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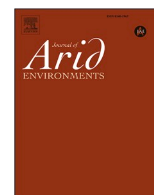

Soil microbial communities and their relationships to soil properties at different depths in an alpine meadow and desert grassland in the Qilian mountain range of China

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ABSTRACT

This study examined whether soil microbial composition would respond differently between alpine meadow and desert grasslands located in the Qilian mountain range in the semi-arid region of northwestern China. The measurements were carried out along a soil profile up to 40 cm. The total nitrogen (TN), total carbon (TC), soil organic carbon (SOC) and soil water content (SWC) were significantly higher (P-value < 0.05) in alpine meadow than in desert. In alpine meadows, all these properties decreased with increasing soil depth, and in desert grassland these properties – except SWC and TN - remained the same at all soil depths. The bacterial phyla Actinobacteria dominated both grasslands, significantly more so in desert grassland (P-value< 0.05). In alpine meadows Proteobacteria, Acidobacteria, Gemmatimonadetes, Planctomycetes and Rokubacteria abundance was significantly higher (P-value < 0.05). The distribution pattern of bacterial phyla along soil depth was different between the two grasslands. The abundance of Ascomycota and Basidiomycota was unaffected by grassland type or soil depth. Alpha and beta diversity analysis revealed two grasslands harbored distinct bacterial and fungal communities. We identified soil carbon, nitrogen and water as important factors that shaped the bacterial and fungal community in these semi-arid grasslands.

1. Introduction

Biodiversity loss has become a global concern as evidence accumulates that these losses will negatively affect ecosystem services on which society depends (Wagg et al., 2014). The below-ground biodiversity is as equally important as above-ground biodiversity because healthy and diverse below-ground communities directly enhance the quantity and quality of food production, the ability of soils to hold water (and thus reduce both flooding and runoff of pollutants like phosphorus), and even human health (Vries and Wallenstein, 2017). It has been well recognized that declining soil biodiversity can impede many ecosystem properties, such as aboveground plant diversity, nutrient retention, and nutrient cycling (Wagg et al., 2014). Soil microbes are distributed throughout soil profiles, from the surface organic matter containing horizon to deeper horizons populated by special microbes (Buckley and Schmidt, 2003). Soil microbial communities in deeper soils have been found to be fundamentally different from surface microbial communities, playing an important role in soil formation, ecosystem biogeochemistry and pollutant degradation, etc. (Deyn and Putten, 2005). Several studies have reported the soil microbial communities are vulnerable to losses due to human activities and climate change (Zhang et al., 2016; Wang et al., 2017). Bacteria and fungi are the key organisms contributing to soil microbial community and are particularly responsible for energy flow and nutrient cycling within an ecosystem (Schulz et al., 2013). The gradients in resource availability in different ecosystems are likely to be primary factors controlling the nature and properties of the microbial communities residing in the soil profile (Fierer et al., 2003).

Microbial community structure is influenced by both biotic and abiotic factors. Soil carbon, nitrogen, organic matter, pH, soil moisture, phosphorus and soil texture appear to be important predictors of the structure of soil microbial communities. Soil pH has been widely reported as a key factor affecting the distribution of soil bacteria, but to a lesser extent for spatial distribution of soil fungi (Lauber et al., 2008), possibly due to wider range of pH adaptability by fungi than bacteria (Rousk et al., 2010). Several studies have reported C availability for microbes as a major factor that determine microbial community

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composition in soil (Ko et al., 2017). Other studies have found that soil moisture had a greater impact on bacterial communities than C or N did, while fungal communities were greatly impacted by soil C and N but not by soil moisture (Singh et al., 2009; Kamble and Bååth, 2018). Soil bulk density affects the soil environment by configuring the space for air, water and plant roots and their movements, consequently influencing microbial populations. Microbial population abundance has been shown to be at their greatest in the low-density soils, presumably due to the favorable soil physical conditions and greater substrate availability provided by plant roots (Uroz et al., 2016; Li et al., 2002).

Grasslands are the largest area and most important land use type in the Qilian mountain region in north west of China (Wang et al., 2016). Among the different grassland types, alpine meadow and desert grassland are widely distributed and have typical regional representation (Liu et al., 2002; Xu et al., 2005). In the Qilian mountain region, alpine meadows and desert grasslands provide an important means of production and livelihood, where they have vital and valuable ecological functions such as protecting biodiversity and maintaining water, soil, and ecological balance (Kang et al., 2015; Zhang et al., 2015; Zhao et al., 2015). The unreasonable use of land resources on the Qilian Mountains in China have caused environmental degradation of grassland areas (Ji and Yang, 2013), potentially impacting the biological functions. A soil microbial community's nature and relative abundance are important indicators to define and evaluate ecosystem functions (Jason et al., 2005) and soil resilience (Bond-Lamberty et al., 2016). While the above ground diversity and productivity in the Qilian Mountain region has been examined previously (Zhang et al., 2015, 2019; Yang et al., 2016), little attention has been paid to soil microbiome studies. In order to contribute to the efforts that fill this research gap, we examined soil bacteria and fungi composition at different soil depths (0–10, 10–20, 20–30, 30–40 cm) in an alpine meadow grassland northeast of the Qilian mountains in the Qinghai province, and a desert grassland in the Hexi corridor of the Ganzhou District. We analyzed the physicochemical properties of soil and microbial (bacteria and fungi) diversity, where the latter was determined by Illumina sequencing of PCR-amplified 16S rRNA and the ITS gene, respectively, and then correlated to the former. We addressed the following two hypotheses in this study: 1) Microbial composition would respond differently to different grassland types, and 2) Soil depths would change the soil physicochemical properties, thereby changing the soil microbial community. In this study we specifically addressed the following scientific questions: 1) What is the composition of soil bacteria and fungi in a soil profile up to 40 cm below the surface in alpine meadow and desert grassland found in the Qilian mountain range? 2) What are the links between soil physicochemical properties and microbial groups? 3) Would the soil physicochemical properties change with soil depth, thereby altering the soil microbial community?

2. Material and methods

2.1. Research area

The soil samples for this study were collected from alpine and desert grasslands in Gangcha County and the Ganzhou District, respectively, where both sites are located in the Qilian mountain range found in north west China. Gangcha County is located in the northeast of the Qinghai Province, which has a typical plateau continental climate with an average annual precipitation of 370.5 mm. In 2018, the average temperature in January was −11.5 °C, the average temperature in July was 13 °C, and the annual average temperature was 1 °C (Fig. 1), The soil type is subalpine meadow soil.

The Ganzhou District is located in the Gansu Province in the middle of the Hexi Corridor, which has a continental desert grassland climate with annual precipitation of 118.4 mm. In 2018, the average temperature in January was −9.4 °C, the average temperature in July was 24 °C, and the annual average temperature was 8.9 °C (Fig. 1). The soil type was Brown desert soil. Both experimental sites were located in conserved areas and minimal human activity was carried out. The details of the soil sampling site at each location is shown in Table 1.

2.2. Sample collection

The soil samples were collected from each grassland site in October 2018. At each sampling site, soil samples were collected from 4 sampling areas which were approximately 100 m apart. In each sampling area, 5 replicate samples were collected along a "M" shape arbitrary line. The soil samples were collected using a 10 cm diameter soil corer from 0 to 10, 10–20, 20–30, 30–40 cm depths. The 40 cm soil depth was selected to cover root zone soils. In alpine meadows, the root zone was up to 15–20 cm while in deserts, roots of some shrub plants had extended up to 40 cm. The five replicate samples from each depth at each sampling area were pooled and mixed thoroughly, resulting in 16 soil samples from each site for further analysis. First, visible roots or other debris were removed from the samples before the soil samples were passed through a 2 mm sieve. Each sample was divided into 3 sub samples. One portion of each soil sample was transported to the laboratory in a portable freezer and stored at – 20 °C for microbial community analysis. Another sub sample was used to analyze the soil water content (SWC). The remaining soil was air dried before measuring for soil physicochemical properties (soil pH, soil total nitrogen (TN), soil total carbon (TC), and soil organic carbon (SOC)). At each site, a separate pit was dug to measure soil bulk density (BD) using a stainless-steel circular cutting ring with 50.46 mm diameter and 50 mm width.

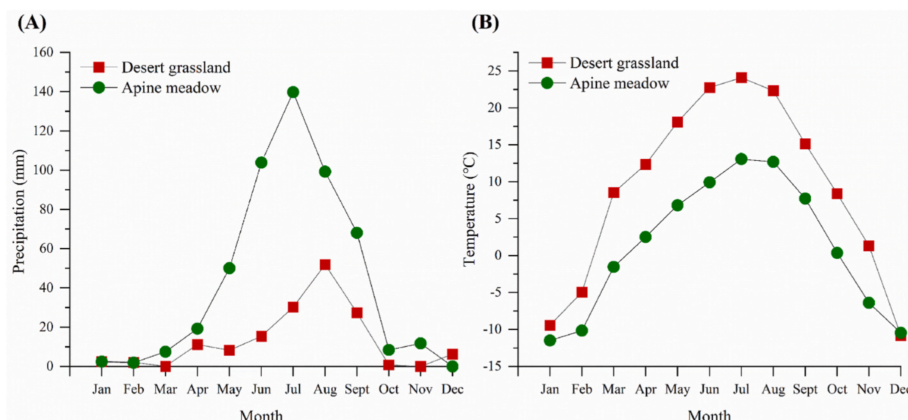

Fig. 1. Average monthly precipitation (A) and temperature (B) during 2018 at the two investigated grasslands. The data were sourced from China Climate Bureau.

Table 1
Basic information of the two investigated grasslands.

	Dominant plant species	Longitude	Latitude	Altitude (m)	Vegetation coverage (%)	Soil type
Alpine meadow	*Stipa capillata, Kobresia myosuroides, Poa annua, Kobresia myosuroides, Koeleria cristata, Thermopsis lanceolata, Leontopodium leontopodioides, Potentilla chinensis* etc.	100°35′01″E	37°17′38″N	3325	95%	Subalpine meadow soil
Desert grassland	*Salsola passerina Bunge, Sympegma regelii Bunge, Kalidium foliatum (Pall.) Moq., Nitraria tangutorum Bobr.* etc.	100°42′54″E	39°11′11″N	1832	20%	Brown desert soil

2.3. Soil physiochemical and microbial community analysis

Gravimetric soil moisture content was determined by drying to a constant weight at 105 °C in an electrothermal blowing oven (DHG - 9240, Shanghai Jing Macro, Shanghai, China). Soil pH was determined with a pH meter, using a slurry with a 1:5 soil-to-water ratio (PE-10, Sartorious, Germany). Total soil C and TN was determined using an elemental analyzer (Elementar Vario EL/micro cube, Hanau, Germany). Soil organic carbon (SOC) was determined by the Walkley-Black wet digestion method with H_2SO_4–$K_2Cr_2O_7$ (Nelson and Sommers, 1996).

2.4. Soil total DNA extraction and 16s rRNA and ITS gene amplification

Total soil genome DNA from each soil sample was extracted from 0.5 g soil using a FastDNA ® spin kit (MP Biomedicals, Santa Ana, CA) according to the manufacturer's instructions. Cell lysis was performed by vigorous shaking in a Bioprep-24 Homogenizer (MP Biomedicals, Ohio, USA) at an intensity of 6 m $s^{-1}$for 45 s. The extracted DNA was dissolved in 100 μL of the DNA elution solution. DNA quantity and purity were determined using the Nanodrop® ND-1000 UV–visible spectrophotometer (Nanodrop technologies, Delaware, USA) and stored in - 20 °C freezer until further use.

The soil microbial community was examined using Illumina MiSeq sequencing analysis. The Illumina MiSeq sequencing libraries for bacteria were prepared by PCR amplification of the V4–V5 hyper variable regions of the bacterial 16S rRNA gene using 515F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 907R (5′-CCGTCAATTCMTTTRAGTTT-3′) primers. Sample specific 7-bp barcodes were incorporated into the primers for multiplex sequencing. Thermal cycling consisted of initial denaturation at 98 °C for 2 min followed by 25 cycles including denaturation at 98 °C for 15 s, annealing at 55 °C for 30 s, extension at 72 °C for 30 s, and finally at 72 °C for 5 min. The Illumina MiSeq sequencing libraries for fungi were prepared by PCR amplification of the internal transcribed spacer (ITS) region using the ITS1 (5′-TCCGTAGGTGAACCTGCGG-3′) and ITS4 (5′-TCCTCCGCTTATTGATATGC-3′) primers. The PCR reaction conditions were at 95 °C for 3 min followed by 30 cycles including denaturation at 95 °C for 40 s, annealing at 55 °C for 45 s, and extension at 72 °C for 1 min, and finally at 72 °C for 10 min.

The PCR amplicons were purified with Agencourt AMPure Beads (Beckman Coulter, Indianapolis, IN) and quantified using the PicoGreen dsDNA Assay Kit (Invitrogen, Carlsbad, CA, USA). After the individual quantification step, amplicons were pooled in equal amounts, and paired-end 2 × 300 bp sequencing was performed using the Illlumina MiSeq platform with the MiSeq Reagent Kit v3 at Shanghai Personal Biotechnology Co., Ltd (Shanghai, China).

2.5. Sequence analysis and OTU generation

The sequencing data was processed using the Quantitative Insights Into Microbial Ecology (QIIME, v1.8.0) pipeline. First, raw sequencing reads with exact matches to the barcodes were assigned to respective

Table 2
Basic soil physical and chemical properties of four soil depths at the two investigated grasslands. The values are mean ± standard error of mean.

Grassland types (T)	Soil depth (D) cm	TN ($g·kg^{-1}$)	TC ($g·kg^{-1}$)	pH	SOC ($g·kg^{-1}$)	SWC (%)	BD ($kg·m^{-3}$)	C/N
Alpine	0–10	4.84 ± 0.07 aA	102.08 ± 3.25 aA	7.07 ± 0.17bB	55.18 ± 1.06 aA	26.21 ± 0.67 cC	0.63 ± 0.01eD	21.10 ± 0.87 aA
	10–20	4.82 ± 0.29 aA	90.02 ± 3.41bB	7.70 ± 0.14 aA	47.99 ± 1.33bB	32.60 ± 1.28abA	0.85 ± 0.01 dC	18.77 ± 0.90bC
	20–30	3.70 ± 0.07bB	49.92 ± 1.43 cC	7.71 ± 0.06 aA	32.69 ± 1.81 cC	31.04 ± 0.28aAB	0.98 ± 0.02bB	13.50 ± 0.40 cB
	30–40	2.56 ± 0.07 cC	43.77 ± 0.77 cC	7.54 ± 0.01 aA	23.48 ± 1.9dD	28.84 ± 1.1bcC	1.05 ± 0.02bA	17.10 ± 0.19bB
	Average (AM 0–40)	3.98 ± 0.29***	71.45 ± 7.63***	7.50 ± 0.08	39.84 ± 3.29***	29.67 ± 0.82***	0.88 ± 0.05	17.62 ± 0.88***
Desert	0–10	1.41 ± 0.04dAB	16.64 ± 0.25 dA	7.59 ± 0.04 aA	4.56 ± 0.51eA	1.71 ± 0.18eC	1.32 ± 0.02 aA	11.80 ± 0.14 cA
	10–20	1.56 ± 0.07 dA	17.37 ± 1.54 dA	7.68 ± 0.05 aA	4.83 ± 0.41eA	3.78 ± 0.26deB	1.19 ± 0.05 aA	11.14 ± 0.78 cA
	20–30	1.25 ± 0.06 dB	14.43 ± 0.99 dA	7.69 ± 0.08 aA	4.1 ± 0.73eA	5.83 ± 0.74 dA	1.24 ± 0.03 aA	11.54 ± 0.26 cA
	30–40	1.55 ± 0.14 dA	17.39 ± 1.53 dA	7.60 ± 0.19 aA	4.57 ± 0.31eA	5.61 ± 0.23 dA	1.27 ± 0.05 aA	11.22 ± 0.14 cA
	Average (DG 0–40)	1.44 ± 0.05	16.46 ± 0.63	7.64 ± 0.05	4.51 ± 0.24	4.23 ± 0.53	1.26 ± 0.02***	11.43 ± 0.20
Statistical significance (P-value)	Grassland types (T)	<0.001	<0.001	0.105	<0.001	<0.001	<0.001	<0.001
	Soil depth (D)	<0.001	<0.001	<0.05	<0.001	<0.001	<0.001	<0.001
	T*D	<0.001	<0.001	0.079	<0.001	<0.001	<0.001	<0.001

TN: Total nitrogen; TC: Total carbon; SOC: Soil organic carbon; SWC: Soil water content; BD: Bulk density; C/N: Ratio of carbon to nitrogen. Different lowercase letters indicate significant differences P-value <0.05 among 8 groups of 4 depths of 2 types of grassland. Different Capital letters indicate significant differences P-value <0.05 among 4 depths within a grassland. * Indicates significant differences P-value <0.05 between the two types of grassland in 0–40 cm, * = significant at P-value <0.05; ** = significant at P ≤ 0.01; *** = significant at P ≤ 0.001. The last three rows are the results of two-way ANOVA using Grassland type (T) and Soil depth (D) as main effects.

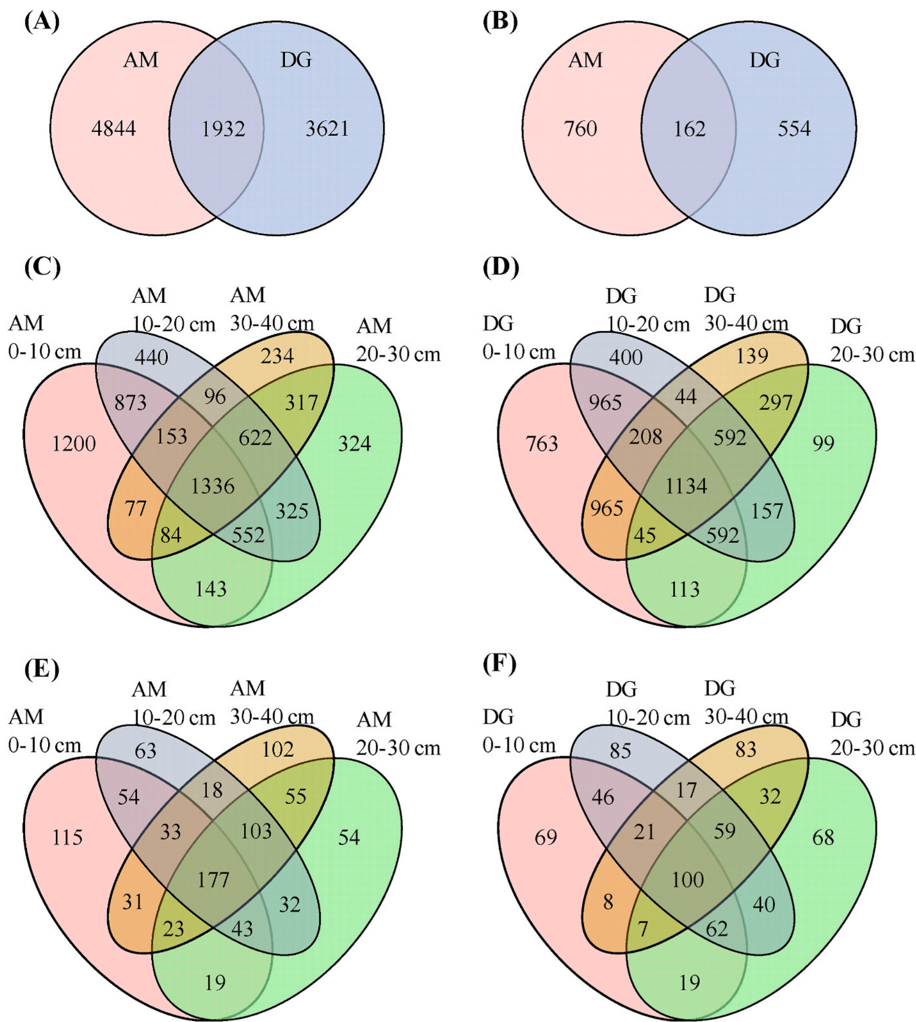

Fig. 2. Venn diagrams illustrating the number of shared and unique bacterial and fungal OTUs in 0–40 cm soil profile of alpine meadow and desert grassland. A = Bacterial OTUs in alpine meadows and desert grassland, B= Fungal OTUs in alpine meadows and desert grassland C= Bacterial OTUs in different depths in alpine meadow, D = Bacterial OTUs in different depths in desert grassland, E = Fungal OTUs in different depths in alpine meadow, F= Fungal OTUs in different depths in desert grassland.

samples and identified as valid sequences. Sequences that had a length of <150 bp, average Phred scores of <20, contained ambiguous bases, and contained mononucleotide repeats of >8 bp were considered as low-quality sequences (Gill et al., 2006; Jiang et al., 2014). The FLASH software (Magoč and Salzberg, 2011) was used to assemble paired end reads. After detecting chimeras, the remaining high-quality sequences were clustered into operational taxonomic units (OTU) at 97% sequence identity using the UCLUST software (Edgar, 2010). A representative sequence was selected from each OTU using default parameters. OTU taxonomic classification was conducted by BLAST searching the representative sequences set against the Greengenes and UNITE database (Desantis et al., 2006; Urmas et al., 2013) using the best hit (Altschul et al., 1997). An OTU table was further generated to record the abundance of each OTU in each sample and the taxonomy of these OTU. OTU containing less than 0.001% of total sequences across all samples were discarded.

2.6. Microbial community composition and diversity analysis

The microbial community composition and diversity was estimated using a rarefied OTU matrix at a consistent sequencing depth. The relative abundance and distribution of phylum, class, order, family and genus in each sample was used to describe the microbial community composition. The shared and unique numbers of OTU in samples were identified by Venn diagram. Alpha diversity (diversity within a sample) of soil bacterial and fungal communities was tested by the community species richness (Chao 1 and ACE) and community evenness (Shannon and Simpson diversity) using QIIME software. The beta diversity (dissimilarity between samples) of the communities was assessed by non-metric multidimensional scaling (NMDS) using a weighted UniFrac distance matrix (Heino et al., 2013).

2.7. Statistical analysis

The effects of grassland type, soil depth and their interactions on alpha diversity indices, relative abundance of bacterial phyla and genera, and soil properties were analyzed using two-way analysis of variance (ANOVA), and the statistical significance of the means were compared by Duncan's multiple range test using Statistical Product and Service Solutions (SPSS) software version 21.0 (SPSS Inc., Chicago, IL, USA). The Shapro-Wilk test was carried out to test the normal distribution of the data. When data did not meet the normal distribution criteria, they were transformed using Box-Cox or Johnson function, and nonparametric rank sum test was used for the data did not meet the normal distribution. Microbial community difference between the two grassland sites and depths were statistically tested by ANOSIM (analysis of similarities) with 999 permutations using QIIME software. The non-metric multidimensional scaling (NMDS) using a weighted UniFrac distance matrix was carried out by R software. Statistical significance in all tests was determined at P-value < 0.05. Spearman correlation and redundancy analysis (RDA) was used to examine the correlations between soil physicochemical properties and microbial communities. RDA analysis was carried out using the Canoco 4.5 software (Microcomputer Power, Ithaca, NY, USA).

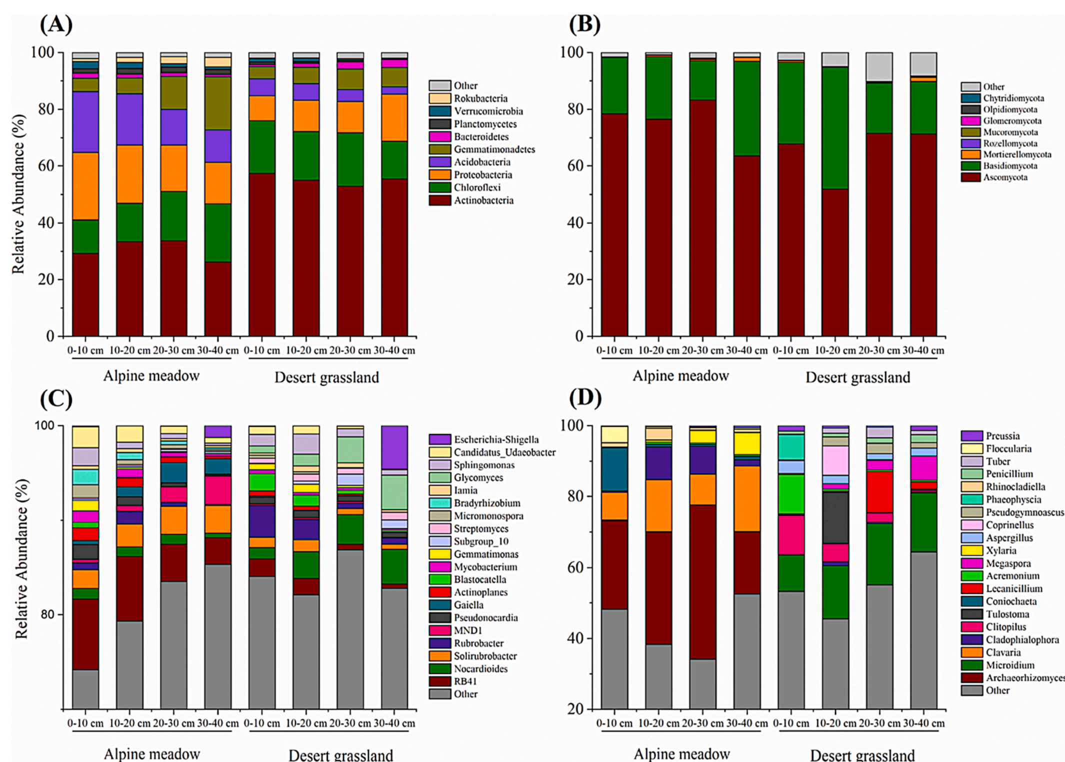

Fig. 3. Relative abundances of bacterial phyla (A), fungal phyla (B), bacterial genera (C) and fungal genera (D) in different soil depths at the investigated two grassland sites.

2.8. *Nucleotide sequence accession numbers*

The nucleotide sequences from this study have been deposited in the NCBI GenBank under the SRA accession PRJNA593866 (Bacteria) and PRJNA593869 (Fungi).

3. Results

3.1. *Soil physicochemical properties*

Differences in soil physiochemical properties in the 0–40 cm soil profile in alpine meadow and desert grassland are shown in Table 2. Except for the soil pH, all other soil properties at different soil depths changed differently in the two grasslands (P-value for the interaction of grassland type × soil depth for pH was >0.05). The contents of TN, TC, SOC and SWC were significantly higher in alpine meadow than in desert. In alpine meadows, these properties decreased with increasing soil depth, but remained the same in all soil depths in desert (except SWC and TN). Soil bulk density in 0–10 and 10–20 cm soil depths were significantly higher in desert than in alpine meadows. In alpine meadows, BD increased with increasing soil depth while in desert it was lower in 10–20 cm soil depth than the other soil depths. The C/N ratio at all soil depths in desert remained the same while it differed between soil depths in alpine meadows.

3.2. *OTU abundance*

In this study, after removing low-quality sequences, a total of 1,558,298 bacterial 16S rRNA sequences and 1,295,324 fungal ITS sequences were obtained. A 97% sequence similarity level was used as the threshold for the OTU classification. Across all samples, 10,397 bacterial OTU and 1476 fungal OTU were obtained. 1932 OTU (19%) were common to both grasslands, while 4844 (47%) and 3621 (34%) were unique to desert and alpine meadow grasslands respectively (Fig. 2A). Among the fungal OTU, 162 OTU (11%) were common to both grasslands, while 760 (51%) and 554 OTU (38%) were unique to desert and alpine meadow soils respectively (Fig. 2B). Soil depth specific OTU were also present at different soil depths in both alpine and desert grasslands (Fig. 2 C, D, E, F). The highest number of unique bacterial OTU were found at 0–10 cm depth in both alpine and desert grasslands. Similarly, the highest number of unique fungal OTU were found at 0–10 cm depth in alpine meadow. In desert soil, however, unique OTU were highest at 10–20 cm depth. 24% and 16% of bacterial OTU were common to all four soil depths in alpine meadow and desert respectively, while 13% and 21% of fungal OTU were common to all four soil depths in alpine meadow and desert respectively.

3.3. *Characteristics of bacterial and fungal community composition*

3.3.1. *Bacterial communities*

Between the two grasslands, a total of 27 phyla were identified in this study. Among them, 15 phyla had an average relative abundance of less than 0.1%, so they were classified into an “other” category. There were 9 phyla with an average relative abundance of more than 1% (Fig. 3A). The most dominant 5 phyla in both grasslands were Actinobacteria, Chloroflexi, Proteobacteria, Acidobacteria, and Gemmatimonadetes, with relative abundances ranging from 26 to 57%, 12–21%, 9–24%, 3–22%, and 4–19%, respectively (Table 3). These 5 phyla represented more than 90% of the sequences in all of the samples from both grasslands. These dominant phyla showed different distribution patterns with increasing depth in both grasslands (Fig. 3A, Table 3).

The relative abundances of bacterial phyla Proteobacteria, Acidobacteria, Gemmatimonadetes, Planctomycetes and Rokubacteria in alpine meadow were significantly higher (P-value<0.05) than in desert grassland, and the relative abundance of actinobacteria was significantly higher in desert grassland than in alpine meadow.

In alpine meadows the relative abundance of Chloroflexi, Gemmatimonadetes and Rokubacteria increased with increasing soil depth, where their relative abundance at 30–40 cm depth was significantly higher than at 0–10 cm depth. In contrast, Proteobacteria, Acidobacteria

Table 3
Relative abundances of taxonomic groups of bacteria at the phylum and genus level. The values are mean ± standard error of mean.

Bacteria		Alpine meadow (AM)					Desert grassland (DG)
Phylum level	Genus level	0–10 cm	10–20 cm	20–30 cm	30–40 cm	Average (AM 0–40 cms)	0–10 cm
Actinobacteria		29.25 ± 3.75bA	33.41 ± 4.79bA	33.80 ± 0.72bA	26.15 ± 1.08bA	30.65 ± 1.61	57.45 ± 1.71 aA
	Nocardioides	1.13 ± 0.27 aA	1.01 ± 0.29 aA	1.04 ± 0.33 aA	0.49 ± 0.09 aA	0.92 ± 0.13	1.19 ± 0.13 aB
	Solirubrobacter	1.99 ± 0.24abA	2.40 ± 0.58 aA	2.95 ± 0.38 aA	2.92 ± 0.36 aA	2.57 ± 0.21***	1.08 ± 0.17bcAB
	Rubrobacter	0.74 ± 0.13cdB	1.36 ± 0.32bcA	0.43 ± 0.11cdBC	0.09 ± 0.03 dC	0.66 ± 0.15	3.36 ± 0.49 aA
	Glycomyces	0b	0b	0b	0b	0	0.73 ± 0.35bB
	Pseudonocardia	1.57 ± 0.32 aA	0.93 ± 0.24bB	0.43 ± 0.03bcAB	0.22 ± 0.04 cC	0.79 ± 0.16	0.71 ± 0.06bcA
	Gaiella	0.40 ± 0.03 dC	1.05 ± 0.17 cB	2.16 ± 0.30 aA	1.65 ± 0.13bA	1.32 ± 0.19***	0.12 ± 0.04 dA
	Actinoplanes	1.35 ± 0.42 aA	0.94 ± 0.25abAB	0.58 ± 0.16bcAB	0.26 ± 0.05 dB	0.78 ± 0.16**	0.53 ± 0.04bcA
	Mycobacterium	1.19 ± 0.15 aA	0.87 ± 0.17bAB	0.49 ± 0.12cBC	0.24 ± 0.06cdC	0.7 ± 0.11**	0.41 ± 0.09cdA
	Streptomyces	0.12 ± 0.01bAB	0.16 ± 0.03bA	0.11 ± 0.01bAB	0.09 ± 0.01bB	0.12 ± 0.01	0.54 ± 0.17 aA
	Micromonospora	1.37 ± 0.47 aA	0.51 ± 0.14bB	0.39 ± 0.10bB	0.16 ± 0.04bB	0.61 ± 0.16*	0.32 ± 0.09bA
	Iamia	0.40 ± 0.05	0.41 ± 0.01	0.26 ± 0.06	0.20 ± 0.04	0.32 ± 0.03	0.24 ± 0.04
Chloroflexi		11.84 ± 1.20 cC	13.53 ± 1.05 cC	17.25 ± 0.69bB	20.63 ± 0.65 aA	15.81 ± 0.97	18.63 ± 0.93abA
Proteobacteria		23.66 ± 3.97 aA	20.58 ± 1.23abAB	16.45 ± 0.96bcB	14.54 ± 0.30cdB	18.81 ± 1.33***	8.77 ± 0.27eB
	Sphingomonas	1.90 ± 0.10 aA	0.69 ± 0.12bcB	0.50 ± 0.13cBC	0.25 ± 0.05 cC	0.83 ± 0.17	1.22 ± 0.02bB
	Escherichia-Shigella	0.11 ± 0.06A	0.03 ± 0.00A	0.06 ± 0.03A	1.24 ± 0.86A	0.36 ± 0.23	0.07 ± 0.03B
	MND1	0.37 ± 0.12cdC	0.58 ± 0.08 cC	1.63 ± 0.15bB	2.99 ± 0.27 aA	1.39 ± 0.28***	0.14 ± 0.03 dA
	Bradyrhizobium	1.64 ± 0.19 aA	0.75 ± 0.11bB	0.42 ± 0.05bcBC	0.19 ± 0.04cdC	0.75 ± 0.15***	0.00 ± 0.00eA
Acidobacteria		21.55 ± 1.80 aA	17.96 ± 3.98aAB	12.49 ± 0.89bC	11.53 ± 0.28bC	15.88 ± 1.45***	5.95 ± 1.06 cA
	RB41	7.44 ± 1.09 aA	6.84 ± 2.02 aA	3.96 ± 0.66bBC	2.81 ± 0.30bcB	5.26 ± 0.73***	1.89 ± 0.85bcA
	Blastocatella	0.59 ± 0.09bcA	0.04±0 cB	0.02 ± 0.01 cB	0.00 ± 0.00 cB	0.16 ± 0.07**	1.84 ± 0.34 aA
	Subgroup_10	0.15 ± 0.08bA	0.18 ± 0.04bA	0.20 ± 0.01bA	0.15 ± 0.04bA	0.17 ± 0.02	0.06 ± 0.03bC
Gemmatimonadetes		4.75 ± 0.38deC	5.59 ± 0.76cdeC	11.66 ± 0.73bB	18.67 ± 0.79 aA	10.17 ± 1.47**	4.33 ± 0.04eA
	Gemmatimonas	1.11 ± 0.26 aA	0.20 ± 0.06 cB	0.08 ± 0.01 cB	0.10 ± 0.01 cB	0.37 ± 0.13	0.65 ± 0.10bB
Bacteroidetes		1.63 ± 0.29bA	1.28 ± 0.18bcAB	1.22 ± 0.17bcAB	0.77 ± 0.07bcB	1.23 ± 0.12	0.62 ± 0.12 cB
Planctomycetes		1.64 ± 0.69abA	2.09 ± 0.16 aA	2.03 ± 0.09 aA	1.76 ± 0.19abA	1.88 ± 0.17***	0.97 ± 0.21bcA
Verrucomicrobia		2.50 ± 1.63	2.09 ± 1.28	1.24 ± 0.10	0.97 ± 0.00	1.70 ± 0.49	1.21 ± 0.15
	Candidatus_Udaeobacter	2.21 ± 1.46	1.70 ± 1.13	0.79 ± 0.10	0.59 ± 0.06	1.32 ± 0.45	0.84 ± 0.18
Rokubacteria		1.07 ± 0.17 dA	1.78 ± 0.20 cB	2.43 ± 0.14bB	3.26 ± 0.34 aA	2.14 ± 0.23***	0.10 ± 0.04eA

Different lowercase letters indicate significant differences (P-value < 0.05) among 8 groups of 4 depths of 2 types of grassland. Different Capital letters indicate significant differences (P-value < 0.05) among 4 depths within a grassland. * Indicates significant differences (P-value < 0.05) between the two types of grassland in 0–40 cm, * = significant at P-value≤0.05; ** = significant at P-value ≤0.01; *** = significant at P-value ≤ 0.001. The last three columns are the results of two-way ANOVA using Grassland type (T) and Soil depth (D) as main effects.

and Bacteroidetes showed a decreasing trend with increasing soil depth, and their relative abundance at 30–40 cm depth was significantly lower than at 0–10 cm depth. The rest of the dominant phyla showed no significant difference with increasing soil depth.

In the desert, Proteobacteria, Gemmatimonadetes and Bacteroidetes tended to increase with increasing soil depth, and the relative abundance in 30–40 cm was significantly higher than at 0–10 cm depth. By contrast, Chloroflexi, Planctomycetes and Verrucomicrobia tended to decrease with increasing soil depth. The vertical distribution changes of Chloroflexi, Bacteroidetes and Proteobacteria showed opposite trends in each grassland; Chloroflexi, and Bacteroides increased with the increasing soil depth in alpine meadows, while in deserts they decreased. The Proteobacteria decreased with the increasing soil depth in alpine meadows, but in deserts they increased.

At lower taxonomic level, 444 bacterial genera were identified in this study. Among them, the most dominant 20 genera belonged to Actinobacteria (11 genera), Proteobacteria (4 genera), Acidobacteria (3 genera) Gemmatimonadetes (1 genus) and Verrucomicrobia (1 genus), where their distribution at different depths in the two grasslands are shown in Fig. 3C and Table 3.

Most Actinobacterial genera in alpine meadows decreased with increasing soil depth. *Solirubrobacter* and *Streptomyces* were distributed evenly at all four soil depths. The *Glycomyces* genus was absent in all soil depths of alpine meadows whereas it was abundant in all soil depths in the desert. In desert soil, the Actinobacterial genera *Nocardioides* and *Glycomyces* increased in abundance with increasing soil depth while *Solirubrobacter*, *Rubrobacter*, *Gaiella*, *Actinoplanes* and *Mycobacterium* abundance decreased with increasing soil depth. The rest of the Actinobacterial genera in the desert were equally abundant in all four soil depths.

The Proteobacterial genera *Sphingomonas* decreased with increasing soil depth in both grasslands, *Escherichia-Shigella* was significantly higher at 30–40 cm soil depth in the desert and *MND1* increased with increasing soil depth in alpine meadows, where in desert it was evenly distributed at all soil depths. *Bradyrhizobium* decreased with increasing soil depth, where in desert it was absent at all soil depths. Acidobacterial genera *RB41* and *Blastocatella* decreased with increasing soil depth in both grasslands. *Subgroup-10* was higher in deeper layers in desert however distributed evenly in all soil depths in alpine meadows. The Gemmatimonadetes genera *Gemmatimona,* and Verrucomicrobial genera *Candidatus-Udaeobacter* decreased in abundance with increasing soil depth in both grasslands.

3.3.2. Fungal communities

Across the two grasslands a total of 8 fungal phyla were identified in this study. These were Ascomycota, Basidiomycota, Mortierellomycota, Rozellomycota, Mucoromycota, Glomeromycota, Olpidiomycota and Chytridiomycota. The distribution of these phyla at different depths in two grasslands are shown in Fig. 3B and Table 4.

Ascomycota was the most dominant in both grasslands, while the next dominant phylum was Basidiomycota. The relative abundance of Ascomycota, Basidiomycota, Rozellomycota, Olpidiomycota and Chytridiomycota was not affected by the grassland type or soil depth. Soil depth had a significant effect on Mortierellomycota, where its abundance was significantly higher at 30–40 cm depth than at other soil depths in both grasslands. The abundance of Mucoromycota and Glomeromycota at different soil depths varied between the two grasslands. Glomeromycota was absent at all the soil depths in the desert where in alpine meadows it was significantly higher at 20–30 cm depth than at 0–10 cm depth.

Desert grassland (DG)				P-value		
10–20 cm	20–30 cm	30–40 cm	Average (DG 0–40 cms)	Grassland types(T)	Soil depth(D)	T*D
55.05 ± 1.47 aA	52.95 ± 1.77 aA	55.44 ± 2.20 aA	55.22 ± 0.91***	<0.01	0.570	0.157
2.85 ± 0.57bA	3.14 ± 0.44bA	3.69 ± 0.66bA	2.72 ± 0.33***	<0.01	0.082	<0.01
1.24 ± 0.27bcA	0.63 ± 0.22cAB	0.52 ± 0.18 cB	0.87 ± 0.12	<0.01	0.821	0.060
2.16 ± 0.49bA	0.56 ± 0.18cdB	0.67 ± 0.32cdB	1.68 ± 0.35**	<0.01	<0.01	<0.01
1.25 ± 0.59bB	2.73 ± 0.60aAB	3.67 ± 0.85 aA	2.10 ± 0.41***	<0.01	<0.05	<0.05
0.8 ± 0.10bA	0.63 ± 0.15bcA	0.55 ± 0.21bcA	0.67 ± 0.07	0.354	<0.01	<0.05
0.05 ± 0.02 dB	0.02 ± 0.01 dB	0.01 ± 0.01 dB	0.05 ± 0.01	<0.01	<0.01	<0.01
0.40 ± 0.02bcA	0.16 ± 0.07 dB	0.04 ± 0.01 dB	0.28 ± 0.05	<0.01	<0.01	0.453
0.30 ± 0.06cdAB	0.27 ± 0.07cdAB	0.13 ± 0.05 dB	0.28 ± 0.04	<0.01	<0.01	<0.05
0.74 ± 0.14 aA	0.61 ± 0.13 aA	0.79 ± 0.26 aA	0.67 ± 0.09***	<0.01	0.749	0.754
0.26 ± 0.07bAB	0.09 ± 0.05bBC	0.01 ± 0.01bC	0.17 ± 0.04	<0.01	<0.01	0.079
0.63 ± 0.25	0.53 ± 0.17	0.25 ± 0.08	0.41 ± 0.08	0.242	0.105	0.240
17.16 ± 0.98bA	18.84 ± 1.14abA	13.43 ± 0.42 cB	17.01 ± 0.69	0.077	<0.05	<0.01
11.05 ± 0.47deB	11.03 ± 0.99deB	16.52 ± 1.87bcA	11.84 ± 0.88	<0.01	0.490	<0.01
2.14 ± 0.37 aA	0.88 ± 0.31bcB	0.56 ± 0.21 cB	1.20 ± 0.19	<0.05	<0.01	<0.01
0.02 ± 0.01B	0.04 ± 0.03B	4.59 ± 2.49A	1.18 ± 0.75	0.224	<0.05	0.207
0.15 ± 0.05 dA	0.16 ± 0.10 dA	0.04 ± 0.02 dA	0.12 ± 0.03	<0.01	<0.01	<0.01
0.00 ± 0.00eA	0eA	0.00 ± 0.00eA	0.00 ± 0.00	<0.01	<0.01	<0.01
5.85 ± 0.95 cA	4.17 ± 1.18cAB	2.63 ± 0.70cAB	4.65 ± 0.57	<0.01	<0.01	0.159
1.71 ± 0.51bcA	0.57 ± 0.40 cA	0.46 ± 0.37 cA	1.16 ± 0.30	<0.01	<0.01	0.308
1.16 ± 0.40bAB	0.41 ± 0.26cBC	0.17 ± 0.11 cC	0.89 ± 0.21	<0.01	<0.01	<0.05
0.31 ± 0.06bBC	1.19 ± 0.43 aA	0.91 ± 0.13aAB	0.62 ± 0.15**	<0.01	<0.01	<0.01
5.76 ± 0.46cdeA	7.25 ± 1.44 cB	6.75 ± 0.43cdB	6.03 ± 0.46	<0.01	<0.01	<0.01
0.87 ± 0.24abAB	0.23 ± 0.07 cA	0.06 ± 0.02cAB	0.45 ± 0.10	0.415	<0.01	<0.01
1.30 ± 0.28bcB	2.44 ± 0.36 aA	2.76 ± 0.51 aA	1.78 ± 0.27	<0.01	<0.05	<0.01
0.72 ± 0.12 cB	0.64 ± 0.12cAB	0.25 ± 0.08 cB	0.65 ± 0.09	<0.01	0.506	0.440
1.14 ± 0.13	0.53 ± 0.19	0.25 ± 0.05	0.78 ± 0.12	0.092	0.308	0.976
0.85 ± 0.12	0.25 ± 0.13	0.08 ± 0.01	0.50 ± 0.11	0.092	0.234	0.906
0.10 ± 0.06eA	0.02 ± 0.02eA	0.00 ± 0.00eA	0.06 ± 0.02	<0.01	<0.01	<0.01

At a lower taxonomic level, 304 fungal genera were identified in this study with the most dominant 20 genera belonging to Ascomycota and Basidiomycota. The distribution of these genera at different soil depths in the two grasslands are shown in Fig. 3D and Table 4. The fungal genera associated with the 0–40 cm soil profile indicate a distinct fungal community in each grassland. In most cases, if a fungal genus is highly abundant in one grassland, its abundance in the other grassland is either none or negligible. For example, *Archaeorhizomyces* was the most dominant in alpine meadows but its relative abundance in desert was negligible. In the desert, *Microidium* was the most dominant and its relative abundance in alpine meadows was low.

3.4. Alpha diversity

The alpha diversity indices of the soil bacterial and fungal communities in the two grasslands are shown in Table 5. Both bacterial and fungal species richness (estimated by Chao1 and ACE) were significantly higher in alpine meadows than in desert. In both grasslands, the bacterial species richness decreased with increasing soil depth while fungal species richness was not affected by the soil depth. The Shannon index indicated the soil bacterial community evenness was significantly different between grasslands, but the Simpson index indicated no significant difference between grasslands. Both Shannon and Simpson indices indicated soil depth had significant effect on bacterial community evenness. The fungal community evenness was not affected by either grassland type or soil depth.

3.5. Beta diversity

The NMDS analysis indicated soil bacterial and fungal communities distinct to each grassland (Fig. 4). The NMDS plot illustrated that, in alpine meadow, bacterial communities had clear dissimilarities at four respective soil depths, while desert bacterial communities at 20–30 cm and 30–40 cm depths were similar (Fig. 4A). Similarly, NMDS analysis showed clear dissimilarities between fungal communities in alpine meadow and desert grassland, but at different depths there were no obvious patterns observed, indicating a somewhat even fungal community distribution across a 0–40 cm depth soil profile in both grasslands (Fig. 4B). ANOSIM analysis indicated that the bacterial and fungal communities of the two grasslands were significantly different ($R = 0.85$, P-value = 0.001 (bacteria); $R = 0.47$, P-value = 0.001 (fungi); The bacterial community was significantly different at different depths in both alpine meadow and desert steppe, but there were no significant fungal differences between depths at both sites (Fig. 4).

3.6. Relationship between bacterial and fungal communities and soil properties

The Spearman correlations of bacterial and fungal alpha diversity with soil parameters are shown in Table 6. Both the bacterial and fungal community richness estimated by Chao1 and ACE was significantly positively correlated with TN, TC, SOC, SWC and C/N (except soil water content and bacterial Chao1 index and ACE index). The BD showed a significant negative correlation with both bacterial and fungal species richness, where bacterial community evenness was estimated by the Shannon index. Bacterial community evenness estimated by the Shannon index showed positive correlations with TN, TC, SOC and C/N ratio, where the fungal community evenness was significantly corelated with SWC.

RDA ordination biplots were used to determine the linkage between bacterial (Fig. 5A) and fungal phyla (Fig. 5B) to soil properties at different soil depths in each grassland. Axis 1 and axis 2 of the RDA ordination biplot for bacterial communities explained 88.6% and 6.3% of the variation respectively. Bacterial phyla Rokubacteria, Planctomycetes, Proteobacteria, Acidobacteria and Verrucomicrobia showed a positive relation to TC, TN, SOC, C/N, and SWC. These relationships are associated in alpine meadows. In deserts, soil pH was linked to Chloroflexi while Bacteroidetes linked to BD. Axis 1 and axis 2 of RDA

Table 4
Relative abundances of taxonomic groups of Fungi at the phylum and genus level. The values are mean ± standard error of mean.

Fungi		Alpine meadow					Desert grassland
Phylum level	Genus level	0–10 cm	10–20 cm	20–30 cm	30–40 cm	Average (AM 0–40 cms)	0–10 cm
Ascomycota		78.47 ± 9.70	76.55 ± 11.50	83.31 ± 4.27	63.58 ± 5.79	75.48 ± 4.18	67.90 ± 8.74
	Archaeorhizomyces	25.00 ± 15.55abcA	31.69 ± 10.3abA	43.40 ± 10.5 aA	17.61 ± 4.67bcA	29.43 ± 5.48***	0.02 ± 0.02c
	Microidium	0.15 ± 0.07 aA	0.11 ± 0.06 aA	0.06 ± 0.04 aA	0.10 ± 0.04 aA	0.11 ± 0.03	10.29 ± 8.95 aA
	Cladophialophora	0.38 ± 0.13	9.25 ± 5.61	7.90 ± 4.48	1.78 ± 0.45	4.83 ± 1.88	0.12 ± 0.10
	Coniochaeta	12.32 ± 8.66	0.77 ± 0.30	0.59 ± 0.40	0.89 ± 0.41	3.64 ± 2.33	0
	Lecanicillium	0.03 ± 0.02	0.09 ± 0.02	0.07 ± 0.02	0.15 ± 0.03	0.08 ± 0.01	0.28 ± 0.07
	Acremonium	0.06 ± 0.06	0.49 ± 0.45	0.35 ± 0.28	0.37 ± 0.30	0.32 ± 0.14	11.05 ± 10.51
	Megaspora	0	0	0	0	0	0.01 ± 0.01
	Xylaria	0.09 ± 0.06bB	0.59 ± 0.26bB	3.41 ± 1.32abAB	6.18 ± 2.67 aA	2.57 ± 0.92*	0.27 ± 0.27bA
	Aspergillus	0.00 ± 0.00bA	0.01 ± 0.01bA	0.05 ± 0.03bA	0.05 ± 0.03bA	0.03 ± 0.01	3.72 ± 1.7 aA
	Pseudogymnoascus	0.00 ± 0.00	0.03 ± 0.02	0.06 ± 0.02	0.10 ± 0.04	0.04 ± 0.02	0.17 ± 0.17
	Phaeophyscia	0	0	0	0	0	7.20 ± 7.19
	Rhinocladiella	1.16 ± 0.18bB	3.28 ± 1.03 aA	0.72 ± 0.29bB	0.78 ± 0.28bB	1.48 ± 0.37***	0.08 ± 0.08bA
	Penicillium	0.02 ± 0.01bB	0.02 ± 0.00bB	0.04 ± 0.02bAB	0.11 ± 0.04bA	0.05 ± 0.01	0.88 ± 0.6abA
	Tuber	0	0.01 ± 0.01	0.01 ± 0.01	0	0.00 ± 0.00	0
	Preussia	0.22 ± 0.18bA	0.29 ± 0.15abA	0.33 ± 0.24abA	0.57 ± 0.55abA	0.35 ± 0.15	1.46 ± 0.19 aA
Basidiomycota		19.84 ± 10.07	22.04 ± 11.60	13.79 ± 4.35	33.42 ± 6.33	22.27 ± 4.26	28.69 ± 8.16
	Clavaria	7.74 ± 7.14 aA	14.61 ± 12.18 aA	8.65 ± 5.28 aA	18.46 ± 8.76 aA	12.36 ± 4.06**	0 aA
	Clitopilus	0.01 ± 0.01bA	0.00 ± 0.00bA	0.00 ± 0.00bA	0.01 ± 0.01bA	0.01 ± 0.00	10.96 ± 6.83 aA
	Tulostoma	0	0	0	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.11
	Coprinellus	0	0	0	0	0	0
	Floccularia	4.55 ± 4.54	0.41 ± 0.40	0.15 ± 0.13	0.35 ± 0.34	1.36 ± 1.13	0
Mortierellomycota		0.04 ± 0.02bB	0.50 ± 0.20abB	0.53 ± 0.12abB	1.28 ± 0.34 aA	0.59 ± 0.15	0.58 ± 0.26abAB
Rozellomycota		0.06 ± 0.04	0.04 ± 0.03	0.07 ± 0.05	0.05 ± 0.03	0.05 ± 0.02	0.06 ± 0.06
Mucoromycota		0.00 ± 0.00b	0.03 ± 0.03b	0.02 ± 0.02b	0.01 ± 0.01b	0.02 ± 0.01	0.00 ± 0.00bB
Glomeromycota		0.03 ± 0.03bB	0.05 ± 0.03bB	0.26 ± 0.11 aA	0.07 ± 0.03bAB	0.10 ± 0.04*	0.01 ± 0.01bA
Olpidiomycota		0	0	0.09 ± 0.09	0.01 ± 0.01	0.03 ± 0.02	0.02 ± 0.01
Chytridiomycota		0.00 ± 0.00	0	0	0	0.00 ± 0.00	0.01 ± 0.01

Different lowercase letters indicate significant differences (P-value < 0.05) among 8 groups of 4 depths of 2 types of grassland. Different Capital letters indicate significant differences (P-value < 0.05) among 4 depths of single grassland. * Indicates significant differences (P-value < 0.05) between the two types of grassland in 0–40 cm, * = significant at P-value ≤ 0.05; ** = significant at P-value ≤ 0.01; *** = significant at P-value ≤ 0.001. The last three columns are the results of two-way ANOVA using Grassland type (T) and Soil depth (D) as main effects.

ordination biplot for fungal communities explained 41.6% and 33.2% of the variation respectively. Fungal phyla Glomeromycota and Olpidiomycota showed a positive link with soil properties TC, TN, SOC, C/N, and SWC. These relationships were associated in alpine meadows. In deserts, soil pH was linked to Rozellomycota, while Mucoromycota was linked to BD.

4. Discussion

The differences in vegetation, climate and geography develop unique soil environments in alpine meadows and desert grasslands (Tables 1 and 2; Fig. 1) which supports distinct soil bacterial and fungal communities (Tables 3 and 4; Figs. 2–4). The soil environment with high C, N, water and air (as indicated by the lower BD) in alpine meadows is more conducive to life compared to the harsh conditions of the desert. This was evident through higher bacterial and fungal species richness in alpine meadows than in desert soils (Table 5). Nevertheless, there were microbial guilds that can thrive in favorable environments as well as more hostile environments, illustrating the resilience (Lombard et al., 2011) of some soil microbes (Table 3, Fig. 3). For example, among the most dominant 20 bacterial genera identified in this study, *RB41*, *Nocardiodes* and *Solirubrobacter* were present in both grasslands, a*lbeit* at lower levels of abundance in the desert.

As found in many previous studies, soil depth can be a significant filter for soil biodiversity (Fierer et al., 2003; Kathryn et al., 2012; Will et al., 2010). In our study, this was more applicable to the alpine meadow where the ecosystem is more conducive to plant growth and litter accumulation than in the desert where the vegetation coverage is low and not diverse. There were obvious changes in soil properties in each of the 10 cm layers along the 40 cm soil profile in alpine meadow. However, apart from the soil moisture and TN, no changes in other soil properties were observed across 10 cm layers in the desert. This difference is most likely due to the limited vegetation coverage in the desert compared to alpine meadows which support diverse and abundant plant communities, contributing to the spatial variation of the belowground environment along each depth by forming soil structure and organic matter, establishing pore space, soil carbon provision by root exudation and changing nutrient availabilities etc. Bacterial community diversity illustrated by the NMDS analysis in Fig. 4A in alpine meadows reflected the pattern of differences in soil properties at different depths. In desert, bacterial community dissimilarity was more obvious between 20 cm layers rather than 10 cm layers. As seen by NMDS analysis in Fig. 4A, microbial communities in 0–10 cm and 10–20 cm depths were similar and the microbial community in 20–30 cm and 30–40 cm were similar. This pattern was similar to the change in soil moisture along soil depth in desert soil, suggesting that soil moisture can be a key determinant in shaping the soil bacterial community in desert. Soil moisture can limit various activities of microorganisms (Eaton et al., 2011). Compared with bacteria, fungal communities often show strong tolerance (Lauber et al., 2008), fungal community diversity wasn't affected by soil depth in either alpine meadow or desert (Fig. 4B, Table 5).

The bacterial and fungal community diversity shifts in alpine meadow and desert alongside the soil depth (Fig. 4) can be explained by the microbial composition changes of different taxonomic groups illustrated in Fig. 5. Despite many differences between the two grassland ecosystems, the members of phylum Actinobacteria dominated both grasslands, indicating their versatility in adapting to different environments (Lombard et al., 2011). The relative abundance of Actinobacteria in desert soil (55.2%) was significantly higher (Table 3) than the meadow soils (30.6%) indicating the dominance of Actinobacteria in arid and desert environments (Silva et al., 2013; Stevenson and Hallsworth, 2014; Wink et al., 2017). Although overall actinobacterial community relative abundance did not vary among the soil depths in both grasslands, at lower taxonomic levels, the relative abundance of several actinobacterial genera either decreased or increased with soil depth (Table 3). The relative abundance of Proteobacteria decreased

Desert grassland				P-value		
10–20 cm	20–30 cm	30–40 cm	Average (DG 0–40 cms)	Grassland types(T)	Soil depth(D)	T*D
51.88 ± 10.97	71.62 ± 8.00	71.37 ± 2.32	65.69 ± 4.21	0.106	0.400	0.294
0.01 ± 0.01c	0.01 ± 0.01c	0.13 ± 0.13c	0.04 ± 0.03	<0.01	0.414	0.407
15.03 ± 7.01 aA	17.30 ± 9.04 aA	16.53 ± 5.07 aA	14.79 ± 3.51***	<0.01	0.920	0.915
1.09 ± 1.09	0.34 ± 0.34	0.30 ± 0.25	0.46 ± 0.28	0.193	0.175	0.135
0.03 ± 0.03	0.02 ± 0.02	0	0.01 ± 0.01	0.107	0.180	0.177
0.27 ± 0.09	11.61 ± 10.35	2.01 ± 0.85	3.54 ± 2.62	0.196	0.371	0.369
0.59 ± 0.3	0.37 ± 0.10	0.46 ± 0.25	3.12 ± 2.63	0.298	0.435	0.378
1.49 ± 1.35	2.82 ± 1.38	6.86 ± 5.82	2.80 ± 1.52	0.081	0.446	0.446
0.00 ± 0.00bA	0.21 ± 0.21bA	0A	0.12 ± 0.08	<0.01	<0.05	<0.05
2.41 ± 0.63abA	1.67 ± 0.82abA	2.26 ± 0.80abA	2.51 ± 0.52***	<0.01	0.610	0.572
2.51 ± 2.51	2.94 ± 1.42	1.49 ± 0.86	1.78 ± 0.73	0.181	0.079	0.076
0.01 ± 0.01	0	0	1.80 ± 1.80	0.326	0.409	0.409
0.01 ± 0.01bA	0.02 ± 0.02bA	0A	0.03 ± 0.02	<0.01	<0.05	<0.05
1.05 ± 0.37abA	1.52 ± 0.81abA	2.26 ± 0.79 aA	1.43 ± 0.33***	<0.01	0.418	0.539
1.44 ± 1.39	2.98 ± 2.95	1.19 ± 1.10	1.40 ± 0.82	0.117	0.679	0.683
0.65 ± 0.22abA	0.40 ± 0.20abA	1.33 ± 0.68abA	0.96 ± 0.21*	<0.05	0.305	0.395
43.04 ± 11.19	17.62 ± 3.96	18.45 ± 3.05	26.95 ± 4.22	0.416	0.239	0.184
0.01 ± 0.01 aA	0.00 ± 0.00 aA	0.00 ± 0.00 aA	0.00 ± 0.00A	<0.01	0.797	0.797
5.08 ± 2.76abA	2.65 ± 1.34bA	0.43 ± 0.25bA	4.78 ± 1.96*	<0.05	0.248	0.248
14.47 ± 14.17	0.04 ± 0.02	0.41 ± 0.30	3.79 ± 3.55	0.295	0.406	0.406
8.35 ± 8.30	0.00 ± 0.00	0	2.09 ± 2.08	0.325	0.405	0.405
0	0	0	0	0.244	0.471	0.471
0.07 ± 0.04bB	0.27 ± 0.14bAB	1.44 ± 0.71 aA	0.59 ± 0.22	0.998	<0.01	0.419
0	0.17 ± 0.17	0.23 ± 0.17	0.12 ± 0.06	0.361	0.561	0.636
0.01 ± 0.01bB	0.09 ± 0.08bB	0.30 ± 0.07 aA	0.10 ± 0.04*	<0.01	<0.01	<0.01
0bA	0bA	0bA	0.00 ± 0.00	<0.01	0.066	<0.05
0.01 ± 0.01	0.02 ± 0.02	0	0.01 ± 0.01	0.627	0.336	0.580
0.05 ± 0.04	0.05 ± 0.05	0	0.03 ± 0.02	0.105	0.585	0.527

with increasing soil depth in alpine meadow, consistent with the view of their copiotrophic life strategy in which the microbes thrive in environments with greater labile soil carbon, such as in rhizosphere soils. A decrease in Proteobacteria with increasing soil depth was also observed by Hansel et al along a geochemically variable soil profile and Will et al. (2010) in German grassland soil. However, the increase of Proteobacterial abundance with depth in desert suggests that under low carbon environments, other factors may play a critical role in their distribution. Romero-Olivares et al. (2017) argued that in low carbon soils, factors other than carbon, such as water and unknown effects of soil depth, can be determinants of microbial community composition. Fierer et al. (2003) reported that water was an important variable for

Table 5
Differences of soil bacterial and fungal alpha diversity indices of four soil depths at the two investigated grasslands. The values are mean ± standard error of mean.

Grassland types(T)		Chao1		ACE		Shannon		Simpson	
	Soil depth (D) cm	bacteria	Fungi	Bacteria	fungi	bacteria	fungi	bacteria	fungi
Alpine meadow	0–10	2550.0 ± 82.5 aA	252.3 ± 31.7 aA	2709.8 ± 102.6 aA	256.1 ± 30.6 aA	10.07 ± 0.10 aA	4.48 ± 0.54 aA	0.997 ± 0.00 aA	0.87 ± 0.04 aA
	10–20	2613.8 ± 59.2 aA	245.8 ± 16.6 aA	2803.8 ± 81.9 aA	248.2 ± 17.1 aA	10.01 ± 0.07abA	4.70 ± 0.27 aA	0.997 ± 0.00 aA	0.88 ± 0.04 aA
	20–30	2450.9 ± 186.5 aA	253.2 ± 14.2 aA	2582.4 ± 159.2 aA	255.6 ± 14.4 aA	9.47 ± 0.19bcB	4.49 ± 0.41 aA	0.992 ± 0.00 cB	0.85 ± 0.04 aA
	30–40	1826.5 ± 217.3bB	270.3 ± 14.3 aA	1875.6 ± 245.9bB	269.6 ± 14.6 aA	8.86 ± 0.07 dC	5.09 ± 0.46 aA	0.987 ± 0.00 dC	0.91 ± 0.04 aA
	Average (AM 0–40 cms)	2360.3 ± 105.7*	255.4 ± 9.5***	2492.9 ± 118.5*	257.4 ± 9.3***	9.60 ± 0.14	4.69 ± 0.20	0.993 ± 0.00	0.88 ± 0.02
Desert grassland	0–10	2292.5 ± 138.9 aA	144.0 ± 7.8bcB	2411.2 ± 137.7 aA	146.0 ± 7.8bcB	9.73 ± 0.12abA	3.99 ± 0.37 aB	0.997 ± 0.00 aA	0.83 ± 0.04 aA
	10–20	2424.7 ± 96.4 aA	187.3 ± 10.8bA	2484.2 ± 73.3 aA	188.6 ± 10.1bB	9.70 ± 0.13abA	4.23 ± 0.33 aB	0.996 ± 0.00abA	0.84 ± 0.06 aA
	20–30	1664.6 ± 214.5bB	158.6 ± 17.9bcAB	1747.9 ± 234.4bB	160.9 ± 18.0bcAB	8.95 ± 0.31cdB	4.61 ± 0.26aAB	0.993 ± 0.00bcAB	0.90 ± 0.02 aA
	30–40	1398.5 ± 147.7bB	133.6 ± 9.5 cB	1459.1 ± 159.8bB	135.3 ± 9.4 cB	8.44 ± 0.27 dB	5.22 ± 0.25 aA	0.989 ± 0.00cdB	0.95 ± 0.01 aA
	Average (DG 0–40 cms)	1945.1 ± 130.2	155.9 ± 7.5	2025.6 ± 133.6	157.7 ± 7.4	9.21 ± 0.17	4.51 ± 0.18	0.994 ± 0.00	0.88 ± 0.02
Statistical significance (P-value)	Grassland types (T)	0.001	<0.001	<0.001	<0.001	0.005	0.508	0.696	0.978
	Soil depth(D)	<0.001	0.724	<0.001	0.722	<0.001	0.115	<0.001	0.148
	T*D	0.237	0.163	0.330	0.182	0.935	0.729	0.549	0.486

Different lowercase letters indicate significant differences (P-value < 0.05) among 8 groups of 4 depths of 2 types of grassland. Different capital letters indicate significant differences (P-value < 0.05) among 4 depths of single grassland. * Indicates significant differences (P-value < 0.05) between the two types of grassland in 0–40 cm, * = significant at P-value≤0.05; ** = significant at P-value ≤0.01; *** = significant at P-value ≤ 0.001. The last three rows are the results of two-way ANOVA using Grassland type (T) and Soil depth (D) as main effects.

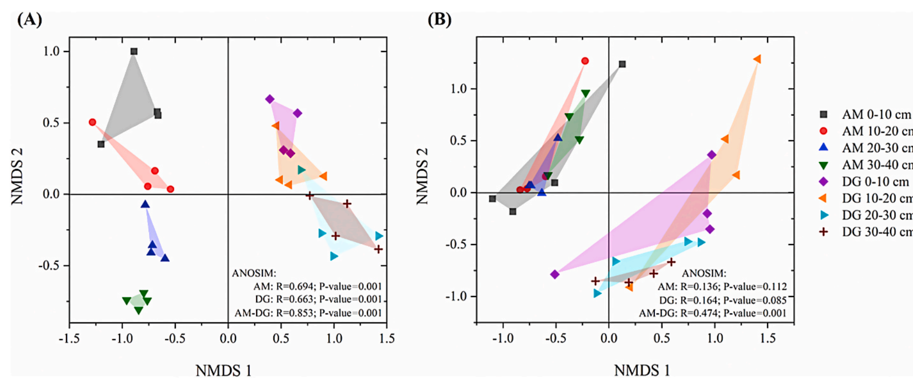

Fig. 4. Non-metric multidimensional scaling (NMDS) plot illustrating the bacterial (A) and fungal (B) communities in different depths of alpine meadow (AM) and desert grassland (DG).

microbial community composition differences along soil depth at their semi-arid research site. The decrease in Acidobacteria with increasing depth in alpine soil can be explained by the increase in soil pH with depth, as generally Acidobacteria abundance is considered to have a negative relationship with soil pH (Lauber et al., 2008). Soil pH was not affected by the depth in desert, and neither was Acidobacteria abundance. Bacterial phyla Chloroflexi and Gemmatimonadetes abundance increased with depth in alpine meadows and was unaffected by the nutrient poor soil layers in desert, indicating their oligotrophic lifestyle (Yan et al., 2018; Yao et al., 2017).

As observed in previous studies (Brodie et al., 2003; Du et al., 2017), members of Ascomycota and Basidiomycota dominated the soil fungal population in both grasslands and their relative abundance was not affected by soil depth. However, at lower taxonomic levels, fungal genera composition of the two grasslands were markedly different (Fig. 3D), resulting in distinct fungal communities in the two grasslands (Fig. 4B). A study conducted across 60 grassland sites in the Tibetan Plateau by Yang et al. (2017) found that plant community diversity is the key determinant for soil fungal diversity. The differences in plant community diversity, together with other differences in soil properties may have caused distinct fungal communities in two grasslands in our study. There were variations of the relative abundance of some of the top 20 dominant fungal genera among different soil depths (Fig. 3D, Table 4) but those differences may not have been substantial, compared to the uniform distribution of other genera throughout the profile, resulting in a uniform fungal community along the 40 cm depth profile in both grasslands (Table 5, Fig. 4B). Similar to our study, Ko et al. (2017) did not observe a clear trend of fungal community responses along a soil profile at a fallow field. In contrast, Jumpponen et al. (2010) found fungal community richness and diversity declined with soil depth at a native tallgrass prairie in eastern Kansas in the USA. The inconsistent pattern of fungal composition along soil depths of different studies may suggest that site specific characteristics are important determinants for shaping the fungal communities.

We found the relationship between soil properties and bacterial/fungal diversity and composition varied in the two grasslands. The importance of soil carbon in shaping the microbial communities has been widely reported by several previous studies (Lauber et al., 2008; Liu et al., 2015; Tian et al., 2017; Yang et al., 2018) and in our study, both bacterial and fungal species richness, bacterial community evenness (estimated by Shannon index), and the relative abundance of some dominant phyla were significantly correlated with TC and SOC (Table 6 , Fig. 5). We found that, especially in alpine grasslands TN, TC, SOC, C/N and SWC were important in structuring bacterial and fungal communities while BD and pH were important in desert soil (Fig. 5). Soil pH has been widely recognized as the best predictor of microbial diversity and richness globally (Fierer and Jackson, 2006; Lauber et al., 2009), in land use regimes (Kaiser et al., 2016) and at a landscape level (Lauber et al., 2008). However, in our study neither bacterial nor fungi species richness and diversity showed a significant correlation with soil pH, possibly due to narrow pH range (7.06–7.69) observed in this study (Table 6).

Consistent with our hypothesis, we found that the two habitats, alpine meadow and desert, harbored distinct microbial populations. The evidence for habitat specificity by microbial communities in dryland China has been previously observed by Wang et al. (2017). Vellend (2010) described four generic processes that potentially contribute to patterns in the composition and diversity of species in ecosystems; 1. Selection - is the outcome of environmental pressures causing variation in survival and reproduction within and among species; 2. Dispersal - mainly refers to the movements of a species to a new location; 3. Drift - reflects population sizes fluctuating in a location owing to inherent chance events; and 4. Speciation - produces new species that are adapted to conditions. Hanson et al. (2012) proposed these four processes also valid for establishing soil microbial biogeographic patterns. In our study, it is plausible that a combination of all four processes have contributed to the differences in microbial composition between two habitats located in the same eco region. We found that 19 and 11% of bacterial and fungal OTUs, respectively, were shared between both sites (Fig. 3) representing either resistant microbial guild to the above

Table 6
Spearman correlation coefficients between bacterial and fungal community alpha diversity indices and soil properties.

		TN	TC	pH	SOC	SWC	BD	C/N
Chao1	Bacteria	0.594**	0.538**	−0.156	0.486**	0.265	−0.588**	0.485*
	Fungi	0.784**	0.772**	−0.239	0.729**	0.667**	−0.774**	0.781**
ACE	Bacteria	0.624**	0.571**	−0.148	0.532**	0.291	−0.603**	0.504*
	Fungi	0.784**	0.772**	−0.257	0.747**	0.667**	−0.774**	0.781**
Shannon	Bacteria	0.621**	0.607**	−0.197	0.518**	0.207	−0.605**	0.570**
	Fungi	0.370	0.352	−0.205	0.067	0.482*	−0.305	0.323
Simpson	Bacteria	0.192	0.187	−0.232	−0.056	0.285	−0.110	0.196
	Fungi	0.411*	0.436*	−0.195	0.279	−0.057	−0.401	0.398

TN: Total nitrogen; TC: Total carbon; SOC: Soil organic carbon; SWC: Soil water content; BD: bulk density; C/N: Ratio of carbon to nitrogen. * and ** indicate that the two variables were significantly correlated at the level of 0.05 and 0.01, respectively.

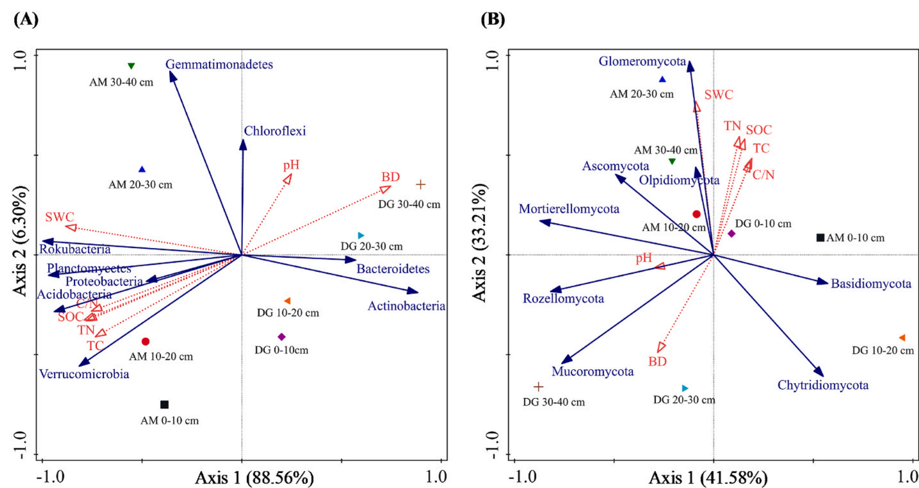

Fig. 5. Redundancy analysis (RDA) ordination plots illustrating the relationships between dominant bacterial (A) and fungal (B) phyla and the soil properties. Solid and dashed vectors indicate the microbial communities and soil parameters, respectively. TN: Total nitrogen; TC: Total carbon; SOC: Soil organic carbon; SWC: Soil water content; BD: bulk density; C/N: Ratio of carbon to nitrogen.

processes or dispersal of microbes from alpine meadows to deserts by wind and water because the Qilian mountain range frequently experiences severe wind and acts as major water resource for the surrounding desert areas in the mountain base. The two sites constantly experience different environmental pressures such as temperature, precipitation, UV radiation, wind, vegetation change and soil erosion, potentially contributing to microbial composition changes through selection, dispersal, drift and speciation occurring to varying degrees at the two sites. Recent years these changes have been occurring severely in some areas of Qilian mountain range (Huang et al., 2007; Ji and Yang, 2013), prompting policy makers to develop actions to prevent desertification. In this context, policies are required to protect soil and soil biodiversity. Soil is most often thought of for its physical and chemical characteristics, not for its biological features. This study generated a large data set about soil biodiversity patterns in two contrasting habitats in the Qilian mountain range, providing useful information for efforts to act against biodiversity loss.

5. Conclusions

We identified distinct bacterial and fungal compositions in soil profiles up to 40 cm below the surface in an alpine meadow and desert grassland, both found on the Qilian mountain range of China. Soil physicochemical properties showed correlations to specific bacterial and fungal taxa. Soil carbon, nitrogen and water changes along the soil depth of alpine meadow influenced the bacterial and fungal species richness and diversity. While there were some bacterial and fungal taxa composition changes present along the depth in desert, more uniform distribution of microbial groups was prevalent in the desert soil profile, emulating the uniformity of soil properties. In contrast to the several previous studies, soil pH was not found as a good predictor for microbial diversity in our study. We identified that soil carbon, nitrogen and water are important factors in shaping the bacterial and fungal community.

CRediT authorship contribution statement

Baotian Kang: Visualization, Investigation, Data curation, Writing - original draft. **Saman Bowatte:** Conceptualization, Supervision, Validation, Visualization, Writing - review & editing. **Fujiang Hou:** Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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