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RESEARCH ARTICLE

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, and 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 against the impacts of local climate on the functions of climate-sensitive alpine grasslands.

KEYWORDS
aboveground-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 differences in aboveground plants and/or belowground microbiomes influence ecosystem functions (Delgado-Baquerizo et al., 2020; Schmid et al., 2009; Tilman et al., 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 et al., 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 et al., 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 et al., 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 et al., 2001; Mokany et al., 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 functions among sites; Mori et al., 2018). For example, Pasari et al. (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 to the spatial turnover of plant- and soil-mediated nutrient pools [i.e., surrogates for ecosystem functions that are 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 et al., 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 these relationships depend on geography, climate, and soil pH. We ask three explicit questions: (a) Do soil bacterial and soil fungal taxa follow the same spatial patterns as plant species, and which factors – geography, climate, and/or soil pH – determine spatial variations in plant and soil microbial species composition? (b) Do plant- and soil-mediated nutrient pools have geographic patterns and, if so,

which factors – geography, climate, and/or soil pH – determine the geographic patterns? (c) 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 do these biotic and abiotic effects vary with spatial scale?

2 | MATERIALS AND METHODS

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 (Supporting Information Figure 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, fieldwork generally followed a sampling order from low elevation sites to high elevation sites ranging from 2,918 to 5,228 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 sampling and plant community surveys. 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 (Shi et al., 2006)]. The mean annual temperature ranges from −5.6 to 3.5°C and mean annual precipitation ranges from 110 to 552 mm/year (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°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 to 321 g/m^2/year (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 the 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 concentrations were measured using the samples of aboveground live plant biomass, which were dried at 60°C to a constant mass. Plant N (%) was 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 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 mesh size) and air-dried in the field. Roots were then oven-dried at 65°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 correcting 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). Soil inorganic C ($CaCO_3$) was measured using a calcimeter (Eijkelkamp, the Netherlands). 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°C prior to DNA extraction) by using a FastDNA Spin kit (Bio 101, Carlsbad, CA, USA) according to the instructions of the manufacturer and stored at −40°C until sequencing analysis. The V4-V5 hypervariable regions of bacterial *16S rRNA* (ribosomal ribonucleic acid) genes were amplified using the universal primer sets: 515 forward (5′-GTGCCAGCMGCCGCGG-3′) with the 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 internal transcribed spacer 2 (ITS2) regions between the *5.8S* and *28S rRNA* genes were amplified for soil fungi using the universal primer sets: ITS3 forward (5′-GCATCGATGAAGAACGCAGC-3′) and ITS4 reverse (5′-TCCTCCGCTTATTGATATGC-3′). Each sample of the *16S rRNA* genes was amplified three times using 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 DNA template and 22 μl double sterile water] under the following conditions: 30 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 30 s, extension at 72°C for 30 s and a final extension at 72°C for

10 min. Each sample of the *ITS2 rRNA* genes was amplified using a 20-μl PCR reaction mixture [0.4 μl FastPfu Polymerase (TransGen Biotech, Beijing, China), 2 μl 5 ng/μl DNA template, 0.8 μl 5 μM forward primer, 0.8 μl 5 μM reverse primer, 1.2 μl 20 mg/l TaKaRa BSA (Bovine Serum Albumin), 4 μl 5 × FastPfu buffer, 2 μl 2.5 mM dNTPs and 8.8 μl sterile water] under the following conditions: one cycle of initialization at 95°C for 3 min, 38 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 30 s, extension at 72°C for 45 s and a final extension at 72°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 T. Yang et al. (2017). In brief, soil bacterial sequences >200 bp in length, with average quality score >25 and no ambiguous characters were included. Sequences were then filtered to remove error sequences and chimeras using the USEARCH algorithm (Edgar, 2010). The remaining sequences were assigned to clusters using the UCLUST method (Edgar, 2010) and assigned to operational taxonomic units (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 OTUs 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, with average quality score >30 and no ambiguous characters were included. Flanking large ribosomal subunit (LSU) and *5.8S* genes and chimeras were also removed using ITSx (version 1.0.11; Bengtsson-Palme et al., 2013) and the UCHIME program (Edgar et al., 2011), respectively. The remaining sequences were assigned to clusters using the UCLUST method (Edgar, 2010) and assigned to OTUs based on a minimum threshold of 97% similarity. All singletons were removed before soil fungal community data analysis, which resulted in 14,207 OTUs and 11,576,489 sequences in total, 3,725 OTUs per site on average (min. = 2,722 OTUs and max. = 4,767 OTUs) and 192,941 sequences per site on average (min. = 123,753 sequences and max. = 341,014 sequences).

Mean annual temperature (BIO1) and mean annual precipitation (BIO12) were obtained from the WorldClim bioclimatic dataset (version 2.0; available from http://www.worldclim.org). The 30 arc-second resolution (*c*. 1 km at the equator) climate data for the period of 1950–2000 were used to estimate the spatial variation in climate for the 60 sampling sites. Climate data were extracted using the World Geodetic System 1984 (WGS-84).

2.2 | Quantifying geographic and environmental distances

We calculated pairwise great circle geographic distance (unit, km) using the geographic locations of sampling sites. Mean annual temperature and mean annual precipitation were two major factors influencing spatial variation in plant and soil microbial α-diversity and individual ecosystem functions in the study areas (Jing et al., 2015; Ma et al., 2010). We used the two climate variables as indicators of climatic differences among sites. A third variable (soil pH) was included to account for site differences in environmental conditions for plant and soil microbial communities (Jing et al., 2021). We standardized the three environmental variables by using *z*-score (Peters et al., 2019). We calculated climatic and soil pH distances using the Euclidean distance (i.e., the square root of the sum of squared differences between environmental variables for any given two sites).

2.3 | Quantifying β-diversity

β-diversity in this study was defined as the directional species compositional turnover along environmental gradients and was measured based on the pairwise dissimilarity between communities (Anderson et al., 2011). Soil bacterial and fungal community data, that is, the OTU table, were rarefied at 11,000 and 123,000 reads per sample, respectively. We first estimated total β-diversity using the Sorensen index. It is a simple measure of differences in species composition between communities by considering the number of species in 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 components, that is, 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 and the two components of Sorensen index (i.e., richness difference and replacement). Since the abundance-based β-diversity index 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 is, they are not true ecosystem functions (Farnsworth et al., 2017; Jax, 2005) and are not recommended to measure in the field of multifunctionality (Garland et al., 2021). However, the eight indicators of ecosystem functions considered are generally associated more with changes in biodiversity than these direct measures of fluxes of energy and matter (Schmid et al., 2009). Indeed, these indicators are 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 et al., 2021; Peters et al., 2019; Zhang et al., 2021) that are especially relevant to the long-term net balance of energy and matter in ecosystems (Garland et al., 2021; Manning et al., 2018). In brief, the eight indicators were used to represent the basic nutrient pools of the alpine grasslands (Supporting Information Table S1). For simplicity, we refer to these indicators as nutrient pools, but for more insights into the debate and research progress on selecting indicators for ecosystem functions (i.e., process rates, nutrient pools versus ecosystem properties), we refer readers to the synthetic review by Garland et al. (2021). We calculated the pairwise Euclidean distance to estimate the spatial turnover of plant- and soil-mediated nutrient pools. Indicators of nutrient pools were standardized by using *z*-score prior to computing the Euclidean distance (Mori et al., 2016; Peters et al., 2019). We assigned equal weights within groups of plant- and soil-mediated nutrient pools because we found only strong autocorrelations among indicators of soil-mediated nutrient pools, but not among indicators of plant-mediated nutrient pools or between indicators of plant- and soil-mediated nutrient pools (Supporting Information Table S2). Since spatial turnover in nutrient pools was derived from the Euclidean distance (i.e., the square root of the sum of squared differences between nutrient pools for any given two sites), the approach considered here cannot assess the compromises of the losses of some nutrient pools and gains in others. Alternatively, investigators might use the schematic analysis of diversity–function relationships to address the question whether two sites with high β-diversity have higher overall functioning at different spatial scales (e.g., box 1 in Mori et al. (2018): functions provided at the plot versus landscape levels).

2.5 | Statistical analyses

We used a distance approach (Tuomisto & Ruokolainen, 2006), that is, simple Mantel tests to examine the associations of geographic distance, climatic distance and soil pH distance with above- and belowground β-diversity as well as the spatial turnover of plant- and soil-mediated nutrient pools. To examine whether the associations of abiotic factors with β-diversity were context dependent, we performed partial Mantel tests. For example, we controlled for the influences of climatic distance, soil pH distance or both when we assessed the bivariate associations between geographic distance and β-diversity. We used the same approach as above to assess the associations of abiotic factors and β-diversity with the spatial turnover of plant- and soil-mediated nutrient pools. We used 9,999 permutations for each Mantel test.

We used structural equation models (SEMs) to compare the direct and indirect effects of biotic and abiotic factors on spatial turnover in nutrient pools. We had two assumptions: (a) geographic, climatic and soil pH distances, which 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 (b) soil microbial β-diversity was influenced by aboveground plant β-diversity (Leff et al., 2018; Prober et al., 2015). We excluded pathways that had non-significant direct effects on plant- or soil-mediated nutrient pools and pathways that had weak associations, for example, 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 in 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 iterations 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 ($n = 1{,}770$ in this study), we considered four alternative indices, including Akaike information criterion (AIC, the lower, the better), comparative fit index (CFI >.90), root mean square error of approximation (RMSEA <.05) and standardized root mean square residual (SRMR <.10) (see summaries by Grace, 2020). All Mantel tests and SEMs were conducted using the Sorensen index for plants and Bray–Curtis dissimilarity for soil bacteria and soil fungi because these indices are associated more with spatial turnover in nutrient pools than the replacement and richness difference components of Sorensen index (see Supporting Information 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 using *z*-score. The procedure of linear regressions was performed by varying the spatial extent of investigated alpine grasslands from

20 to 1,000 km. In other words, the analysis was run on all sites at distances of 0–20, 0–40, 0–60, …, 0–1,000 km.

All statistical analyses were performed in R version 3.6.1 (R Development Core Team, 2019) using data aggregated at site level, that is, 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 et al., 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), SEMs using the *lavaan* package (Rosseel, 2012), and linear regression models using the *lmPerm* package (Wheeler et al., 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 (Figure 1), suggesting that in this study variation in soil microbial community composition is shaped by the same suite of factors as that in plant communities. However, there were differences in the relative importance of each of these abiotic factors. Specifically, climatic distance was moderately correlated with plant β-diversity (Spearman correlation coefficient, hereafter $\rho = .44$), soil bacterial β-diversity ($\rho = .48$) and soil fungal β-diversity ($\rho = .41$) (Figure 1a). These bivariate associations were retained when geographic and soil pH distances were statistically controlled for (Figure 1b). Furthermore, we found that soil pH distance was moderately correlated with soil bacterial β-diversity ($\rho = .42$) but was weakly correlated with plant ($\rho = .12$) and soil fungal β-diversity ($\rho = .16$) (Figure 1a). When we controlled for the influences of geographic and climatic distances, the significant bivariate associations were retained between soil pH and soil bacterial β-diversity, while the bivariate associations became weak for plant β-diversity and soil fungal β-diversity (Figure 1b). In contrast, geographic distance was more strongly correlated with soil fungal β-diversity than with soil pH distance even though we controlled for the environmental covariates, that is, differences in climate and soil pH (Figure 1a,b).

3.2 | Geography of plant- and soil-mediated nutrient pools

Changes in plant- and soil-mediated nutrient pools were driven by geography, climate, and soil pH (Figure 2). However, the main factors influencing the geographic patterns of plant- and soil-mediated nutrient pools were different. Specifically, we found that climatic distance was weakly associated with plant-mediated nutrient pools but moderately associated with soil-mediated nutrient pools (all eight indicators of nutrient pools, hereafter overall, $\rho = .30$; plant-mediated nutrient pools, $\rho = .17$; soil-mediated nutrient pools, $\rho = .30$; Figure 2a), even when geographic distance and soil pH distance were statistically controlled for (Figure 2b). The associations between plant-mediated nutrient pools and geographic distance were as strong as those with climatic distance (all cases, $\rho = .17$; Figure 2a,b). Finally, soil-mediated nutrient pools were associated more with soil pH distance than with geographic and climatic distances (Figure 2).

3.3 | β-diversity and nutrient pool relationships

We asked whether three abiotic factors – geographic, climatic and soil pH distances – would alter the relationships between β-diversity and spatial turnover in nutrient pools. To test this idea, we compared the effects of β-diversity on plant- and soil-mediated nutrient pools before (Figure 3a) and after (Figure 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 but weakly associated with plant-mediated nutrient pools (overall, $\rho = .35$; plant-mediated nutrient pools, $\rho = .20$; soil-mediated nutrient pools, $\rho = .38$; Figure 3a). Soil bacterial β-diversity was also moderately associated with the spatial turnover of overall and soil-mediated nutrient pools but weakly associated with plant-mediated nutrient pools (overall, $\rho = .37$; plant-mediated nutrient pools, $\rho = .16$; soil-mediated nutrient pools, $\rho = .43$; Figure 3a). These bivariate associations were retained when geographic, climatic and soil pH distances or their combinations were controlled for (Figure 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 (Figure 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, $r = .12$; Figure 4). This result thus supports classifying plant- and soil-mediated nutrient pools separately. The SEM (AIC = 31,684) explained 23% and 6% of the variance in the spatial turnover of soil- and plant-mediated nutrient pools, respectively (Figure 4; Supporting Information Table S4). Specifically, plant β-diversity had slightly stronger direct effects on both plant- (standardized path coefficient, $\beta_{std} = .13$) and soil-mediated nutrient pools ($\beta_{std} = .21$) than did soil bacterial β-diversity ($\beta_{std} = .07$ for plant-mediated nutrient pools and $\beta_{std} = .14$ for soil-mediated nutrient pools) or soil fungal β-diversity ($\beta_{std} = -.06$ for plant-mediated

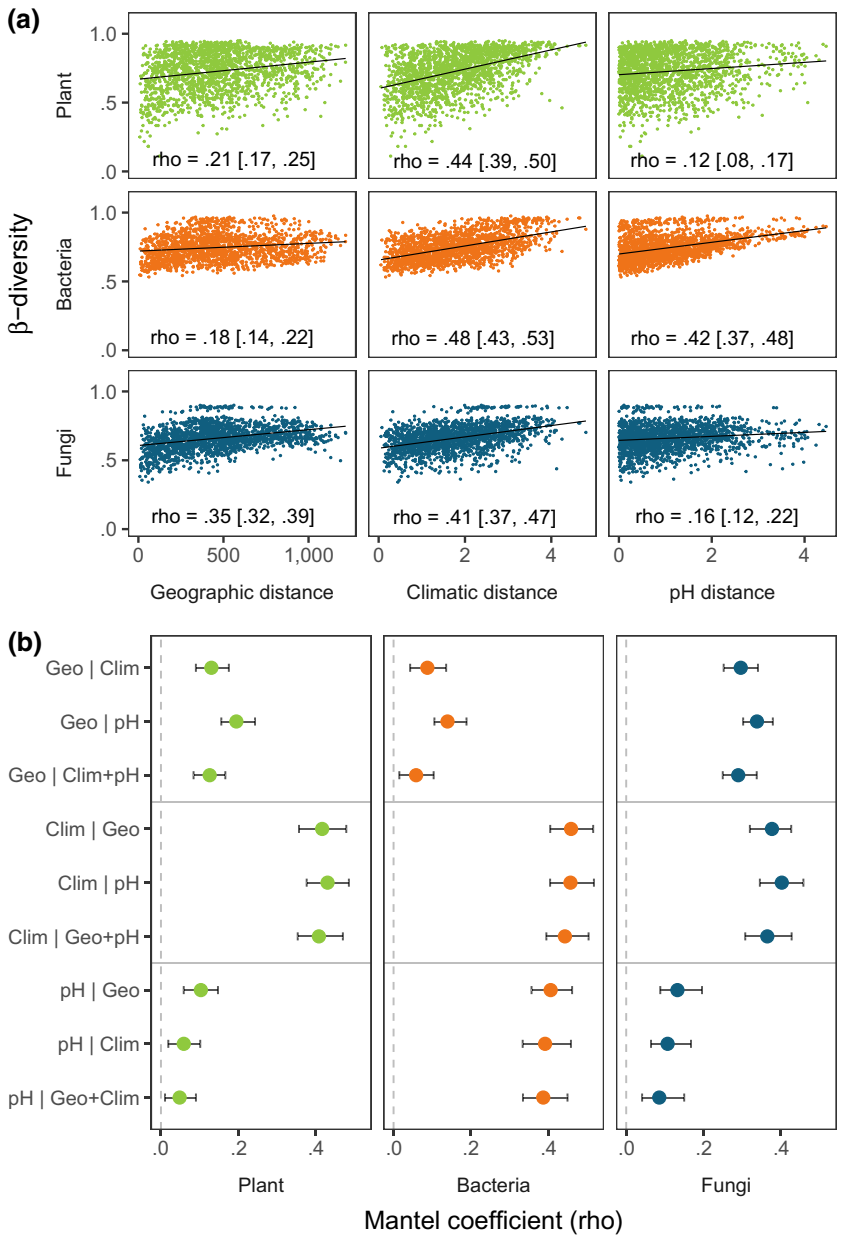


FIGURE 1 Biogeographic patterns of plant and soil microbial β-diversity. (a) Simple Mantel tests for relationships between abiotic factors (geographic, climatic and pH distances) and β-diversity. Lines are fitted by general linear regressions illustrating the direction of the bivariate associations. Spearman correlation coefficients (ρ) and the lower and upper 95% confidence intervals are given. (b) Partial Mantel tests for the relationships 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 to the right of |. Geo, geographic distance (km); Clim, climatic distance (unitless); pH, soil pH distance (unitless)

nutrient pools) (Figure 4; Supporting Information Table S4). In addition, the effects of plant β-diversity on soil bacterial β-diversity (β_{std} = .41; Figure 4; Supporting Information Table S4) were greater than those on soil fungal β-diversity (β_{std} = .31; Figure 4; Supporting Information Table S4). Soil bacterial β-diversity was moderately associated with soil fungal β-diversity (r = .47; Figure 4). We found that the alternate SEM did not substantially increase the R^2 values for plant and soil microbial β-diversity (Supporting Information Figure S2). However, the alternate SEM had a higher AIC value (AIC = 31,698 vs. 31,684; Supporting Information Tables S4 and S5), suggesting that plant- and soil-mediated nutrient pools were more likely driven by β-diversity.

We found that the magnitudes of the effects of β-diversity on spatial turnover in plant- and soil-mediated nutrient pools varied across spatial scales (Figure 5). At relatively small scales (e.g., <200 km), plant replacement was a more important (or at least as important) predictor of spatial turnover in plant-mediated nutrient pools than was soil bacterial replacement. At relatively large scales, we found moderately strong effects of soil bacterial replacement on spatial turnover in overall and soil-mediated nutrient pools but weak effects of soil bacterial replacement on spatial turnover in plant-mediated nutrient pools (Figure 5; Supporting Information Table S6). Further, we found that richness difference was a less important driver of spatial turnover in plant- and soil-mediated nutrient pools than replacement, geographic, climatic and soil pH distances (Figure 5 and Supporting Information Figure S3). However, we found a stronger effect of plant richness difference than soil microbial richness difference on spatial turnover in plant- and soil-mediated nutrient pools at relatively large scales (e.g., >200 km; Figure 5; Supporting Information Table S6).

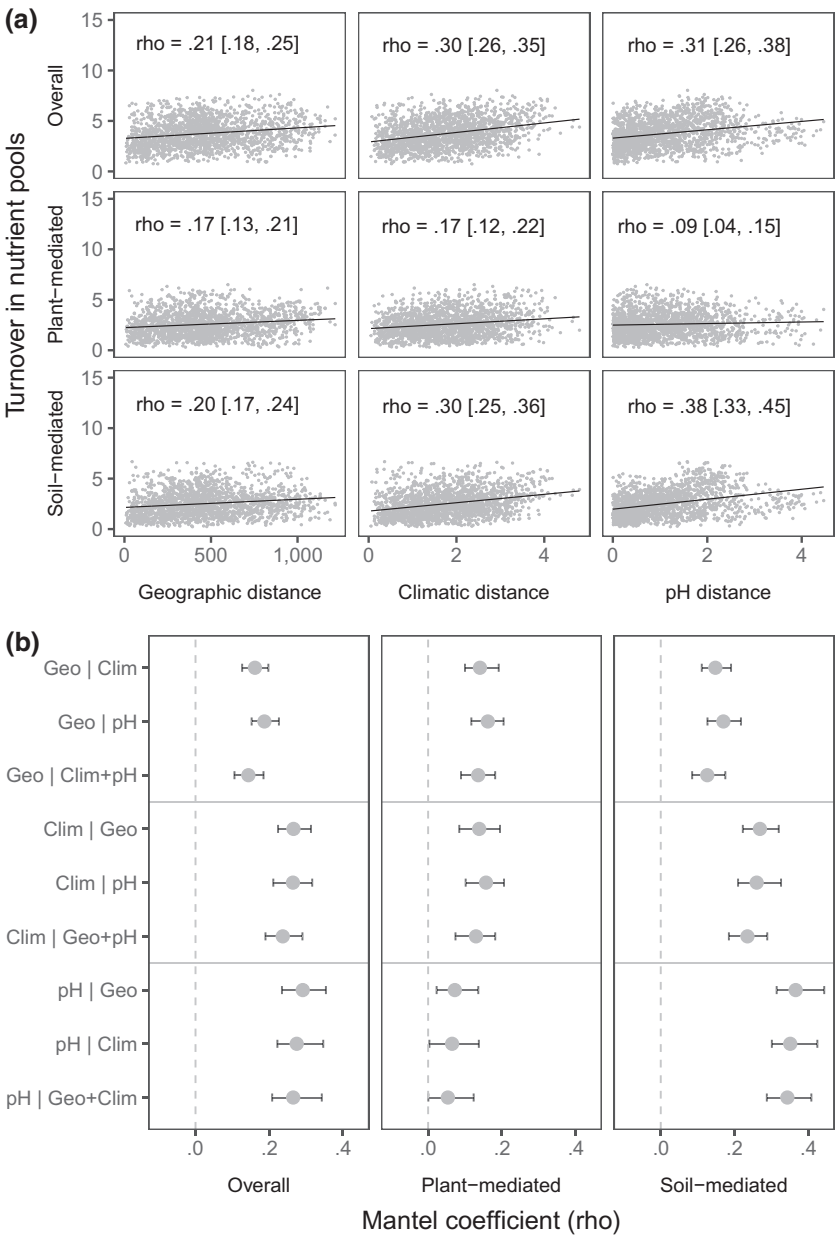


FIGURE 2 Geographic patterns of plant- and soil-mediated nutrient pools. (a) Simple Mantel tests for relationships between abiotic factors (geographic, climatic and soil pH distances) and spatial turnover in nutrient pools. Spearman correlation coefficients (ρ) and the lower and upper 95% confidence 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 to the right of |. Geo, geographic distance (km); Clim, climatic distance (unitless); pH, soil pH distance (unitless)

4 | DISCUSSION

This study investigated how above- and belowground species composition are concurrently connected with spatial turnover in plant- and soil-mediated nutrient pools in the alpine grasslands on the Qinghai-Tibetan Plateau, and pinpointed changes in plant and soil bacterial species composition that are directly associated not only with soil-mediated nutrient pools, but also with plant-mediated nutrient pools. The abiotic factor most consistently associated with the β-diversity of plants, soil bacteria and soil fungi was climate, while the influence of climate on plant- and soil-mediated nutrient pools was mostly indirect, and occurred through changes in plant and soil bacterial species composition. We discuss these findings in the context of plant and soil microbial biogeography with a focus on species composition–ecosystem function relationships across environmental gradients.

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 are not randomly distributed or 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 as climate and soil pH. Among the three abiotic factors examined here (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

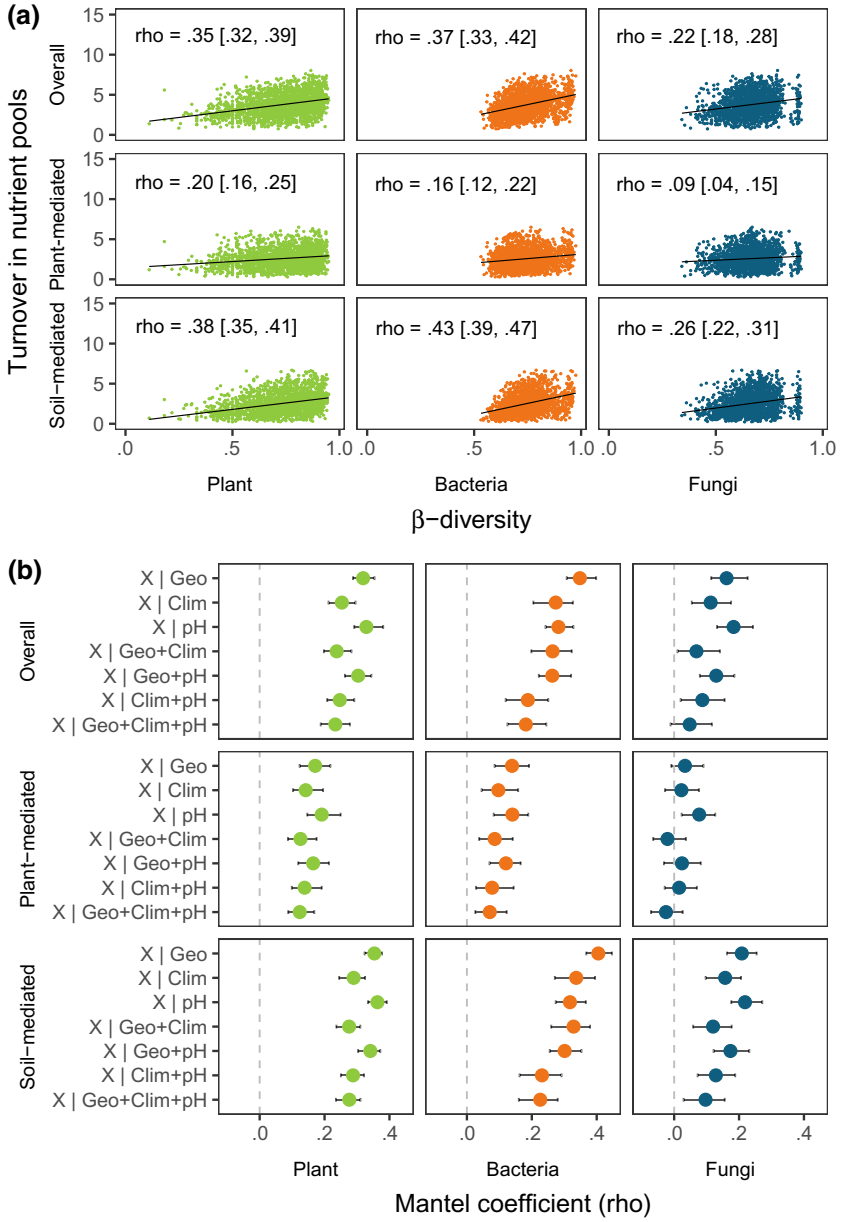


FIGURE 3 Relationships between β-diversity and spatial turnover in nutrient pools. (a) Simple Mantel tests for the relationships between β-diversity and spatial turnover in nutrient pools. Spearman correlation coefficients (ρ) and the lower and upper 95% confidence intervals are given. Lines are fitted by general linear regressions illustrating the direction of the bivariate associations. (b) Partial Mantel tests for the relationships 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 to the right of |. Geo, geographic distance; Clim, climatic distance; pH, soil pH distance

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 (Figure 1). This result suggests that the ongoing soil acidification in many Chinese grasslands (Y. 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 (Figure 1a,b). This suggests that dispersal limitation is also one of the important processes shaping the spatial turnover of soil fungal 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 simultaneously manipulate levels of above- and belowground biodiversity (Eisenhauer, 2011; Naeem et al., 1994; Scherber et al., 2010).

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

Our results highlight that abiotic factors, for example, climate and soil pH, are 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 are

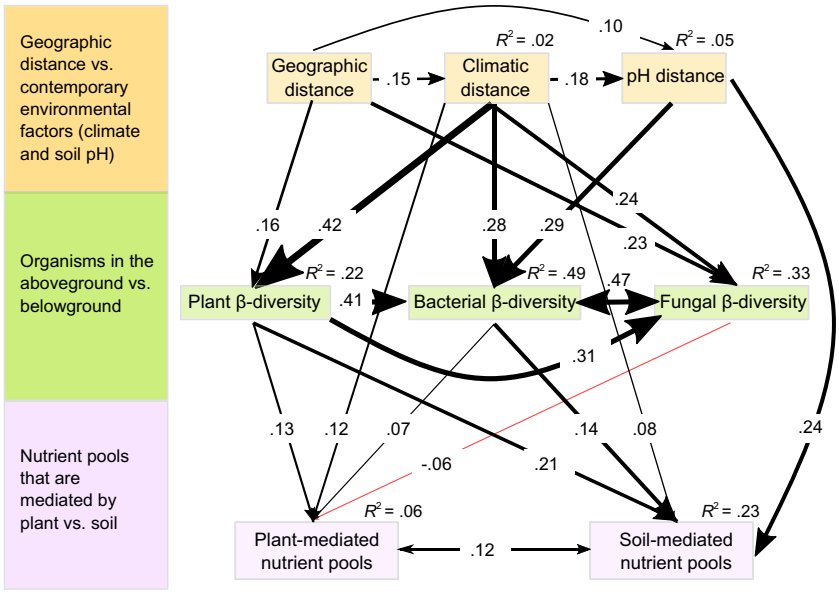
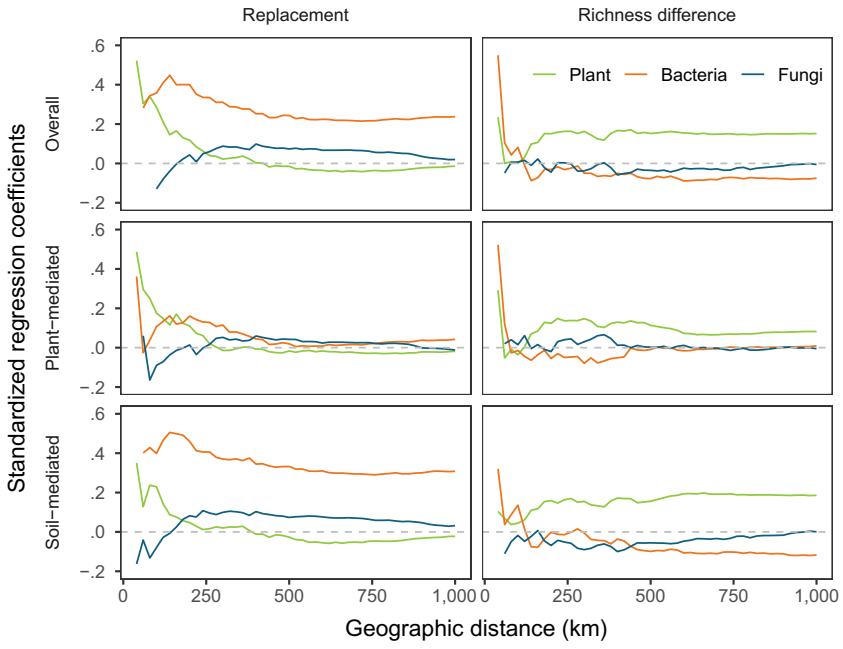


FIGURE 4 Direct and indirect effects of abiotic and biotic factors on plant- and soil-mediated nutrient pools. Arrows represent the direct and indirect pathways through which abiotic and biotic factors affect plant- and soil-mediated nutrient pools. Black arrows represent significantly positive pathways, and red arrows represent significantly negative pathways. Double-headed arrows represent residual correlations, that is, bacterial versus fungal β-diversity and plant- versus 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 Supporting Information Table S4

FIGURE 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 Supporting Information Table S6



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 are 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 are the same as those that influence patterns of plants and soil fungi, while those of soil-mediated nutrient pools are 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 for (Duffy et al., 2017). However, unlike the predictions of this meta-analysis, our work suggests that when more abiotic factors were controlled for, the effects of plant and soil bacterial β-diversity on spatial turnover in nutrient pools became weaker (Figure 3b), which is also 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 important 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 controlled for (Figure 3b). Our results therefore do not support the findings of an earlier landscape-scale study in forest ecosystems, in which the highly positive associations of soil fungal β-diversity with spatial turnover in ecosystem functions remained significant after geographic and environmental distances were controlled for (Mori et al., 2016).

An increasing number of studies show that soil fungal and bacterial diversity consistently and interactively promote a wide range of soil- and plant-mediated ecosystem functions, such as decomposing organic matter and enhancing plant nutrient uptake and growth (Delgado-Baquerizo et al., 2020; van der Heijden et al., 2008). However, contrary to our expectation, although soil fungal β-diversity was highly correlated with soil bacterial β-diversity, soil fungal β-diversity had weak effects on both spatial turnover in plant- and soil-mediated nutrient pools in the Qinghai-Tibetan alpine grasslands (Figure 4). One explanation is that large changes in soil fungal composition may be associated with small changes in ecosystem functions, that is, functional redundancy (Martinez-Almoyna et al., 2019; Peay et al., 2016; Talbot et al., 2014). Previous work has shown that functional redundancy may arise because of functional homogenization due to disturbance by exotic species (Peay et al., 2013). Here, however, functional homogenization was not one of the main driving factors because the study sites are relatively undisturbed natural alpine grasslands with little documented impacts of exotic species or direct impacts by humans (Jing et al., 2015). In the Qinghai-Tibetan grasslands, belowground microorganisms generally adjust their activities to the stressful environments, such as low annual temperature, high climatic seasonality, and short growing season (Jing et al., 2014; Wang et al., 2014). As a result, these adaptive strategies may lead to a high degree of functional redundancy of soil fungal communities across the unique and stressful environmental conditions in these (and similar) alpine grassland ecosystems.

Among the three abiotic factors studied here, soil pH distance had significant effects on soil-mediated nutrient pools but not on plant-mediated nutrient pools, while climatic distance had slightly positive effects on both plant- and soil-mediated nutrient pools (Figure 4; Supporting Information Table S4). As shown in the SEM, the effects of abiotic factors were mainly indirect, and occurred through changes in above- and belowground β-diversity (Figure 4). Specifically, abiotic factors accounted for 49%, 33% and 22% of the variance in soil bacterial, soil fungal and plant β-diversity, respectively (Figure 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 by 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 intermediate spatial scales (Supporting Information Figure 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 value 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 driving differences in β-diversity for 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 et al., 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 β-diversity was directly associated with spatial turnover in plant- and soil-mediated nutrient pools, while plant β-diversity was also indirectly associated with the spatial turnover of nutrient pools through changes in soil bacterial β-diversity. Our work further indicates that the replacement component of soil bacterial β-diversity, rather than differences in richness, was one of the more important drivers of spatial turnover in nutrient pools when geographic, climatic and soil pH distances were controlled for (Figure 5). The associations are likely explained by the fact that soil bacteria exhibit higher values of the replacement component of β-diversity than do plants and soil fungi (Supporting Information Figure S4). Our work thus indicates the necessity of investigating the role of above- and belowground linkages and additive partitioning components of β-diversity in maintaining spatial variability in multiple ecosystem

functions (Eisenhauer et al., 2019; Martinez-Almoyna et al., 2019; Soliveres et al., 2016; Trivedi et al., 2020). It also highlights the importance of changes in abiotic factors, including both geographic distance and contemporary environmental factors, in generating the biogeographic patterns of above- and belowground community structure and jointly affecting regional spatial turnover in ecosystem functions.

In summary, our study provides a comprehensive assessment of the biogeography of plant and soil microbial communities and their potential functions in natural alpine grassland ecosystems. We show that the relative importance of abiotic processes generating above- and belowground community structure differs, which suggests the rapid and ongoing environmental changes in alpine grasslands and elsewhere may have differential impacts on above- and belowground components of ecosystems. For example, soil acidification can substantially alter soil bacterial community composition, dispersal limitations can constrain spatial variation in soil fungal composition, and local climate can influence all above- and belowground taxa in the alpine grasslands. We further show that the impacts of local climate on spatial turnover in plant- and soil-mediated nutrient pools are mainly indirect, and occur through changes in plant and soil bacterial β-diversity, rather than through changes in soil fungal β-diversity. The direct associations of the replacement component of soil bacterial β-diversity and the richness difference of plant β-diversity with plant- and soil-mediated nutrient pools highlight that above- and belowground biodiversity may jointly safeguard against the impacts of local climate change on the functioning of climate-sensitive alpine grasslands at regional scales.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

NJS, XJ, ATC, J-SH, BZ, CMP and NJG developed the research questions. XJ analysed 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.

DATA AVAILABILITY STATEMENT

Soil bacterial sequence data have been deposited in the DNA Data Bank of Japan (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).

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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.

SUPPORTING INFORMATION

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