Temperature drives plant and soil microbial diversity patterns across an elevation gradient from the Andes to the Amazon

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Summary

1. Climate strongly regulates plant community composition and diversity, exemplified by gradients in plant diversity and community structure with elevation. However, we do not know if soil bacteria and fungi, key drivers of terrestrial biogeochemical cycling, follow similar biogeographical patterns determined by the same climatic drivers.

2. We studied an Andean tropical forest transect traversing 3.5 km in elevation. The species richness (α-diversity) and compositional dissimilarity of communities (β-diversity) were determined for plants, bacteria and fungi. We determined the environmental drivers of these patterns, using 31 environmental and edaphic predictor variables, and the relationship between microbial communities and soil organic matter cycling (extracellular enzymes).

3. We found co-ordinated changes with elevation in the species richness and composition of plants, soil bacteria and fungi. Across all groups, α-diversity declined significantly as elevation increased, and β-diversity increased with increased elevation difference. Temperature was the dominant driver of these diversity gradients, with only weak influences of edaphic properties, including soil pH, which did not vary substantially across the study transect. The gradients in microbial diversity were strongly correlated with the activities of enzymes involved in soil organic matter cycling, and were accompanied by a transition in microbial traits, towards slower-growing, more oligotrophic taxa at higher elevations.

4. We provide the first evidence of co-ordinated temperature-driven patterns in the diversity and distribution of plants, soil bacteria and fungi in tropical ecosystems. This finding suggest that, across landscape scales of relatively constant soil pH, shared patterns and environmental drivers of plant and microbial communities can occur, with large implications for tropical forest communities under future climate change.

Introduction

Climate regulates plant community composition and diversity, exemplified by the existence of plant diversity and community structure changes with elevation along mountainsides – first reported in a classical 19th century study of the tropical Andes (von Humboldt and Bonpland 1805). However, we do not know if soil bacteria and fungi, key drivers of terrestrial biogeochemical cycling, follow similar biogeographical patterns determined by the same climatic drivers. Microbes are the most diverse and abundant organisms on Earth (Whitman et al. 1998) and perform vital metabolic processes including the decomposition of organic matter, recycling of nutrients, and formation of root symbioses, all of which generate feedbacks affecting the productivity and diversity of plants (Bardgett and van der Putten 2014). Given their small size, abundance and rapid life cycles relative to plants and animals, microorganisms were long-assumed to be cosmopolitan in their distributions (Baas Becking 1934). Recent work has challenged this paradigm, highlighting the importance of environmental filtering, historical events, stochastic speciation and dispersal processes in shaping microbial biogeography (Fierer and Jackson 2006, Martiny et al. 2006, Tedersoo et al. 2014). Relationships between plant and soil microbes are now starting to be revealed (Barberán et al. 2015, Prober et al. 2015), but important questions concerning their relationships over landscape gradients within the tropics remain open, especially for forests. As tropical rainforests are highly productive (Pan et al. 2011) and more species-rich than any other terrestrial biome (Pianka 1966), strong associations between plant and microbe communities are likely, potentially leading to co-ordinated changes in biota across climatic gradients.

The large temperature gradients on mountains have proven invaluable for understanding how climate influences plant diversity, community composition and productivity (Colwell et al. 2008). They can also help understand the influence of climate on the diversity and functional attributes of soil microbial communities (Bryant et al. 2008) and their role in soil organic matter cycling (Bardgett and van der Putten 2014). However, such studies are scarce (Bryant et al. 2008, Fierer et al. 2011, Singh et al. 2012, Shen et al. 2014), with the diversity and functional attributes of bacteria and fungi along elevation gradients in tropical forests especially poorly resolved. Shifts in the diversity of plant and animal taxa across mountainsides are thought to result principally from differences in energy limitation and/or niche differentiation, leading to a typically monotonic decrease or mid-elevation peak in above-ground species richness with elevation (Rahbek 2005). No coordinated shifts in plant and soil microbial diversity with elevation have yet been identified globally, although this may be a consequence of insufficient sampling intensity (Fierer et al. 2011) or confounding variation in rainfall and soil pH (Bryant et al. 2008, Shen et al. 2014).

In this study we address two fundamental but unresolved questions in tropical forest ecology. First, are biogeographical patterns in plant, bacterial and fungal species diversity (α-diversity) and compositional dissimilarity of communities (β-diversity) related, and do they occur in response to the same drivers across large environmental gradients? Second, do shifts in diversity reflect differences in soil resource quality and organic matter cycling? We would expect the biogeographical patterns of plants and soil microbes to be related, as suggested by studies that associate microbial communities with plant leaf litter traits (Orwin et al. 2010, de Vries et al. 2012, Handa et al. 2014), and a strong relationship between plants and soil microbes has been hypothesised for tropical forests where there is wide inter-specific variation in leaf traits (Hattenschwiler et al. 2008). However, a relationship of this sort was not evident at local scale in a study of a single, albeit large, tropical forest plot (Barberán et

al. 2015), but the issue has not been investigated across tropical forest landscapes. Hence, relevant studies to date are partly contradictory, and although some work points towards the possibility of related biogeographical patterns among plant and microbial communities, strong evidence has been lacking. A global study of grasslands found relationships between plant, bacterial and fungal β-diversity, but not α-diversity (Prober et al. 2015). Plant and fungal α-diversity were positively related across a global latitudinal gradient, but this pattern was not observed for bacteria (Bardgett and van der Putten 2014, Tedersoo et al. 2014, Prober et al. 2015), possibly due to the wide variation in soil pH which influences biogeographical patterns in bacteria (Fierer and Jackson 2006).

We used a 3450 m tropical elevation gradient (~ 6.5 to 26.4 ^{o}C temperature gradient) in the Peruvian Andes, where variation in the important co-variants of soil pH and moisture was constrained (pH in organic horizons was 3.9 ± 0.1 (± one standard error) and in mineral horizons 4.0 ± 0.1; with no significant seasonal soil moisture limitation; Table S1). We sampled at relatively high density (22 sites in total, with soil data in separate horizons for 14 sites) significantly improving spatial resolution compared with previous studies of elevation gradients (Fierer et al. 2011, Shen et al. 2014).

Materials and Methods

Study sites and sample collection

The elevation transect under study lies on the Eastern flank of the Andes in South Eastern Peru, in the upper Madre de Dios/Madeira watershed. The transect spans 3.4 km in elevation from 194 to 3644 m above sea level (asl) and consists of 22 sites, each with a 1 ha

122 permanent sampling plot, in old growth tropical forest and one site on high elevation
123 grassland (soil properties and microbial diversity were determined for 14 sites; plant diversity
124 was determined for 19 sites; Table S1). Mean annual temperature (MAT) decreases with
125 increasing elevation (26 to 6 ^{o}C) but mean annual precipitation (MAP) does not vary
126 consistently with elevation, ranging from 1506-5302 mm yr^{-1}, with no evidence of soil
127 moisture constraints at any site. The sites are situated on predominantly Paleozoic (~450 Ma)
128 meta-sedimentary mudstone (~80%), with plutonic intrusions (granite) underlying the sites
129 between 1500 and 2020 m asl. The soils at the sites above 2520 m are Umbrisols
130 (Inceptisols), while the soils from 1000 to 2020 m are Cambisols (Inceptisols). The soils at
131 the two lowland sites are Haplic Allisols (Ultisols) (194 m asl) and Haplic Cambisols
132 (Inceptisols) (210 m asl) (according to FAO, with USDA Soil Taxonomy in parentheses).
133 Further descriptions of soil, climate and floristic composition of these sites are reported
134 elsewhere (Rapp et al. 2012, Whitaker et al. 2014). Trees were recorded in 19 of the 1 ha
135 plots, where every individual tree ≥ 10 cm diameter at breast height, 1.3 m (d.b.h.) was
136 measured, tagged and identified to species or morphospecies. Soil was collected during
137 January 2012 from five systematically distributed sampling points within 14 of the 1 ha plots.
138 These systems are highly aseasonal, with no significant variation in mean annual temperature
139 and no seasonal soil or plant moisture constraints (Zimmermann et al. 2010, van de Weg et
140 al. 2014), therefore the comparison of sites at a single time point was not confounded by
141 strong seasonality. We used composite soil samples representing spatial replication of three
142 for DNA extraction, or five spatial replicates for all other analyses. Although we sampled and
143 analysed soil in spatial replicates (within 1 ha), our treatment unit for all analyses is the plot
144 mean. Organic horizons and the surface 0-10 cm layer of mineral horizons were collected
145 separately. Soil samples were stored for < 14 days at < 4^{o}C until DNA extraction and

146 determination of nutrients and enzyme activities, which has been shown to have negligible
147 effect on these soil properties (Lauber et al. 2010, Turner and Romero 2010).

148

149 **Soil analyses: DNA sequencing, nutrients and extracellular enzyme activities**

150 For each soil sample, DNA was extracted using the MoBio PowerSoil DNA isolation
151 kit (MoBio Laboratories, Carlsbad, CA) following manufacturer instructions. For bacterial
152 community composition, the 16S rRNA gene was amplified in triplicate PCR reactions using
153 the 515f and 806r primers for bacterial and archaeal taxa. For fungal community
154 composition, the first internal transcribed spacer region (ITS1) of the rRNA gene was
155 amplified using the ITS1-F and ITS2 primer pair. Primers were modified to incorporate 12bp
156 error-correcting barcodes, and 16S rRNA amplicons and ITS amplicons were pooled
157 separately prior to sequencing with two separate runs on an Illumina MiSeq instrument at the
158 University of Colorado at Boulder. Raw sequence data were processed using the QIIME v1.7
159 pipeline, where sequences were demultiplexed using their unique barcode specific to
160 individual samples and assigned to phylotypes (at 97% similarity) using the 'open reference'
161 clustering approach recommended in the pipeline. Samples were rarefied to 1,850 and 100
162 sequences per sample for bacteria/archaea and fungi, respectively. The lower rarefaction
163 depth for fungi, which was used to increase sample number and statistical power for the
164 ecological analyses, but was sufficient to characterise diversity and community composition
165 characteristics; and these diversity patterns were highly correlated to those found when using
166 higher rarefaction depth (300; $\rho = 0.98$). Representative sequences for each phylotype were
167 assigned taxonomic classifications using the Ribosomal Database Project classifier trained on
168 the Greengenes and UNITE databases for 16S rRNA and ITS phylotypes, respectively.

Relatively abundant phylotypes were checked using BLAST and comparison against sequences contained within GenBank.

Total C and N were determined for dried, ground soil samples using a TruSpec CN Elemental Determinator (LECO, USA). Total P was determined by ignition (550°C, 1 h) followed by extraction in 1 M H_2SO_4, with phosphate detection in neutralised extracts at 880 nm by automated molybdate colorimetry using a Lachat Quikchem 8500 (Hach Ltd, Loveland, CO, USA). Mineral N and P availability were determined using ion exchange resins (Nottingham et al. 2015). Other organic and inorganic phosphorus fractions were determined using a modification of Hedley sequential extraction (in 1M NaOH, 1M HCl) (Hedley et al. 1982) and exchangeable cations extracted in 0.1 M BaCl (Hendershot and Duquette 1986), Soil pH was determined in H_2O (soil solution, 1:2.5 w:v). Gravimetric moisture content, bulk density (dried for 24 h at 105 ^{o}C) and water holding capacity (the amount of water remaining in the soil after being saturated and left to drain for 12 h) were calculated for composite soil samples for each site.

Enzyme activities for seven enzymes involved in carbon and nutrient cycling were determined for 14 study sites, using microplate fluorimetric assays with 100 µM methylumbelliferone (MU)-linked substrates to measure activity of β-glucosidase (degradation of β -bonds in glucose), cellobiohydrolase (degradation of cellulose), *N*-acetyl β-glucosaminidase (degradation of *N*-glycosidic bonds), phosphomonoesterase (degradation of monoester-linked simple organic phosphates) and β-xylanase (degradation of hemicellulose). Phenol oxidase (degradation of phenolic compounds) was measured using 5 mM L-dihydroxyphenyalanine (L-DOPA) as substrate. Further information on protocols for enzyme analyses is reported elsewhere (Nottingham et al. 2015).

193 **Statistical analyses**

194 We determined species richness (α-diversity) using Shannon diversity index,
195 according to total species abundance for plants or OTUs for soil bacteria and fungi.
196 Community composition (β-diversity) was determined using Sorrenson indices for plants and
197 Bray Curtis dissimilarity matrices for soil bacteria and fungi. We tested whether patterns in
198 bacterial and fungal diversity and community composition were explained by biotic
199 interactions with plant communities, by using Spearman's correlation (α-diversity) and
200 Mantel tests (β-diversity) among biotic groups and comparing the relationships between
201 plants and microbes in organic and mineral soil horizons. Permutational MANOVA and
202 Principal Co-ordinates Analyses to explore differences in β-diversity with elevation or soil
203 horizon. The environmental or edaphic drivers of these patterns in plant, bacterial or fungal
204 diversity and community composition were determined univariate and multivariate
205 correlation. Multivariate correlation was performed using the BEST trend correlation
206 function (Primer; version 6.1.12), to show how multivariate biotic data are shaped by 31
207 predictor variables including soil nutrients (total, organic, exchangeable), soil micronutrients,
208 soil enzymes (obtained by fluorogenic or absorption assays), and climatic and soil abiotic
209 properties. We quantified the functional consequences of changes in soil microbial β-
210 diversity by using Mantel tests of bacterial and fungal community composition and enzymatic
211 activity for seven enzymes (obtained by fluorogenic or absorption assays). For all analyses,
212 we only included sites for which we have combined plant, microbial, soil edaphic and
213 environmental data. The combined methodology allowed us to 1) determine whether diversity
214 patterns in plants, bacteria and fungi are co-related; 2) identify the β-diversity principle
215 environmental or edaphic drivers of these patterns and 3) test whether the diversity and
216 community composition of soil microorganisms influence soil processes along a tropical

environmental gradient. All statistical analyses were performed in either Primer (version 6.1.12) or R (version 2.15.2).

Results

The α-diversity of plants, soil bacteria and fungi declined as elevation increased along our study transect (Fig. 1). The α-diversity of plants declined most steeply, followed by bacteria in organic horizons and fungi in mineral horizons. The decline in diversity was linear for plants and fungi, but non-linear for bacteria. Bacterial α-diversity declined more steeply at higher elevations, especially in the mineral horizon, whereas the linear decline in fungal α-diversity with elevation was partly driven by the high fungal diversity in the two lowland forest sites. There was a stronger coupling of plant and bacterial diversity compared to plant and fungal diversity (Fig. 2). Mean annual temperature (MAT) was the strongest predictor of the patterns in α-diversity for plants and bacteria in both soil horizons and for fungi in the mineral horizon (Table S2).

The composition of plant, bacterial and fungal communities also differed with elevation (Figs. 3 & S1), and between organic and mineral horizons for soil microorganisms (Fig. S2), although fungi differed to a lesser extent between horizons than bacteria. For bacteria, increased elevation was associated with an increased dominance of *Acidobacteria* and *Betaproteobacteria*, and decreased dominance of Actinobacteria and *Deltaproteobacteria*; the patterns occurred in both horizons, although mineral horizons contained a greater proportion of *Acidobacteria* and *Archaea* (Fig. 3). For fungi, increased elevation was associated with increased dominance of Ascomycota (*Archaeorhizomycetes*, *Leotiomycetes*), Basidiomycota (*Microbotryomycetes*), and decreased dominance of other Ascomycota (*Sodariomycetes*, *Dothideomycetes*, *Eurotiomycetes*), Glomeromycota and

241 Zygomycota (Fig. 3; Table S3). Bacteria exhibited the largest compositional dissimilarities of
242 communities with elevation (β-diversity) followed by plant and then fungal communities, and
243 the β-diversity patterns observed for bacteria and fungi were correlated with those observed
244 for plants (Fig. 4). Thus, plants and several major taxonomic groups of both bacteria and
245 fungi showed clear changes in composition with elevation, suggesting shared environmental
246 drivers in community structure.

247 As with α-diversity, MAT was the strongest correlate of patterns in β-diversity. MAT
248 was the most significant parameter in multivariate models for β-diversity of plants, bacteria
249 in both organic and mineral horizons, and fungi in mineral horizons (Table 1). There were
250 additional significant correlations between the β-diversity of bacteria and fungi, and organic
251 nutrient concentrations and their ratios; these were stronger in the organic compared to
252 mineral horizons (Fig. S4). Nutrients other than nitrogen and phosphorus also influenced β-
253 diversity, including potassium for plants and sodium for bacteria (Table 1). Soil pH was
254 correlated with bacterial β-diversity but not fungal β-diversity.

255 To assess whether soil microbial distributions were related to differences in rates of
256 organic matter cycling, we determined the activities of seven enzymes involved in the
257 degradation of different organic compounds. The activity of the different soil enzymes
258 decreased with increased elevation but at different rates, and independently of differences in
259 ambient temperature (Fig. S5). These patterns reflected responses in the microbial
260 community to shifts in substrate availability. For example, relative microbial investment into
261 different enzymes shifted with increased elevation, from enzymes that degrade phosphorus-
262 to nitrogen– containing organic compounds (Nottingham et al. 2015). Strong relationships
263 between the differential activity of these seven enzymes and differences in β-diversity were
264 found for bacteria ($\rho = 0.75$) and fungi ($\rho = 0.74$) in organic horizons (Fig. S6). Together

265 these findings suggest that, in addition to temperature, differences in organic nutrient cycling
266 are related to the β-diversity of bacteria and fungi in organic soil horizons.

267

268 **Discussion**

269 Overall, our results demonstrate a fundamental role for environment, principally
270 temperature, in co-ordinating the diversity and community composition of plants, soil
271 bacteria and fungi. Although environmental filtering at large geographic scales has been
272 suggested to shape community composition for plants and soil bacteria and fungi
273 independently (Tedersoo et al. 2014), this has not been observed for both diversity (species
274 richness) and community composition across all three biotic groups. Evidence for this
275 environmental filtering comes from both multivariate models and correlations between
276 distance matrices, where temperature and, to a lesser extent, organic nutrient concentrations,
277 were strongly associated with variation in bacterial and fungal α- and β-diversity (Table 1).

278 The role of temperature in determining microbial β-diversity is also illustrated by an
279 increased relative abundance of *Acidobacteria* and the fungi *Archaerhizomycetes* with
280 increased elevation, but a decreased relative abundance of Actinobacteria and
281 *Alphaproteobacteria* (Fig. 3). These major taxonomic groups have been associated with
282 oligotrophic (Acidobacteria, *Archaerhizomycetes*) and copiotrophic (Actinobacteria,
283 *Alphaproteobacteria*) life history strategies, respectively (Fierer et al. 2007, Rosling et al.
284 2011), which is consistent with evidence for increased energy limitation of microbial activity
285 at higher elevations, favoring slower growth (Nottingham et al. 2015). The strong
286 correlations between the β-diversity of plants, soil bacteria and fungi (Fig. 4) further
287 indicated that similar environmental factors, primarily temperature (Table 1), drive these
288 patterns across the three biotic groups. The high relative abundance of the Ascomycota,

289 *Archaerhizomycetes* at higher elevations (Fig. 3) is of particular interest because this class of
290 fungi was identified only very recently, in tundra soils (Schadt et al. 2003) and their global
291 distribution is poorly understood because many previous analyses failed to identify them
292 because of amplification biases (Rosling et al. 2011). They are understood to be typically
293 oligotrophic and root-associated fungi, colonizing typical ectomycorrhizal habitats beneath
294 pine and ericaceous plants (Rosling et al. 2011), which is consistent with our current
295 understanding of tropical montane forest habitats being energy-limited (Bruijnzeel et al.
296 2011). This important class of fungi, which until very recently was unknown, dominate the
297 fungal biomass in these tropical montane forests.

298 Temperature was also the principal correlate of plant β-diversity (Table 1).
299 Temperature has previously been shown to be a major determinant of tree community
300 composition across this transect (Rapp et al. 2012) and up-slope movement of tree species'
301 ranges has been observed under recent climatic warming (Duque et al. 2015). Patterns in
302 plant species composition and richness on tropical mountains are thought to be driven mainly
303 by the effect of narrow temperature ranges on niche separation (by directly affecting
304 metabolism and indirectly affecting resource availability), while further constrained by land
305 area, lithology and disturbance history (Janzen 1967, Colwell et al. 2008). Although the high
306 landslide activity and soil erosion in the humid Eastern Andean Cordillera (Clark et al. 2013)
307 may be significant factors in constraining diversity at higher elevations in this region, our
308 study identifies a central underlying role for temperature. Analogous observations have been
309 made along latitudinal gradients where plant/fungal species richness ratios decrease with
310 distance from the equator (Tedersoo et al. 2014). Our data indicate a stronger coupling
311 between the α-diversity of plants and bacteria compared to fungi (Fig. 2), but a stronger
312 coupling between the β-diversity of plants and fungi as compared to bacteria (Fig. 4).

There was a secondary role for edaphic properties in shaping these diversity patterns, with direct influences of nutrient ratios on microbial β-diversity and potassium on plant β-diversity (Table 1). Our data also suggest that this role of edaphic processes on microbial α- and β-diversity is more significant in organic horizons, where the community-wide differences in plant litter traits is largest (Hattenschwiler et al. 2008). Multiple lines of evidence suggest an influence of plant organic matter inputs on soil microbes: (i) the large difference in microbial diversity between organic and mineral soil horizons (Figs. S1 & S2); (ii) the existence of stronger correlations between microbial β-diversity and soil organic nutrients in organic horizons compared to mineral horizons (Table 1; Fig. S3); (iii) the overall strong correlation between plant and soil microbial diversity (Figs. 2 & 4); and (iv) the correlation between soil microbial β-diversity and the dissimilarity among sites in enzymatic activity, indices of organic nutrient degradation (Nottingham et al. 2015) (Fig. S6). Laboratory incubations of soils from this transect also support the link between differences in microbial community composition and the rate at which different organic substrates undergo degradation (Whitaker et al. 2014). Together these findings point towards a relationship between the high soil microbial diversity in lowland forests and the diverse complexity and stoichiometry of plant organic matter inputs to soil, through the high inter- and intra-species chemical diversity in leaf-litter (Hattenschwiler et al. 2008).

Our results, from a 3450 m elevation range, contrast with findings from studies of other elevation gradients that only examined plant and bacterial diversity, and have not found such strongly-related diversity gradients. The fundamental climate-diversity relationships we observed here were probably obscured in previous studies because of insufficient sampling density and wider variation in soil pH and soil moisture. For example, the importance of sampling intensity is demonstrated by the contrast between findings from this study of 14 sites with an earlier report from 6 locations along the same Andean transect where no

338 elevation gradient in soil bacterial diversity was found (Fierer et al. 2011): if we reduce our
339 dataset to include only those sites represented in the earlier study, no strong elevation trends
340 are apparent (Fig S6). While the importance of soil pH and rainfall variation in determining
341 patterns in bacterial diversity was demonstrated for a 1850 m elevation gradient in South
342 Korea (Singh et al. 2014). Similarly, these factors also likely accounted for the lack of clear
343 patterns for two temperate zone elevation transect studies which sampled six locations over
344 1670 m in Northeast China (Shen et al. 2014) and five locations over 920 m in the Rocky
345 mountains, the latter indicating a small single-taxon increase with elevation, but no
346 community-wide trend (Bryant et al. 2008).

347 This elevation gradient study in the Peruvian Andes demonstrates how temperature
348 fundamentally shapes plant, bacterial and fungal diversity in tropical forests. Consistent
349 trends in both α- and β-diversity were observed across the principal organismal groups of
350 plants, bacteria and fungi, also suggesting that stronger interactions occur among these
351 groups than has been recognised previously. Our findings imply that, where other potential
352 influences such as soil pH and moisture remain relatively constrained, anticipated future
353 temperature change will have significant co-ordinated impacts on the identity and functioning
354 (above- and below-ground) of tropical biota.

355

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Figure legends

Figure 1. The α-diversity (Shannon diversity index) of bacteria and fungi declined with increased elevation in Andean tropical forests. There were significant relationships between elevation and the α-diversity of plants, and each of bacteria and fungi in both organic and mineral soils. Models were selected based on AIC values; linear models were the best fit in all cases except for logistic models for bacteria (where $p < 0.001$).

Figure 2. The relationships between the ratios of plant to bacterial and plant to fungal α-diversity and elevation, in organic and mineral soil horizons. Regression lines are shown with increasing number of dashes for bacterial mineral (solid line), bacterial organic, fungal mineral and fungal organic (shortest dashes). The stronger coupling of plant and bacterial diversity (Spearman's correlation: $\rho = 0.76, 0.70$; organic and mineral horizons, respectively) compared to plant and fungal diversity ($\rho = 0.14, 0.64$), was further reflected in a greater decline with elevation for the species richness ratio of plants-to-fungi (slope of 1.02) compared to plants-to-bacteria (slope of 0.59).

Figure 3. The (A) positive and (B) negative trends in the relative abundances of specific bacterial and fungal taxa in soils along an elevation gradient in Andean tropical forest. Bacteria taxa are Acidobacteria, Actinobacteria, *Beta-Proteobacteria* and *Delta-Proteobacteria*; and fungal taxa are Actinomycetes, *Sordariomycetes* and *Archaeorhizomycetes* (by phyla or, where italicised, by class). All data are for organic horizons except for Acidobacteria, which is for mineral horizon. The full data for all taxa in organic and mineral horizons (which follow similar trends) are in Fig. S1 and Table S3 (Fig. S1 also shows dissimilarity of communities among sites using heat-maps and Table S3 shows correlations between relative abundance of taxa and elevation).

519

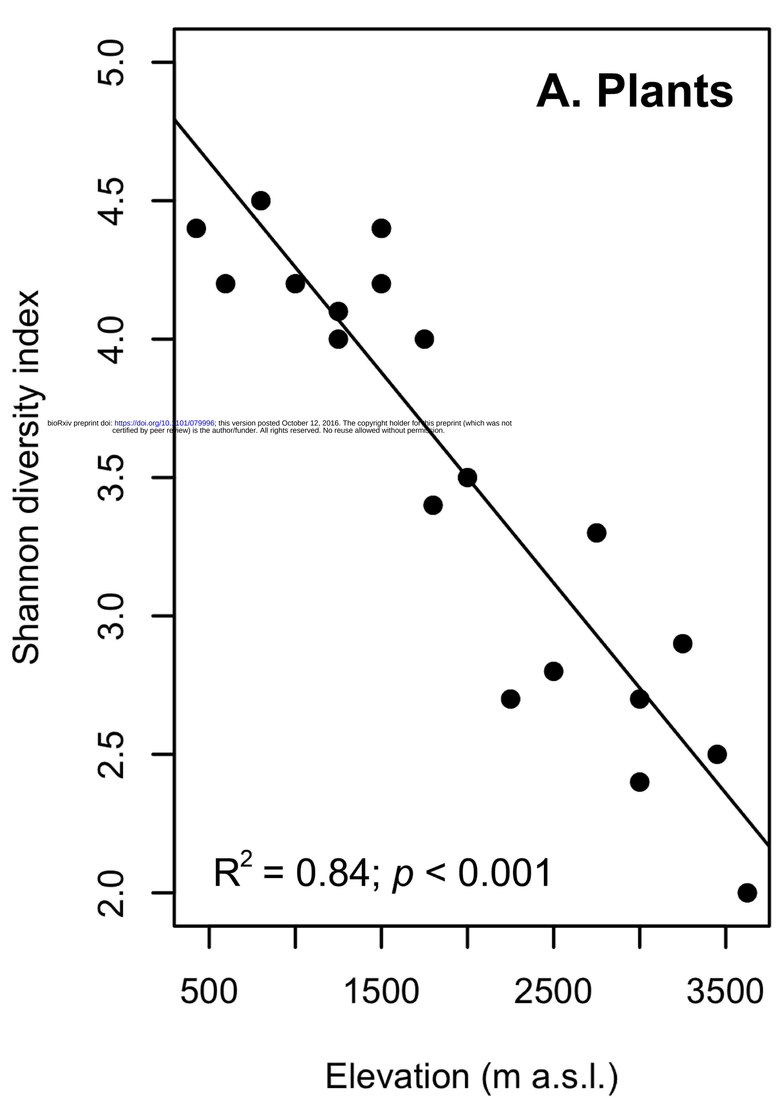
520 **Figure 4. Elevation comparisons of indices of plant ß-diversity, bacteria and fungal ß-**
521 **diversity in organic horizons.** The overall decline with increased elevation indicates
522 increased dissimilarity in ß-diversity between sites with greater difference in elevation. ß-
523 diversity was determined by Sorensen's indices for plants, and by Bray Curtis indices for
524 bacteria and fungi. Patterns in ß-diversity were correlated between plants and bacteria
525 (organic horizon $\rho = 0.81$; mineral horizon $\rho = 0.88$) and plants and fungi (organic horizon ρ
526 $= 0.67$; mineral horizon $\rho = 0.79$; by Mantel tests*;* $p < 0.001$ for all comparisons

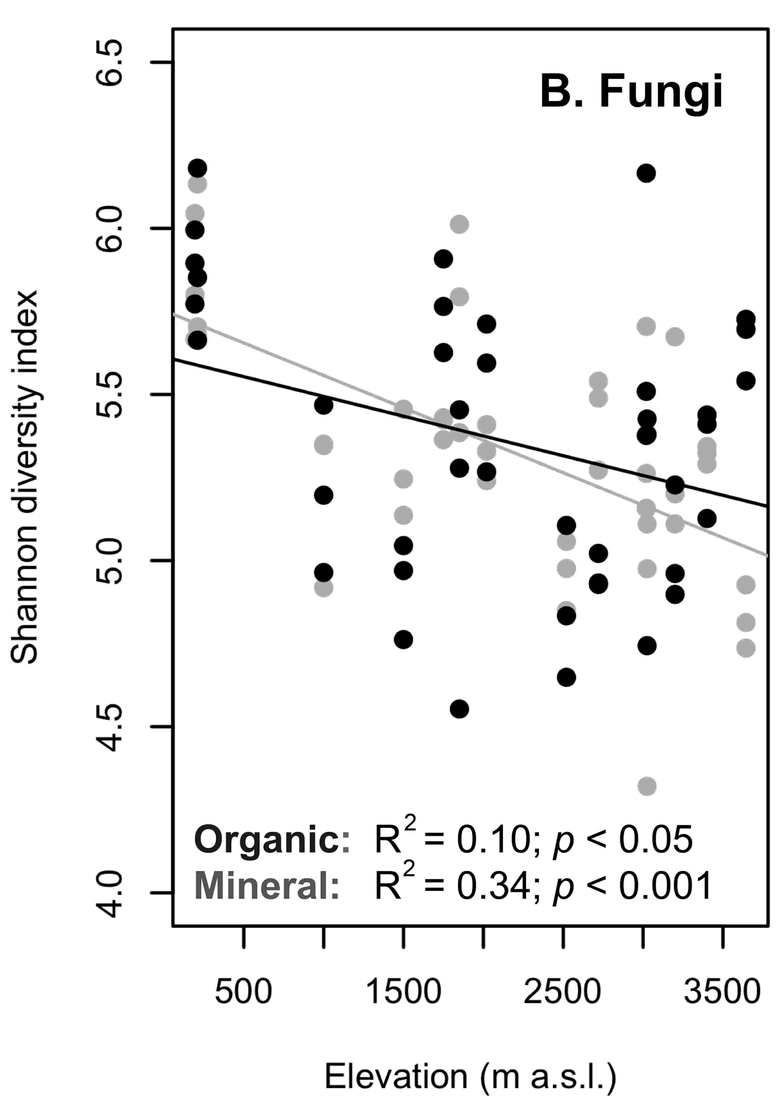
Table 1

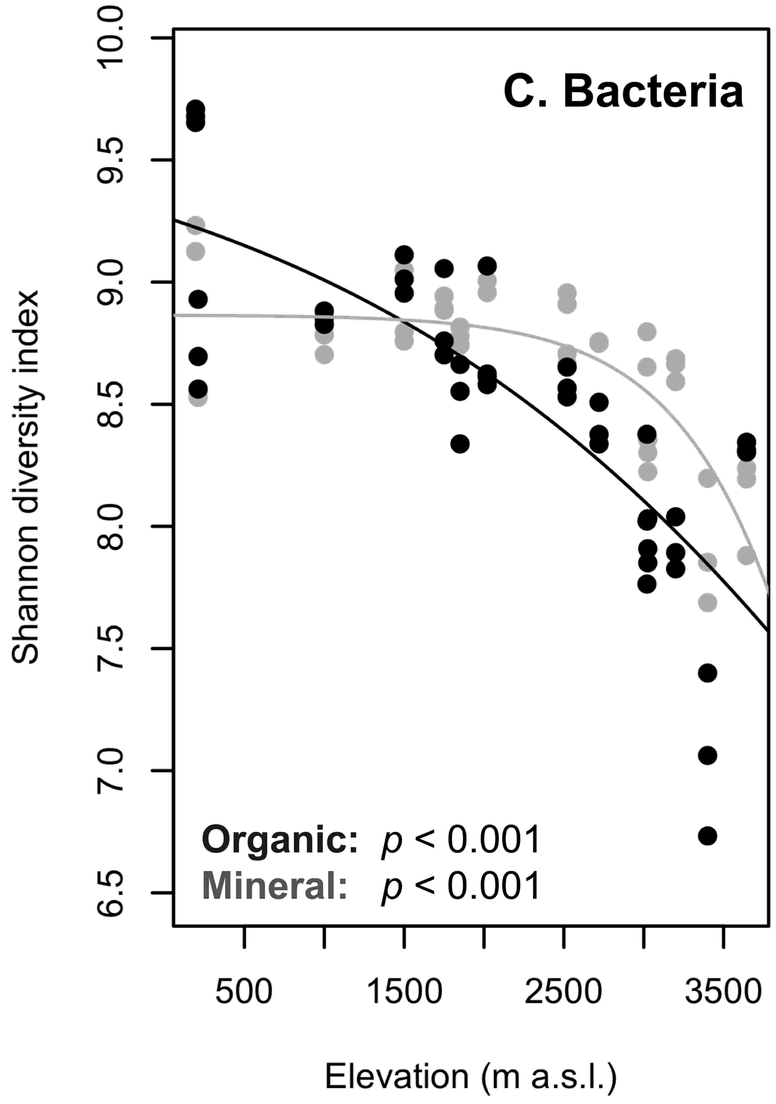
The relationship between plant, bacterial and fungal β-diversity and environmental and edaphic variables.

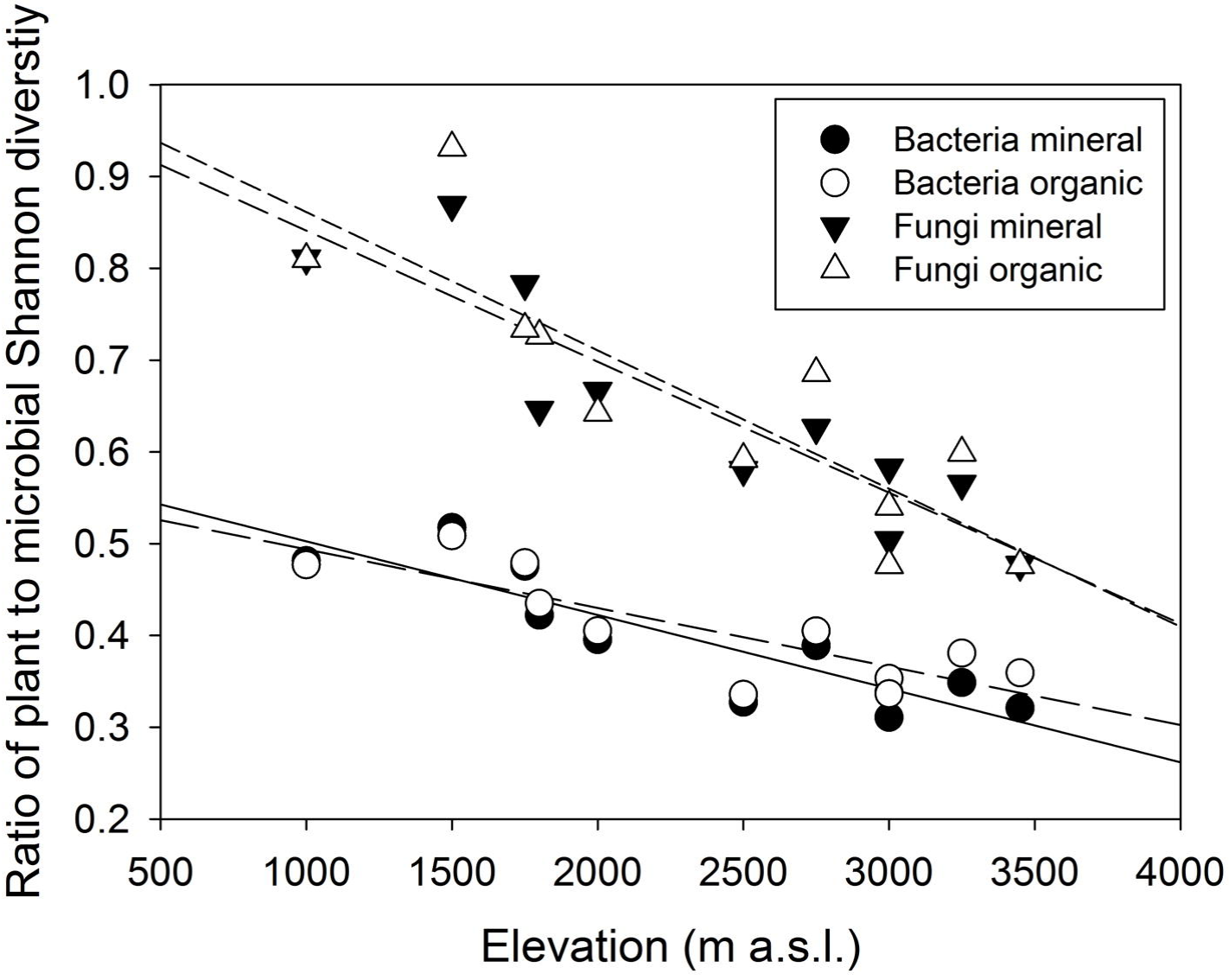
	Plants	Bacteria	Fungi	Bacteria	Fungi
		Organic horizon		Mineral horizon	
MAT	*** (0.91)	*** (0.77)	* (0.67)	*** (0.88)	*** (0.59)
Soil pH	ns	* (0.57)	ns	** (0.47)	ns
Total C:N	ns	** (0.68)	ns	ns	** (0.38)
Total C:P	ns	ns	** (0.70)	ns	ns
Na	ns	ns	ns	* (0.22)	ns
K	** (0.44)	ns	ns	ns	ns
N-acetyl β-glucosasminidase	ns	ns	*** (0.74)	ns	ns
Complete model	0.93	0.88	0.80	0.91	0.65

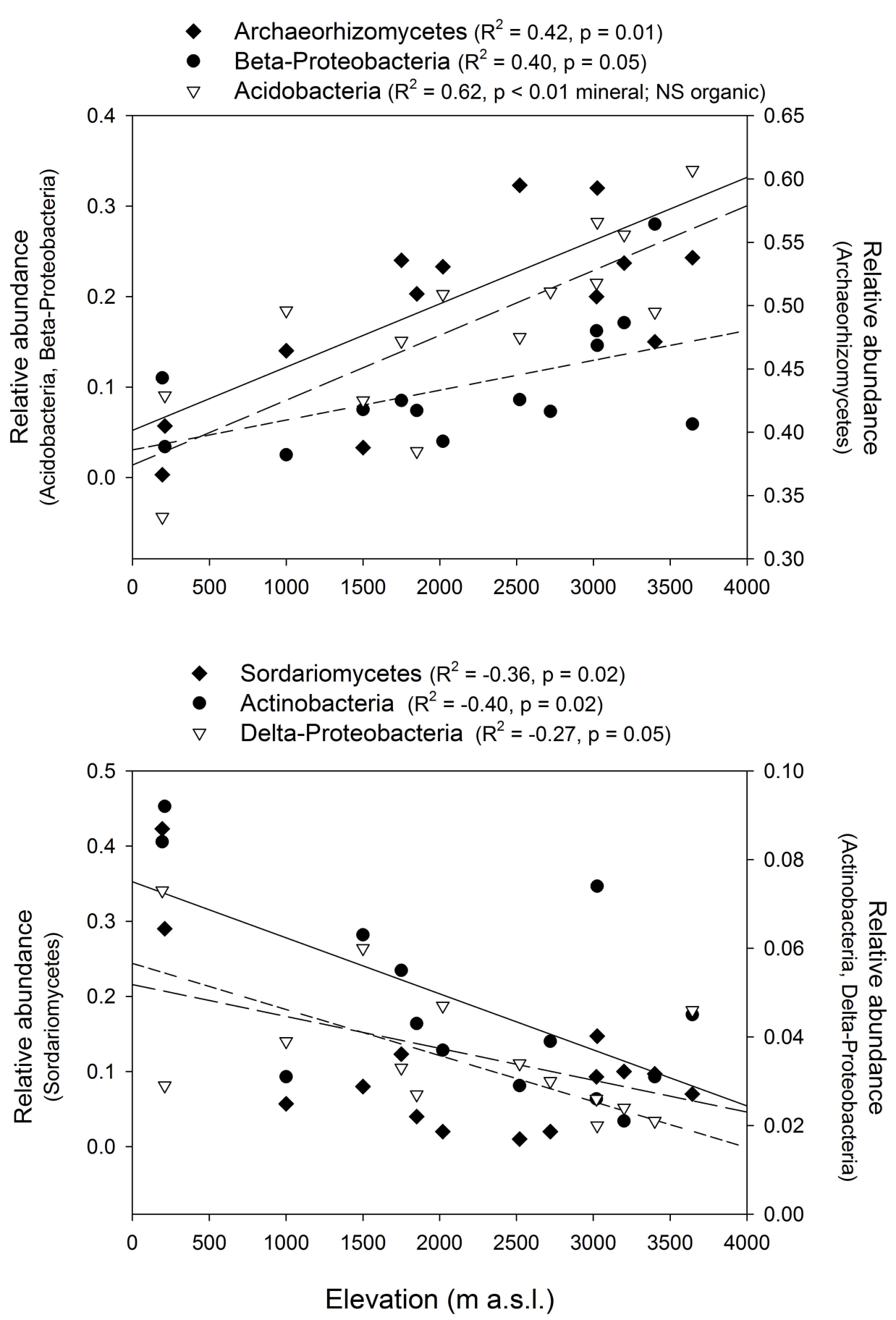
Models were determined using step-wise selection based on dissimilarity between variables by Euclidean distance (biotic and environmental matching function in Primer). A total of 31 properties were included in models for plants and bacteria and fungi in organic soils (25 for bacteria and fungi in mineral soils), including MAP, soil pH, total soil nutrients (CNP) and their ratios, available soil nutrients, soil phosphorus fractions, cations, cation exchange capacity; and the activities of seven enzymes in organic horizons. For plants, organic horizon soil properties were included in analyses (when we included mineral soil data the model included MAT (0.91) and Fe (0.16). Variables are ranked in order of significance by number of asterisks; the correlation coefficients (Mantel tests) for each individual variable are shown in parentheses.

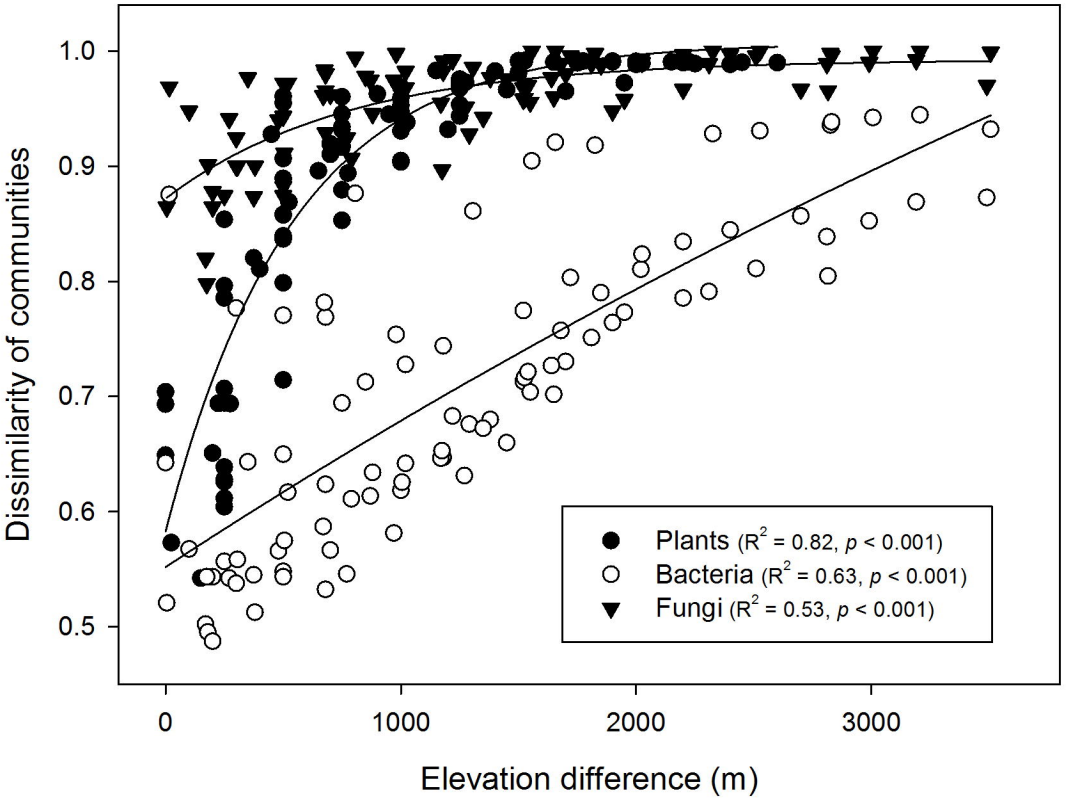







Ratio of plant to microbial Shannon diverstiy
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
500
1000
1500
2000
2500
3000
3500
4000
Elevation (m a.s.l.)
Bacteria mineral
Bacteria organic
Fungi mineral
Fungi organic


Archaeorhizomycetes (R^2 = 0.42, p = 0.01)
Beta-Proteobacteria (R^2 = 0.40, p = 0.05)
Acidobacteria (R^2 = 0.62, p < 0.01 mineral; NS organic)
Relative abundance (Acidobacteria, Beta-Proteobacteria)
Relative abundance (Archaeorhizomycetes)
0.4
0.3
0.2
0.1
0.0
0.65
0.60
0.55
0.50
0.45
0.40
0.35
0.30
0
500
1000
1500
2000
2500
3000
3500
4000
Sordariomycetes (R^2 = -0.36, p = 0.02)
Actinobacteria (R^2 = -0.40, p = 0.02)
Delta-Proteobacteria (R^2 = -0.27, p = 0.05)
Relative abundance (Sordariomycetes)
Relative abundance (Actinobacteria, Delta-Proteobacteria)
0.5
0.4
0.3
0.2
0.1
0.0
0.10
0.08
0.06
0.04
0.02
0.00
0
500
1000
1500
2000
2500
3000
3500
4000
Elevation (m a.s.l.)


Dissimilarity of communities
1.0
0.9
0.8
0.7
0.6
0.5
0
1000
2000
3000
Elevation difference (m)
Plants (R^2 = 0.82, p < 0.001)
Bacteria (R^2 = 0.63, p < 0.001)
Fungi (R^2 = 0.53, p < 0.001)