Title: The influence of aboveground and belowground species composition on spatial turnover in nutrient pools in alpine grasslands

Running title: β-diversity and nutrient pools

Xin Jing[1*], Case, M. Prager[2], Litong Chen[3], Haiyan Chu[4,5], Nicholas J. Gotelli[6], Jin-Sheng He[7,8], Yu Shi[4,5,9], Teng Yang[4,5], Biao Zhu[7], Aimée T. Classen[2], Nathan J. Sanders[1,2]

[1]Natural History Museum of Denmark, Copenhagen, Denmark

[2]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA

[3]Key Laboratory of Adaptation and Evolution of Plateau Botany, Northwest Institute of Plateau Biology, Chinese Academy of Science, Xinning Road No 23, Xining 810008, China

[4]State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, 71 East Beijing Road, Nanjing, 210008, China

[5]University of Chinese Academy of Sciences, Beijing, 100049, China

[6]Department of Biology, University of Vermont, Burlington, VT 05405, USA

[7]Institute of Ecology, College of Urban and Environmental Sciences, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing 100871, China

[8]State Key Laboratory of Grassland Agro-Ecosystems, and College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou, 730000, Gansu, China

[9]State Key Laboratory of Crop Stress Adaptation and Improvement, School of Life Sciences, Henan University, Kaifeng, Henan, China

***Author for correspondence:**

Xin Jing, E-mail: jingxin0123@gmail.com

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/GEB.13442

Natural History Museum of Denmark, Universitetsparken 15, DK-2100, Copenhagen, Denmark

Biosketch: We are a group of researchers interested in the spatial distribution of above- and belowground species composition and the linkages of biodiversity and ecosystem functioning.

Author contributions: NJS, XJ, ATC, J-SH, BZ, CMP, and NJG developed the research questions. XJ analyzed the data with inputs from NJS, NJG and CMP. XJ, LC, HC, J-SH, YS and TY collected data. XJ wrote the first draft of the paper with contributions from all authors.

Acknowledgements: We thank the members of A. Classen's lab and Wenting Feng for helpful comments and discussions. We thank Bonnie Waring and two anonymous reviewers for helpful comments that improved the manuscript. This work was supported by a Semper Ardens grant from the Carlsberg Foundation (N.J.S.).

Data availability: Soil bacterial sequence data have been deposited in the DDBJ sequence read archive under accession number DRA001226 and soil fungal sequence data have been deposited in the European Nucleotide Archive under the accession number PRJEB16010. The data and code supporting these results are publicly available in the Zenodo repository (https://doi.org/10.5281/zenodo.5644360).

Competing interests: The authors declare no competing interests.

DR. XIN JING (Orcid ID : 0000-0002-7146-7180)

DR. LITONG CHEN (Orcid ID : 0000-0002-9797-296X)

PROFESSOR HAIYAN CHU (Orcid ID : 0000-0001-9004-8750)

DR. BIAO ZHU (Orcid ID : 0000-0001-9858-7943)

Article type : Research Article

Title: The influence of aboveground and belowground species composition on spatial turnover in nutrient pools in alpine grasslands

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Abstract

Aim: An important research question in ecology is how climate and the biodiversity of aboveground plants and belowground microbiomes affect ecosystem functions such as nutrient pools. However, little is studied on the concurrent role of above- and belowground species composition in shaping the spatial distribution patterns of ecosystem functions across environmental gradients. Here, we investigated the relationships between the taxonomic composition of plants, soil bacteria and soil fungi and spatial turnover in nutrient pools, assessed how species composition-nutrient pool relationships were mediated by contemporary climatic conditions.

Location: Qinghai-Tibetan Plateau.

Time period: Current.

Major taxa studied: Plants, soil bacteria and soil fungi.

Methods: We surveyed plant assemblages, sampled the taxonomic composition of soil bacteria and soil fungi, and measured plant- and soil-mediated nutrient pools at 60 alpine grasslands on the Qinghai-Tibetan Plateau. Using Mantel tests, structural equation models and general linear models, we investigated the relative importance of the taxonomic composition of plant, soil bacterial, and soil fungal communities on the spatial turnover of alpine grassland nutrient pools.

Results: We found that the taxonomic composition of plant, soil bacterial, and soil fungal communities was associated with local climate. However, the effects of local climate on the spatial turnover of plant- and soil-mediated nutrient pools were mainly indirect and mediated through plant and soil bacterial species composition, but not through soil fungal species composition. We further found that the replacement component of soil bacterial β-diversity and the richness difference of plant β-diversity were the direct predictors of nutrient pools in the alpine grasslands.

Main conclusions: These results highlight that belowground bacterial composition together with aboveground plant species composition are related to spatial turnover in nutrient pools, perhaps even driving it. Conserving above- and belowground biodiversity may therefore safeguard the impacts of local climate on the functions of climate-sensitive alpine grasslands.

Keywords: Above- and belowground linkages, beta-diversity, Climate change, Dispersal limitation, Ecosystem functions, Environmental selection, Naturally assembled communities, Spatial turnover

1 | Introduction

Biodiversity varies from place to place: the number of species at two sites might differ (i.e., there is variation in local diversity, hereafter α-diversity), and such difference in aboveground plants and/or belowground microbiomes influences ecosystem functions (Delgado-Baquerizo et al., 2020; Schmid et al., 2009; Tilman, Isbell, & Cowles, 2014; van der Plas, 2019). Similarly, the identities of species might vary from place to place (i.e., there is variation in species composition, hereafter β-diversity) (Whittaker, 1972), and that variation in above- and/or belowground species composition might also

influence ecosystem functions (Burley et al., 2016; Mori, Isbell, & Seidl, 2018). However, there are few studies on the concurrent role of above- and belowground species composition in shaping the spatial distribution patterns of ecosystem functions across environmental gradients (e.g., Jing et al., 2015; Soliveres et al., 2016; Yuan et al., 2020).

Unlike those biodiversity experiments conducted at small scales (see summaries by Gonzalez et al., 2020), multiple biogeographic processes generate and maintain spatial variation in species composition among sites across environmental gradients (Engel et al., 2020; Peay, Kennedy, & Talbot, 2016; Wardle, 2016). For example, spatial variation in species composition can be determined by stochastic processes (e.g., historical contingencies, dispersal limitation) (Myers et al., 2013) or by differences in climate and soil properties (Nottingham et al., 2018). Importantly, to understand why β-diversity varies spatially, it is essential to know how the two processes lead to differences in species composition across environmental gradients (Kraft et al., 2011; Martiny, Eisen, Penn, Allison, & Horner-Devine, 2011). Such information will also strengthen our ability to predict the consequences of changes in species composition for ecosystem functions (Mori et al., 2018).

While a growing number of studies have begun to elucidate mechanisms governing spatial variation in β-diversity, in particular for belowground taxa (Martiny et al., 2006; Peay et al., 2016; Xu et al., 2020), ecosystem ecologists have only just begun to explore whether β-diversity influences ecosystem functions and services (Burley et al., 2016; Fukami, Naeem, & Wardle, 2001; Mokany, Burley, & Paini, 2013; Nottingham et al., 2018; Thompson et al., 2021; Winfree et al., 2018). Most studies to date have focused on the β-diversity of a single trophic level (typically primary producers) and its influence on spatial variation in individual ecosystem functions. Notably, only a few studies have explored how β-diversity in any trophic level influences spatial turnover in multiple ecosystem functions (i.e., differences in multiple ecosystem function among sites) (Mori et al., 2018). For example, Pasari, Levi, Zavaleta, and Tilman (2013) found that plant β-diversity reduced the variability, but not the mean, of multiple ecosystem functions in a local-scale grassland biodiversity experiment. When climate and soil properties were

statistically controlled for, Martinez-Almoyna et al. (2019) found that only the β-diversity of soil saprophytic fungi was significantly associated with the spatial turnover of multiple ecosystem functions along an elevational gradient. In contrast, Mori et al. (2016) found a highly positive effect of soil fungal β-diversity on spatial turnover in multiple forest ecosystem functions at landscape scale, while Jing et al. (2021) found spatial turnover in multiple grassland functions is driven more by plant β-diversity than by soil fungal diversity at a continental scale. While these studies do not provide consistent findings, there are strong indicators that some abiotic processes are responsible for shaping the biogeographic patterns of above- and belowground species composition that are also important for shaping the spatial distribution patterns of ecosystem functions across environmental gradients and spatial scales (Burley et al., 2016). Specifically, abiotic processes may directly influence the spatial turnover of ecosystem functions (Graham et al., 2014). For example, changes in climate and land use intensity have stronger effects on plant-mediated ecosystem functions than soil-mediated ecosystem functions (Peters et al., 2019). Meanwhile, abiotic processes may indirectly influence spatial turnover in multiple ecosystem functions through altering above- and belowground species composition (Barnes et al., 2016; Jing et al., 2021; Martinez-Almoyna et al., 2019; Yuan et al., 2020).

Here, we are most interested in β-diversity in both above- and belowground communities, why it varies spatially, and what its variation might mean for multiple ecosystem functions. Our aim is therefore to investigate the relative importance of aboveground and belowground species composition on the spatial turnover of plant- and soil-mediated nutrient pools [i.e., surrogates for ecosystem functions that is defined as stocks of energy/matter representing the long-term effects of biological processes (Garland et al., 2021)]. We assembled a regional-scale dataset from 60 sites in the alpine grasslands of the Qinghai-Tibetan Plateau. In previous studies, climate change and soil acidification, more so than human activities, have been identified as two important aspects of global change drivers in many alpine natural grasslands, including the ones studied here (Dong, Shang, Gao, & Boone, 2020; Yang et al., 2012). Climate change and soil acidification

also mediate the relationship between α-diversity and spatial variation in multiple ecosystem functions (Jing et al., 2015; Ma et al., 2010). In the present study, we extend our research to examine the linkages among plant, soil bacterial and soil fungal β-diversity to plant- and soil-mediated nutrient pools, and examine how those relationships depend on geography, climate, and soil pH. We ask three explicit questions: (i) Do soil bacterial and soil fungal taxa follow the same spatial patterns as plant species, and which factors - geography, climate, or soil pH - determine spatial variations in plant and soil microbial species composition? (ii) Do plant- and soil-mediated nutrient pools have geographic patterns and, if so, which factors - geography, climate, or soil pH - determine the geographic patterns? (iii) How do plant and soil microbial β-diversity compare to these abiotic factors in predicting the spatial turnover of plant- and soil mediated nutrient pools, and how these biotic and abiotic effects varied with spatial scale?

2 | Methods and Materials

2.1 | Study sites and data collection

We used an observational dataset from alpine grasslands on the Qinghai-Tibetan Plateau, China (Jing et al., 2015). In brief, soil sampling and plant community surveys were conducted at 60 sites in 2011 (Fig. S1). Three plots (1 m × 1 m) were established along a 100-m transect at each site. A total of 180 plots were surveyed over 40 days in the field between late July and late August. To track the peak-growing season of the alpine grasslands, field work generally followed a sampling order from low elevation sites to high elevation sites ranging from 2918 m to 5228 m above sea level. The sampling design thus minimizes the influence of seasonal differences from the sampling of early samples to the sampling of late samples on soil samples and plant community survey. In addition, study sites were selected to reduce the influence of grazing and other anthropogenic disturbances on soils and plant communities. The sampling sites were in one of the three typical alpine vegetation types (alpine meadow, alpine steppe, and desert steppe) and in one of the 11 soil types (brown pedocals, castanozems, chernozems, cold calcic soils, dark felty soils, felty soils, frigid calcic soils, frigid frozen soils, grey-brown desert soils, grey-cinnamon soils, and meadow soils; Genetic Soil Classification of China). The mean

annual temperature ranges from –5.6 to 3.5 ^{o}C and mean annual precipitation ranges from 110 to 552 mm yr^{-1} (data source: WorldClim version 2, http://www.worldclim.org).

Plant communities were surveyed along the 100-m transect at each site. Aboveground live plant biomass was collected from the same vegetation survey plot and dried at 60 ^{o}C to a constant mass. Since the vegetation surveys were conducted in the peak-growing season, we considered the aboveground live plant biomass as the annual aboveground productivity (Shi et al., 2013), which ranges from 25–321 g m^{-2} yr^{-1} (averaged over three plots per site) across the 60 sampling sites. Vascular plants were identified to species. Percent cover for each species was visually estimated within each 1 m × 1 m plot per site in the field. Plant species were pooled over three plots at each site at the stage of data analysis, which led to 2–28 species per site and 153 species across all of 60 sampling sites. Since the visually estimated plant cover data were subjective (Damgaard & Irvine, 2019), we used site-level plant species presence/absence data for all subsequent community data analysis. Plant N and P contents were measured using the samples of aboveground live plant biomass that were dried at 60 ^{o}C to a constant mass. Plant N (%) were measured using a CHN element analyzer (2400 II CHN element analyzer, PerkinElmer, MA, USA). Plant P (%) was measured by the molybdenum blue method using an ultraviolet-visible spectrophotometer (UV-2550, Shimadzu, Kyoto, Japan).

Soil samples (five to seven soil cores, 5 cm in diameter at 0–5 and 5–10 cm soil depths) were collected from the vegetation survey plot, homogenized, and shipped in portable refrigerators to the laboratory for later use. Since soils in 10% of the sampling sites were shallow (0–10 cm), we measured soil abiotic and biotic properties to the top 10 cm soil depth. Due to the costs of laboratory assays, soil total P, available N and microbial molecular sequencing were measured only in the top 5 cm soil depth. Specifically, soil pH was measured using a pH probe (S220, Mettler-Toledo, Switzerland) in a 1:5 ratio of air-dried soil to deionized water. Root samples were collected by soil cores (7 cm in diameter, six soil cores per plot on average) at 0–5 cm and 5–10 cm soil depths. Root samples from the same soil layers were pooled by plot and stored in nylon mesh bags, washed using a sieve (0.5 mm in mesh size) and air-dried in the field. Roots were then

oven-dried at 65 ^{o}C to a constant mass and weighed for biomass in the lab. Live root biomass (g m^{-2}) for each plot was calculated by taking the sum of root biomass density for the sampled top 10 cm soil depth and corrected with a ratio of 56% for dead root biomass (Jing et al., 2015). Soil total C was measured using a CHN element analyzer (2400 II CHN element analyzer, PerkinElmer, MA, USA). Soil inorganic C ($CaCO_3$) was measured using a Calcimeter (Eijkelkamp, Netherland). Soil organic C was calculated as the difference between soil total C and inorganic C. Soil total N and P (%) were measured using the same methods as the measurements of plant N and P. The density of soil organic C, soil total N and soil total phosphorus (i.e., carbon and nutrient stocks g cm^{-2}) was calculated taking into account soil depth, bulk density, carbon/nutrient concentration and the percentage of rock fraction (see Chen et al., 2017 for details of the estimation). Soil available inorganic and organic N (the sum of ammonium, nitrate and dissolved organic N) was measured using a TOC-TN analyzer (Shimadzu, Kyoto, Japan).

Soil DNA was extracted from 0.5 g soil samples (stored at –80 ^{o}C prior to DNA extraction) by using the FastDNA Spin kit (Bio 101, Carlsbad, CA, USA) according to the instructions of manufacturer and stored at –40 ^{o}C until sequencing analysis. The V4-V5 hypervariable regions of bacterial 16S rRNA genes were amplified using the universal primer sets: 515 forward (5′-GTGCCAGCMGCCGCGG-3′) with Roche 454 A pyrosequencing adapter and a unique 7 bp barcode sequence, and 907 reverse (5′-CCGTCAATTCMTTTRAGTTT-3′) with the Roche 454 B sequencing adapter. The ITS2 between the 5.8S and 28S rRNA genes were amplified for soil fungi using the universal primer sets: ITS3 forward (5′-GCATCGATGAAGA ACGCAGC-3′) and ITS4 reverse (5′-TCCTCCGCTTATTGATATGC-3′). A 50 μl PCR reaction mixture (25 μl 2 × premix (TaKaRa, Shiga, Japan), 0.5 μl 20 mM forward primer, 0.5 μl 20 mM reverse primer, 2 μl 25 ng μl^{-1} DNA template and 22 μl double sterile water) of 16S rRNA gene amplification was performed in triplicate under the following conditions: 30 cycles of denaturation at 94 ^{o}C for 30 s, annealing at 55 ^{o}C for 30 s, extension at 72 ^{o}C for 30 s and a final extension at 72 ^{o}C for 10 min. A 20 μl PCR

reaction mixture (0.4 μl FastPfu Polymerase (TransGen Biotech, Beijing, China), 2 μl 5 ng μl^{-1} DNA template, 0.8 μl 5 μM forward primer, 0.8 μl 5 μM reverse primer, 1.2 μl 20 mg l^{-1} TaKaRa BSA, 4 μl 5 × FastPfu buffer, 2 μl 2.5 mM dNTPs and 8.8 μl sterile water) of ITS2 rRNA gene amplification was performed under the following conditions: one cycle of initialization at 95 ^{o}C for 3 min, 38 cycles of denaturation at 94 ^{o}C for 30 s, annealing at 55 ^{o}C for 30 s, extension at 72 ^{o}C for 45 s and a final extension at 72 ^{o}C for 10 min. The triplicate PCR products of soil bacteria were combined and purified with a TaKaRa agarose gel DNA purification kit and quantified in a NanoDrop ND-1000 spectrophotometer (Thermo Scientific, Omaha, NE, USA). Different sequencing technologies were used to estimate the community composition of soil bacteria and soil fungi. Specifically, soil bacterial samples were sequenced on the Roche FLX454 pyrosequencing instruments at the Beijing Genomics Institute (BGI-Shenzhen, China), and soil fungal samples were sequenced on the Illumina MiSeq instruments (Illumina PE250, San Diego, CA, USA) at the Novogene Bioinformatics Technology Co., Ltd. (Beijing, China). Note that different sequencing technologies may lead to technical biases in quantifying bacterial and fungal communities (Ramirez et al., 2018).

Soil bacterial and fungal sequence data were processed using the Quantitative Insights Into Microbial Ecology (QIIME) pipeline (version 1.9.0) (Caporaso et al., 2010) following the protocols presented by Jing et al.(2015), Ladau et al.(2018) and Yang et al.(2017). In brief, soil bacterial sequences < 200 bp in length, average quality score < 25 and ambiguous characters were excluded. Sequences were then filtered to remove error sequences and chimeras using USEARCH algorithm (Edgar, 2010). The remaining sequences were assigned to cluster using UCLUST method (Edgar, 2010) and assigned to OTUs based on a minimum threshold of 97% similarity. All singletons were removed before soil bacterial community data analysis, which resulted in 65,874 OTUs and 926,609 sequences in total, 5,837 OUTs per site on average (min = 2,975 OTUs and max = 7,280 OTUs) and 15,443 sequences per site on average (min = 11,062 sequences and max = 23,602 sequences). Soil fungal sequences < 280 bp in length, average quality score < 30 and ambiguous characters were excluded. Flanking large ribosomal subunit (LSU) and 5.8S genes and chimeras were also removed using ITSx (version 1.0.11) (Bengtsson-

241 Palme et al., 2013) and UCHIME program (Edgar, Haas, Clemente, Quince, & Knight,
242 2011), respectively. The remaining sequences were assigned to cluster using UCLUST
243 method (Edgar, 2010) and assigned to OTUs based on a minimum threshold of 97%
244 similarity. All singletons were removed before soil fungal community data analysis,
245 which resulted in 14,207 OTUs and 11,576,489 sequences in total, 3,725 OUTs per site
246 on average (min = 2,722 OTUs and max = 4,767 OTUs) and 192,941 sequences per site
247 on average (min = 123,753 sequences and max = 341,014 sequences).
248
249 Mean annual temperature (BIO1) and mean annual precipitation (BIO12) were obtained
250 from the WorldClim bioclimatic dataset (version 2.0; available from
251 http://www.worldclim.org). The 30 arc-second resolution (~ 1 km at the equator) climate
252 data for the period of 1950–2000 were used to estimate the spatial variation in climate for
253 the 60 sampling sites. Climate data were extracted using the World Geodetic System
254 1984 (WGS-84).
255
256 **2.2 | Quantifying geographic and environmental distances**
257 We calculated pair-wise great circle geographic distance (unit, km) using the geographic
258 locations of sampling sites. Mean annual temperature and mean annual precipitation were
259 two main factors influencing spatial variation in plant and soil microbial α-diversity and
260 individual ecosystem functions in the study areas (Jing et al., 2015; Ma et al., 2010). We
261 used the two climate variables as indicators of climatic differences among sites. A third
262 variable (soil pH) was included to account for site differences in environmental
263 conditions for plant and soil microbial communities (Jing et al., 2021). We standardized
264 the three environmental variables by z-score (Peters et al., 2019). We calculated climatic
265 and soil pH distances using the Euclidean distance (i.e., the square root of the sum of
266 squared differences between environmental variables for any given two sites).
267
268 **2.3 | Quantifying β-diversity**
269 β-diversity in this study was defined as the directional species compositional turnover
270 along environmental gradients and was measured based on the pair-wise dissimilarity
271 between communities (Anderson et al., 2011). Soil bacterial and fungal community data,

i.e., the OTU table, were rarefied at 11,000 and 123,000 reads per sample, respectively. We first estimated total β-diversity using Sorensen index. It is a simple measure of differences in species composition between communities by considering the number of species common in two communities and the number of species unique to each community. We then additively decomposed the Sorensen β-diversity index (total β-diversity) into two complementary indices, i.e., richness difference (differences in species richness between communities) and replacement (species turnover/changes in species identity between communities along environmental gradients) (Legendre, 2014; Podani & Schmera, 2011). The beta.div.comp function (Legendre, 2014) was used to compute the Sorensen index, the richness difference, and the replacement of Sorensen index. Since the abundance-based β-diversity metric is commonly used in microbial ecology, we computed the Bray-Curtis dissimilarity for soil bacteria and soil fungi.

2.4 | Quantifying spatial turnover in nutrient pools

Eight indicators of ecosystem functions were selected. These indicators included four plant-mediated nutrient pools (i.e., aboveground plant biomass, root biomass, aboveground plant N and plant P) and four soil-mediated nutrient pools (i.e., soil organic C, soil available N, soil total N and soil total P). Note that these indicators are not direct measures of fluxes of energy and matter (e.g., decomposition, carbon sequestration, nitrification and nutrient recycling) that are often defined as true ecosystem functions (Farnsworth, Albantakis, & Caruso, 2017; Jax, 2005) and recommended to measure in the field of multifunctionality (Garland et al., 2021). However, the eight indicators of ecosystem functions considered are generally more associated with changes in biodiversity than these direct measures of fluxes of energy and matter (Schmid et al., 2009) and are often considered as important properties determining ecosystem functions in numerous studies (e.g., Allan et al., 2013; Hautier et al., 2018; Hu et al., 2021; Jing et al., 2015; Liu, Chang, Power, Bell, & Manning, 2021; Peters et al., 2019; Zhang et al., 2021) that were especially relevant to the net balance of inputs and outputs of energy and matter in the long term (Garland et al., 2021; Manning et al., 2018). In brief, the eight indicators were used to reflect basic nutrient pools of the alpine grasslands (Table S1). Here, we refer to these indicators as nutrient pools for simplicity, but we refer to the

303 synthetic review by Garland et al. (2021) for more insights into the debate and research
304 progress on selecting indicators for ecosystem functions (process rates, nutrient pools vs.
305 ecosystem properties). We calculated the pair-wise Euclidean distance to estimate the
306 spatial turnover of plant- and soil-mediated nutrient pools. Indicators of nutrient pools
307 were standardized by z-score prior to computing the Euclidean distance (Mori et al., 2016;
308 Peters et al., 2019). We assigned equal weights within groups of plant- and soil-mediated
309 nutrient pools because we found only strong autocorrelations among indicators of soil-
310 mediated nutrient pools, but not among indicators of plant-mediated nutrient pools or
311 between indicators of plant- and soil-mediated nutrient pools (Table S2). Since spatial
312 turnover in nutrient pools was derived from the Euclidean distance (i.e., the square root
313 of the sum of squared differences between nutrient pools for any given two sites), the
314 approach considered here cannot assess the compromises of the losses of some nutrient
315 pools and gains in others. In other words, investigators might use the schematic analysis
316 of diversity-function relationships to address the question whether two sites with high β-
317 diversity have higher overall functioning at different spatial scales (e.g., Box 1 in Mori et
318 al. (2018): functions provided at the plot vs. landscape levels).
319
320 **2.5 | Statistical analyses**
321 We used a distance approach (Tuomisto & Ruokolainen, 2006), i.e., simple Mantel tests
322 to examine the associations of geographic distance, climatic distance and soil pH distance
323 with above- and belowground β-diversity as well as the spatial turnover of plant- and
324 soil-mediated nutrient pools. To examine whether the associations of abiotic factors with
325 β-diversity were context dependent, we performed partial Mantel tests. For example, we
326 controlled the influences of climatic distance, soil pH distance or both when we assessed
327 the bivariate associations between geographic distance and β-diversity. We used the same
328 approach as above to assess the associations of abiotic factors and β-diversity with the
329 spatial turnover of plant- and soil-mediated nutrient pools. We used 9,999 permutations
330 for each Mantel test.
331
332 We used structural equation models (SEMs) to compare the direct and indirect effects of
333 biotic and abiotic factors on spatial turnover in nutrient pools. Two assumptions were

applied to the framework of SEM: (i) geographic, climatic and soil pH distances that are proxies for historical and contemporary environmental factors (Martiny et al., 2006; Shade et al., 2018; Xu et al., 2020) directly and indirectly affected plant- and soil-mediated nutrient pools through changes in plant and soil microbial β-diversity (Burley et al., 2016; Martinez-Almoyna et al., 2019); and (ii) soil microbial β-diversity was influenced by aboveground plant β-diversity (Leff et al., 2018; Prober et al., 2015). We excluded pathways that had nonsignificant direct effects on plant- or soil-mediated nutrient pools and pathways that had weak associations, e.g., soil pH distance and plant β-diversity. In addition, we included two residual correlations between soil bacterial and soil fungal β-diversity, and between plant- and soil-mediated nutrient pools. Since the indicators associated with plant- and soil-mediated ecosystem functions can be considered factors that drive plant and soil microbial diversity (van der Plas, 2019), we conducted an alternate SEM by switching the direction of pathways and examined the effects of plant- and soil-mediated nutrient pools on plant and soil microbial β-diversity. If the variation of β-diversity (i.e., R^2 values) increased substantially in the alternate SEM, we therefore expected that these plant- and soil-mediated nutrient pools influenced β-diversity and not the other way around. We performed the significance tests for path coefficients using a bootstrap procedure with 9,999 random sampling as presented by Martinez-Almoyna et al. (2019). Since the χ^2 statistic is not suitable for the evaluation of global model fits when the sample size is large (n = 1770 in this study), we considered four alternative indices, including Akaike information criterion (AIC, the lower, the better), comparative fit index (CFI > 0.90), root mean square error of approximation (RMSEA < 0.05) and standardized root mean square residual (SRMR < 0.10) (see summaries by Grace, 2020). All Mantel tests and SEMs were conducted using Sorensen index for plants and Bray-Curtis dissimilarity for soil bacteria and soil fungi because these metrics are more associated with spatial turnover in nutrient pools than the replacement and richness difference of Sorensen index (see Table S3 for sensitivity analysis).

To determine whether the effects of abiotic and biotic predictors on spatial turnover in plant- and soil-mediated nutrient pools varied with spatial scales, we used linear regression models with permutation tests. The linear regression models included geographic distance, environmental distance (i.e., climate and soil pH), and the replacement and richness difference components of plant, soil bacterial and soil fungal β-diversity. Since replacement is highly associated with richness difference (Legendre, 2014), we separately conducted the linear regression models for the two indices. To estimate the relative strength of predictors, variables were standardized by z-score. The procedure of linear regressions was performed by varying the spatial extent of investigated alpine grasslands from 20 km to 1000 km. In other words, the analysis was run on all sites at distances of 0-20 km, 0-40 km, 0-60 km, …, 0-1000 km.

All statistical analyses were performed in R version 3.6.1 (R Development Core Team, 2019) using data aggregated at site level, i.e., pooling species by sites or taking the mean of values for soil pH and indicators of nutrient pools at each site. We used permutations throughout all the statistical analyses to address the non-independent observations in distance matrices (Dietz, 1983). Climate data were extracted from the WorldClim database using the raster package (Hijmans, 2021). Geographic distance was calculated using the 'rdist.earth' function in the fields package (Furrer, Nychka, & Sain, 2015) and environmental distance and the spatial turnover of nutrient pools using the 'distance' function in the ecodist package (Goslee & Urban, 2007). The simple and partial Mantel tests were performed using the 'mantel' function in the ecodist package (Goslee & Urban, 2007), SEM using the lavaan package (Rosseel, 2012), and linear regression models using the lmPerm package (Wheeler, Torchiano, & Torchiano, 2016).

3 | Results

3.1 | Biogeography of plant, soil bacteria and soil fungi

Plant, soil bacterial and soil fungal β-diversity were all positively associated with geographic, climatic and soil pH distances (Fig. 1), suggesting that variation in soil microbial community composition is shaped by the same suite of factors considered in this study as that in plant communities. However, there were differences in the relative

394 importance of each of these abiotic factors. Specifically, climatic distance was
395 moderately correlated with plant β-diversity (Spearman correlation coefficient, hereafter
396 $\rho = 0.44$), soil bacterial β-diversity ($\rho = 0.48$) and soil fungal β-diversity ($\rho = 0.41$) (Fig.
397 1a). These bivariate associations were retained when geographic and soil pH distances
398 were statistically controlled (Fig. 1b). Furthermore, we found that soil pH distance was
399 moderately correlated with soil bacterial β-diversity ($\rho = 0.42$) but was weakly correlated
400 with plant ($\rho = 0.12$) and soil fungal β-diversity ($\rho = 0.16$) (Fig. 1a). When we controlled
401 the influences of geographic and climatic distances, the significant bivariate associations
402 were retained between soil pH and soil bacterial β-diversity, while the bivariate
403 associations became weak for plant β-diversity or soil fungal β-diversity (Fig. 1b). In
404 contrast, geographic distance was more correlated with soil fungal β-diversity than
405 climatic distance even though we controlled environmental covariates, i.e., differences in
406 climate and soil pH (Fig. 1a-b).
407
408 **3.2 | Geography of plant- and soil-mediated nutrient pools**
409 Plant- and soil-mediated nutrient pools were driven by geography, climate, and soil pH
410 (Fig. 2). However, the main factors influencing the geographic patterns of plant- and soil-
411 mediated nutrient pools were different. Specifically, we found that climatic distance was
412 weakly associated with plant- mediated nutrient pools while moderately associated with
413 soil-mediated nutrient pools (all eight indicators of nutrient pools, hereafter overall, $\rho =$
414 0.30; plant-mediated nutrient pools, $\rho = 0.17$; soil-mediated nutrient pools, $\rho = 0.30$; Fig.
415 2a), even if geographic distance and soil pH distance were statistically controlled for (Fig.
416 2.b). The associations between plant-mediated nutrient pools and geographic distance
417 were as strong as those with climatic distance (all cases, $\rho = 0.17$) (Fig. 2a-b). Finally,
418 soil-mediated nutrient pools was always more likely associated with soil pH distance than
419 with geographic and climatic distances (Fig. 2).
420
421 **3.3 | β-diversity and nutrient pool relationships**
422 We asked whether these abiotic factors - geographic, climatic and soil pH distances -
423 would alter the relationship between β-diversity and spatial turnover in nutrient pools. To
424 test this idea, we compared the effects of β-diversity on these plant- and soil-mediated

nutrient pools before (Fig. 3a) and after (Fig. 3b) controlling for geographic, climatic and soil pH distances. We found that plant β-diversity was moderately associated with the spatial turnover of overall and soil-mediated nutrient pools while weakly associated with plant-mediated nutrient pools (overall, $\rho = 0.35$; plant-mediated nutrient pools, $\rho = 0.20$; soil-mediated nutrient pools, $\rho = 0.38$; Fig. 3a). Soil bacterial β-diversity was also moderately associated with the spatial turnover of overall and soil-mediated nutrient pools while weakly associated with plant-mediated nutrient pools (overall, $\rho = 0.37$; plant-mediated nutrient pools, $\rho = 0.16$; soil-mediated nutrient pools, $\rho = 0.43$; Fig. 3a). These bivariate associations were retained when geographic, climatic and soil pH distances or their combinations were controlled for (Fig. 3b). Soil fungal β-diversity was only positively associated with soil-mediated nutrient pools when geographic, climatic and soil pH distances were simultaneously controlled for (Fig. 3b).

3.4 | The impacts of abiotic factors on β-diversity and nutrient pool relationships

Spatial turnover in plant-mediated nutrient pools was weakly correlated with spatial turnover in soil-mediated nutrient pools (residual correlation coefficient, $r = 0.12$) (Fig. 4). This result thus supports classifying plant- and soil-mediated nutrient pools separately, which suggests spatial turnover in plant-mediated nutrient pools are weakly associated with spatial turnover in soil-mediated nutrient pools. The structural equation model (AIC = 31,684) explained 23% and 6% of the variance in the spatial turnover of soil- and plant-mediated nutrient pools, respectively (Fig. 4; Table S4). Specifically, plant β-diversity had slightly stronger direct effects on both plant- (standardized path coefficient, $\beta_{std} = 0.13$) and soil-mediated nutrient pools ($\beta_{std} = 0.21$) than did soil bacterial β-diversity ($\beta_{std} = 0.07$ for plant-mediated nutrient pools and $\beta_{std} = 0.14$ for soil-mediated nutrient pools) or soil fungal β-diversity ($\beta_{std} = -0.06$ for plant-mediated nutrient pools) (Fig. 4; Table S4). In addition, the effects of plant β-diversity on soil bacterial β-diversity ($\beta_{std} = 0.41$; Fig. 4; Table S4) were greater than those on soil fungal β-diversity ($\beta_{std} = 0.31$; Fig. 4; Table S4). Soil bacterial β-diversity was moderately associated with soil fungal β-diversity ($r = 0.47$; Fig. 4). We found that the alternate structural equation model did not substantially increase the R^2 values for plant and soil microbial β-diversity (Fig. S2). However, the alternate structure equation model had a higher AIC value (AIC = 31,698

456 vs. 31,684) (Tables S4 and S5) suggesting that plant- and soil-mediated nutrient pools
457 were more likely driven by β-diversity.
458
459 We found that the magnitudes of the effects of β-diversity on spatial turnover in plant-
460 and soil-mediated nutrient pools varied across spatial scales (Fig. 5). At relatively small
461 scales (e.g., < 200 km), plant replacement was a more important (or at least as important)
462 predictor of spatial turnover in plant-mediated nutrient pools than was soil bacterial
463 replacement. At relatively large scales, we found moderately strong effects of soil
464 bacterial replacement on spatial turnover in overall and soil-mediated nutrient pools
465 while weak effects of soil bacterial replacement on spatial turnover in plant-mediated
466 nutrient pools (Fig. 5; Table S6). Further, we found that richness difference was the less
467 important driver of spatial turnover in plant- and soil-mediated nutrient pools than
468 replacement, geographic, climatic and soil pH distances (Figs. 5 and S3). However, we
469 found a stronger effect of plant richness difference than soil microbial richness difference
470 on spatial turnover in plant- and soil-mediated nutrient pools at relatively large scales
471 (e.g., > 200 km) (Fig. 5; Table S6).
472

473 **4 | Discussion**

474 This study investigates how above- and belowground species composition concurrently
475 connected with spatial turnover in plant- and soil-mediated nutrient pools in the alpine
476 grasslands on the Qinghai-Tibetan Plateau, and pinpoints changes in plant and soil
477 bacterial species composition that are directly associated not only with soil-mediated
478 nutrient pools, but also with plant-mediated nutrient pools. The abiotic factor most
479 consistently associated with the β-diversity of plants, soil bacteria and soil fungi was
480 climate, while the influences of climate on plant- and soil-mediated nutrient pools was
481 mostly indirect, and through changes in plant and soil bacterial species composition. We
482 discuss these findings in the context of plant and soil microbial biogeography with a
483 focus on species composition-ecosystem function relationships across environmental
484 gradients.
485

4.1 | Do soil bacterial and soil fungal taxa follow the same spatial patterns as plant species?

Overall, despite both macro- and micro-organisms exhibiting similar biogeographic patterns in β-diversity (Martiny et al., 2006; Shade et al., 2018), the processes that generate and maintain those biogeographic patterns depend on the taxa considered. Our results suggest that plant and soil microbial communities were not randomly distributed nor randomly assembled (De Laender et al., 2016; van der Plas, 2019). Put another way, species composition is similar when sites are close to one another or, regardless of distance between them, because they share similar environmental conditions such climate and soil pH. Among the three abiotic factors (geography, climate, and soil pH), we found that local climate consistently influenced the biogeographic patterns of aboveground plants and belowground microorganisms. This finding suggests that contemporary climatic conditions are one of the most important environmental filters causing changes in above- and belowground species composition in the alpine grasslands on the Qinghai-Tibetan Plateau. However, in addition to the impacts of climate, our findings have important implications for soil microbial communities. For example, we found moderately strong bivariate associations between soil bacterial β-diversity and differences in soil pH (Fig. 1). This results suggest that the ongoing soil acidification in many Chinese grasslands (Yang et al., 2012) may lead to dramatic shifts in soil bacterial community composition. However, soil fungal communities are less influenced by soil pH because of their high tolerance to changes in acidic conditions (Rousk et al., 2010). In contrast, geographic distance was highly associated with soil fungal β-diversity in addition to climatic distance (Fig. 1a-b). This suggests that the spatial turnover of soil fungal composition is more likely influenced by dispersal limitation than the spatial turnover of plant and soil bacterial community composition. Therefore, although the biogeographic patterns are similar among taxa examined in this study, the processes that generate above- and belowground communities are not the same. This incongruence has rarely been considered in studies of biodiversity and ecosystem function relationships that were implemented by simultaneously manipulating levels of above- and belowground biodiversity (Eisenhauer, 2011; Naeem, Thompson, Lawler, & Lawton, 1994; Scherber et al., 2010).

4.2 | Do plant- and soil-mediated nutrient pools have geographic patterns?

Our results highlight that those abiotic factors, e.g., climate and soil pH, were important for predicting the spatial variation in the turnover of plant- and soil-mediated nutrient pools in the Qinghai-Tibetan alpine grasslands. Previous work in the same alpine grasslands has shown that climate and soil properties were key predictors of plant aboveground productivity (Ma et al., 2010) and multiple grassland ecosystem functions (Jing et al., 2015). Unlike these studies, our work provides the first evidence that the magnitudes of the effects of abiotic factors on plant- and soil-mediated nutrient pools were different. For example, the spatial turnover of plant-mediated nutrient pools was influenced more by geographic and climatic distances than by soil pH distance. In contrast, soil-mediated nutrient pools were more associated with soil pH than with geographic distance. Taken together, these findings suggest that the factors that influence geographic patterns of plant-mediated nutrient pools were the same as those that influence patterns of plants and soil fungi, while those of soil-mediated nutrient pools were the same as soil bacteria. However, in the following discussion we show that the influences of abiotic factors on the spatial turnover of plant- and soil-mediated nutrient pools are mostly indirect.

4.3 | How do abiotic factors mediate the effects of β-diversity on spatial turnover in nutrient pools?

A recent meta-analysis reported that the effects of biodiversity (in this case, α-diversity) on ecosystem productivity remained strong after the effects of environmental covariates were controlled (Duffy, Godwin, & Cardinale, 2017). However, unlike the predictions of this meta-analysis, our work suggests that when more abiotic factors were controlled, the effects of plant and soil bacterial β-diversity on spatial turnover in nutrient pools became weaker (Fig. 3b), which is true for the effects of plant diversity (α-diversity) on aboveground plant productivity in the Qinghai-Tibetan grasslands (Ma et al., 2010). We found that the effects of covariates were particularly not negligible for soil fungal β-diversity. That is, the effects of soil fungal β-diversity on spatial turnover in plant-mediated nutrient pools disappeared when both geographic and climatic distances were

548 controlled (Fig. 3b). Our results therefore do not support the finding that the highly
549 positive associations of soil fungal β-diversity with spatial turnover in ecosystem
550 functions remained significant, which was found in a landscape-scale study in forest
551 ecosystems (Mori et al., 2016).
552
553 An increasing number of studies show that soil fungal and bacterial diversity consistently
554 and interactively promote a wide range of soil- and plant-mediated ecosystem functions,
555 such as decomposing organic matter and enhancing plant nutrient uptake and growth
556 (Delgado-Baquerizo et al., 2020; van der Heijden, Bardgett, & van Straalen, 2008).
557 However, contrary to our expectation, although soil fungal β-diversity was highly
558 correlated with soil bacterial β-diversity, soil fungal β-diversity had weak effects on both
559 spatial turnover in plant- and soil-mediated nutrient pools in the Qinghai-Tibetan alpine
560 grasslands (Fig. 4). One explanation is that large changes in soil fungal composition may
561 be associated with small changes in ecosystem functions, i.e., functional redundancy
562 (Martinez-Almoyna et al., 2019; Peay et al., 2016; Talbot et al., 2014). Previous work has
563 shown that functional redundancy may arise because of functional homogenization due to
564 disturbance by exotic species (Peay, Dickie, Wardle, Bellingham, & Fukami, 2013). Here,
565 however, functional homogenization was not one of the main driving factors because the
566 study sites are relatively undisturbed natural alpine grasslands with little documented
567 impacts of exotic species or direct impacts by humans (Jing et al., 2015). In the Qinghai-
568 Tibetan grasslands, belowground microorganisms generally adjust their activities to the
569 stressful environments, such as low annual temperature, high climatic seasonality, and
570 short growing season (Jing et al., 2014; Wang et al., 2014). As a result, these adaptive
571 strategies may lead to a high degree of functional redundancy of soil fungal communities
572 across the unique and stressful environmental conditions in these (and similar) alpine
573 grassland ecosystems.
574
575 Among the three abiotic factors, soil pH distance had significant effects on soil-mediated
576 nutrient pools but not on plant-mediated nutrient pools, while climatic distance had
577 slightly positive effects on both plant- and soil-mediated nutrient pools (Fig. 4; Table S4).
578 As shown in the structural equation model, the effects of abiotic factors were mainly

indirect through changes in above- and belowground β-diversity (Fig. 4). Specifically, abiotic factors accounted for 49%, 33% and 22% of the variance in soil bacterial, soil fungal and plant β-diversity, respectively (Fig 4). Climatic distance had the strongest effects on β-diversity both above- and belowground, which indirectly affected spatial turnover in nutrient pools. These findings are supported by an earlier study of Martinez-Almoyna et al. (2019), who found that spatial variation in climate indirectly, rather than directly, affected spatial turnover in multiple ecosystem functions. However, our work indicates that the relative importance of climatic distance and soil pH difference on spatial turnover in plant- and soil-mediated nutrient pools varies with spatial scale. For example, we found a slightly positive effect of climate on both plant- and soil-mediated nutrient pools at both small and large scales, but not at the intermediate spatial scales (Fig. S3; Table S6). This finding highlights the role of spatial scale in determining the relative importance of environmental conditions on spatial turnover in ecosystem functions, which underlines the initiatives of scaling up biodiversity and ecosystem function research (Burley et al., 2016; Gonzalez et al., 2020; Thompson et al., 2021).

Our work lends support to the conceptual predictions that changes in species composition influence spatial variation in ecosystem functions (Mori et al., 2018). However, we acknowledge that one could argue about the directionality of these relationships; differences in ecosystem properties of course drive patterns of β-diversity. In our study, however, we argue that β-diversity drives differences in ecosystem processes rather than ecosystem processes drive β-diversity two reasons. First, our AIC analyses provide some support for the models in which β-diversity drives ecosystem processes. Second, our work is in line with previous work in this system and others indicating that biodiversity both responds to changes in environmental conditions and drives multiple ecosystem functions above and beyond the effects of environmental conditions (Grman, Zirbel, Bassett, & Brudvig, 2018; Jing et al., 2021; Jing et al., 2015; Martinez-Almoyna et al., 2019; Mori et al., 2016; Mori et al., 2018; Pasari et al., 2013; van der Plas, 2019). Moreover, our work highlights that changes in both plant and soil bacterial β-diversity are key pathways associated with spatial turnover in ecosystem functions. For example, plant

609 β-diversity was directly associated with spatial turnover in plant- and soil-mediated
610 nutrient pools, while plant β-diversity was also indirectly associated with the spatial
611 turnover of nutrient pools through changes in soil bacterial β-diversity. Our work further
612 indicates that the replacement component of soil bacterial β-diversity, rather than
613 differences in richness, was one of the more important drivers of spatial turnover in
614 nutrient pools when geographic, climatic and soil pH distances were controlled for (Fig
615 5). The associations could be explained by the fact that soil bacteria exhibit higher values
616 of replacement component of β-diversity than do plants and soil fungi (Fig. S4). Our
617 work thus indicates the necessity of investigating above- and belowground linkages and
618 additive partitioning components of β-diversity in maintaining spatial variability in
619 multiple ecosystem functions (Eisenhauer et al., 2019; Martinez-Almoyna et al., 2019;
620 Soliveres et al., 2016; Trivedi, Leach, Tringe, Sa, & Singh, 2020). It also highlights the
621 importance of changes in abiotic factors including both geographic distance and
622 contemporary environmental factors for generating the biogeographic patterns of above-
623 and belowground community structure and jointly affecting regional spatial turnover in
624 ecosystem functions.
625
626 In summary, our study provides a comprehensive assessment of the biogeography of
627 plant and soil microbial communities and their potential functions in natural alpine
628 grassland ecosystems. We show that the relative importance of abiotic processes
629 generating above- and belowground community structure differs, which suggests the
630 rapid and ongoing environmental changes in alpine grasslands and elsewhere may have
631 differential impacts on above- and belowground components of ecosystems. For example,
632 soil acidification can substantially alter soil bacterial community composition, dispersal
633 limitations could constrain spatial variation in soil fungal composition, and local climate
634 can influence all above- and belowground taxa in the alpine grasslands. We further show
635 that the impacts of local climate on spatial turnover in plant- and soil-mediated nutrient
636 pools are mainly indirect and through changes in plant and soil bacterial β-diversity,
637 rather than through changes in soil fungal β-diversity. The direct associations of the
638 replacement component of soil bacterial β-diversity and the richness difference of plant
639 β-diversity with plant- and soil-mediated nutrient pools highlight that above- and

640 belowground biodiversity may jointly safeguard the impacts of local climate change on
641 the functioning of climate-sensitive alpine grasslands at regional scales.
642
643 **References**

644 Allan, E., Weisser, W. W., Fischer, M., Schulze, E. D., Weigelt, A., Roscher, C., . . . Schmid, B.
645 (2013). A comparison of the strength of biodiversity effects across multiple functions.
646 Oecologia, 173(1), 223-237. doi:10.1007/s00442-012-2589-0
647 Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., . . .
648 Davies, K. F. (2011). Navigating the multiple meanings of β diversity: a roadmap for the
649 practicing ecologist. Ecology Letters, 14(1), 19-28. doi:10.1111/j.1461-0248.2010.01552.x
650 Barnes, A. D., Weigelt, P., Jochum, M., Ott, D., Hodapp, D., Haneda, N. F., & Brose, U. (2016).
651 Species richness and biomass explain spatial turnover in ecosystem functioning across tropical
652 and temperate ecosystems. Philosophical Transactions of the Royal Society B: Biological
653 Sciences, 371(1694), 20150279. doi:10.1098/rstb.2015.0279
654 Bengtsson-Palme, J., Ryberg, M., Hartmann, M., Branco, S., Wang, Z., Godhe, A., . . . Nilsson, R.
655 H. (2013). Improved software detection and extraction of ITS1 and ITS2 from ribosomal ITS
656 sequences of fungi and other eukaryotes for analysis of environmental sequencing data.
657 Methods in Ecology and Evolution, 4(10), 914-919. doi:10.1111/2041-210X.12073
658 Burley, H. M., Mokany, K., Ferrier, S., Laffan, S. W., Williams, K. J., & Harwood, T. D. (2016).
659 Macroecological scale effects of biodiversity on ecosystem functions under environmental
660 change. Ecology and Evolution, 6(8), 2579-2593. doi:10.1002/ece3.2036
661 Caporaso, J. G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F. D., Costello, E. K., . . .
662 Knight, R. (2010). QIIME allows analysis of high-throughput community sequencing data.
663 Nature Methods, 7, 335-336. doi:10.1038/nmeth.f.303
664 Chen, L., Jing, X., Flynn, D. F., Shi, Y., Kühn, P., Scholten, T., & He, J.-S. (2017). Changes of
665 carbon stocks in alpine grassland soils from 2002 to 2011 on the Tibetan Plateau and their
666 climatic causes. Geoderma, 288, 166-174. doi:10.1016/j.geoderma.2016.11.016
667 Damgaard, C. F., & Irvine, K. M. (2019). Using the beta distribution to analyse plant cover data.
668 Journal of Ecology, 107(6), 2747-2759. doi:10.1111/1365-2745.13200
669 De Laender, F., Rohr, J. R., Ashauer, R., Baird, D. J., Berger, U., Eisenhauer, N., . . . Van den
670 Brink, P. J. (2016). Reintroducing environmental change drivers in biodiversity-ecosystem
671 Functioning Research. Trends in Ecology and Evolution, 31(12), 905-915.
672 doi:10.1016/j.tree.2016.09.007

673 Delgado-Baquerizo, M., Reich, P. B., Trivedi, C., Eldridge, D. J., Abades, S., Alfaro, F. D., . . .
674 Singh, B. K. (2020). Multiple elements of soil biodiversity drive ecosystem functions across
675 biomes. Nature Ecology & Evolution, 4(2), 210-220. doi:10.1038/s41559-019-1084-y
676 Dietz, E. J. (1983). Permutation tests for association between two distance matrices. Systematic
677 Biology, 32(1), 21-26.
678 Dong, S., Shang, Z., Gao, J., & Boone, R. B. (2020). Enhancing sustainability of grassland
679 ecosystems through ecological restoration and grazing management in an era of climate
680 change on Qinghai-Tibetan Plateau. Agriculture, Ecosystems & Environment, 287, 106684.
681 doi:10.1016/j.agee.2019.106684
682 Duffy, J. E., Godwin, C. M., & Cardinale, B. J. (2017). Biodiversity effects in the wild are
683 common and as strong as key drivers of productivity. Nature, 549, 261-264.
684 doi:10.1038/nature23886
685 Edgar, R. C. (2010). Search and clustering orders of magnitude faster than BLAST.
686 Bioinformatics, 26, 2460-2461. doi:10.1093/bioinformatics/btq461
687 Edgar, R. C., Haas, B. J., Clemente, J. C., Quince, C., & Knight, R. (2011). UCHIME improves
688 sensitivity and speed of chimera detection. Bioinformatics, 27, 2194-2200.
689 doi:10.1093/bioinformatics/btr381
690 Eisenhauer, N. (2011). Aboveground–belowground interactions as a source of complementarity
691 effects in biodiversity experiments. Plant and Soil, 351(1-2), 1-22. doi:10.1007/s11104-011-
692 1027-0
693 Eisenhauer, N., Schielzeth, H., Barnes, A. D., Barry, K. E., Bonn, A., Brose, U., . . . Ebeling, A.
694 (2019). A multitrophic perspective on biodiversity–ecosystem functioning research. In
695 Advances in Ecological Research (Vol. 61, pp. 1-54): Elsevier.
696 Engel, T., Blowes, S. A., McGlinn, D. J., May, F., Gotelli, N. J., McGill, B. J., & Chase, J. M.
697 (2020). Resolving the species pool dependence of beta-diversity using coverage-based
698 rarefaction. bioRxiv 2020.04.14.040402. doi:10.1101/2020.04.14.040402
699 Farnsworth, K. D., Albantakis, L., & Caruso, T. (2017). Unifying concepts of biological function
700 from molecules to ecosystems. Oikos, 126(10), 1367-1376. doi:10.1111/oik.04171
701 Fukami, T., Naeem, S., & Wardle, D. A. (2001). On similarity among local communities in
702 biodiversity experiments. Oikos, 95(2), 340-348.
703 Furrer, R., Nychka, D., & Sain, S. (2015). Fields: tools for spatial data.
704 www.image.ucar.edu/fields: R package version 8.4-1.

Garland, G., Banerjee, S., Edlinger, A., Oliveira, E. M., Herzog, C., Wittwer, R., . . . van der Heijden, M. G. A. (2021). A closer look at the functions behind ecosystem multifunctionality: A review. Journal of Ecology, 109(2), 600-613. doi:10.1111/1365-2745.13511

Gonzalez, A., Germain, R. M., Srivastava, D. S., Filotas, E., Dee, L. E., Gravel, D., . . . Loreau, M. (2020). Scaling-up biodiversity-ecosystem functioning research. Ecology Letters, 23, 757-776. doi:10.1111/ele.13456

Goslee, S. C., & Urban, D. L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software, 22(7), 1-19. doi:10.18637/jss.v022.i07

Grace, J. (2020). A 'Weight of Evidence' approach to evaluating structural equation models. One Ecosystem, 5, e50452. doi:10.3897/oneeco.5.e50452

Graham, E. B., Wieder, W. R., Leff, J. W., Weintraub, S. R., Townsend, A. R., Cleveland, C. C., . . . Nemergut, D. R. (2014). Do we need to understand microbial communities to predict ecosystem function? A comparison of statistical models of nitrogen cycling processes. Soil Biology and Biochemistry, 68(0), 279-282. doi:10.1016/j.soilbio.2013.08.023

Grman, E., Zirbel, C. R., Bassett, T., & Brudvig, L. A. (2018). Ecosystem multifunctionality increases with beta diversity in restored prairies. Oecologia, 188(3), 837-848. doi:10.1007/s00442-018-4248-6

Hautier, Y., Isbell, F., Borer, E. T., Seabloom, E. W., Harpole, W. S., Lind, E. M., . . . Hector, A. (2018). Local loss and spatial homogenization of plant diversity reduce ecosystem multifunctionality. Nature Ecology & Evolution, 2(1), 50-56. doi:10.1038/s41559-017-0395-0

Hijmans, R. J. (2021). raster: Geographic data analysis and modeling. R package version 3.4-10. https://CRAN.R-project.org/package=raster.

Hu, W., Ran, J., Dong, L., Du, Q., Ji, M., Yao, S., . . . Deng, J. (2021). Aridity-driven shift in biodiversity-soil multifunctionality relationships. Nature Communications, 12(1), 5350. doi:10.1038/s41467-021-25641-0

Jax, K. (2005). Function and "functioning" in ecology: what does it mean? Oikos, 111(3), 641-648. doi:10.1111/j.1600-0706.2005.13851.x

Jing, X., Prager, C. M., Borer, E. T., Gotelli, N. J., Gruner, D. S., He, J.-S., . . . Sanders, N. J. (2021). Spatial turnover of multiple ecosystem functions is more associated with plant than soil microbial β-diversity. Ecosphere, 12(7), e03644. doi:10.1002/ecs2.3644

Jing, X., Sanders, N. J., Shi, Y., Chu, H. Y., Classen, A. T., Zhao, K., . . . He, J. S. (2015). The links between ecosystem multifunctionality and above- and belowground biodiversity are mediated by climate. Nature Communications, 6, 8159. doi:10.1038/ncomms9159

738 Jing, X., Wang, Y., Chung, H., Mi, Z., Wang, S., Zeng, H., & He, J.-S. (2014). No temperature
739 acclimation of soil extracellular enzymes to experimental warming in an alpine grassland
740 ecosystem on the Tibetan Plateau. Biogeochemistry, 117, 39-54. doi:10.1007/s10533-013-
741 9844-2
742 Kraft, N. J., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., . . .
743 Anderson, M. J. (2011). Disentangling the drivers of β diversity along latitudinal and
744 elevational gradients. Science, 333(6050), 1755-1758. doi:10.1126/science.1208584
745 Ladau, J., Shi, Y., Jing, X., He, J. S., Chen, L., Lin, X., . . . Chu, H. (2018). Existing climate
746 change will lead to pronounced shifts in the diversity of soil Prokaryotes. mSystems, 3(5),
747 e00167-00118. doi:10.1128/mSystems.00167-18
748 Leff, J. W., Bardgett, R. D., Wilkinson, A., Jackson, B. G., Pritchard, W. J., De Long, J. R., . . .
749 Fierer, N. (2018). Predicting the structure of soil communities from plant community
750 taxonomy, phylogeny, and traits. The ISME Journal, 12(7), 1794-1805. doi:10.1038/s41396-
751 018-0089-x
752 Legendre, P. (2014). Interpreting the replacement and richness difference components of beta
753 diversity. Global Ecology and Biogeography, 23(11), 1324-1334. doi:10.1111/geb.12207
754 Liu, D., Chang, P. S., Power, S. A., Bell, J. N. B., & Manning, P. (2021). Changes in plant
755 species abundance alter the multifunctionality and functional space of heathland ecosystems.
756 New Phytologist, 232(3), 1238-1249. doi:10.1111/nph.17667
757 Ma, W., He, J.-S., Yang, Y., Wang, X., Liang, C., Anwar, M., . . . Schmid, B. (2010).
758 Environmental factors covary with plant diversity-productivity relationships among Chinese
759 grassland sites. Global Ecology and Biogeography, 19, 233-243. doi:10.1111/j.1466-
760 8238.2009.00508.x
761 Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F. T., Mace, G., . . . Fischer, M.
762 (2018). Redefining ecosystem multifunctionality. Nature Ecology & Evolution, 2(3), 427-436.
763 doi:10.1038/s41559-017-0461-7
764 Martinez-Almoyna, C., Thuiller, W., Chalmandrier, L., Ohlmann, M., Foulquier, A., Clément, J.
765 C., . . . Münkemüller, T. (2019). Multi-trophic β-diversity mediates the effect of
766 environmental gradients on the turnover of multiple ecosystem functions. Functional Ecology,
767 33, 2053-2064. doi:10.1111/1365-2435.13393
768 Martiny, J. B., Bohannan, B. J., Brown, J. H., Colwell, R. K., Fuhrman, J. A., Green, J. L., . . .
769 Staley, J. T. (2006). Microbial biogeography: putting microorganisms on the map. Nature
770 Review Microbiology, 4(2), 102-112. doi:10.1038/nrmicro1341

771 Martiny, J. B., Eisen, J. A., Penn, K., Allison, S. D., & Horner-Devine, M. C. (2011). Drivers of
772 bacterial beta-diversity depend on spatial scale. Proceedings of the National Academy of
773 Sciences, USA, 108(19), 7850-7854. doi:10.1073/pnas.1016308108
774 Mokany, K., Burley, H. M., & Paini, D. R. (2013). β diversity contributes to ecosystem processes
775 more than by simply summing the parts. Proceedings of the National Academy of Sciences,
776 USA, 110(43), E4057. doi:10.1073/pnas.1313429110
777 Mori, A. S., Isbell, F., Fujii, S., Makoto, K., Matsuoka, S., & Osono, T. (2016). Low
778 multifunctional redundancy of soil fungal diversity at multiple scales. Ecology Letters, 19(3),
779 249-259. doi:10.1111/ele.12560
780 Mori, A. S., Isbell, F., & Seidl, R. (2018). β-Diversity, community assembly, and ecosystem
781 functioning. Trends in Ecology & Evolution, 33(7), 549-564. doi:10.1016/j.tree.2018.04.012
782 Myers, J. A., Chase, J. M., Jimenez, I., Jorgensen, P. M., Araujo-Murakami, A., Paniagua-
783 Zambrana, N., & Seidel, R. (2013). Beta-diversity in temperate and tropical forests reflects
784 dissimilar mechanisms of community assembly. Ecology Letters, 16(2), 151-157.
785 doi:10.1111/ele.12021
786 Naeem, S., Thompson, L. J., Lawler, S. P., & Lawton, J. H. (1994). Declining biodiversity can
787 alter the performance of ecosystems. Nature, 368, 734 - 737. doi:10.1038/368734a0
788 Nottingham, A. T., Fierer, N., Turner, B. L., Whitaker, J., Ostle, N. J., McNamara, N. P., . . . Meir,
789 P. (2018). Microbes follow Humboldt: temperature drives plant and soil microbial diversity
790 patterns from the Amazon to the Andes. Ecology, 99(11), 2455-2466. doi:10.1002/ecy.2482
791 Pasari, J. R., Levi, T., Zavaleta, E. S., & Tilman, D. (2013). Several scales of biodiversity affect
792 ecosystem multifunctionality. Proceedings of the National Academy of Sciences, USA, 100,
793 10219-10222. doi:10.1073/pnas.1220333110
794 Peay, K. G., Dickie, I. A., Wardle, D. A., Bellingham, P. J., & Fukami, T. (2013). Rat invasion of
795 islands alters fungal community structure, but not wood decomposition rates. Oikos, 122(2),
796 258-264. doi:10.1111/j.1600-0706.2012.20813.x
797 Peay, K. G., Kennedy, P. G., & Talbot, J. M. (2016). Dimensions of biodiversity in the Earth
798 mycobiome. Nature Reviews Microbiology, 14(7), 434-447. doi:10.1038/nrmicro.2016.59
799 Peters, M. K., Hemp, A., Appelhans, T., Becker, J. N., Behler, C., Classen, A., . . . Steffan-
800 Dewenter, I. (2019). Climate–land-use interactions shape tropical mountain biodiversity and
801 ecosystem functions. Nature, 568(7750), 88-92. doi:10.1038/s41586-019-1048-z
802 Podani, J., & Schmera, D. (2011). A new conceptual and methodological framework for
803 exploring and explaining pattern in presence–absence data. Oikos, 120(11), 1625-1638.
804 doi:10.1111/j.1600-0706.2011.19451.x

Prober, S. M., Leff, J. W., Bates, S. T., Borer, E. T., Firn, J., Harpole, W. S., . . . Fierer, N. (2015). Plant diversity predicts beta but not alpha diversity of soil microbes across grasslands worldwide. Ecology Letters, 18(1), 85-95. doi:10.1111/ele.12381

R Development Core Team. (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ramirez, K. S., Knight, C. G., de Hollander, M., Brearley, F. Q., Constantinides, B., Cotton, A., . . . de Vries, F. T. (2018). Detecting macroecological patterns in bacterial communities across independent studies of global soils. Nature Microbiology, 3(2), 189-196. doi:10.1038/s41564-017-0062-x

Rosseel, Y. (2012). lavaan: An R Package for Structural Equation Modeling. Journal of Statistical Software, 48(2), 1-36. doi:10.18637/jss.v048.i02

Rousk, J., Bååth, E., Brookes, P. C., Lauber, C. L., Lozupone, C., Caporaso, J. G., . . . Fierer, N. (2010). Soil bacterial and fungal communities across a pH gradient in an arable soil. The ISME Journal, 4(10), 1340-1351. doi:10.1038/ismej.2010.58

Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., . . . Tscharntke, T. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature, 468(7323), 553-556. doi:10.1038/nature09492

Schmid, B., Balvanera, P., Cardinale, B. J., Godbold, J., Pfisterer, A. B., Raffaelli, D., . . . Srivastava, D. S. (2009). Consequences of species loss for ecosystem functioning: Meta-analyses of data from biodiversity experiments. In S. Naeem, D. E. Bunker, A. Hector, M. Loreau, & C. Perrings (Eds.), Biodiversity, ecosystem functioning, and human wellbeing: An ecological and economic perspective (pp. 14-29): Oxford University Press.

Shade, A., Dunn, R. R., Blowes, S. A., Keil, P., Bohannan, B. J. M., Herrmann, M., . . . Chase, J. (2018). Macroecology to unite all life, large and small. Trends in Ecology & Evolution, 33(10), 731-744. doi:10.1016/j.tree.2018.08.005

Shi, Y., Wang, Y., Ma, Y., Ma, W., Liang, C., Flynn, D., . . . He, J.-S. (2013). Field-based observations of regional-scale, temporal variation in net primary production in Tibetan alpine grasslands. Biogeosciences, 10, 16843-16878. doi:10.5194/bg-11-2003-2014

Soliveres, S., van der Plas, F., Manning, P., Prati, D., Gossner, M. M., Renner, S. C., . . . Allan, E. (2016). Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature, 536(7617), 456-459. doi:10.1038/nature19092

Talbot, J. M., Bruns, T. D., Taylor, J. W., Smith, D. P., Branco, S., Glassman, S. I., . . . Peay, K. G. (2014). Endemism and functional convergence across the North American soil mycobiome.

Proceedings of the National Academy of Sciences, USA, 111(17), 6341-6346. doi:10.1073/pnas.1402584111

Thompson, P. L., Kéfi, S., Zelnik, Y. R., Dee, L. E., Wang, S., de Mazancourt, C., . . . Gonzalez, A. (2021). Scaling up biodiversity–ecosystem functioning relationships: the role of environmental heterogeneity in space and time. Proceedings of the Royal Society B, 288(1946), 20202779. doi:10.1098/rspb.2020.2779

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and Ecosystem Functioning. Annual Review of Ecology, Evolution, and Systematics, 45(1), 471-493. doi:10.1146/annurev-ecolsys-120213-091917

Trivedi, P., Leach, J. E., Tringe, S. G., Sa, T., & Singh, B. K. (2020). Plant–microbiome interactions: from community assembly to plant health. Nature Reviews Microbiology, 18(11), 607-621. doi:10.1038/s41579-020-0412-1

Tuomisto, H., & Ruokolainen, K. (2006). Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. Ecology, 87(11), 2697-2708. doi:10.1890/0012-9658(2006)87[2697:AOEBDU]2.0.CO;2

van der Heijden, M. G. A., Bardgett, R. D., & van Straalen, N. M. (2008). The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecology Letters, 11, 296-310. doi:10.1111/j.1461-0248.2007.01139.x

van der Plas, F. (2019). Biodiversity and ecosystem functioning in naturally assembled communities. Biological Reviews of the Cambridge Philosophical Society, 94(4), 1220-1245. doi:10.1111/brv.12499

Wang, Y. H., Liu, H. Y., Chung, H., Yu, L. F., Mi, Z. R., Geng, Y., . . . He, J. S. (2014). Non-growing-season soil respiration is controlled by freezing and thawing processes in the summer monsoon-dominated Tibetan alpine grassland. Global Biogeochemical Cycles, 28(10), 1081-1095. doi:10.1002/2013gb004760

Wardle, D. A. (2016). Do experiments exploring plant diversity–ecosystem functioning relationships inform how biodiversity loss impacts natural ecosystems? Journal of Vegetation Science, 27(3), 646-653. doi:10.1111/jvs.12399

Wheeler, B., Torchiano, M., & Torchiano, M. M. (2016). lmPerm: Permutation tests for linear models. R Package Version 2.1.0. https://CRAN.R-project.org/package=lmPerm.

Whittaker, R. H. (1972). Evolution and measurement of species diversity. Taxon, 21(2-3), 213-251.

Winfree, R., Reilly, J. R., Bartomeus, I., Cariveau, D. P., Williams, N. M., & Gibbs, J. (2018). Species turnover promotes the importance of bee diversity for crop pollination at regional scales. Science, 359(6377), 791-793. doi:10.1126/science.aao2117

Xu, X. F., Wang, N. N., Lipson, D., Sinsabaugh, R., Schimel, J., He, L. Y., . . . Tedersoo, L. (2020). Microbial macroecology: In search of mechanisms governing microbial biogeographic patterns. Global Ecology and Biogeography, 29, 1870-1886. doi:10.1111/geb.13162

Yang, T., Adams, J. M., Shi, Y., He, J. S., Jing, X., Chen, L., . . . Chu, H. (2017). Soil fungal diversity in natural grasslands of the Tibetan Plateau: Associations with plant diversity and productivity. New Phytologist, 215(2), 756-765. doi:10.1111/nph.14606

Yang, Y., Ji, C., Ma, W., Wang, S., Wang, S., Han, W., . . . Smith, P. (2012). Significant soil acidification across northern China's grasslands during 1980s–2000s. Global Change Biology, 18, 2292-2300. doi:10.1111/j.1365-2486.2012.02694.x

Yuan, Z. Q., Ali, A., Ruiz-Benito, P., Jucker, T., Mori, A. S., Wang, S. P., . . . Loreau, M. (2020). Above- and below-ground biodiversity jointly regulate temperate forest multifunctionality along a local-scale environmental gradient. Journal of Ecology, 108, 2012-2024. doi:10.1111/1365-2745.13378

Zhang, R., Tian, D., Chen, H. Y. H., Seabloom, E. W., Han, G., Wang, S., . . . Schrodt, F. (2021). Biodiversity alleviates the decrease of grassland multifunctionality under grazing disturbance: A global meta-analysis. Global Ecology and Biogeography, 00, 1-13. doi:10.1111/geb.13408

Figure legends

Fig. 1 Biogeographic patterns of plant and soil microbial β-diversity. (**a**) Simple Mantel tests for relationships between abiotic factors (geographic, climatic and pH distances) and β-diversity. Lines are fitted by general linear regressions illustrating the direction of bivariate associations. Spearman correlation coefficients (ρ) and the lower and upper 95% confidence intervals are given. (**b**) Partial Mantel tests for the relationship between abiotic factors and β-diversity given geographic, climatic and soil pH distances or their combinations. Points represent the Spearman correlation coefficients and error bars represent the 95% confidence intervals. | represents the partial Mantel effects, which

account for the influence of other abiotic factors in the left of |. Geo, geographic distance (km); Clim, climatic distance (unitless); pH, soil pH distance (unitless).

Fig. 2 Geographic patterns of plant- and soil-mediated nutrient pools. (**a**) Simple Mantel tests for relationships between abiotic factors (geographic, climatic and soil pH distances) and spatial turnover in nutrient pools. Spearman correlation coefficients (ρ) and the lower and upper 95% confidence intervals are given. Lines are fitted by general linear regressions illustrating the direction of the bivariate associations. (**b**) Partial Mantel tests for the relationships between abiotic factors and spatial turnover in nutrient pools given geographic, climatic and soil pH distances or their combinations. Points represent the Spearman correlation coefficients and error bars represent the 95% confidence intervals. | represents the partial Mantel effects, which account for the influence of other abiotic factors in the left of |. Geo, geographic distance (km); Clim, climatic distance (unitless); pH, soil pH distance (unitless).

Fig. 3 Relationships between β-diversity and spatial turnover in nutrient pools. (**a**) Simple Mantel tests for the relationships between β-diversity and spatial turnover in nutrient pools. Spearman correlation coefficients (ρ) and the lower and upper 95% confidence intervals are given. Lines are fitted by general linear regressions illustrating the linear bivariate associations. (**b**) Partial Mantel tests for the relationship between β-diversity and spatial turnover in nutrient pools given geographic, climatic and soil pH distances or their combinations. Points represent the Spearman correlation coefficients and error bars represent the 95% confidence intervals. Xs represent β-diversity of plant and soil microorganisms. | represents the partial Mantel effects, which account for the influence of other abiotic factors in the left of |. Geo, geographic distance; Clim, climatic distance; pH, soil pH distance.

Fig. 4 Direct and indirect effects of abiotic and biotic factors on plant- and soil-mediated nutrient pools. Arrows represent the direct and indirect pathways through which abiotic and biotic factors affect plant- and soil-mediated nutrient pools. Black arrows represent significantly positive pathways, and red arrows represent significantly negative pathways. Double-headed arrows represent residual correlations, i.e., bacterial vs. fungal β-diversity and plant- vs. soil-mediated nutrient pools. Arrow width is proportional to the

standardized path coefficients. The R^2 of each response variable is given. Details of the structural equation model can be found in Table S4.

Fig. 5 Scale dependence of the impacts of above- and belowground β-diversity on plant- and soil-mediated nutrient pools. Two components of β-diversity are compared: replacement (left) and richness difference (right). Lines show changes in standardized regression coefficients with geographic distances. Significance tests for the standardized regression coefficients are given in Table S6.

Fig. S1. Map of sampling location in 2011. A total of 60 sites were surveyed across three main vegetation types, including alpine meadow, alpine steppe, and desert steppe. Adapted from the supplementary Figure 2 of Jing et al. (2015) [Jing, X., Sanders, N., Shi, Y. et al. The links between ecosystem multifunctionality and above- and belowground biodiversity are mediated by climate. Nat Commun 6, 8159 (2015). https://doi.org/10.1038/ncomms9159]

Fig. S2. An alternate structural equation model illustrating the effects of plant- and soil-mediated nutrient pools on plant and soil microbial β-diversity. Double-headed arrows represent residual correlations, i.e., bacterial vs. fungal β-diversity and plant- vs. soil-mediated nutrient pools. Arrow width is proportional to the standardized path coefficients. R^2 of each response variable is given. Details of this structural equation model can be found in Table S5.

Fig. S3. Relative importance of geographic, climatic and soil pH distances on plant- and soil-mediated nutrient pools across spatial scales. Lines show changes in standardized regression coefficients over geographic distances. The permutation significance tests of regression coefficients are given in Table S6.

Fig. S4. Probability density distributions of replacement and richness difference of plant and soil microbial β-diversity. (**a**) replacement, (**b**) richness difference. Points represent median β-diversity. Thick and thin error bars represent 66% and 95% confidence intervals, respectively.