Microbes follow Humboldt: temperature drives plant and soil microbial diversity patterns from the Amazon to the Andes

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Summary

More than 200 years ago, von Humboldt reported decreases in tropical plant species richness with increasing elevation and decreasing temperature. Surprisingly, co-ordinated patterns in plant, bacterial and fungal diversity on tropical mountains are yet to be observed, despite the central role of soil microorganisms in terrestrial biogeochemistry. We studied an Andean transect traversing 3.5 km in elevation to test whether the species diversity and composition of tropical forest plants, soil bacteria and fungi can follow similar biogeographical patterns with shared environmental drivers. We found co-ordinated changes with elevation in all three groups: species richness declined as elevation increased, and the compositional-dissimilarity of communities increased with increased separation in elevation, although changes in plant diversity were larger than in bacteria and fungi. Temperature was the dominant driver of these diversity gradients, with weak influences of edaphic properties, including soil pH. The gradients in microbial diversity were strongly correlated with the activities of enzymes involved in organic matter cycling, and were accompanied by a transition in microbial traits towards slower-growing, oligotrophic taxa at higher elevations. We provide the first evidence of co-ordinated temperature-driven patterns in the diversity and distribution of three major biotic groups in tropical ecosystems: soil bacteria, fungi and plants. These findings suggest that, across landscape scales of relatively constant soil pH, inter-related patterns of plant and microbial communities with shared environmental drivers can occur, with large implications for tropical forest communities under future climate change.

Keywords: biogeography, elevation gradient, microbial ecology, plant ecology, Peru, phylogenetic diversity, tropical forests

1. Introduction

Climate regulates plant community composition and diversity. This observation is exemplified by the existence of changes in plant species diversity and community structure with elevation along mountainsides – first reported in a classical study of the tropical Andes by the 19th century naturalist Alexander von Humboldt (von Humboldt and Bonpland 1805). However, it is not clear 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 functions including the decomposition of organic matter, recycling of nutrients, and formation of root symbioses, all of which can affect the productivity and diversity of plants (Bardgett and van der Putten 2014). Given their small size, abundance and short 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 (Tedersoo et al. 2014, Barberán et al. 2015, Prober et al. 2015, Zhou et al. 2016), but important questions concerning their relationships over landscape gradients remain open, especially for tropical forests. The high productivity and species richness of tropical rainforests (Pianka 1966, Pan et al. 2011) translates to a greater quantity and chemical diversity of organic matter inputs to their soils and a greater diversity of plant-microbial associations. Together, these characteristics point towards more opportunities for associations between plant and microbial species than in temperate or high-latitude biomes (Hattenschwiler et al. 2008, Mangan et al. 2010, Fanin et al. 2014),

74 potentially leading to co-ordinated changes in biota across climatic gradients within tropical
75 forests.

76 The large temperature gradients on mountains have proven invaluable for
77 understanding how temperature influences plant diversity, community composition and
78 productivity (Colwell et al. 2008). Shifts in the diversity of plant and animal taxa with
79 changes in elevation along mountainsides globally are thought to result principally from
80 differences in energy limitation and/or niche differentiation, leading to a typically monotonic
81 decrease or mid-elevation peak in above-ground species richness with elevation (Rahbek
82 2005). Elevation gradients can also help us to understand the influence of temperature on the
83 diversity and functional attributes of soil microbial communities and their role in soil organic
84 matter cycling (Bryant et al. 2008, Geml 2017). However, such studies have not shown the
85 strong elevation-related pattern of diversity observed for plants. Studies of bacterial richness
86 have revealed contrasting patterns, strongly influenced by multiple additional drivers,
87 particularly the large between-sample variations in rainfall or soil pH that have accompanied
88 such studies (Bryant et al. 2008, Shen et al. 2013, Singh et al. 2014, Peay et al. 2017).
89 Similarly contrasting patterns have been found in studies of fungal richness, which have
90 generally targeted specific groups that vary in their elevation relationship by functional type
91 and plant-host specificity (reviewed in (Geml 2017, Kivlin et al. 2017)). Any of these sources
92 of sample variance could obscure an underlying temperature-microbial diversity relationship.
93 The diversity and functional attributes of bacteria and fungi along elevation gradients in
94 tropical forests are especially poorly resolved.

95 We would expect the biogeographical patterns of plants and soil microbes to be
96 related, as suggested by studies that have associated microbial communities with plant leaf
97 litter traits (Orwin et al. 2010, de Vries et al. 2012, Handa et al. 2014); and a strong
98 association between plant leaf traits (i.e. chemical diversity) and soil microbial species

assemblages has been hypothesised for tropical forests where there is sufficiently wide inter-specific variation in leaf traits (Hattenschwiler et al. 2008). Where this question has been addressed in the tropics, a relationship between the chemical composition of leaf-litter and the underlying microbial community composition has been demonstrated in an incubation experiment (Fanin et al. 2014), but there was no overall relationship between plant and soil microbial species diversity in a study of a single, albeit large, forest plot (Barberán et al. 2015). However, the issue has not yet been investigated at a larger biogeographical scale in the tropics. 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 (Tedersoo et al. 2014) and detailed relationships have been shown for specific groups of fungi (Geml 2017, Kivlin et al. 2017). These biogeographical patterns have not been observed for bacteria (Bardgett and van der Putten 2014, Prober et al. 2015), possibly due to the wide variation in soil pH which likely confounds sampling for biogeographical patterns in bacteria in studies that do not constrain its variation (Fierer and Jackson 2006). In summary, some work points towards related biogeographical patterns among plant and microbial communities (Tedersoo et al. 2014, Prober et al. 2015), elsewhere evidence is inconclusive or partly contradictory (de Vries et al. 2012, Barberán et al. 2015) and especially so for tropical forest.

In this study, we used a 3.5 km tropical elevation gradient (~ 6.5 to 26.4 ^{o}C mean annual temperature range) in the Peruvian Andes (figure 1), to ask: do related biogeographical patterns in plant, bacterial and fungal species diversity (α-diversity) and compositional dissimilarity of communities (β-diversity) occur across large environmental gradients, and does temperature drive these patterns where other environmental variables are constrained? Importantly, the variation along this elevation gradient in the key environmental variables of soil pH and moisture was very limited (table S1), meaning that

our data would be minimally affected by other key potential environmental factors that may confound any effect of temperature on soil biota. We sampled at high density considering the logistical challenges of the environment (14 sites in total, with soil data from two separate horizons). We determined the α-diversity and β-diversity for plants and soil microbes, by using field surveys of 1 ha permanent sample plots for plants and high-throughput sequencing for soil microbes. We analysed a large suite of environmental and soil properties, including soil extracellular enzymes, to determine the environmental drivers of these plant and microbial diversity patterns, and how those patterns were related to indices of organic matter cycling.

2. Materials and Methods

2.1 Study sites

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 (figure 1) (Nottingham et al. 2015b). The transect spans 3450 m in elevation from 194 to 3644 m above sea level (asl) and consists of 14 sites, each with a 1 ha permanent sampling plot, all in old growth tropical forest except for one site on high elevation grassland (figure 1, table S1). The sites are roughly evenly distributed by elevation but not spatial separation: the transect is approximately 270 km in length, with 35 km between the upper 12 sites and 12 km between the upper 9 sites. Mean annual temperature (MAT) decreases with increasing elevation across the transect (dropping from 26 ^{o}C to 6 ^{o}C), but mean annual precipitation (MAP) does not vary consistently with elevation, ranging from 1506-5302 mm yr^{-1} among the sites, with no evidence of soil moisture constraints at any (Zimmermann et al. 2010). The plots are situated on predominantly Paleozoic (~450 Ma) meta-sedimentary mudstone (~80%), with plutonic intrusions (granite) underlying the sites between 1500 and 2020 m asl. The soils at the sites

148 above 2520 m are Umbrisols (Inceptisols), while the soils from 1000 to 2020 m are
149 Cambisols (Inceptisols). The soils below 1000 m, at the two lowland sites, are Haplic Allisols
150 (Ultisols) (194 m asl) and Haplic Cambisols (Inceptisols) (210 m asl) (according to FAO,
151 with USDA Soil Taxonomy in parentheses). Further descriptions of soil, climate and floristic
152 composition of these sites are reported elsewhere (Rapp et al. 2012, Whitaker et al. 2014).

153 *Plant and soil data collection.* Soil and microbial properties were determined for 14
154 sites (13 forest, 1 high elevation grassland). Plant diversity was determined in the 13 forest
155 sites, resulting in 13 sites with both tree and microbial data. For the 13 forest sites, trees were
156 measured in each 1 ha plot, where every individual tree ≥ 10 cm diameter at breast height
157 (1.3 m) was measured, tagged and identified to species or morphospecies. Plants were
158 censused during 2007-2012; for further details on methodology see Rapp et al. (2012). For all
159 sites, soil samples were collected during January 2012 from five systematically distributed
160 sampling points in the 1 ha plots. These ecosystems are highly aseasonal, with no significant
161 intra-annual variation in mean monthly temperature and no evidence of seasonal soil or plant
162 moisture constraints (Zimmermann et al. 2010, van de Weg et al. 2014), therefore the
163 comparison of soil properties for these sites at a single time point was representative of
164 patterns likely to be found throughout the year. We used composite soil samples composed of
165 three replicates for DNA extraction because our aim, for both plants and soil microorganisms,
166 was to characterize the overall diversity and community composition by plot (rather than to
167 investigate the spatial variation within the plot). However, we used five spatial replicates for
168 all other analyses, to quantify the within-plot variation for edaphic properties. We collected
169 and analysed samples from both organic and mineral horizons, with the mineral horizon
170 samples coming from the upper 10 cm of the mineral layer. Soil samples were stored for < 14
171 days at < 4 ^{o}C until DNA extraction and determination of nutrient content and enzyme

activities; this method has been shown to have negligible effects on these soil properties (Lauber et al. 2010, Turner and Romero 2010).

Soil analyses: DNA sequencing, nutrients and extracellular enzyme activities

Microbial diversity was assessed using high-throughput sequencing to characterise the variation in marker gene sequences (Fierer et al. 2012). For bacterial community composition, the 16S rRNA gene was amplified in triplicate PCR reactions using the 515f and 806r primers. For fungal community composition, the first internal transcribed spacer region (ITS1) of the rRNA gene was amplified using the ITS1-F and ITS2 primer pair. Raw sequence data were processed using the QIIME v1.7 pipeline, where sequences were de-multiplexed using their unique barcode specific to individual samples and assigned to phylotypes (operational taxonomic units, OTUs, at 97% similarity). Taxonomy was determined for each phylotype using the RDP classifier (Wang et al. 2007) trained on the Greengenes (McDonald et al. 2012) and UNITE (Abarenkov et al. 2010) databases for bacterial and fungal sequences (see Supplementary Information for further detail).

Soil characteristics: We determined the following edaphic variables: total carbon (C), total nitrogen (N), total phosphorus (P), organic P, resin-extractable P (resin P), resin-N, cation exchange capacity (ECEC) and exchangeable cations (Al, Ca, Cl, Fe, K, Mn, Mg, Na), soil pH, bulk density, moisture content and activities of seven soil enzymes (Nottingham et al. 2012) (see Supplementary Information for further detail).

2.3 Measures of α- and β-diversity

We analysed estimates of α- and β-diversity for each biotic group. For plants, α-diversity measures came from Shannon species diversity indices for each plot and therefore constituted a single measure per site (n = 13 sites in total, as there was no plant diversity measure from the grassland site). Bacterial and fungal α-diversity were determined using Shannon species

196 diversity indices based on the abundance of OTUs for soil bacteria and fungi. We determined
197 β-diversity (community composition) using dissimilarity matrices (Sørensen and Bray-Curtis
198 for plants and soil microbes, respectively). The process was repeated separately for the
199 organic and the mineral horizons. Our data-set therefore consisted of the following five
200 measures of α-diversity and β-diversity for each site: plants, fungal-organic, fungal-mineral,
201 bacterial-organic and bacterial-mineral.

202 **2.4 Statistical analyses**

203 Our main hypotheses that 1) α- and β-diversity measures across biotic groups are
204 related and 2) have shared environmental drivers, were addressed by using linear and linear
205 mixed-models for α-diversity (mixed effects models) and multivariate methods for β-
206 diversity (permutational-MANOVA (PERMANOVA), Principal Co-ordinates Analyses
207 (PCA), Mantel tests and multivariate correlation models). The effects of elevation on α-
208 diversity were tested using a linear model for plant diversity and linear mixed-effects models
209 for each of the four measures of microbial diversity. Elevational differences in β-diversity
210 were examined using PERMANOVA, PCA and Mantel tests. The effects of climate and
211 edaphic variables on α-diversity were addressed by testing for effects of six specific variables
212 on α-diversity: MAT, MAP, pH, total C, ECEC and resin P, using a linear model for plant
213 diversity, and linear mixed models for each of the four measures of soil microbial diversity.
214 To test for the effects of climate and edaphic variables on β-diversity we used BIO-ENV
215 multivariate correlation models (Clarke and Ainsworth 1993), which creates a model by step-
216 wise selection, determining high-rank correlations between species dissimilarity matrices and
217 resemblance matrices generated from environmental variables (31 in total). Detailed
218 descriptions of these statistical tests are provided in supplementary material. All statistical
219 analyses were performed in either R (version 3.4.1) or PRIMER (version 6.1.12; PRIMER-E,
220 Plymouth, UK). The combined analysis allowed us to: 1) determine whether diversity

patterns in plants, bacteria and fungi are related; 2) infer the principal environmental or edaphic drivers of the observed patterns in diversity; and 3) test whether the diversity and community composition of soil microorganisms influence soil processes along a tropical environmental gradient.

3. Results

Effect of elevation on α-diversity. There were significant differences between biotic groups in their average levels of α-diversity (linear mixed model, group effect: $F = 1093$; $df = 4, 165$; $p < 0.001$), which increased in the order: plants < fungi < bacteria (figure 2). For each group, all α-diversity measures declined with increased elevation, except for fungal diversity in the organic horizon (table S2). For plant, fungal-mineral and bacterial-organic α-diversity, the decline with elevation was best described with a linear model (table S2a, c, d). For fungal-organic and bacterial-mineral α-diversity, the change was non-linear: for fungal-organic, α-diversity was lowest at mid-elevation (figure 2b, table S2b) whereas for bacterial-mineral, α-diversity only showed significant declines at the higher elevations (figure 2c, table S2e). The effects of elevation on α-diversity were therefore mostly negative, but there were also significant differences among groups in the exact pattern of change with elevation (combined linear mixed model, group: elevation interaction: $F = 23.48$; $df = 5, 87$; $p < 0.001$; between group and elevation^2: $F = 7.80$; $df = 5,86$; $p < 0.001$). Plants showed the steepest decline in α-diversity with elevation (slope = -0.753 ± 0.094; table S2).

Effects of climate and edaphic variables on α-diversity. Mean annual temperature (MAT) was the dominant determinant of the patterns in α-diversity for all biotic groups and in both soil horizons, with the exception, again, of fungal-organic (table 1). Plant α-diversity increased significantly with MAT, but also increased with mean annual precipitation (MAP; table 1a). Fungal-organic α-diversity was not correlated to either climatic variable, but

instead declined significantly with increasing ECEC (table 1b). For both mineral horizon measures (fungal and bacterial), the only variable with any significant effect was MAT (table 1c, 1e). Bacterial-organic α-diversity was also positively affected by MAT, and additionally by resin-P (table 1d). Full models with all six variables showed the same qualitative results (table S3). In summary, temperature (MAT) had a nearly-universally significant positive effect on α-diversity, but precipitation (MAP), ECEC and resin-P were all also relevant for certain biotic group-soil horizon combinations.

Correlations between α-diversity of different groups. Plant α-diversity was most strongly positively correlated with that of bacteria α-diversity, especially in the organic horizon (r = 0.83; table S4). The coupling of plant and bacterial α-diversity also appeared to be more conserved than for plant and fungal α-diversity: the ratio in the Shannon diversity index for plants:bacteria varied with elevation by less than half that for plants:fungi, in both mineral and organic horizons (figure 3). There were also strong positive correlations between α-diversity for the two soil horizons for bacteria (r = 0.81), but not for fungi (r = 0.30). Overall, the fungal organic α-diversity showed the weakest coupling to any of the other measures (table S4).

Elevation patterns in β-diversity of different groups. The composition of plant, bacterial and fungal communities differed with elevation (differences in β-diversity; all comparisons by PERMANOVA; $p < 0.001$; figure 4), were characterised by exponential relationships whereby community compositional dissimilarity tended towards a maximum (dissimilarity = 1) with increased elevational separation (figure 4). Fungi exhibited the largest compositional dissimilarities of communities with elevation, followed by plant and then bacteria communities. The β-diversity of bacteria and fungi also differed between organic and mineral horizons (figure S2), although fungi differed to a lesser extent than bacteria (all comparisons by PERMANOVA; $p < 0.001$). The differences in soil microbial *β-diversity*

with elevation were reflected by shifts in dominant phyla (figure S3). 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* (figure S3a). For fungi, increased elevation was associated with increased dominance of Ascomycota (*Archaeorhizomycetes*, *Leotiomycetes*), Basidiomycota (*Microbotryomycetes*), and decreased dominance of other Ascomycota (*Sodariomycetes*, *Dothideomycetes*, *Eurotiomycetes*) and Glomeromycota (figure S3b; table S5). The β-diversity patterns observed for bacteria and fungi were correlated with those observed for plants (figure 4). Patterns in ß-diversity were correlated between plants and bacteria (organic horizon $\rho = 0.81$; mineral horizon $\rho = 0.88$) and plants and fungi (organic horizon $\rho = 0.67$; mineral horizon $\rho = 0.79$; by Mantel tests; $p < 0.001$ for all comparisons). Thus, plants and several major taxonomic groups of both bacteria and fungi showed clear and correlated changes in composition with elevation.

Effects of climate and edaphic variables on β-diversity. As with α-diversity, MAT was the strongest correlate of patterns in β-diversity. MAT was the most significant parameter in multivariate models for β-diversity of plants, bacteria in both organic and mineral horizons, and fungi in mineral horizons (table 2). There were additional correlations between the β-diversity of bacteria and fungi, and dissimilarity matrices of organic nutrient concentrations and their ratios; these were stronger in the organic compared to mineral horizons (figure S4). Nutrients other than N and P were also correlated with β-diversity, including K for plants and Na for bacteria (table 2). Soil pH affected bacterial β-diversity, but not fungal β-diversity (table 2).

Soil β-diversity and function. The activities of seven soil enzymes decreased with increased elevation but at different rates, and independently of differences in ambient

295 temperature (figure S5). These patterns reflected responses in the microbial community to
296 shifts in substrate availability in the soil. For example, relative microbial investment into
297 different enzymes shifted with increased elevation, from enzymes that degrade P- to N-
298 containing organic compounds (Nottingham et al. 2015a). Strong relationships between the
299 differential activity of these seven enzymes and differences in β-diversity were found for
300 bacteria ($\rho = 0.75$) and fungi ($\rho = 0.74$) in organic horizons (figure S6; by Mantel tests*;* $p <$
301 0.001 for all comparisons).

302 **4. Discussion**

303 Overall, our results demonstrate a fundamental role for environment, principally temperature,
304 in co-ordinating the diversity and community composition of plants, soil bacteria and fungi
305 along an extensive 3.5 km elevation gradient in tropical forest. For all three biotic groups,
306 species richness (α-diversity) declined as elevation increased, and the compositional
307 dissimilarity of communities (β-diversity) increased with increased elevation difference
308 between communities, although the changes in plant α-diversity were larger than in bacteria
309 and fungi (figures 2, 3). While environmental filtering at large geographic scales has been
310 suggested to shape community composition for plants, soil bacteria and fungi independently
311 (Tedersoo et al. 2014, Prober et al. 2015), this has not been reported before for both α-
312 diversity and β-diversity and across all three biotic groups together. Fundamentally,
313 temperature, and to a much lesser extent rainfall and edaphic properties, were strongly
314 associated with variation in plant, bacterial and fungal α-diversity (from linear models; table
315 1) and β-diversity (from multivariate models; table 2).

316 The role of temperature in determining microbial β-diversity is also illustrated by
317 shifts in the relative abundance of specific taxonomic groups. For example, there was an
318 increased relative abundance of *Acidobacteria* and the fungi *Archaerhizomycetes* with

319 increased elevation, but a decreased relative abundance of Actinobacteria and
320 *Alphaproteobacteria* (figure S3). These major taxonomic groups have been associated with
321 oligotrophic (Acidobacteria, *Archaerhizomycetes*) and copiotrophic (Actinobacteria,
322 *Alphaproteobacteria*) life history strategies, respectively (Fierer et al. 2007, Rosling et al.
323 2011), which is consistent with evidence for increased energy limitation at higher, cooler
324 elevations (Bruijnzeel et al. 2011, Nottingham et al. 2015a), favouring slower growth. The
325 high relative abundance of the Ascomycota, *Archaerhizomycetes* at higher elevations (figure
326 S3) is of particular interest because this class of fungus was discovered only recently and
327 their global distribution is poorly understood, partly because many previous analyses failed to
328 identify them due to amplification biases (Rosling et al. 2011). They were recently identified
329 in a range of global biomes, but generally represented <1% of relative abundance [6], which
330 contrasts with their high abundance in our upper montane forest sites (26%; figure S1B).
331 They are understood to be typically oligotrophic and root-associated fungi (Choma et al.
332 2016), colonizing typical EM fungal habitats (Rosling et al. 2011). This important class of
333 fungi, which until very recently was unknown, are a major component of the fungal biomass
334 in these tropical montane forests.

335 Temperature was also the principal correlate of plant α-diversity (table 1) and β-
336 diversity (table 2). Temperature has previously been shown to be a major determinant of tree
337 community composition across this transect (Rapp et al. 2012), and up-slope movement of
338 tree species' lower-range limits has been observed under recent climatic warming (Duque et
339 al. 2015). Patterns in plant species composition and richness on tropical mountains are
340 thought to be driven mainly by the effect of geographically narrow temperature ranges on
341 niche separation (by directly affecting metabolism and indirectly affecting resource
342 availability), further constrained by land area, lithology and disturbance history (Janzen 1967,
343 Colwell et al. 2008). Although the high landslide activity and soil erosion in the humid

344 Eastern Andean Cordillera (Clark et al. 2013) may be significant factors in constraining
345 diversity at higher elevations in this region, our study identifies a central underlying role for
346 temperature.

347 Diversity gradients were steeper for plants compared to microorganisms (figures 2-3),
348 which is consistent with the widespread view that microorganisms are more cosmopolitan
349 than plants in their distributions (Martiny et al. 2006). Analogous plant/microbial diversity
350 relationships have been shown along latitudinal gradients where plant/microbial species
351 richness ratios decrease with distance from the equator (Tedersoo et al. 2014, Zhou et al.
352 2016). Our data indicate a stronger coupling between the α-diversity of plants and bacteria
353 compared to fungi (figure 3; table S4), but a stronger coupling between the β-diversity of
354 plants and fungi than for bacteria (figure 4). The stronger coupling between the β-diversity of
355 plants and fungi can be explained by coordinated shifts in the presence of obligate plant hosts
356 among sites for symbiotic fungi (Geml 2017); which can also explain the absence of a clear
357 elevation pattern in fungal α-diversity in organic soil horizons (figure 4). Consistent with this
358 idea, correlations between plant and fungal β-diversity alongside high variation in α-diversity
359 patterns among specific fungal phyla (especially those that form plant-associations), have
360 been observed across elevation gradients in a range of ecosystems (Geml et al. 2014, Merckx
361 et al. 2015, Looby et al. 2016, Geml 2017, Geml et al. 2017). For example, along other
362 elevation gradients, the presence of EM and endophytic fungal hosts explained correlations in
363 plant and fungal β-diversity (Geml et al. 2014) and opposing α-diversity patterns have been
364 observed for AM and EM fungi (Geml et al. 2017, Kivlin et al. 2017). The lack of clear
365 relationship between temperature and α-diversity we observed for the distinct fungal
366 communities in organic horizons (figures 3, S2), may therefore reflect a stronger signal of
367 plant-host associations on total fungal α–diversity.

368 There was a secondary role for other environmental and edaphic properties in shaping
369 these diversity patterns (tables 1, 2, S3; figures S4, S6), in addition to the main effect of
370 MAT. For α-diversity, cation exchange capacity explained significant variation of fungal α-
371 diversity in organic horizons, while mean annual precipitation and soil pH explained minor
372 amounts of variation in α-diversity of plants and bacteria (table 1). For β-diversity, there were
373 secondary influences of nutrient ratios on microbes (C:N and C:P) and K on plants (table 4).
374 Our data suggest that this influence of edaphic properties on microbial α- and β-diversity is
375 more significant for fungal α-diversity and in organic horizons (tables 2, S3). Fungi are the
376 primary decomposers of plant-derived lignocellulosic biomass and the upper part of the soil
377 profile is where decomposition processes reflect the early stages of carbohydrate polymer
378 breakdown. Thus, elevation-related shifts in plant litter chemistry (van de Weg et al. 2009,
379 Salinas et al. 2010), which are known to affect soil microbial community composition (Orwin
380 et al. 2010, de Vries et al. 2012, Fanin et al. 2014), may determine fungal α-diversity patterns
381 in organic horizons, and be an additional determinant of fungal β-diversity and its coupling
382 with plant β-diversity.

383 Multiple lines of evidence suggest an influence of plant organic matter inputs on soil
384 microbes, where these inputs are in turn determined by temperature effects on plant
385 communities and production (van de Weg et al. 2014), for example: (i) the large difference in
386 microbial diversity (α and β) between organic and mineral soil horizons (figures S1, S2); (ii)
387 the stronger correlations between microbial β-diversity and nutrients in organic horizons
388 compared to mineral horizons (table 2, figure S4); (iii) the overall strong correlation between
389 plant and soil microbial diversity (table S4, figure 3); (iv) the correlation between soil
390 microbial β-diversity and enzymatic activity, indices of organic nutrient degradation
391 (Nottingham et al. 2015a) (figure S6); (v) fungal α-diversity in organic horizons significantly
392 increased above the treeline, coinciding with an abrupt change in plant organic matter inputs

393 from vegetation dominated by grassland (figure 2). Laboratory incubations of soils from this
394 transect (Whitaker et al. 2014) and studies from tropical forest in French Guiana (Fanin et al.
395 2011, Fanin et al. 2014), also support the link between differences in microbial community
396 composition and organic matter inputs and their rate of degradation. Together these findings
397 point towards a relationship between the high soil microbial diversity in tropical forests and
398 plant organic matter inputs to soil, through the high inter- and intra-species chemical diversity
399 in leaf litter.

400 Our results, from a 3.5 km elevation range, contrast with findings from studies of
401 elevation gradients that examined plant and microbial α-diversity and did not find such strong
402 α-diversity correlations (Bryant et al. 2008, Fierer et al. 2011, Shen et al. 2013, Geml et al.
403 2014, Shen et al. 2014, Singh et al. 2014). The fundamental temperature-microbial diversity
404 relationships we have observed here were likely obscured in previous studies by the
405 confounding influence of wider natural among-site variation in soil pH, soil moisture, plant-
406 host distributions (for fungi, in particular) and, in some instances, by insufficient sampling
407 intensity or elevation range. For example, variation in bacteria diversity along a 1850 m
408 elevation gradient in South Korea was related to the large variation in rainfall (1713 – 3743
409 mm) and soil pH (3.7 – 5.8) (Singh et al. 2014); large variation in rainfall (280 – 3280 mm)
410 and soil pH also explained microbial diversity along a 950 m elevation gradient in Hawaii
411 (Peay et al. 2017). Soil pH effects on fungal α-diversity along mountain gradients have also
412 been demonstrated (Geml 2017), including a positive effect on the α-diversity of AM fungi
413 along a large gradient in subtropical forest where soil pH varied widely (3.8 – 7.2) (Geml et
414 al. 2014). The majority of fungal diversity studies on mountain gradients have focussed on
415 specific phyla, reporting high variation in α-diversity patterns (Geml et al. 2014, Merckx et
416 al. 2015, Looby et al. 2016, Geml 2017, Geml et al. 2017) and strong associations with plant-
417 host distributions such as with AM and EM-fungal associated communities (Kivlin et al.

418 2017); as previously outlined, these factors can partly explain differences in fungal α-
419 diversity patterns in organic and mineral horizons in this study. The importance of sampling
420 intensity is demonstrated by the contrast between findings from this study of 14 sites with an
421 earlier report from six locations along the same Andean transect where no elevation gradient
422 in soil bacterial α-diversity was found (Fierer et al. 2011): if we reduce our dataset to include
423 only those sites represented in the earlier study, no strong elevation trends are apparent
424 (figure S7). Similarly, these factors may have accounted for the lack of clear patterns in
425 bacterial diversity for two temperate–zone elevation transect studies which sampled only six
426 locations over 1670 m in Northeast China (Shen et al. 2014), and five locations over 920 m in
427 the Rocky Mountains, the latter indicating a single-taxon increase with elevation, but no
428 community-wide trend (Bryant et al. 2008). Last, the detection of these elevation diversity
429 patterns may also depend on the length and, therefore, temperature range of the transect. For
430 example, the absence of bacterial diversity patterns along a 900 m gradient in tropical
431 montane forest in Hawaii may have been because the 5^{o}C temperature difference did not
432 affect plant community composition (Selmants et al. 2016). In contrast, the temperature-
433 driven diversity patterns in bacteria and fungi demonstrated for this large Peruvian gradient
434 (20^{o}C temperature difference) resulted, in part, from indirect temperature effects on plant
435 communities – thus leading to correlated diversity patterns among these three biotic groups.

436 This elevation gradient study in the Peruvian Andes demonstrates how temperature
437 fundamentally shapes plant, bacterial and fungal diversity in tropical forests, whether directly
438 for each group, or indirectly for microbial groups through temperature effects on plant
439 communities and production. Consistent trends in both α- and β-diversity were observed
440 across the principal organismal groups of plants, bacteria and fungi, suggesting that stronger
441 interactions occur among these groups than has been recognised previously. The role of
442 temperature in driving these co-ordinated patterns was revealed by the occurrence in our

study transect of constrained variation in soil pH and moisture, and by intensive sampling across space, and in separate soil horizons. We suggest that this relationship is often obscured across unconstrained environmental gradients often associated with differences in elevation and latitude (Bryant et al. 2008, Tedersoo et al. 2014), and its detection is further hindered by shallower diversity gradients for soil microbes compared to plants (figures 2-3) (Tedersoo et al. 2014, Zhou et al. 2016). Our findings imply that, where other influences such as soil pH and moisture remain relatively constrained, anticipated future temperature change will have significant co-ordinated impacts on the identity and functioning (above- and below-ground) of tropical biota.

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Table 1. Final models of effects of climatic and edaphic parameters on α-diversity in the five groups. Final models after removal of all non-significant variables: linear model for plants (n = 13) and linear mixed models for fungi/bacteria (with site as random effect; n = 42). MAT: mean annual temperature; MAP: mean annual precipitation; ECEC: cation exchange capacity; resinP: resin-extractable P (for full models with all six variables for each measure of α-diversity, see table S3). 'Prop. variance' gives the proportion of variance explained by each fixed effect; 'Marginal R^2' that explained by all the fixed effects together; conditional R^2 that explained by both fixed and random effects (see Methods).

(a) Plants	Parameter	SE	t	p-value	Prop. variance
(Intercept)	1.312	0.179	7.324	0	
MAT	0.108	0.009	12.29	0	0.821
MAP	2.393×10^{-4}	0.438×10^{-4}	5.461	0	0.119
R^2	0.940				
(b) Fungal organic	Parameter	SE	t	p-value	
(Intercept)	5.904	0.158	37.449	0	
ECEC	-0.012	0.003	-3.823	0.002	0.385
Random effects variance					
Site	0.040				
Residual	0.066				
Marginal R^2	0. 385	Conditional R^2	0. 619		
(c) Fungal mineral	Parameter	SE	t	p-value	
(Intercept)	4.834	0.16	30.201	0	
MAT	0.034	0.01	3.382	0.004	0.342
Random effects variance					
Site	0.037				
Residual	0.049				
Marginal R^2	0.342	Conditional R^2	0. 627		
(d) Bacterial organic	Parameter	SE	t	p-value	
(Intercept)	8.056	0.247	32.64	0	
MAT	0.048	0.013	3.645	0.003	0.575
resinP	-2.33×10^{-3}	-0.58×10^{-3}	-3.972	0.001	0.199
Random effects variance					
Site	0.057				
Residual	0.029				
Marginal R^2	0. 774	Conditional R^2	0. 922		
(e) Bacterial mineral	Parameter	SE	t	p-value	
(Intercept)	8.213	0.19	43.2	0	
MAT	0.031	0.012	2.568	0.022	0.294
Random effects variance					
Site	0.071				
Residual	0.013				
Marginal R^2	0. 294	Conditional R^2	0. 889		

672 **Table 2. The effects of environmental and edaphic variables on plant, bacterial and**
673 **fungal β-diversity, determined by multivariate correlation models.** The final models were
674 determined by step-wise selection to determine which resemblances matrices for 47 initial
675 predictor variables best describe community composition dissimilarity matrices. Significance
676 of individual parameters in each model were determined by Mantel tests between β-diversity
677 and the specific variable, shown in parentheses. Values are correlation coefficients and *** p
678 < 0.001, ** p < 0.01, p < 0.05, ns = not significant.

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	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

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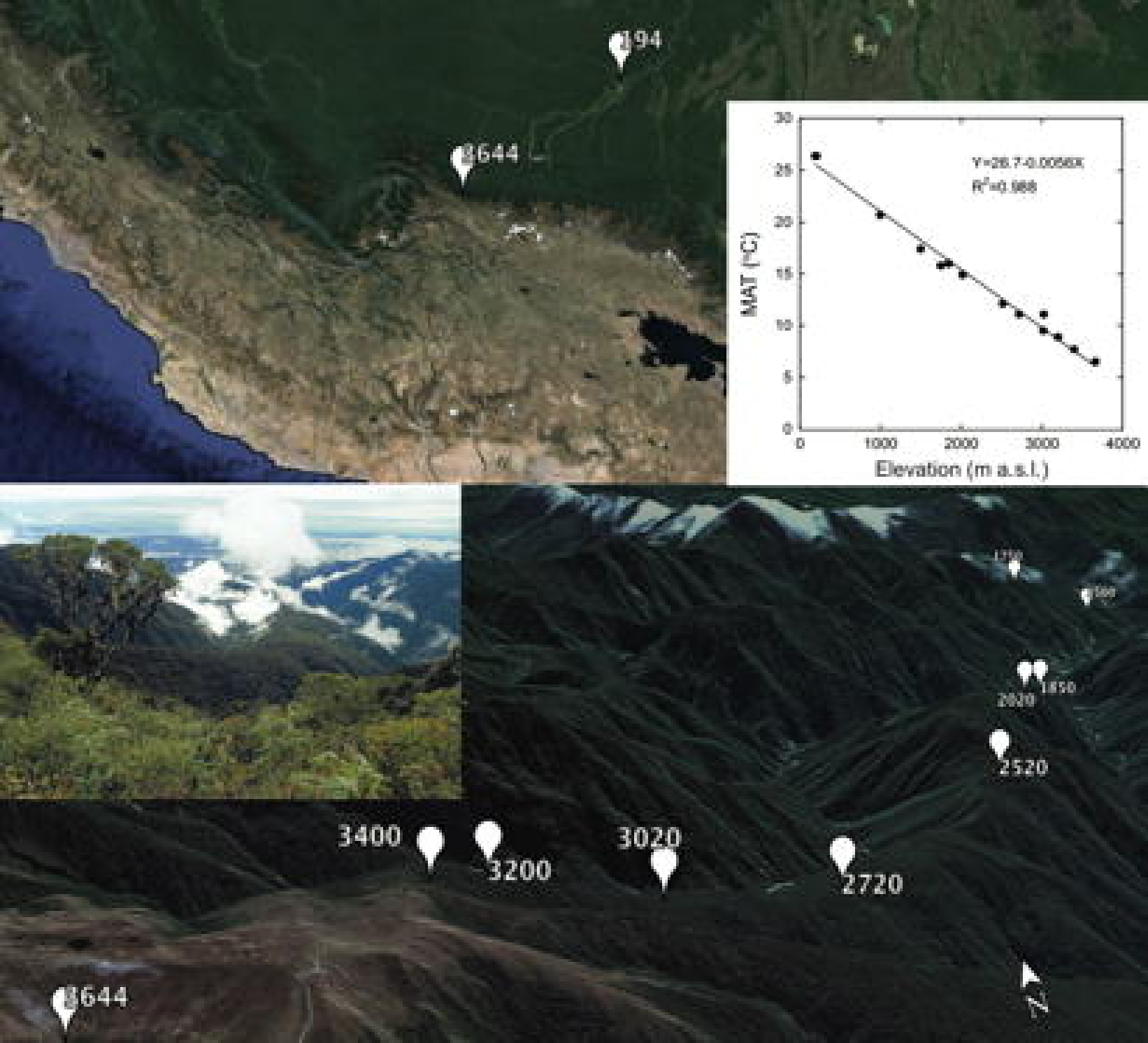
Figure legends

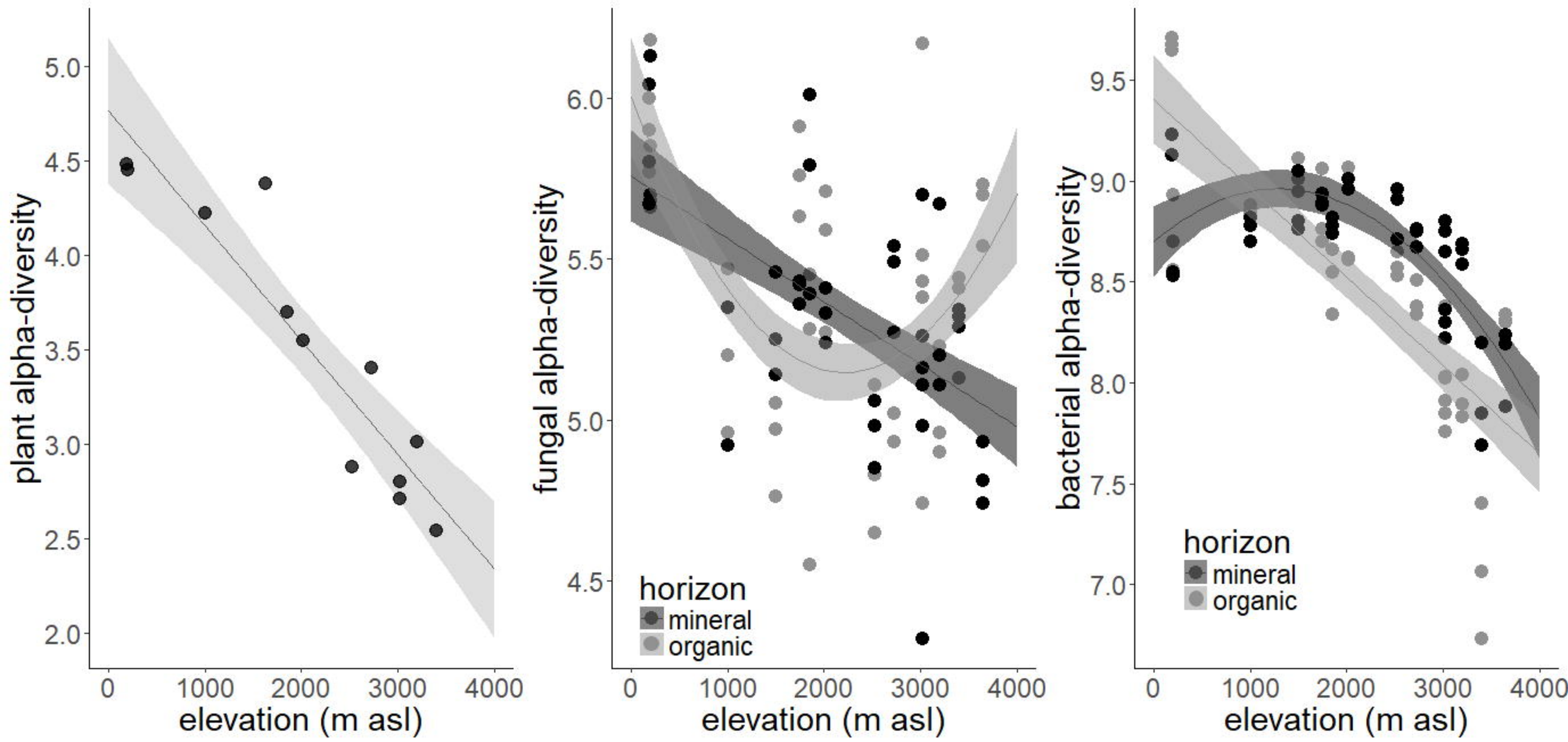
Figure 1. The Kosñipata elevation transect, Manu National Park, Peru. The top panel shows the highest (3644 m a.s.l.) and lowest elevation (194 m a.s.l.) sites and the relationship between elevation and mean annual temperature (MAT). The bottom panel shows all sites from 3644 m a.s.l. to 1500 m a.s.l. viewed facing approximately northeast from the top of the transect and a photograph of the transect of the same view.

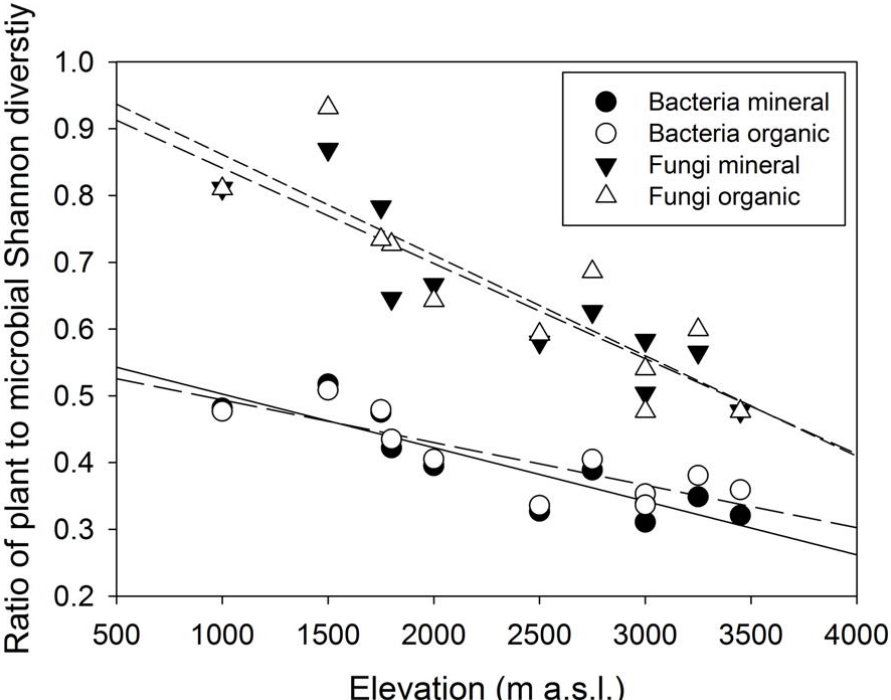
Figure 2. Changes in α-diversity with elevation ('elev', in m a.s.l.) in plants, fungi and bacteria. Fungi and bacteria were sampled from both the organic and the mineral soil horizon, and each site is represented by three data points. Note the different scales on the y-axes. The solid lines and confidence intervals show predicted relationships and 95% confidence intervals from models equivalent to those shown in table S2 but excluding quadratic terms where they were non-significant. i.e. for the plants, fungal-organic and bacterial-mineral groups.

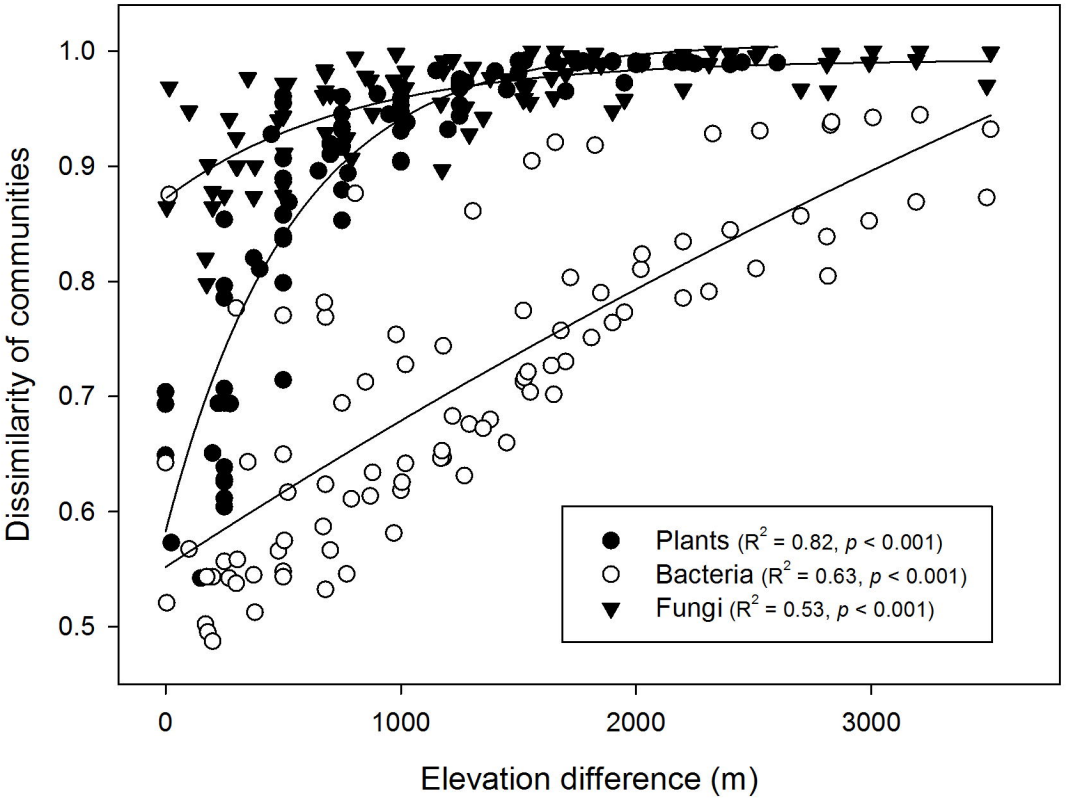
Figure 3. The relationships between the ratios of plant to bacterial and plant to fungal α-diversity and elevation, in organic and mineral soil horizons. Regression lines are shown with increasing number of dashes for bacterial mineral (solid line), bacterial organic, fungal mineral and fungal organic (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 4. The relationship between ß-diversity of plants, bacteria and fungi (dissimilarity of communities) with elevation difference. ß-diversity for all groups differed with elevation (plants: $p < 0.001$, F = 79.2, DF = 19; bacteria: $p < 0.001$. F = 4.5, DF = 69; fungi: $p < 0.001$, F = 3.3, df = 83; by PERMANOVA). Soil microbial data are shown for organic soil horizons (there were consistent patterns in mineral horizons). The overall decline with increased elevation indicates increased dissimilarity in ß-diversity between sites with greater difference in elevation. Elevational declines were fitted with exponential models [y = a[1-exp(-bx)]; with parameter estimates for bacteria (a = 1.27, 0.001), fungi (a = 0.12, b = 0.0013) and plants (a = 0.424, b = 0.0019)].


3644
Y=28.7-0.0056X
R²=0.988
MAT (°C)
Elevation (m a.s.l.)
0
5
10
15
20
25
30
0
1000
2000
3000
4000
1850
2820
2520
3400
3200
3020
2720
3644
N


plant alpha-diversity
5.0
4.5
4.0
3.5
3.0
2.5
2.0
0
1000
2000
3000
4000
elevation (m asl)
fungal alpha-diversity
6.0
5.5
5.0
4.5
horizon
mineral
organic
0
1000
2000
3000
4000
elevation (m asl)
bacterial alpha-diversity
9.5
9.0
8.5
8.0
7.5
7.0
horizon
mineral
organic
0
1000
2000
3000
4000
elevation (m asl)


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


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)