

ORIGINAL ARTICLE

Co-ordinated elevational diversity patterns for soil bacteria, fungi, and plants in alkaline soils of arid northwestern China

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Abstract

Plants often show remarkable elevational distribution patterns in arid-montane ecosystems. However, it is not clear if soil microbes follow elevational diversity patterns, even though they represent the majority of biodiversity and drive varieties of ecological processes. Here, we conducted a survey of fungal and bacterial communities across an elevational gradient from 2350 to 3850 m in a typical mountainous grassland of arid northwestern China. Our results revealed co-ordinated alpha and beta diversity patterns for soil microbes and plants along the elevational gradient, and the richness and Shannon diversity of bacteria, fungi, and plants exhibited a unimodal elevational pattern. The unimodal diversity pattern for soil microbes was further confirmed by the shifts in the relative abundance of dominant bacterial phyla (*Actinobacteria*, *Firmicutes* and *Nitrospirae*) and fungal phyla (*Zygomycota*) along the elevational gradient. Soil variables (soil pH, organic carbon, total nitrogen, available phosphorus, and nitrate nitrogen) explained the largest proportion of the variability in both bacterial and fungal communities, followed by plant (richness and Shannon diversity) and climatic (mean annual temperature and precipitation) variables. These environmental factors together explained a larger proportion of variability in bacterial communities (54.88%) than in fungal communities (24.15%). Our results strongly supported the existence of co-ordinated elevational diversity patterns for soil microbes and plants in arid-montane ecosystems, and highlighted that the importance of soil pH in microbial elevational patterns was also apparently in alkaline soils.

Highlights

- Soil bacteria and fungi follow elevational diversity patterns of plants.
- Species richness and Shannon diversity index exhibited unimodal elevational patterns.
- Soil, plant, and climatic factors are co-responsible for microbial diversity.
- These factors explained more variation in bacteria than that in fungi.
- Microbial diversity is more vulnerable to precipitation than temperature.

KEYWORDS

alpine grasslands, arid-montane ecosystems, bacterial community, elevational diversity gradients, environmental drivers, fungal community

1 | INTRODUCTION

Montane ecosystems are unique habitats, often characterised by dramatic changes in temperature, precipitation, and light (Körner, 2007; Peng et al., 2018). High variability in topographic, climatic, and edaphic conditions over short distances regulate biotic turnover and distribution, and often result in distinct altitudinal biozones in montane ecosystems (Bryant et al., 2008; Cardelus et al., 2006; Z. Wang et al., 2013). Biodiversity in these ecosystems received considerable attention from ecologists globally (Fierer et al., 2011; Luo et al., 2019; J. T. Wang et al., 2015). Furthermore, a large body of research has documented that montane ecosystems and associated species are particularly sensitive and vulnerable to climate change (Beniston et al., 1997; Gobiet et al., 2014; Thuiller, 2007). Elevational gradients can serve as excellent natural experiments to explore potential effects of climate-related factors on biota (Frenne et al., 2013; Körner, 2007; Siles & Margesin, 2016; Zi et al., 2018). Increased understanding of biological elevational diversity patterns can aid in prediction of the potential ecological consequences of climate change in montane regions.

To that end, spatial patterns in biodiversity of plants and animal taxa along elevational gradients have been intensively investigated over several decades (Alexander et al., 2011; Fu et al., 2007; Zhang et al., 2013). By contrast, elevational patterns in microbial communities remain poorly understood, even though they represent the majority of biodiversity in terrestrial ecosystems and drive a variety of ecological processes (Dequiedt et al., 2009; Nemergut et al., 2013). With the development and application of modern molecular approaches, altitudinal changes in microbial community have attracted increasing attention (Fierer et al., 2011; Zhou et al., 2015). However, different and sometimes contradictory results have been reported in different studies (Luo et al., 2019; Siles & Margesin, 2016; Singh et al., 2014). For example, a declining pattern in soil acidobacterial diversity with elevation was first documented by Bryant et al. (2008) in the Rocky Mountains of Colorado, and by Shen et al. (2014) for bacterial diversity in Nyainqentanglha Mountains in the central Tibetan Plateau. In contrast, Siles and Margesin (2016) observed an increase in bacterial alpha diversity and no clear pattern in archaeal community in the Italian Alps. Meng et al. (2013) and Peng et al. (2018) reported a unimodal pattern in bacterial alpha diversity in

Halla Mountain in South Korea and Taibai Mountain in China, respectively. The inconclusive results indicate that further investigations of mountain ecosystems are needed to deepen our understanding of microbial patterns over altitudinal gradients (Aurore et al., 2014; Meng et al., 2013; Shen et al., 2019; Siles & Margesin, 2016).

Furthermore, the mechanisms underlying microbial community assembly over altitudinal gradients are still only hypothetical (Siles & Margesin, 2016; Peng et al., 2018). Some authors have used the mid-domain effect mode to explain the mid-elevational richness 'peak' for macroorganisms and the unimodal pattern of microbial communities with elevation (Colwell & Lees, 2000; J. T. Wang et al., 2015). However, Bryant et al. (2008) reported that the elevational diversity pattern in microbial communities in the Rocky Mountains of Colorado was better interpreted by edaphic variables, especially soil pH, than by mid-domain effect mode. These findings were then confirmed by Shen et al. (2014), Siles and Margesin (2016) and Cho et al. (2018), who highlighted the role of soil pH and nutrient availability in regulating elevational microbial distribution patterns in montane ecosystems. Climatic factors have often been considered as a principal predictor of the declining trend for plant and animal diversity with elevation. Evidence from Singh et al. (2013) on Halla Mountain in South Korea indicated that climate-related factors, notably temperature and precipitation, contributed most variability to the strong elevational trends in soil bacterial community composition. Nottingham et al. (2018) also reported that temperature was the principal driver shaping the decreasing diversity pattern for both plants and microbes along an elevation transect in the Peruvian Andes. Peng et al. (2018) documented that plant characteristics also contributed large proportions of variation in microbial communities over altitudinal gradients through modification of microclimate, litter production and quality, and interactions with root symbiotic organisms. Likewise, there is no single environmental factor consistently explaining the microbial patterns over altitudinal gradients, although climate, soil, and plant variables are often among the most important predictors (Deng et al., 2019; Peng et al., 2018; Siles & Margesin, 2016).

The Qilian Mountains constitute one of the largest and highest mountain ranges, and a major biodiversity hotspot in arid northwestern China. Grasslands occupy more than 60% of the total area (He et al., 2012). The mountains are characterised by complex topography with steep

elevations, generating remarkable elevational distribution patterns for climate and vegetation (Chen et al., 2016; Jia et al., 2016). The unique climate and ecological gradients make it an optimal environment to investigate microbial elevational patterns and the underlying assembly mechanisms. Thus far, only a bacterial diversity study has been conducted in Tianshan Mountains, another typical mountain range in arid northwestern China (Y. T. Zhao et al., 2018). Furthermore, global climate change has already resulted in an increase in temperature in this area of about 0.29°C per decade since the 1960s (Lin et al., 2017). Therefore, an investigation of the changes in microbial communities along large elevational gradients in this zone will increase the understanding of the response of soil microbes to future climate change, and will aid in biodiversity conservation in arid-montane ecosystems. In this study, we aimed to explore the elevational patterns of microbial communities and the environmental driving factors along an altitudinal gradient. For this purpose, we selected a typical elevational gradient from 2350 to 3850 m a.s.l in a montane grassland in the Qilian Mountains. We hypothesised that (1) soil bacteria and fungi follow elevational diversity patterns similar to those of plants, and (2) soil, plant, and climatic characteristics are co-responsible for the variability in bacterial and fungal microbial communities along altitudinal gradients.

2 | METHODS

2.1 | Study sites

The study area is located in the Dayekou watershed (2250–3980 m a.s.l, 100°13′–100°16′E, 38°16′–38°33′N) in Sunan County, Gansu Province, which is part of the Qilian Mountains. The mean annual temperature (MAT) was 2°C and the mean annual precipitation (MAP) was about 376 mm according to meteorological observations (from 2000 to 2018) at Pailugou station (located at 2700 m a.s.l in the Dayekou watershed and affiliated to Linze Inland River Basin Research Station, Chinese Academy of Sciences). Grasslands are the main landscape types in the zone, and are mainly found on sunny, south-facing, and semi-shaded, east- or west-facing slopes; scrublands and forests, dominated by the Qinghai spruce (*Picea crassifolia*), are found primarily on shaded, north-facing slopes.

2.2 | Experimental design, soil sampling, and vegetation survey

We sampled in August 2018 in six long-term observation sites (established in August 2013) along an altitudinal

gradient at 2350, 2650, 2950, 3250, 3550, and 3850 m a.s.l on a south-facing slope (Table 1). At each site, three replicate plots of 30 m × 30 m were randomly established; the plots were spaced at least 50 m apart in order to avoid edge effects. Precipitation for MAP of the plots was determined with standing tipping-bucket pluviographs. MAT for each plot was monitored by thermo-hygrometer (EL-USB-2-LCD, Lascar Electronics).

Twelve samples of topsoil (0–20 cm) were randomly collected in each plot using a soil auger after removing the litter layer; these samples were then mixed into one sample. Samples were divided into two parts: one part was stored at –80°C for DNA analysis; the other part was air-dried for chemical analysis. Further, 10 quadrats of 1 × 1 m² were randomly located in each plot to investigate species composition and percent cover of the herbaceous community. Plants were dug up and dried to obtain the biomass (include both aboveground and root biomass). The number of species identified in each quadrat was used to estimate species richness (R_{plant}); Shannon diversity index (H_{plant}) of plant community was calculated using the equation: $H = -\sum_{i=1}^n (P_i \ln P_i)$, where P_i is the relative abundance of species i (calculated by percentage biomass), and n is the number of species (Chen et al., 2016; W. Zhao et al., 2009).

2.3 | Analysis of soil physicochemical properties

We analysed soil pH, soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP), ammonium nitrogen (NH₄⁺-N), nitrate nitrogen (NO₃⁻-N), and available phosphorus (AP) (Table 2). Detailed soil physicochemical analyses were described in Chen et al. (2020).

2.4 | DNA extraction and sequencing

DNA was extracted from 0.50 g of fresh soil using the Power Soil DNA Isolation kit (MoBio Laboratories, Carlsbad, CA). The primers 338F and 806R were used to amplify the V3-V4 hyper variable region of 16S rRNA gene in bacteria. The internal transcribed spacer (ITS) rRNA gene in fungi was amplified using the PCR primers ITS1F and ITS2R. PCR reactions were performed in triplicate with 20 µl mixtures, containing 4 µl of 5 × FastPfu Buffer, 2 µl of 2.5 mM dNTPs, 0.8 µl of forward and reverse primers (5 µM), 0.4 µl of FastPfu Polymerase, 0.2 µl of BSA, and 10 ng Template DNA. Details of the purification and quantification were described in Chen et al. (2020). After purification and quantification, PCR

TABLE 1 Site characteristics along an altitudinal gradient

Sites	Altitude (m)	Slope		MAT (°C)	MAP (mm)	Dominant plant species
		aspect	Slope gradient			
38E	3850	S	19°	-4.8 ± 0.1	553.5 ± 6.3	<i>Polygonum viviparum</i> ; <i>Kobresia humilis</i> ; <i>Plantago depressa</i> ; <i>Kobresia capillifolia</i>
35E	3550	SE	21°	-3.1 ± 0.3	595.6 ± 10.4	<i>Kobresia humilis</i> ; <i>Polygonum viviparum</i> ; <i>Potentilla multifida</i> ; <i>Plantago depressa</i>
32E	3250	S	18°	-1.3 ± 0.1	516.1 ± 6.7	<i>Kobresia humilis</i> ; <i>Carex atrata</i> ; <i>Polygonum viviparum</i> ; <i>Potentilla chinensis</i>
29E	2950	S	16°	0.4 ± 0.2	447.0 ± 4.8	<i>Elymus cylindricus</i> ; <i>Agropyron cristatum</i> ; <i>Carex atrata</i> ; <i>Potentilla supina</i>
26E	2650	SW	17°	2.1 ± 0.1	387.2 ± 2.5	<i>Agropyron cristatum</i> ; <i>Elymus cylindricus</i> ; <i>Heteropappus altaicus</i> ; <i>Carex atrata</i>
23E	2350	SE	15°	4.0 ± 0.2	336.3 ± 3.1	<i>Peganum harmala</i> ; <i>Heteropappus altaicus</i> ; <i>Stipa breviflora</i> ; <i>Allium chrysanthum</i>

Note: 23E, 26E, 29E, 32E, 35E and 38E represent sites at 2350, 2650, 2950, 3250, 3550, and 3850 m.

Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature.

amplicons were pooled at equimolar ratios, and then paired-end sequenced (2 × 250) bp on the Illumina Miseq PE 250 platform. The raw sequences were deposited in the NCBI Sequence Read Archive (accession number SRP316310).

2.5 | Processing of sequencing data

The obtained raw sequences were quality-filtered and chimera checked using the QIIME software. Quality-filtered sequences at 97% nucleotide similarity were assigned to the same operational taxonomic units (OTUs) with the UPARSE software. 16S rRNA sequences and ITS sequences were assigned taxonomy based on the bacterial SILVA reference database (Release 132; <http://www.arb-silva.de>) and the Unite reference database (Release 7.2; <http://unite.ut.ee/index.php>) using the Ribosomal Database Project classifier. Alpha diversity indices including Good's coverage, Chao1, and Shannon's index were obtained using MOTHR.

2.6 | Statistical analysis

One-way analysis-of-variance, followed by a least significant difference multiple comparison ($p < 0.05$), was used to evaluate the differences in soil and plant characteristics along the altitudinal gradient ('multcomp' package in R v.3.2.3). Ordinary least squares regression was used to assess the relationship of elevation with alpha diversity indices for plant, bacterial, and fungal communities ('basicTrendline' package in R v.3.2.3). We

tested four models (quadratic, linear, logarithm, and exponent) to describe the relationships. The model was selected based on adjusted R^2 , root mean square error, and akaike information criterion, and the significance of the fits were evaluated by Wald-test. Principal coordinates analysis (PCoA) was performed to detect the overall differences in plants, bacterial, and fungal community composition based on Bray-Curtis distances along the elevational gradient ('ape' package in R v.3.2.3). Pearson correlation analysis was used to assess the relationships between alpha and beta diversity indices of plant, bacterial, and fungal communities, the relationships between alpha and beta diversity indices of bacterial and fungal communities and environmental factors, and the relationships between dominant bacterial and fungal phyla and environmental variables ('psych' package in R v.3.2.3). Redundancy analysis (RDA) was used to identify the correlations among environment variables (soil, plant, and climatic variables) and the bacterial and fungal community based on Hellinger pre-transformed community data ('vegan' package in R v.3.2.3). Variance inflation factor (VIF) was measured to judge the collinearity among different environmental factors by the functions of envfit (permu = 999) and vif.cca ('car' package in R v.3.2.3), and the environmental factors with VIF > 10 were removed from the RDA analysis. The VIF values of SOC, TN, TP, and plant cover were higher than 10 and removed. The contributions of the soil, plant, and climatic characteristics (selected by RDA analysis) to the bacterial and fungal community changes were determined by variance partition analysis (VPA) ('vegan' package in R v.3.2.3).

TABLE 2 Soil and vegetation characteristics along an altitudinal gradient

Sites	Soil pH	Vegetation characteristics									
		SOC (g kg ⁻¹)	TN (g kg ⁻¹)	TP (g kg ⁻¹)	NH ₄ ⁺ -N (mg kg ⁻¹)	NO ₃ ⁻ -N (mg kg ⁻¹)	AP (mg kg ⁻¹)	CO (%)	BI (g cm ⁻³)	R _{plant}	H _{plant}
38E	7.29 ± 0.06d	79.90 ± 3.86b	7.85 ± 0.15b	1.51 ± 0.26d	3.61 ± 1.45a	91.54 ± 8.15b	12.37 ± 0.31c	50.1 ± 3.6d	122.3 ± 11.9 cd	15 ± 1a	2.09 ± 0.09ab
35E	6.72 ± 0.04e	91.22 ± 5.46a	7.96 ± 0.01b	2.01 ± 0.11bc	4.65 ± 1.06a	126.21 ± 4.43a	11.84 ± 0.43c	59.3 ± 3.2c	142.0 ± 7.4c	16 ± 2a	2.23 ± 0.09ab
32E	6.68 ± 0.02e	92.89 ± 4.60a	9.35 ± 0.17a	3.27 ± 0.12a	4.71 ± 1.69a	127.24 ± 2.31a	16.19 ± 0.17a	90.0 ± 2.9a	220.5 ± 7.9a	13 ± 1ab	2.35 ± 0.16a
29E	8.10 ± 0.03c	42.30 ± 3.63c	4.34 ± 0.02c	2.13 ± 0.09b	3.87 ± 1.97a	61.04 ± 16.39bc	8.06 ± 0.18d	70.0 ± 2.9b	172.3 ± 7.3b	11 ± 2b	2.26 ± 0.23ab
26E	8.31 ± 0.02b	35.11 ± 2.26d	3.29 ± 0.04d	1.72 ± 0.27 cd	2.25 ± 1.50a	49.02 ± 21.19c	7.79 ± 0.30d	45.3 ± 2.2d	111.2 ± 8.1de	10 ± 2bc	2.04 ± 0.08ab
23E	8.93 ± 0.10a	20.98 ± 2.23e	1.15 ± 0.05e	1.65 ± 0.13d	1.93 ± 1.17a	9.51 ± 0.77a	14.78 ± 0.29b	38.0 ± 2.5e	89.9 ± 12.8e	7 ± 2c	1.42 ± 0.15c
F	90.714	261.271	388.975	39.379	1.844	47.782	23.170	42.224	37.716	11.965	16.093
p	***	***	***	***	0.179	***	***	***	***	***	***

Note: Values (±SD) followed by different lowercase letters within rows are significantly different at $p < 0.05$. 23E, 26E, 29E, 32E, 35E and 38E represent sites at 2350, 2650, 2950, 3250, 3550, and 3850 m. Abbreviations: AP, available phosphorus; BI, plant biomass; CO, plant cover; H_{plant}, Shannon diversity; NH₄⁺-N, ammonia nitrogen; NO₃⁻-N, nitrate nitrogen; R_{plant}, species richness; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus.

*** $p < 0.001$.

3 | RESULTS

3.1 | Soil and vegetation characteristics along the altitudinal gradient

Concentrations of SOC, TN, TP, and NO₃⁻-N increased with elevation and then decreased ($p < 0.001$), with the highest values at 3250 m. Soil pH decreased with elevation and then increased ($p < 0.001$), and was lowest at 3250 m (Table 2). Concentrations of AP show no apparent patterns along the altitudinal gradient, although some differences were statistically significant. No significant differences were observed in NH₄⁺-N among elevational sites ($p > 0.05$).

Plant community composition differed significantly among elevational sites. Specifically, plant cover, biomass, R_{plant}, and H_{plant} increased initially and then decreased with elevation, with plant cover, biomass, and H_{plant} reaching the highest values at 3250 m, while R_{plant} at 3550 m (Table 2). Both R_{plant} and H_{plant} exhibited unimodal patterns with elevation (Figure 1).

The PCoA plot indicated clear differences along coordinate 1 in plant community composition, and plant communities formed three separate clusters along the altitudinal gradient: plant communities at 3850, 3550, and 3250 m clustered together, those at 2950 and 2650 m clustered together, and both were separated from the ones at 2350 m (Figure 3a).

3.2 | Diversity and composition of soil bacterial community along the altitudinal gradient

A total of 3786 bacterial OTUs were identified and assigned to 37 phyla. The dominant phyla (relative abundance >1%) were *Actinobacteria* (22.90%–32.81%), *Proteobacteria* (15.20%–31.60%), *Acidobacteria* (13.89%–19.75%), and less than 10% each of *Chloroflexi*, *Bacteroidetes*, *Firmicutes*, *Gemmatimonadetes*, *Cyanobacteria*, *Verrucomicrobia*, *Nitrospirae*, and *Planctomycetes* (Table S4). Notably, the relative abundance of *Actinobacteria*, *Firmicutes*, *Gemmatimonadetes*, *Cyanobacteria*, and *Nitrospirae* differed significantly along the elevational gradient; *Actinobacteria*, *Firmicutes*, and *Nitrospirae* exhibited unimodal patterns with elevation, while *Gemmatimonadetes* and *Cyanobacteria* exhibited hollow patterns with elevation (Table S4; Table S5).

Bacterial alpha diversity indices varied along the elevational gradient, and both the Chao and Shannon indices showed unimodal patterns with elevation (Figure 1). Similarly, the number of bacterial classes, families, species, and OTUs also showed unimodal patterns with elevation (Figure 2).

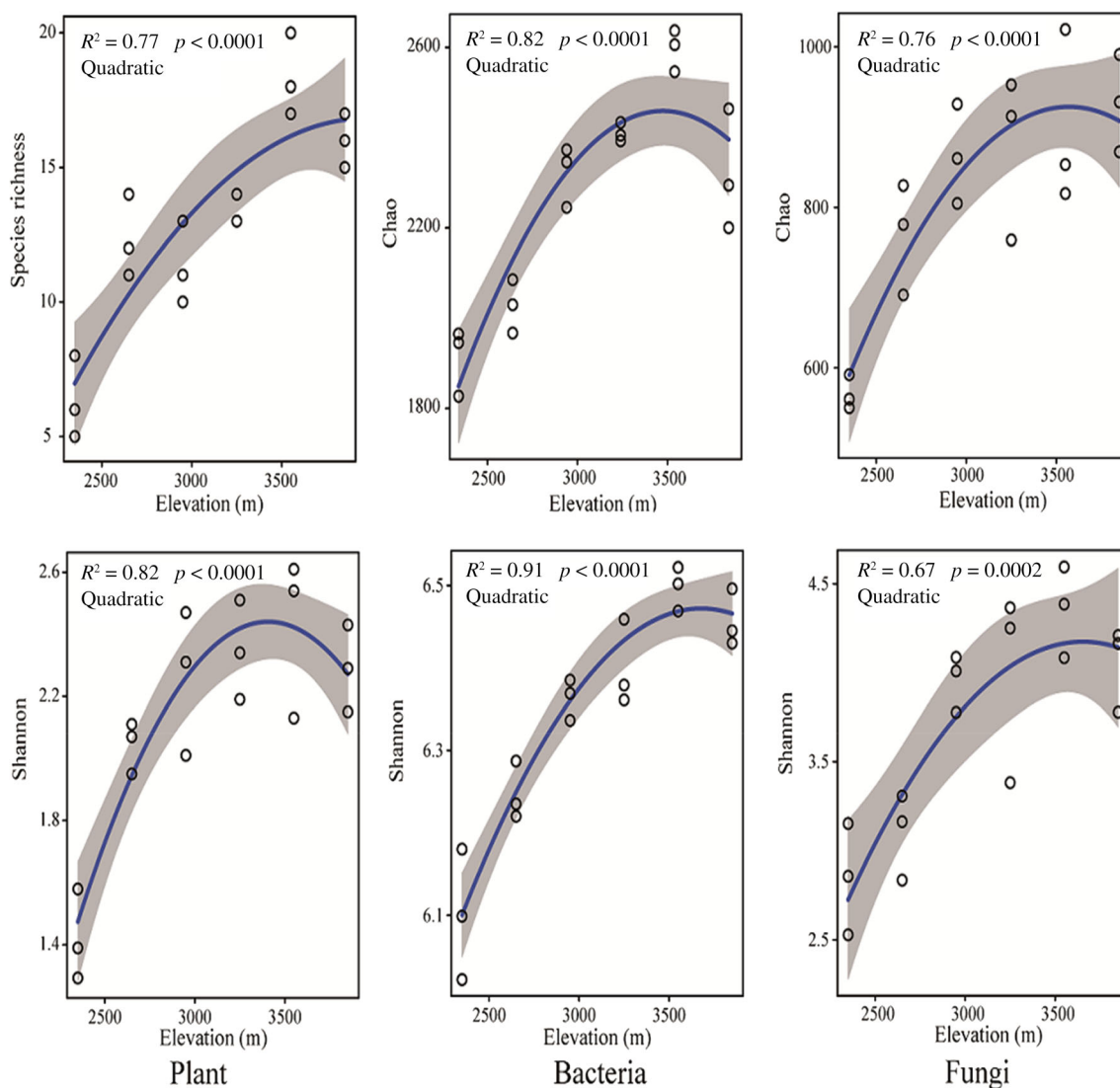


FIGURE 1 Relationships between elevation and alpha diversity indices for plant, bacterial and fungal communities. The relationships were described by quadratic models. The model was selected based on adjusted R^2 , root mean square error and akaike information criterion. p -Values indicated how significant the models were

The PCoA plot indicated clear differences along coordinate 1 in bacterial community composition, and bacterial communities formed three separate clusters along the altitudinal gradient: bacterial communities at 3850, 3550, and 3250 m clustered together, those at 2950 and 2650 m clustered together, and both were separated from the ones at 2350 m (Figure 3b).

3.3 | Diversity and composition of soil fungal community along the altitudinal gradient

A total of 3367 fungal OTUs were identified and assigned to 9 phyla. The dominant phyla (relative

abundance >1%) were *Ascomycota* (55.27%–84.92%), *Basidiomycota* (6.61%–30.59%), *Zygomycota* (0.51%–13.06%), and *Chytridiomycota* (0.28%–1.44%) (Table S4). Notably, the relative abundance of *Zygomycota* differed significantly along the elevational gradient and showed unimodal pattern with elevation (Table S4; Table S5).

The fungal alpha diversity indices also varied along the elevational gradient, and both the Chao and Shannon indices showed unimodal patterns with elevation (Figure 1). Similarly, the number of fungal classes, families, species, and OTUs also showed unimodal patterns with elevation (Figure 2).

The PCoA plot also indicated clear differences along coordinate 1 in fungal community composition,

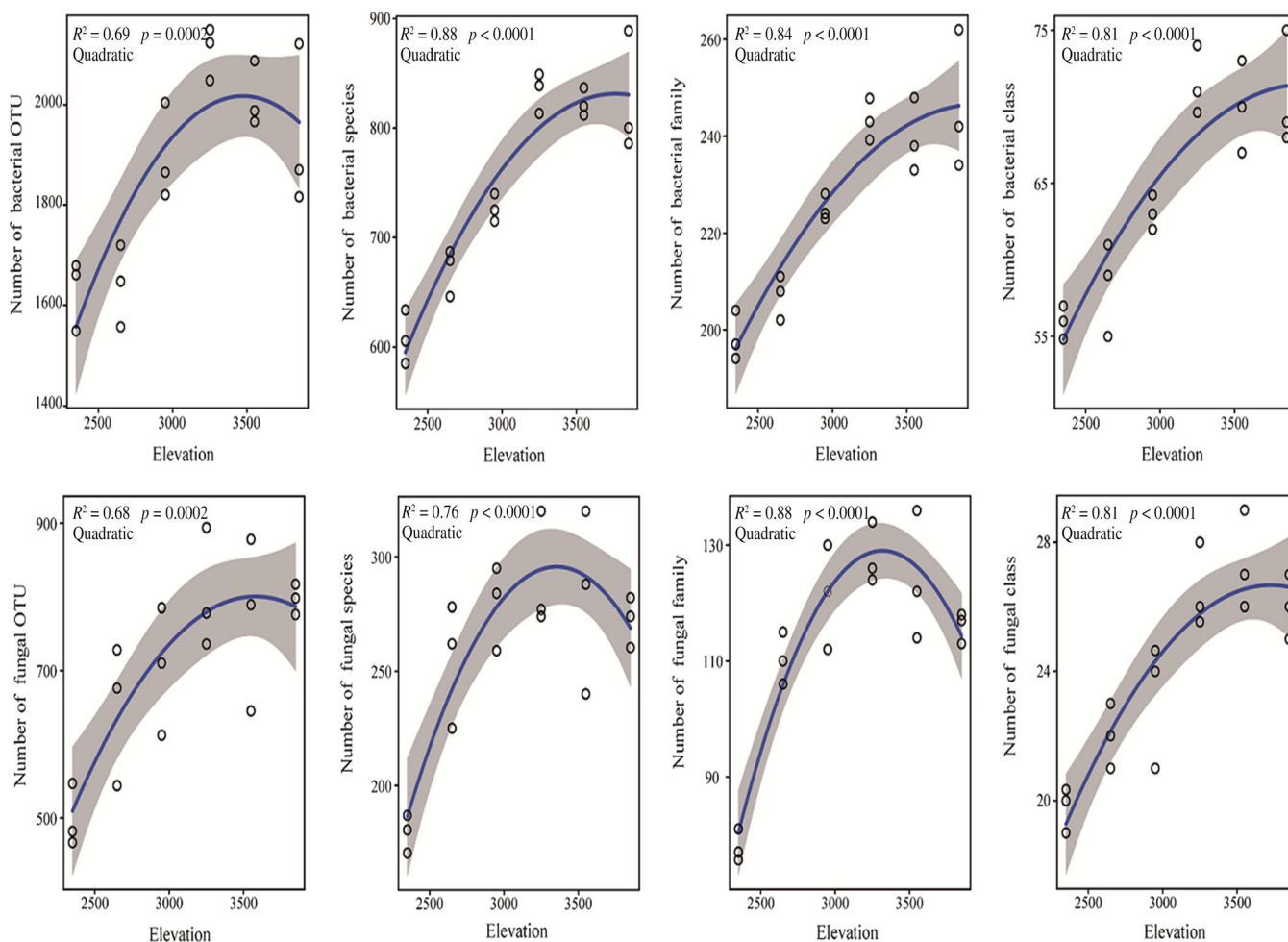


FIGURE 2 Number of classes, families, species, and operational taxonomic units (OTUs) for bacteria and fungi along the altitudinal gradient and their relationships with elevation. The relationships were described by quadratic models. The model was selected based on adjusted R^2 , root mean square error and akaike information criterion. p -Values indicated how significant the models were

and fungal communities formed three separate clusters along the altitudinal gradient: fungal communities at 3850, 3550, and 3250 m clustered together, fungal communities at 2950 and 2650 m clustered together, and both were separated from those at 2350 m (Figure 3c).

3.4 | Relationships between soil microbial community and environmental factors

RDA showed that soil pH ($r^2 = 0.90$), MAP ($r^2 = 0.87$), AP ($r^2 = 0.86$), NO_3^- -N ($r^2 = 0.83$), MAT ($r^2 = 0.78$), H_{plant} ($r^2 = 0.73$), and R_{plant} ($r^2 = 0.66$) were the most significant environmental factors explaining variability in bacterial community composition (Figure 4a; Table 3). VPA further revealed that these factors together

explained 54.88% of the variance in bacterial community along the altitudinal gradient (Figure 4c). The contribution of soil (soil pH, AP and NO_3^- -N), plant (H_{plant} and R_{plant}), and climatic (MAP and MAT) characteristics explained 35.47, 23.59, and 8.83%, respectively, of bacterial community changes.

RDA showed that soil pH ($r^2 = 0.83$), H_{plant} ($r^2 = 0.78$), MAP ($r^2 = 0.78$), NO_3^- -N ($r^2 = 0.76$), AP ($r^2 = 0.74$), R_{plant} ($r^2 = 0.71$), and MAT ($r^2 = 0.65$) were the most significant environmental parameters explaining the variability in fungal community composition (Figure 4b; Table 3). VPA further revealed that these parameters together explained 24.15% of the variance in fungal community along the altitudinal gradient (Figure 4d). The contribution of soil (soil pH, AP and NO_3^- -N), plant (H_{plant} and R_{plant}), and climatic (MAP and MAT) characteristics explained 6.69, 2.70, and 1.51%, respectively, of fungal community changes.

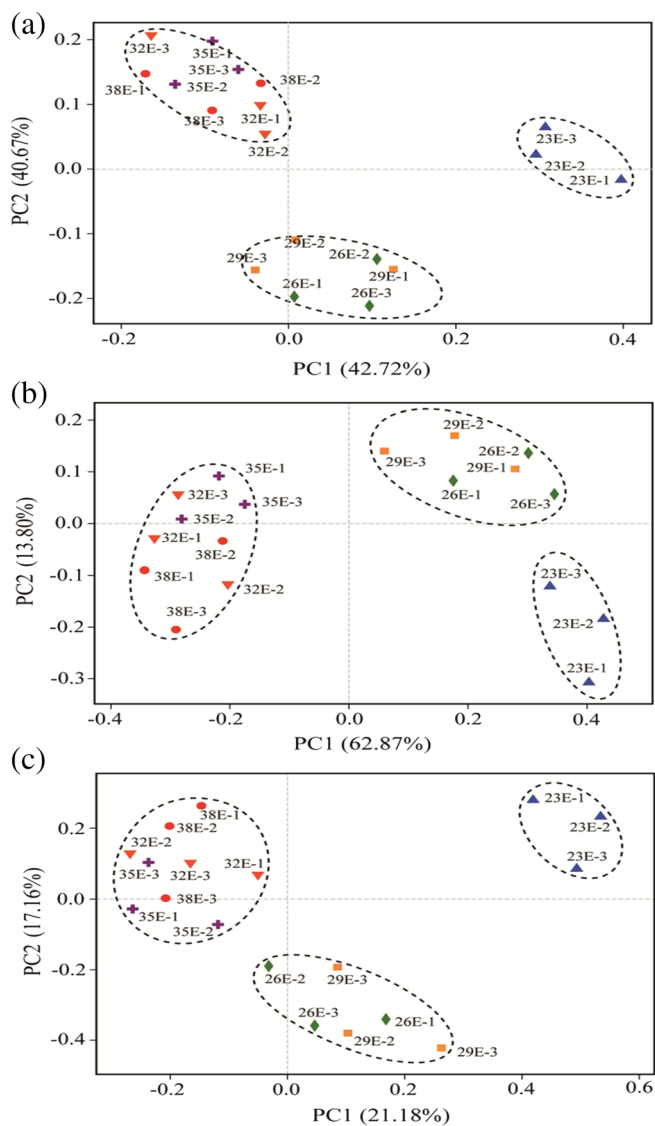


FIGURE 3 Principal coordinates analysis of plant (a), bacterial (b) and fungal (c) community composition along the elevational gradient. Values at axes 1 and 2 are the percentages that can be explained by the corresponding axis. 23E, 26E, 29E, 32E, 35E and 38E represent sites at 2350, 2650, 2950, 3250, 3550, and 3850 m

4 | DISCUSSION

4.1 | Distribution patterns of soil bacterial and fungal communities along an elevation gradient

Steep elevation gradients along with high variability in climatic conditions result in remarkable plant distribution patterns in arid-montane ecosystems (Chen et al., 2016; Jia et al., 2016; Y. T. Zhao et al., 2018). The results of this study demonstrated co-ordinated alpha and beta diversity patterns for soil microbes and plants along the elevational gradient in the arid-montane ecosystem:

the richness and diversity of bacteria, fungi, and plants exhibited significant quadratic relationships with elevation (a unimodal pattern); the community composition of all three groups formed three separate clusters along the altitudinal gradient, specifically, communities at 3850, 3550, and 3250 m clustered together, communities at 2950 and 2650 m clustered together, and both were separated from those at 2350 m. Significant correlations ($p < 0.01$) between the alpha and beta diversity indices of bacteria, fungi, and plants, confirming the co-ordinated elevational diversity patterns for soil bacteria, fungi, and plants (Table S2). These findings confirm our basic hypothesis, and indicated that plant diversity dynamics have important implications for the prediction of soil microbial diversity changes under climate change scenarios in the arid-montane ecosystem, which may be of great significance for biodiversity conservation.

Distinct elevational patterns of bacterial diversity above and below the treeline were reported by G. Li et al. (2016). Shen et al. (2019) reviewed more than 20 soil microbial studies from 2008 to 2018 and further found that the elevational diversity patterns for microbial communities were related to the treeline. Soil microbes above the treeline often showed decreasing diversity trends with elevation (Bryant et al., 2008; G. Li et al., 2016; Shen et al., 2019), while those that extended across the treeline showed other trends, such as unimodal (Peng et al., 2018), hollow (Singh et al., 2014), and increasing (Siles & Margesin, 2016). In the present study, a unimodal diversity pattern was detected for both bacterial and fungal communities across an elevational gradient from 2350 to 3850 m (treeline was at about 3250 m), similar to the results of Meng et al. (2013) from Halla Mountain in South Korea, and Peng et al. (2018) from Taibai Mountain in China.

The dominant phyla in bacterial and fungal communities in this study were also documented in other alpine ecosystems (Peng et al., 2018; Shen et al., 2019; Siles & Margesin, 2016), and were generally consistent along an elevational gradient. However, their relative abundance varied with elevation in this study. The unimodal diversity pattern for soil microbes was further confirmed by the shifts in the relative abundance of dominant bacterial and fungal phyla along the elevational gradient. For example, bacterial phyla of *Actinobacteria*, *Firmicutes*, and *Nitrospirae*, and fungal phyla of *Zygomycota* showed unimodal patterns with elevation. These major taxonomic groups have been associated with copiotrophic life history strategies and prefer nutrient-rich environments (Lim et al., 2014; Nottingham et al., 2018). Thus, the unimodal distribution patterns for these phyla could be explained by the initial increase and then decrease in the levels of C and other nutrients with elevation. Our

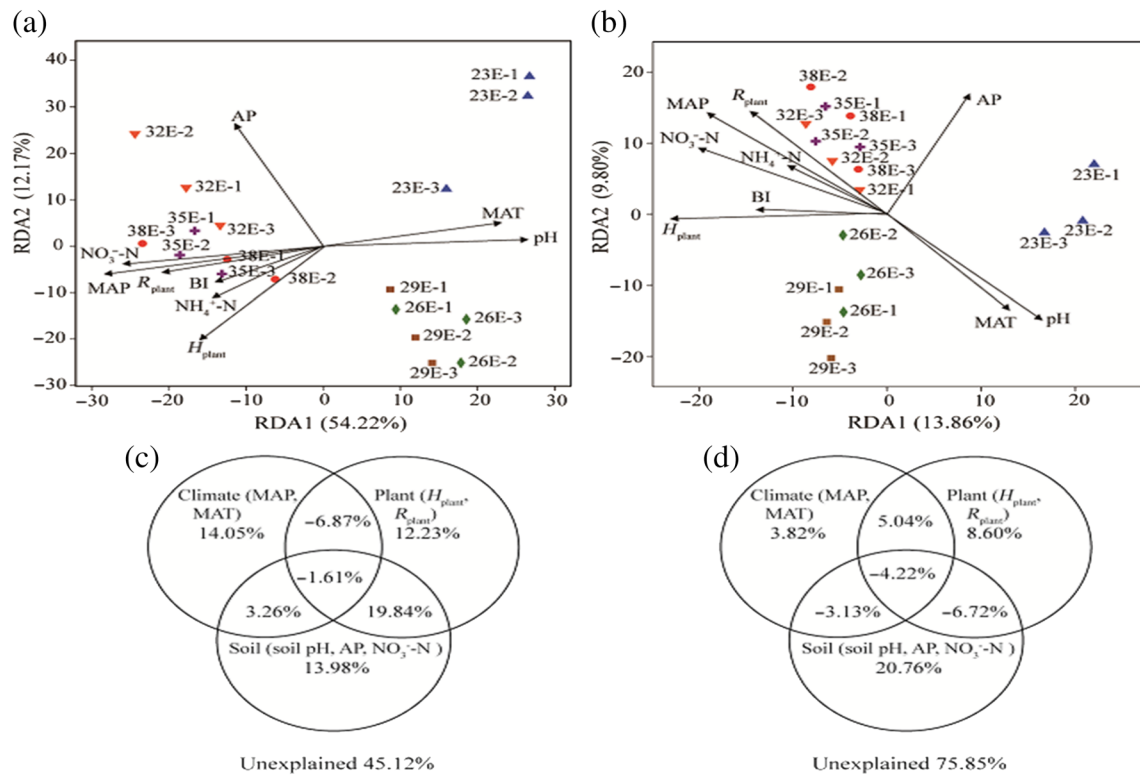


FIGURE 4 Redundancy analysis identifying the relationships between bacterial (a) and fungal (b) communities and environmental factors. Values at axes 1 and 2 are the percentages explained by the corresponding axis. Venn diagram of the variance partitioning analysis displaying the partitioning of the contributions of soil, plant, and climatic characteristics to the bacterial (c) and fungal (d) community changes. 23E, 26E, 29E, 32E, 35E, and 38E represent sites at 2350, 2650, 2950, 3250, 3550, and 3850 m. AP, available phosphorus; BI, plant biomass; H_{plant} , Shannon diversity; MAP, mean annual precipitation; MAT, mean annual temperature; $\text{NH}_4^+\text{-N}$, ammonium nitrogen; $\text{NO}_3^-\text{-N}$, nitrate nitrogen; R_{plant} , species richness

TABLE 3 Correlation between soil properties and soil bacterial and fungal abundances at the operational taxonomic unit level, and redundancy analysis (RDA) axes

	VIF	Bacteria				Fungi			
		RDA1	RDA2	r^2	p	RDA1	RDA2	r^2	p
MAT	5.369	0.978	0.209	0.781	***	0.8000	-0.600	0.647	***
MAP	7.051	-0.982	-0.191	0.868	***	-0.823	0.569	0.780	***
pH	9.063	0.997	0.072	0.897	***	0.799	-0.602	0.833	***
$\text{NO}_3^-\text{-N}$	6.708	-0.987	-0.163	0.828	***	-0.869	0.495	0.756	***
$\text{NH}_4^+\text{-N}$	2.215	-0.950	-0.312	0.325	0.057	-0.862	0.507	0.288	0.084
AP	2.347	-0.407	0.914	0.857	***	0.442	0.897	0.735	***
BI	4.107	-0.980	-0.201	0.299	0.072	-0.998	0.061	0.296	0.080
R_{plant}	4.642	-0.982	-0.191	0.655	***	-0.809	0.588	0.705	***
H_{plant}	6.035	-0.756	-0.655	0.725	***	-0.998	-0.052	0.782	**

Abbreviations: AP, available phosphorus; BI, plant biomass; H_{plant} , Shannon diversity; MAP, mean annual precipitation; MAT, mean annual temperature; $\text{NH}_4^+\text{-N}$, ammonia nitrogen; $\text{NO}_3^-\text{-N}$, nitrate nitrogen; R_{plant} , species richness.

*** $p < 0.001$, ** $p < 0.01$.

conclusion is supported by the significant positive correlation detected between SOC and nutrient content and the abundance of these phyla along the elevational

gradient in this study (Table S7). However, we also found different elevational patterns for the rare bacterial phyla. For example, *Cyanobacteria* are assigned to oligotrophic

groups and are less abundant in more nutrient-rich environments (Goldfarb et al., 2011; Zi et al., 2018), while *Gemmatimonadetes* prefer arid conditions (DeBruyn et al., 2011), supporting their hollow patterns with elevation.

4.2 | Factors responsible for the variability in bacterial and fungal microbial communities along an elevation gradient

In this study, RDA revealed that both bacterial and fungal patterns over an altitudinal gradient were significantly affected by soil (soil pH, AP, and NO_3^- -N), plant (H_{plant} and R_{plant}), and climatic (MAP and MAT) variables, as confirmed by the Pearson correlation between alpha and beta diversity indices of bacterial and fungal communities, and environmental factors (Table S6). These findings support our hypothesis (2) that soil, plant, and climatic characteristics are co-responsible for the variability in bacterial and fungal microbial communities along altitudinal gradients. Our study further revealed that these abiotic and biotic environmental factors together explained a larger proportion of variation in bacterial communities (54.88%) than that in fungal communities (24.15%). Previous microbial ecology studies have shown that abiotic and biotic environmental factors, often referred to as deterministic (Luo et al., 2019; Maren et al., 2018; Zhou & Ning, 2017), and stochastic processes (e.g., extinction, colonisation, and dispersal limitations) are co-responsible for microbial community assemblies (Caruso et al., 2011; S. Li et al., 2018), however, their relative importance is the subject of debate (Zhou & Ning, 2017). Some recent findings have showed that dispersal limitation is an underlying determinant of fungal communities at both large- and fine-scale (Davison et al., 2012; Higgins et al., 2014; S. Li et al., 2018; Peay & Bruns, 2014). Thus, the relatively low proportion of variation in fungal community explained by soil, plant, and climatic characteristics may be attributed to the role of dispersal limitation in shaping fungal communities along elevational gradients.

The results of VPA showed that soil variables (soil pH, AP, and NO_3^- -N) explained the largest proportion of the variation in both bacterial and fungal communities. The fundamental role of soil pH and nutrient levels in microbial elevational patterns has been demonstrated in other montane ecosystems (Cho et al., 2018; Shen et al., 2013; Siles & Margesin, 2016). Our observations confirmed previous research. Interestingly, soil pH in previous studies was consistently acidic, while soil pH in our study is alkaline and is likely to reflect soil pH range in

arid-montane ecosystems. Our results extended the importance of soil pH for microbial elevational patterns to alkaline soils.

In addition to soil variables, we also found that plant (H_{plant} and R_{plant}) and climatic (MAP and MAT) characteristics played a secondary role in shaping bacterial and fungal communities along the elevational gradient, and plant characteristics contributed a larger proportion of variation relative to climatic characteristics. The strong coupling between the alpha and beta diversity of plant and fungal communities has been reported in forests and grasslands at multiple scales (S. Li et al., 2018; Prober et al., 2015). Our observations supported previous research, and further demonstrated the strong and consistent associations between the diversity of plant and bacterial communities. Bacterial diversity has been shown to be closely related to the quality or composition of soil organic matter (Millard & Singh, 2010; Nielsen et al., 2010). In arid-montane ecosystems, an increase in plant diversity is also often associated with an increase in plant biomass (Chen et al., 2016; Jia et al., 2016); consequently, organic matter inputs to soils may be greater and have more diverse composition, providing a more suitable environment for microbial growth and an increase in bacterial diversity (Nottingham et al., 2018; F. Z. Zhao et al., 2019).

Based on the metabolic theory of ecology, temperature has long been recognised as the principal climatic variable influencing microbial elevational distribution by directly regulating metabolism and indirectly regulating soil resource availability (Liu et al., 2020; Nottingham et al., 2018; Shen et al., 2019). However, in the present study, precipitation has been observed to play a more important role than temperature in structuring bacterial and fungal communities. Water availability was the major limiting factor for biota growth in arid-montane ecosystems, and biodiversity can be expected to be regulated by precipitation gradients (Báez et al., 2013; Cregger et al., 2012; Sun et al., 2017). At our experimental site, precipitation increased initially and then decreased with elevation, possibly supporting unimodal diversity pattern for both soil microbes and plants.

5 | CONCLUSIONS

Our study strongly supported the existence of coordinated elevational diversity patterns for soil microbes and plants in arid-montane ecosystems. Therefore, plant diversity dynamics have important implications for the prediction of soil microbial diversity changes under climate change scenarios, which might be of great significance for biodiversity conservation. Our study further

revealed the fundamental role of soil variables (soil pH and nutrient levels) in shaping microbial elevational patterns, highlighting that the importance of soil pH in microbial elevational patterns is also apparently in alkaline soils. Given the stronger links between microbial diversity and precipitation along elevational gradients than temperature, our results suggest that the diversity of soil microbial communities might be more vulnerable to changes in precipitation than temperature in alpine grassland ecosystems of northwestern China.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Ming-Dan Song: Investigation (supporting). **Yuan Gao:** Investigation (supporting).

DATA AVAILABILITY STATEMENT

The data used to support the findings of this study are available from the corresponding author upon request.

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