1**). The weak influence of elevational gradients on soil microbial diversity was further confirmed by fitting linear and quadratic models for each mountain (**Fig. 4B**). Only bacterial richness in the Catalina and Santa Rita mountains showed significant hump-shaped and increasing linear trends, respectively. For soil fungal communities, richness showed significant U-shaped trends for the Huachuca and Santa Rita mountains.

Table 1. Linear mixed-effects model results of the effects of vegetation biome and mountain on soil microbial diversity. Bold values indicate significant effects ($P < 0.05$).

	F	P	Marginal R ² (vegetation)	Conditional R ² (vegetation+mountain)
Bacterial/archaeal richness	1.83	0.15	0.06	0.12
Bacterial/archaeal Shannon	1.2	0.32	0.04	0.17
Fungal richness	2.33	0.08	0.07	0.16
Fungal Shannon	3.65	0.02	0.11	0.12

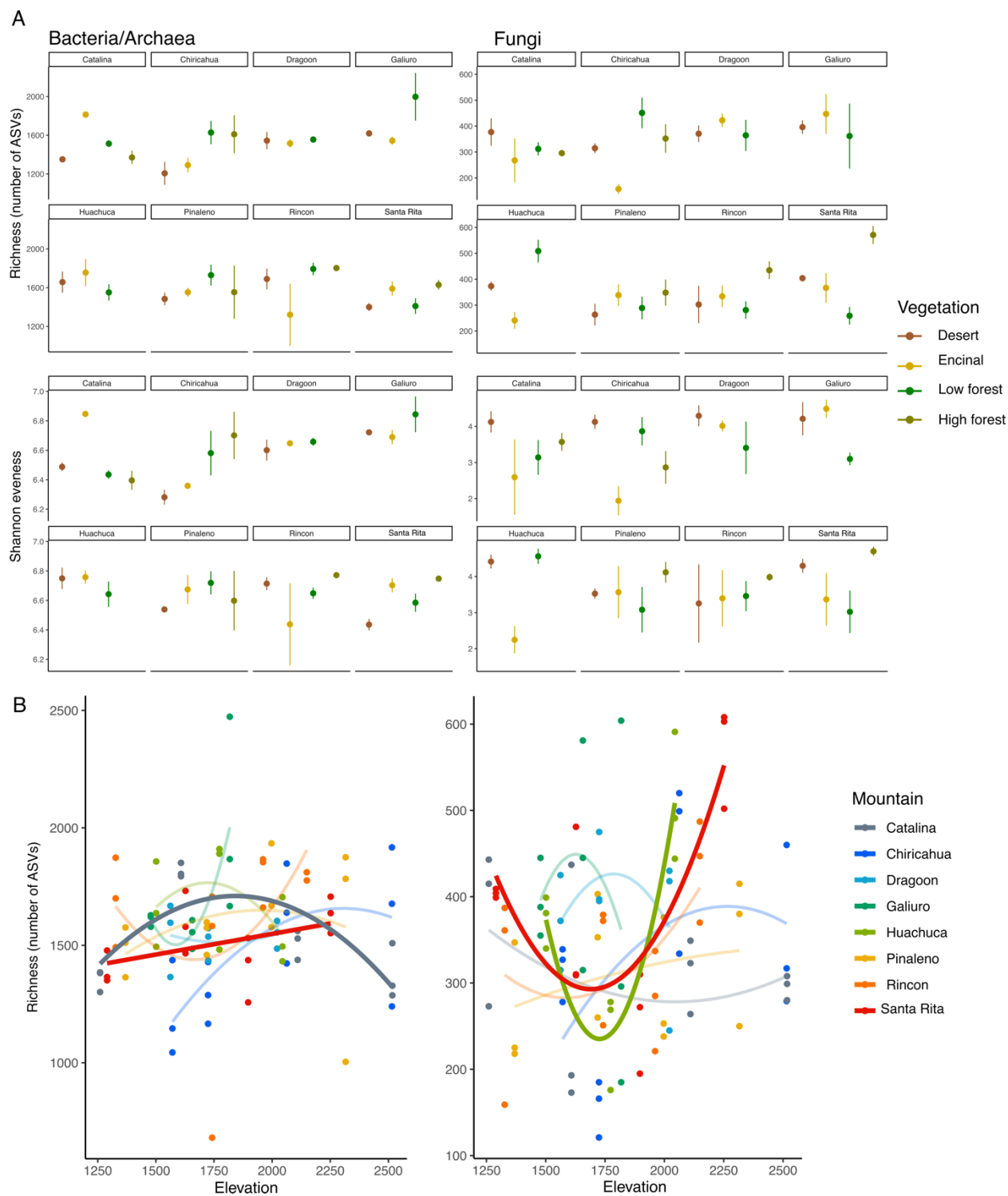


Figure 4. A) Soil microbial richness and evenness across vegetation biomes and different mountains. Point ranges show means and standard errors. B) Soil microbial richness along elevation for each mountain. The best model (linear or quadratic) based on AIC is represented. Significant relationships ($P < 0.05$) are indicated by bolded lines.

3.3 Soil microbial community composition

Soil bacterial/archaeal communities were dominated by Actinobacteria (36.53%), Proteobacteria (27.90%), Acidobacteria (12.02%), Chloroflexi (3.97%), Firmicutes (3.86%), and Gemmatimonadetes (3.68%). Soil fungal communities were dominated by Ascomycota (55.06%), Basidiomycota (39.14%), Mortierellomycota (3.42%), and Mucoromycota (1.05%) (Fig. 5). Compositional differences between low and high vegetation biomes were already visible at broad phylogenetic resolution. Actinobacteria and Ascomycota tended to be more abundant in desert and encinal, while Proteobacteria and Basidiomycota were more abundant

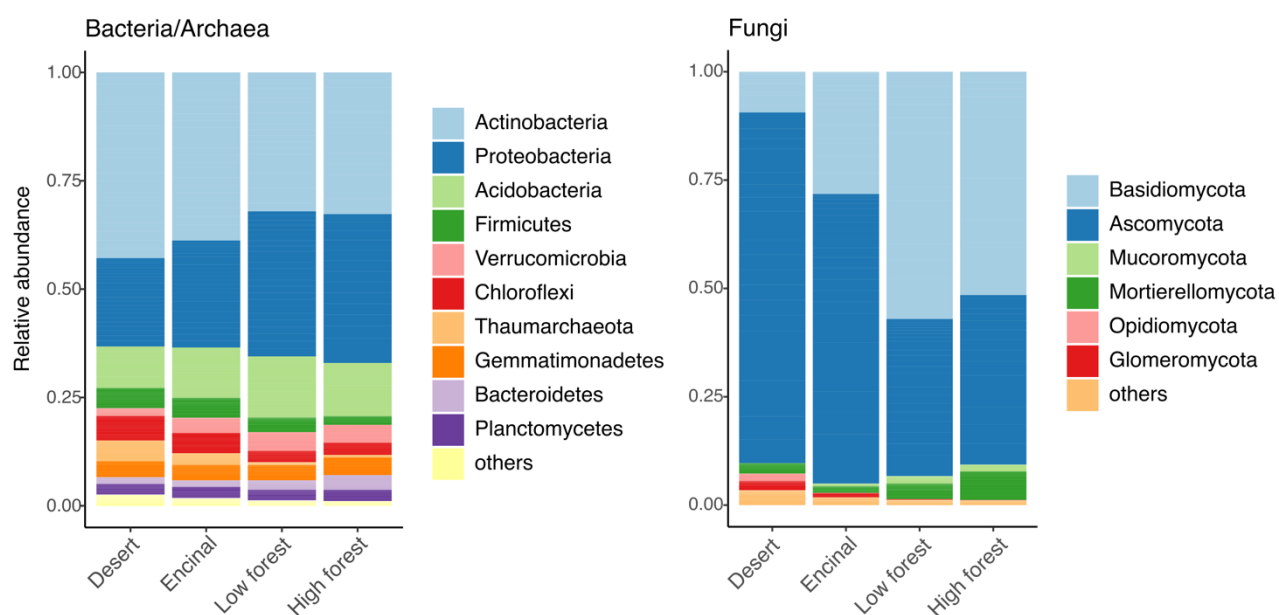


Figure 5. Relative abundance of different bacterial/archaeal and fungal phyla across vegetation biomes.

in the forest biomes (Fig. 5).

Soil bacterial/archaeal and fungal compositional dissimilarity were significantly different across vegetation biomes within mountains (PERMANOVA for Bacteria/Archaea: $R^2 = 0.50$, $P < 0.001$; PERMANOVA for Fungi: $R^2 = 0.39$, $P < 0.001$ Fig. 6A). This trend was further confirmed by significant positive associations between microbial compositional dissimilarity and elevational distance (Fig. 7A). Soil microbial composition also differed across geographic locations (i.e., different mountains), even though the explanatory power was lower

than for vegetation (PERMANOVA for Bacteria/Archaea: $R^2 = 0.15$, $P < 0.001$; PERMANOVA for Fungi: $R^2 = 0.12$, $P < 0.001$; **Fig. 6B**). Accordingly, we observed an almost flat response of microbial compositional dissimilarity with increasing geographical distance (**Fig. 7B**).

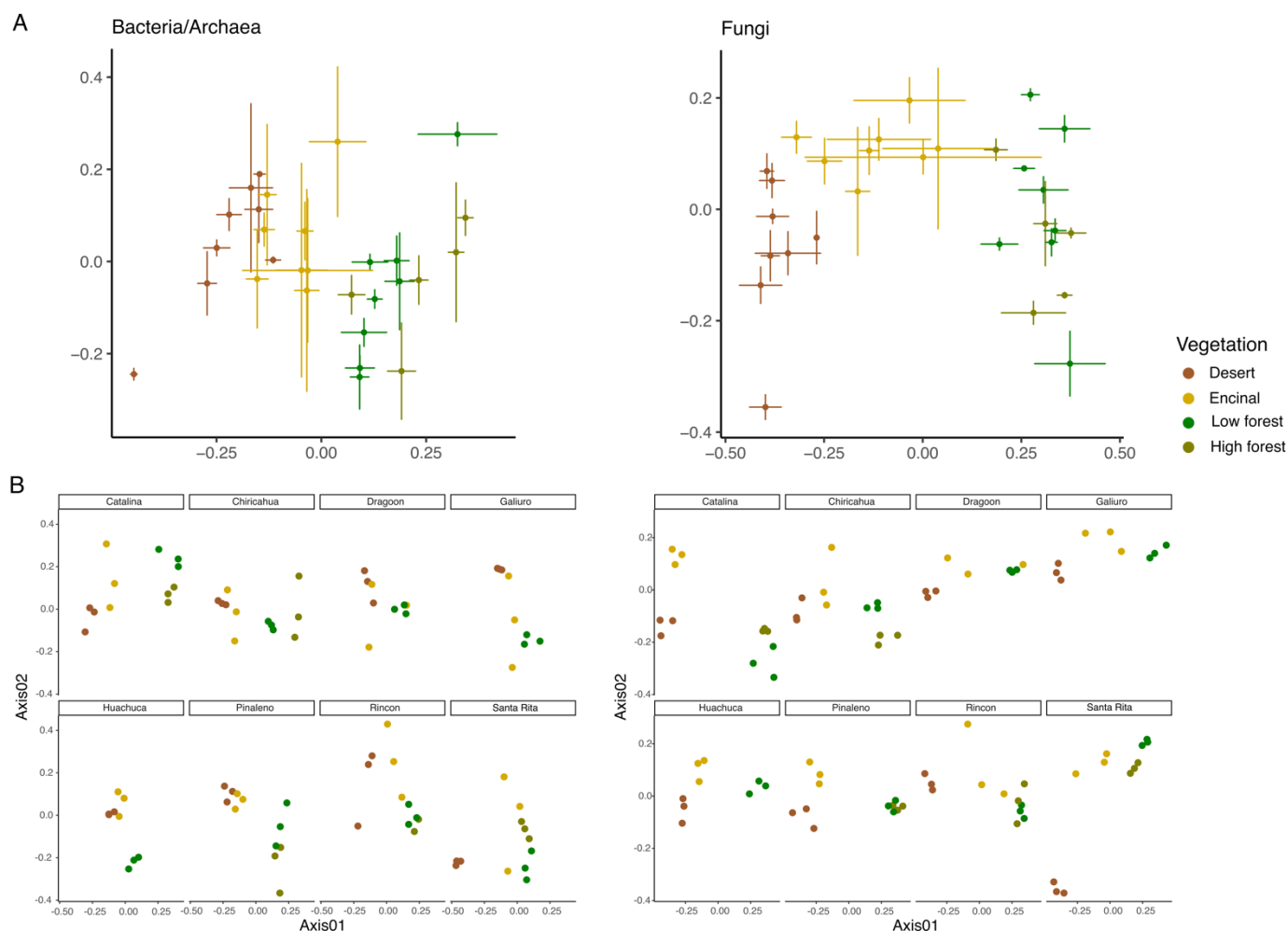


Figure 6. Non-metric multidimensional scaling (NMDS) ordination plots of soil microbial community dissimilarity. A) Soil samples from the same transect plotted together to visualize clustering based on vegetation. (stress=0.10 and 0.12, respectively). B) Individual soil samples separated by mountain.

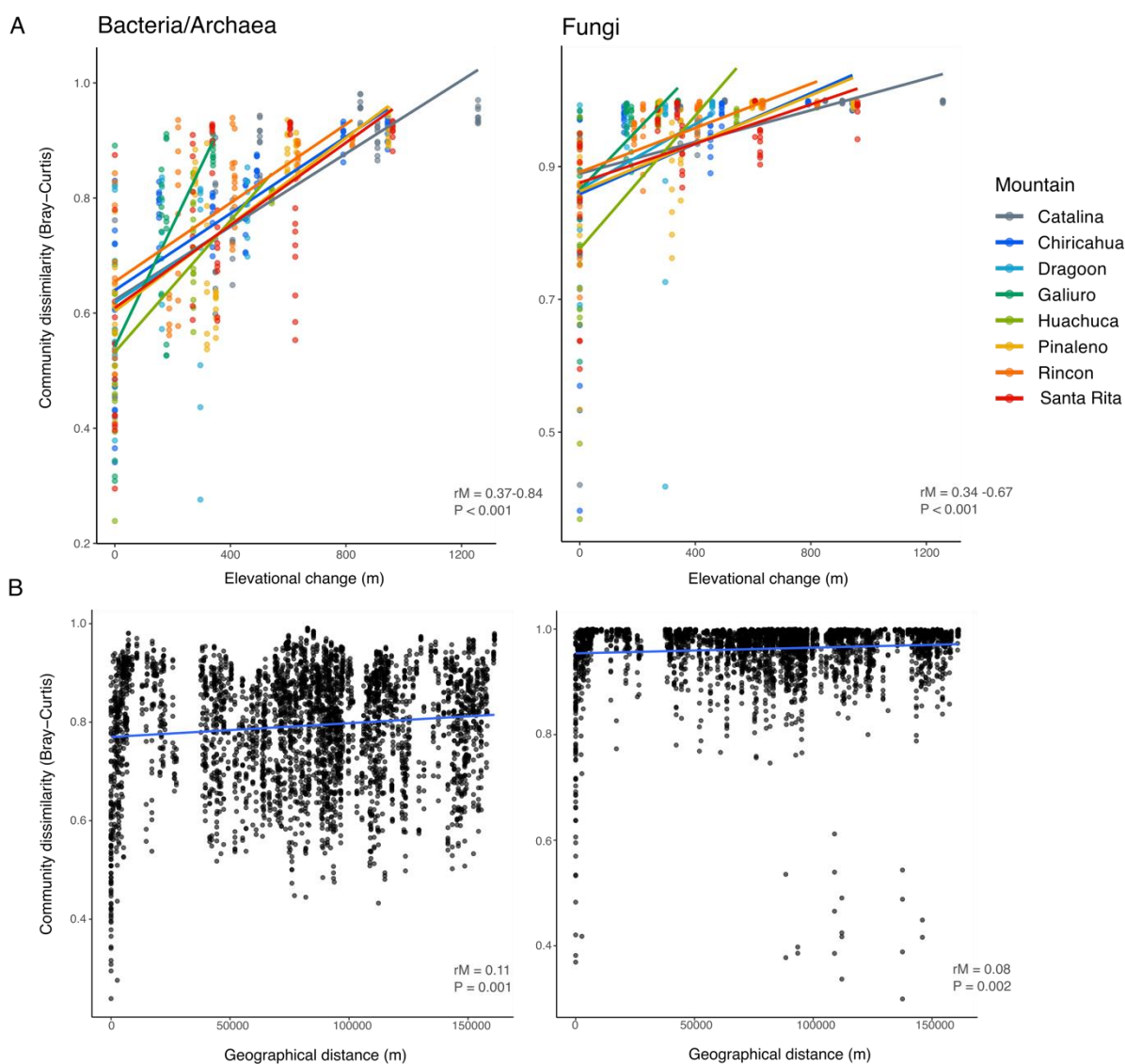


Figure 7. A) Patterns of bacterial/archaeal and fungal compositional dissimilarity across elevational changes. B) Patterns of bacterial/archaeal and fungal compositional dissimilarity across geographical distances.

3.4 Soil microbial functional groups

The abundance of soil microbial functional groups along elevation showed distinct patterns (Fig. 8). Using structural equation models including mountain as random effects, we were able to tease apart the direct and the indirect (i.e., mediated by soil) effects of elevation (including the climatic, topographical and biotic factors that co-vary along the gradient) while controlling

for geographical location (i.e., mountain and the factors that co-vary across space). In general, the indirect effect of elevation was mainly positive (except for fermenters, methylotrophs, nitrifiers, oxygenic photoautotrophs, arbuscular mycorrhizal fungi, and fungal plant pathogens) and larger than the direct elevation effect which tended to be close to zero (except for cellulolytic bacteria, denitrifiers, N fixers, and ectomycorrhizal fungi) (**Fig. 9**). Overall, soil had a stronger significant effect on microbial richness and on the abundance of functional groups than elevation (**Fig. 9**).

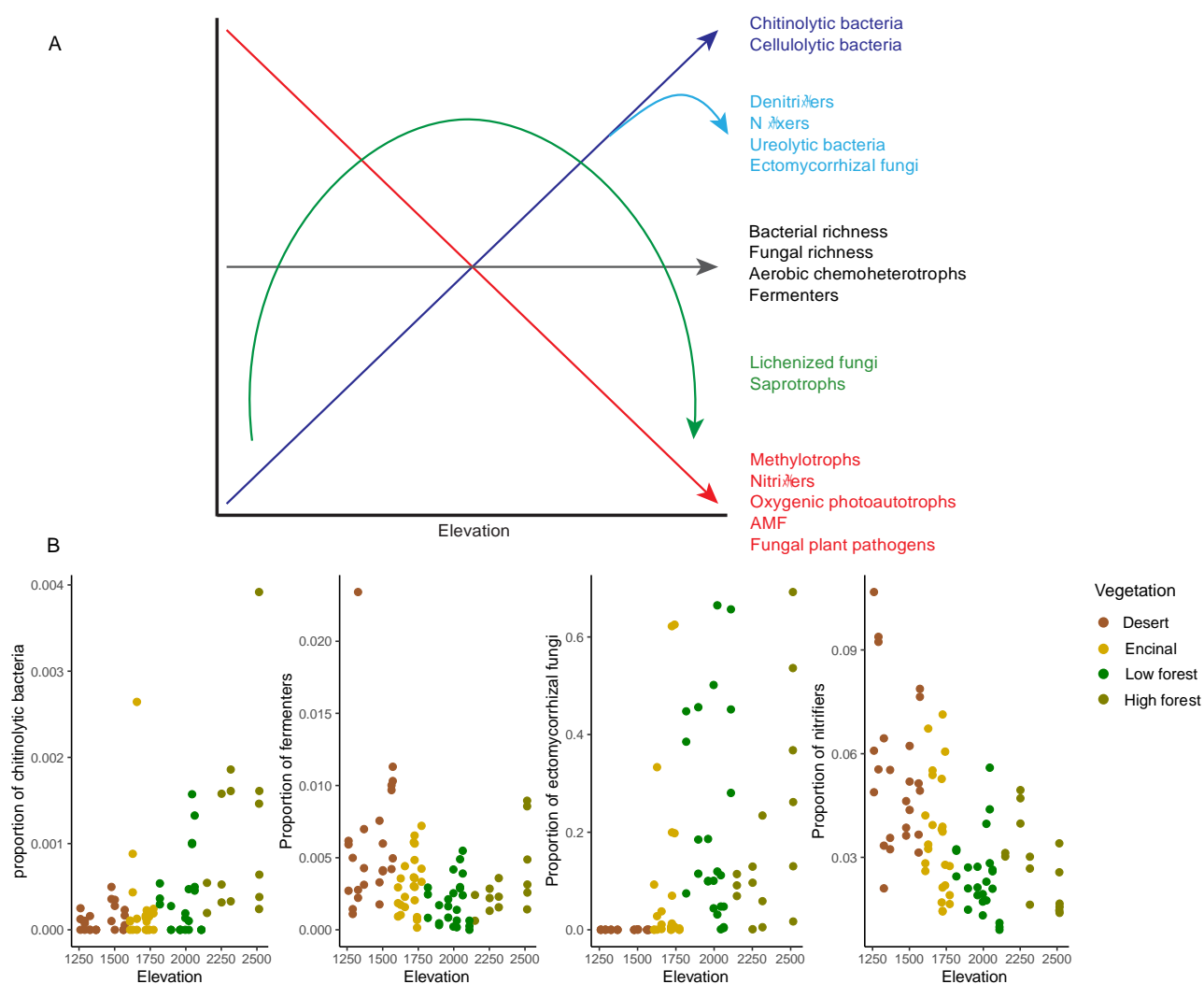


Figure 8. A) Overview of elevation patterns for functional groups abundance and richness. B) Examples of functional groups abundance patterns.

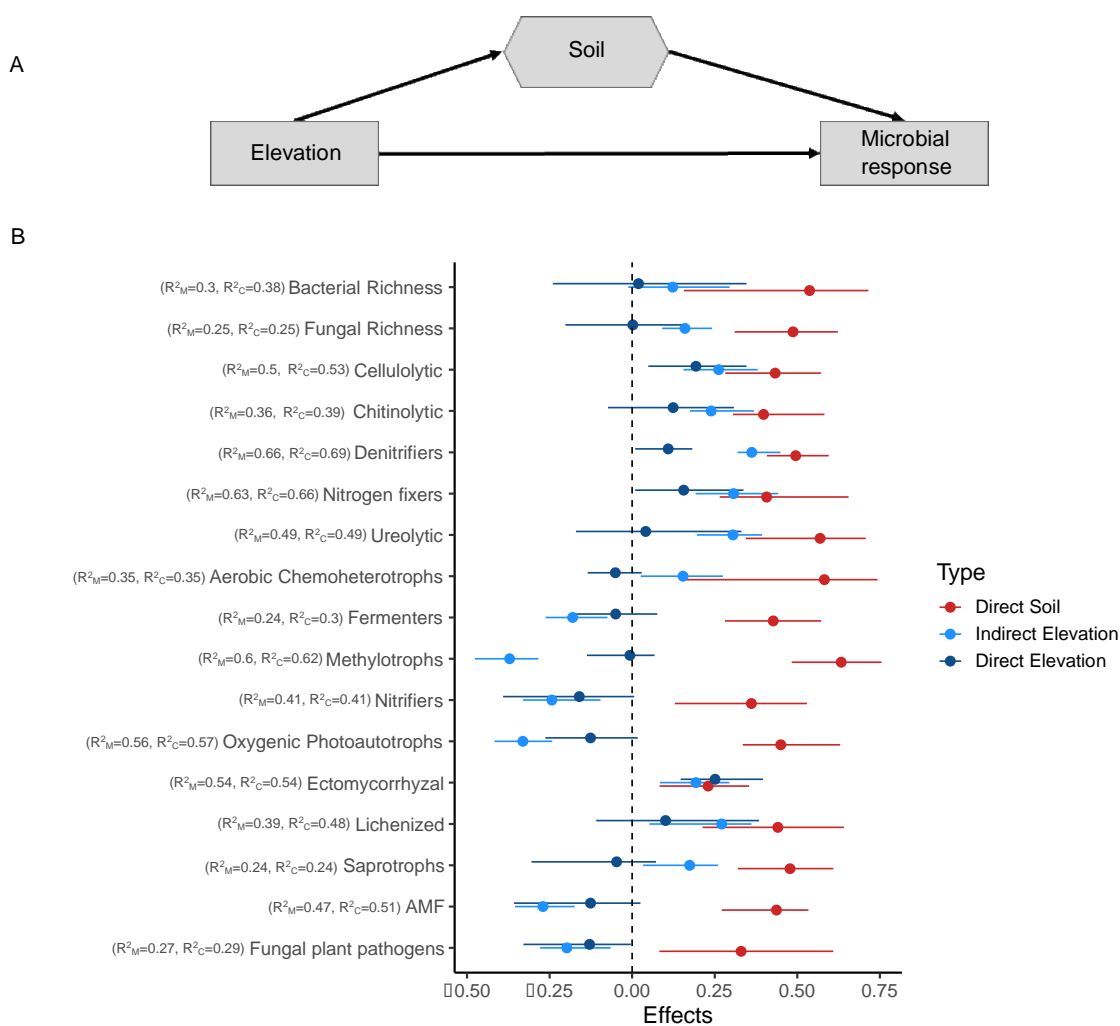


Figure 9. Structural causal model showing direct and indirect effects of soil and elevation on microbial response variables (i.e., microbial richness and functional group abundances). B) Standardized effects of elevation and soil on microbial response variables. Error bars represent 95% confidence intervals. R^2_m refers to marginal R^2 (only fixed effects) and R^2_c refers to conditional R^2 (fixed and random effects).

4. DISCUSSION

Investigating soil microbial communities along montane gradients and the environmental factors behind these patterns provides insight into microbial biogeography and how climate change impacts on ecosystem functioning (Pugnaire et al., 2019). In this study, we studied soil microbial diversity and composition along elevational gradients in the Sky Islands of southeastern Arizona, and we found that while elevational diversity gradients are not

consistent across different mountains, elevation (and the co-varying climatic, topographical and biotic factors) and soil characteristics strongly influenced overall composition and the abundance of key functional groups.

4.1 Soil microbial richness along elevational gradients

Early naturalists noticed that the number of plant and animal species tended to decrease from low to high mountain elevations (Lomolino, 2001). However, unimodal (i.e., hump-shaped) patterns have been more commonly documented (Rahbek, 1995). In general, patterns of microbial richness along elevation tend to be more varied (i.e., flat, increasing, decreasing, hump-shaped and U-shaped) and weaker than for plants and animals (Looby & Martin, 2020; Wang et al., 2022). Our results in the Arizona Sky Islands support this general trend. We only found two out of eight mountains with significant elevation trends in bacterial richness, one being an increasing trend and the other hump-shaped. While for fungi, the two significant trends were U-shaped patterns.

Many mechanisms (i.e., climate, productivity, space, topography, biotic interactions, evolutionary history) have been proposed to explain elevational gradients (Gaston, 2000; Michalet et al., 2006; Nogués-Bravo et al., 2008; Rahbek et al., 2019). Overall, the most important factors for plants and animals appear to be climatic and taxonomy-specific (McCain, 2007, 2009, 2010). Although these drivers certainly also influence microbial communities (Martiny et al., 2006), soil characteristics (mainly pH) are recognized as the dominant influence of microbial community diversity and composition (Fierer & Jackson, 2006). For instance, a recent meta-analysis showed that soil pH exerts a larger influence than climate on microbial mountain diversity (Wang et al., 2022; but see Singh et al., 2013). Similarly, our SEM results confirm that soil (as a composite variable generated from soil properties, nutrients and micronutrients) has a stronger effect shaping microbial richness than the total effects of elevation (including co-varying climatic and other factors) while controlling for geographical location (and factors that co-vary across space). Overall, higher microbial dispersal ability compared to plant and animals (Barberán, 2014) and experiencing spatial heterogeneity at

much smaller scales than macroorganisms (Rowe & Lidgard, 2009) might blur clear elevational richness patterns.

4.2 Soil microbial composition along elevational gradients

By contrast and consistent with the zonation of plants and animals, we observed clear and for the most part uniform elevational patterns in overall soil microbial community composition in the Arizona Sky Islands. As a matter of fact, elevational changes were far more determinant of microbial composition than geographical distance. That is, based on our results, we expect more distinct communities along a 1,000 m elevational gradient within the same mountain than across mountains separated by 150 km. In this arid landscape where soil is exposed to wind erosion due to sparse vegetation, microbial airborne dispersal via dust is an important mechanism for long-distance connectivity (Kellogg & Griffin, 2006; Schiro et al., 2022)

Major phyla followed expected abundance patterns along the elevation gradient. For example, actinobacterial abundance generally declined at higher altitudes, while Basidiomycota increased. Actinobacteria are widespread in desert soils and tolerant to desiccation (Chen et al., 2021; Mohammadipanah & Wink, 2016), while Basidiomycota dominate at cooler temperatures and in high-precipitation areas (Peay et al., 2016). This segregation was further confirmed by assessing changes in the abundance of main microbial functional groups along the elevation gradient. Overall, these abundance patterns were mainly driven by soil factors and indirect effects of elevation mediated through soil. This is expected as strong relationships among topography, soil and vegetation exist in the Sky Islands with lower elevations characterized by steep slopes, thin soils, low organic matter and low plant biomass, and high elevations characterized by gentler slopes, thicker organic-rich soils and higher biomass (Pelletier et al., 2013; Poulos et al., 2007). Indeed, soil transplantation experiments across different elevations have shown changes in microbial community composition and associated ecosystem functions such as decomposition rates (Baker et al., 2018; Looby & Treseder, 2018; Zimmermann et al., 2009).

We observed a general increase of cellulolytic and chitinolytic bacteria along the

elevational gradient. Previous studies found monotonic increases in the potential to metabolize recalcitrant carbon compounds along the Tibetan Plateau (Zhao et al., 2017), or U-shaped patterns along Mount Kilimanjaro (Dai et al., 2021). It is expected that fire occurrence and frequency might directly affect the enzymatic activity associated with the degradation of these recalcitrant polysaccharides (Fairbanks et al., 2020). In the Sky Islands region, invasive grasses create a fire hazard by increasing fuel loads and continuity (Fusco et al., 2019; McDonald & McPherson, 2013), and these changes in the fire regime can have belowground repercussions in organic matter degradation.

Denitrifiers and nitrogen (N) fixers tended to be more abundant at higher elevations although they peaked at the low forest biome. A similar hump-shaped pattern of denitrifier communities was previously reported along an elevational gradient in China (Kou et al., 2021), while a monotonic increase of N fixers abundance was observed along Mount Kilimanjaro (Shen et al., 2020) and in the Swiss Alps (Jacot et al., 2000). The abundance decline at the uppermost elevations could be explained by slower rates of mineralization and decomposition processes due to lower temperatures (Zhang et al., 2012) and sensitivity to soil moisture variations (Groffman et al., 2009). Nitrifier abundance, on the other hand, decreased monotonically along the Sky Islands. Several studies have confirmed this general trend, and proposed that a combination of altitude-related factors (mainly temperature and soil pH) shape the overall abundance of nitrifiers (Shen et al., 2020; Wang et al., 2015; Zhang et al., 2009; Zhao et al., 2017). Similarly, to nitrifiers, methylotrophs (i.e., a diverse group of microorganisms that reduce one-carbon compounds) and oxygenic photoautotrophs (i.e., cyanobacteria) decreased monotonically with elevation. Methylotrophs are present in alkaline soils (such as those found at lower elevations in the Sky Islands) and have the ability to promote plant growth (Iguchi et al., 2015; Kumar et al., 2019). A previous study similarly reported declining abundances of methylotrophs with altitude (Hofmann et al., 2016). Cyanobacteria are known to survive in arid environments with high temperatures and low water and nutrient

availability (such as those in the Sky Islands lower elevations), while contributing to primary production and soil stabilization (Chamizo et al., 2018).

Plants influence soil microbial communities by modifying the soil physical environment, and by shaping the quantity and quality of litter supply (Hooper et al., 2000; Wu et al., 2018). In general, it is expected that plant diversity and composition directly influence fungal altitudinal distributions (Carteron et al., 2022; Kazenel et al., 2019; Kivlin et al., 2022). The abundance of ectomycorrhizal, saprotroph and lichenized fungi followed a unimodal (hump-shaped) pattern. This pattern matches higher plant productivity and diversity at mid elevation in the Sky Islands (Whittaker & Niering, 1975). These fungal groups are known to be highly associated with leaf litter inputs (Asplund & Wardle, 2017; Lindahl & Tunlid, 2015; Marañón-Jiménez et al., 2021; Tripp et al., 2016). On the other hand, arbuscular mycorrhizal fungi (AMF) and fungal plant pathogens abundances tended to decrease with elevation in the Arizona Sky Islands, in contrast with a study on Mount Kilimanjaro reporting a U-shaped trend for AMF abundance and no apparent pattern for fungal plant pathogens (Shen et al., 2020). The manifest geographical, environmental, and floristic differences between these two areas might explain this variability. At the global scale, the proportion of soil-borne pathogens tends to increase with warming (Delgado-Baquerizo et al., 2020), and AMF are known to promote drought stress resistance in native plant of arid ecosystems (Madouh & Quoreshi, 2023). Both observations can likewise explain our AMF and fungal plant pathogen declining trends with altitude. In a meta-analysis of plant-associated fungi along montane gradients, ectomycorrhizal fungal abundance increased with elevation, while AMF abundance declined (Kivlin et al., 2017). In our study, we did not observe a trade-off in ectomycorrhizal and saprotrophic fungi (i.e., ectomycorrhizal fungi are generally adapted to colder temperatures; (Qin et al., 2023) along elevation as reported in several studies (Eduardo et al., 2018; Gadgil & Gadgil, 1971; Looby et al., 2016; Saitta et al., 2018).

4.3 Implications for climate change adaptability

Climatic models predict higher temperatures and increased drought periods in Southwestern North America (Seager et al., 2007). In addition, the arid Southwestern USA is experiencing one of the fastest population growths in the country (Stehfest et al., 2019). Given that climate change and human impacts are associated with diversity and composition changes in soil microbial communities (Chen et al., 2020; B. Singh et al., 2010), our results along elevation gradients in the Arizona Sky Islands underscore how environmental changes will impact belowground communities, plant-soil interactions and ecosystem functions (Morrissey et al., 2019).

As climate warms and seasonality changes, montane communities shift in response. Increasing plant species numbers on summits (Steinbauer et al., 2018), generally replacements of small- by large-ranged species (Stauder et al., 2022) and more non-native species (Iseli et al., 2023), have already been observed. In addition to changes in species numbers, upward shifts in species composition are frequently reported. For example, lowland birds have started breeding in montane cloud-forest habitat (Pounds et al., 1999), alpine flora have expanded toward the summits (Grabherr et al., 1994), lower elevational limits of butterfly species have risen (Wilson et al., 2005), and small mammal species have moved up in elevation (Moritz et al., 2008). These shifts can lead to severe range contractions or even extinctions of mountaintop species (Beever et al., 2003).

Understanding plant-soil interactions is key to predict population declines, range shifts and ecosystem functions under climate change, particularly carbon and nitrogen (N) cycling (Pugnaire et al., 2019; Van Nuland et al., 2017). With warming, decomposition rates will likely increase at higher elevations, causing feedbacks on soil carbon dynamics, particularly changing mountains from carbon sinks to sources of atmospheric CO₂ (Nottingham et al., 2019; Salazar et al., 2020). According to our results and previous studies, we can expect a shift from ectomycorrhizal fungi to arbuscular mycorrhizal fungi (AMF) towards higher elevations in the Arizona Sky Islands (Steidinger et al., 2019; Miyamoto et al., 2018; Steidinger et al., 2020).

The shift from ectomycorrhizal fungi to AMF driven by warming might be further aggravated because while ectomycorrhizal fungi are limited by dispersal (Bowman & Arnold, 2018), AMF tend to disperse more efficiently including by human mediation (Davison et al., 2018). Moreover, anthropogenic N deposition on mountaintops decreases N limitation and thus the value of ectomycorrhizal fungi, which exchange soil N for plant photosynthate (Lilleskov et al., 2002). This shift will have profound consequences, specifically it will promote faster N turnover because AMF cannot decompose soil organic matter and are restricted to the use of mineral forms of N (Mushinski et al., 2021). Our results also hint to a potential increase in pathogens with warming (Delgado-Baquerizo et al., 2020). More soil-borne pathogens would benefit range-shifting plant species released from negative plant-soil feedbacks (Engelkes et al., 2008).

In Southwestern North America, drying (i.e., reduction of precipitation and soil moisture) will be more limiting than warming (Park Williams et al., 2013; Seager & Vecchi, 2010). For example, a litter-bag experiment in Arizona mountains reported increased decomposition rates toward colder but wetter higher elevations (Murphy et al., 1998). Drought can modify plant competitive interactions and plant-soil interactions via decreased litter quantity and quality (i.e., more recalcitrant carbon compounds), causing large changes in nutrient cycling by slowing down mineralization rates (Carrera & Bertiller, 2010; Delgado-Baquerizo et al., 2013; Kaisermann et al., 2017; Karlowsky et al., 2018). Besides litter, plants under drought change their root exudate composition producing more phytohormones, osmolytes and antioxidants (Preece et al., 2018). Drought-driven changes in rhizodeposition are expected to promote fungi in detriment of bacteria (Preece & Peñuelas, 2016). In arid ecosystems, soil microorganisms such as N fixers and AMF can buffer the negative effects of drought (Madouh & Quoreishi, 2023; Rubin et al., 2017) and thus, we might expect their abundances (and those of plant species that fix N and/or form AMF) to increase.

5. APPENDIX

Table 1. Geographic and climatic variables. Mean annual precipitation (MAP), mean annual temperature (MAT), normalized difference vegetation index (NDVI).

Mountain	Vegetation	Elevation (m)	Coordinates	NDVI	MAP (mm)	MAT (°C)
Santa Catalina	Desert	1260	32°19'11.71"N 110°42'36"W	0.28	513.95	18.59
	Encinal	1608	32°20'49.42"N 110°43'26.4"W	0.31	626.66	16.09
	Low forest	2110	32°23'3.48"N 110°41'45.6"W	0.52	751.65	13.12
	High forest	2517	32°24'3.56.1"N 110°43'51.6"W	0.59	845.22	10.35
Santa Rita	Desert	1290	31°40'3.26"N 110°56'52.8"W	0.31	456.52	18.58
	Encinal	1627	31°40'13.73"N 110°54'54"W	0.32	538.43	16.27
	Low forest	1897	31°40'19.42"N 110°53'31.2"W	0.53	649.71	15.44
	High forest	22512	31°40'49.19"N 110°52'51.6"W	0.61	704.29	13.07
Huachuca	Desert	1501	31°27'7.42"N 110°15'46.8"W	0.34	481.59	16.72
	Encinal	1773	31°24'53.03"N 110°16'40.8"W	0.49	615.78	15.22
	Low forest	2044	31°24'18.61"N 110°17'34.8"W	0.61	760.15	12.62

Dragoon	Desert	1562	31°52'16.97"N 109°55'22.8"W	0.29	469.52	16.51
	Encinal	1725	31°52'21.83"N 109°57'10.8"W	0.41	481.86	15.8
	Low forest	2021	31°51'4.46"N 109°56'31.2"W	0.49	473.76	14.01
Chiricahua	Desert	1571	31°51'4.46"N 109°56'31.2"W	0.28	421.58	15.6
	Encinal	1571	32°0'22.93"N 109°23'16.8"W	0.43	503.65	14.22
	Low forest	2063	31°56'9.89"N 109°16'37.2"W	0.5	746.11	12.45
	High forest	2515	31°54'53.57"N 109°16'8.4"W	0.41	818.09	10.32
Pinaleño	Desert	1369	32°40'44.44"N 109°46'26.4"W	0.35	327.99	17.01
	Encinal	1719	32°39'41.98"N 109°48'3.6"W	0.45	455.8	15.24
	Low forest	1997	32°38'57.88"N 109°48'57.6"W	0.65	624.96	12.71
	High forest	2316	32°37'45.91"N 109°49'15.6"W	0.65	719.91	11.65
Galiuro	Desert	14778	32°30'38.95"N 110°12'18"W	0.24	405.33	16.36
	Encinal	1656	32°30'50.72"N 110°15'39.6"W	0.51	445.2	14.66
	Low forest	1818	32°30'58.57"N 110°16'30"W	0.49	457.25	14.19
Rincon	Desert	1327	32°16'41.66"N 110°33'39.6"W	0.28	421.58	15.6
	Encinal	1742	32°14'50.68"N 110°32'24"W	0.43	503.65	14.22
	Low forest	1961	32°14'22.92"N 110°32'20.4"W	0.5	746.11	12.45

	High forest	2149	32°14'4.74"N 110°31'58.8"W	0.41	818.09	10.32
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Table 2. Soil properties. Standard deviation across each transect is indicated in parenthesis.

Mountain	Vegetation	H ₂ O (%)	pH	EC (uS/cm)	N (%)	C (%)
Santa Catalina	Desert	7.6(1.69)	6.9(0.28)	23.48(7.18)	0.11(0.05)	1.5(0.82)
	Encinal	3.67(0.31)	7.07(0.16)	9.86(2.23)	0.26(0.17)	4.03(2.78)
	Low forest	5.77(1.11)	6.13(0.39)	13.13(1.08)	0.16(0.09)	2.93(1.44)
	High forest	9.1(0.44)	6.62(0.13)	42.9(13.38)	0.17(0.12)	2.29(1.76)
Santa Rita	Desert	10.4(1.6)	8.41(0.39)	65.11(21.38)	0.14(0.03)	5.81(0.11)
	Encinal	11.64(4.05)	6.86(0.71)	68.64(64.12)	0.29(0.13)	3.75(1.89)
	Low forest	11.37(4.67)	7.93(0.94)	65.61(24.8)	0.3(0.18)	4.74(2.88)
	High forest	8.57(0.78)	6.79(0.6)	125.64(104.44)	0.4(0.17)	5.14(2.17)
Huachuca	Desert	9.2(0.61)	7.25(0.5)	34.13(8.8)	0.21(0.04)	2.43(0.38)
	Encinal	6.87(1.74)	7(0.42)	18.1(8.68)	0.09(0.03)	1.31(0.35)
	Low forest	15.54(5.52)	7.43(0.19)	135.3(40.54)	0.7(0.25)	11.8(4.29)
Dragoon	Desert	7.74(1.46)	6.65(0.32)	25.25(10.6)	0.16(0.06)	2.27(1.18)
	Encinal	76.14(116.98)	7.42(0.33)	145.55(190.23)	0.2(0.13)	3.67(2.17)
	Low forest	12.4(1.69)	6.37(0.35)	56.41(20.21)	0.39(0.08)	7.97(1.75)
Chiricahua	Desert	6.4(1.36)	7.81(0.69)	24.09(7.09)	0.11(0.01)	1.27(0.05)

	Encinal	9(2.46)	7.26(0.31)	25.39(12.01)	0.18(0.03)	2.55(0.7)
	Low forest	4.84(1.38)	7(0.2)	30.77(12.14)	0.15(0.05)	2.49(0.89)
	High forest	4.64(3.91)	7.13(1.2)	15.51(7.23)	0.08(0.07)	1.71(1.48)
Pinaleño	Desert	3.37(0.57)	7.13(0.03)	17.79(4.42)	0.08(0.02)	1.03(0.21)
	Encinal	4.17(0.36)	7.33(0.48)	13.79(5.12)	0.06(0.02)	0.82(0.22)
	Low forest	6.54(2.24)	7.33(0.15)	27.94(13.09)	0.14(0.07)	2.66(1.48)
	High forest	20.07(17.65)	7.33(0.36)	125.79(100.45)	0.48(0.31)	9.72(5.99)
Galiuro	Desert	6.57(1.37)	7.2(0.56)	16.99(1.77)	0.17(0.14)	2.81(2.83)
	Encinal	16.9(7.57)	7.14(0.79)	111.13(93.4)	0.35(0.38)	4.84(5.92)
	Low forest	11.27(5.09)	7.19(0.48)	85.34(36.42)	0.29(0.26)	4.12(3.47)
Rincon	Desert	6.4(1.36)	6.84(0.13)	26.68(17.29)	0.12(0.05)	1.4(0.44)
	Encinal	9(2.46)	7.19(0.59)	19.34(8.79)	0.16(0.09)	2.13(1.18)
	Low forest	4.84(1.38)	6.9(0.43)	33.78(10.36)	0.14(0.04)	2.42(0.69)
	High forest	4.64(3.91)	6.77(0.22)	59.18(25.99)	0.13(0.06)	1.75(0.83)

Table 3. Micronutrient concentrations (mg/kg). Standard deviation across each transect is indicated in parenthesis.

Mountain	Vegetation	Fe	Cu	K	Mg	Ca	P	Mn	S
Santa Catalina	Desert	56.34(5.21)	5.5(2.18)	221.97(58.48)	326.04(63.41)	2161.47(449.58)	68.2(19.67)	162.07(56.42)	7.6(1.69)
	Encinal	65.1(6.9)	3.4(1.23)	72.44(7.73)	157.4(17.68)	886.77(182.28)	19.2(3.73)	76.44(50.06)	3.67(0.31)
	Low forest	185.17(42.06)	3.9(0.86)	91.07(25.66)	86.27(21.32)	595.47(96.38)	11.44(1.77)	152.77(65.13)	5.77(1.11)
	High forest	236.34(81.14)	5.6(1.83)	263.97(73.42)	291.2(18.22)	2521.94(368.89)	33.9(14.8)	60.67(19.96)	9.1(0.44)

Santa Rita	Desert	5.47(2.74)	2.74(1.2)	118.47(8.16)	312.14(12.13)	19912.2(3890.58)	9.04(3.96)	32.07(16.47)	10.4(1.6)
	Encinal	99.54(26.07)	6.27(0.21)	299.2(230.58)	614.2(485.78)	3177.6(2057.91)	44.37(15.9)	332.57(162.52)	11.64(4.05)
	Low forest	147.14(34.48)	6.97(0.29)	227.27(66.51)	590.9(148.23)	5187.7(2326.65)	78.6(29.36)	101.27(36.33)	11.37(4.67)
	High forest	161.74(5.11)	5.27(0.33)	285.34(166.87)	409.87(58.19)	3367.87(428.42)	49.17(8.64)	63.1(14.02)	8.57(0.78)
Huachuca	Desert	94.24(8.79)	8.17(0.41)	400.5(54.32)	217.1(25.54)	1919.67(184.66)	42.14(9.72)	93.84(13.94)	9.2(0.61)
	Encinal	137.97(18.34)	6.94(3.24)	115.64(45.1)	196.34(89.32)	1272.14(454.25)	35.94(9.14)	323.6(98.36)	6.87(1.74)
	Low forest	154.84(16.31)	15.67(3.66)	234.67(27.46)	480.84(13.23)	7218.57(630.88)	61.84(54.23)	254.9(70.46)	15.54(5.52)
Dragoon	Desert	95.17(14.49)	3.44(0.48)	231.4(44.93)	173.7(34.44)	1602.67(635.27)	43.9(4.78)	184.97(41.11)	7.74(1.46)
	Encinal	74.37(12.24)	5.54(1.06)	97.24(7.26)	150.24(30.23)	2478.4(1317.41)	16.64(5.34)	269.47(105.48)	76.14(116.98)
	Low forest	144.4(21.12)	9.5(2.56)	229.77(36.09)	339.37(66.62)	3186.37(400.13)	26.54(4.75)	296.57(31.06)	12.4(1.69)
Chiricahua	Desert	57.94(6.66)	5.27(0.48)	518.27(76.89)	721.07(53.75)	2861.57(255.9)	30.4(4.02)	116.67(14.78)	6.4(1.36)
	Encinal	105.44(15.3)	4(0.87)	216.47(26.91)	182.84(29)	2148.2(847.7)	40.4(8.29)	348.04(41.21)	9(2.46)
	Low forest	239.4(66.7)	5.47(1.71)	237(74.82)	754.87(149.98)	3365.7(664.12)	51.97(17.69)	81.64(3.38)	4.84(1.38)
	High forest	184.1(126.54)	1.8(1.22)	282.64(193.55)	537.27(209.6)	3744.14(405.9)	40.54(40.18)	107.6(39.31)	4.64(3.91)
Pinaleño	Desert	109.5(37.11)	1.84(0.31)	151.54(28.69)	101.07(21.79)	1038.24(210.7)	77.34(34.66)	47.17(19.12)	3.37(0.57)
	Encinal	84.37(16.92)	2.54(0.48)	82.8(9.73)	72.67(5.77)	857.64(193.91)	33.3(10.86)	33.47(10.75)	4.17(0.36)
	Low forest	269.77(19.96)	2.54(0.31)	106.6(7.34)	250.6(57.4)	1841.44(956.8)	70.97(9.73)	127.14(72.34)	6.54(2.24)

	High forest	210.7(84.62)	4.9(2.22)	414.4(232.09)	495.17(176.2)	6073.24(4586.18)	103.94(87.42)	199.84(114.23)	20.07(17.65)
Gailuro	Desert	77.34(2.35)	6.67(0.51)	311.04(55.64)	278.14(38.88)	1200.54(165.58)	25.37(5.86)	75.3(7.02)	6.57(1.37)
	Encinal	81.7(36.85)	13.64(5.08)	369.6(114.91)	497.57(87.9)	6900.77(5133.25)	28.37(12.18)	339.1(152.23)	16.9(7.57)
	Low forest	93.84(5.63)	8.74(4.74)	1015.6(179.78)	369.67(67.3)	3503.97(1184.11)	15.17(3.33)	305.6(135.29)	11.27(5.09)
Rincon	Desert	71.7(20.88)	5.44(0.5)	131.54(24.31)	249.57(152.33)	1269.77(474.78)	59.34(73.63)	87.54(53.97)	8.54(5.37)
	Encinal	127.4(40.56)	36.5(19.79)	127.54(88.09)	318.2(37.26)	1717.37(783.16)	16.77(3.89)	87.74(48.45)	8.17(1.56)
	Low forest	235.3(21.39)	5.24(1.01)	167.77(56.55)	179.14(50.01)	1743.27(263.01)	10.3(1.39)	181.37(99.16)	6.64(0.77)
	High forest	340.97(101.53)	5.7(1.75)	328.5(219.51)	335.44(162.72)	3120.74(1810.66)	28.47(8.81)	48.54(58.63)	6.4(1.61)

Table 4. Linear mixed-effects model results of the effects of vegetation biome and mountain on soil properties and soil micronutrients. Bold values indicate significant effects ($P < 0.05$).

	F	P	Marginal R ² (vegetation)	Conditional R ² (vegetation+mountain)
pH	1.49	0.224	0.04	0.19
EC	5.69	0.001	0.13	0.38
moisture	67.39	<0.001	0.59	0.76
C	5.3	0.002	0.14	0.27
N	3.64	0.016	0.1	0.23
Fe	26.97	<0.001	0.43	0.56
Cu	2.88	0.04	0.06	0.41

K	8.49	<0.001	0.15	0.52
Mg	4.66	0.005	0.1	0.4
Ca	3.22	0.027	0.08	0.36
P	0.98	0.407	0.03	0.21
Mn	6.24	<0.001	0.15	0.34
S	0.78	0.506	0.02	0.21

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