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The influence of biocrusts on the spatial pattern of soil bacterial communities: A case study at landscape and slope scales

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ABSTRACT

Biocrusts are a functional unit in arid and semiarid areas, their development has significant recruitment and screening effects on soil microbial communities. Microbial composition of biocrusts exhibits significant geographical patterns, but the regulation of biocrust development on the geographical patterns in unclear. In this study, we examined bacterial communities from cyanobacterial-lichen and moss crust soils in five desert habitats in northern China, and evaluated the relative importance of environmental factors and biocrust development *versus* geographic distance to the distance–decay relationship. To explore the effects of the sampling scale on geographical patterns, we also examined soil bacterial communities along the slope of sand dunes. Across the five desert habitats, bacterial α-diversity, phylogenetic diversity, and the dominant bacterial phyla in cyanobacterial-lichen crusts did not increase consistently with precipitation increase, instead bacterial community composition was mainly impacted by soil nutrients (SOC, TP) and biocrust development (thickness, cover and Chl a). Bacterial β-diversity in both cyanobacterial-lichen and moss crusts showed strong distance-decay relationships across the landscape scale; bacterial community composition in cyanobacterial-lichen crusts differed significantly among five desert habitats. Environmental and biocrust development variables explained bacterial community variation better than geographic distance, suggesting a weaker influence of dispersal limitation on the bacterial communities in biocrusts. In addition, the distance-decay rate was higher at the slope than that at the landscape scale, suggesting a fast turnover rate of bacterial community communities induced by topography. Our study implies that soil attributes and biocrust development have more profound impacts on soil bacterial communities than precipitation, which provides novel insights into the geographical distribution and assemblage of soil bacterial communities in deserts. Moreover, our study is significant with respect to understanding the potential responses of soil microbial communities to climate change in desert areas under the scenario of increasing precipitation variation.

1. Introduction

Geographical distribution patterns of plants and microorganisms have been studied at local (Wang et al., 2015b, 2017; Scola et al., 2018) and continental scales (Fierer and Jackson, 2006; Wang et al., 2017). Precipitation (Scola et al., 2018), soil salinity (Zhang et al., 2019), soil pH (Fierer and Jackson, 2006) and soil texture (Pasternak et al., 2013) are crucial determinants for the geographical variation of soil microbial communities in arid and semiarid regions. Until now, however, few studies have focused on the modification effects of biocrust development on soil microbes. Biocrusts are widely distributed and make up 40% of the soil surface living cover, and they are significant to ecosystem sustainability and stabilization (Belnap and Lange, 2003; Weber et al., 2016). Biocrusts show dynamic development and succession after their inhabitation in bare soils, during this process, soil nutrient accumulate and water availability changes, which may generate different microbial communities from bare soils (Garcia-Pichel et al., 2001; Liu et al., 2017). However, it remains unclear how spatial patterns of soil bacterial

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communities occur in terms of biocrust development (Garcia-Pichel et al., 2001, 2003; Dvořák et al., 2012).

In the process of biocrust development, the transition of dominant functional groups from cyanobacteria to lichen and moss alters the structure of bacterial communities due to different nursing effects on soil bacteria, consequently, this generates contrasting bacterial communities (Steven et al., 2013; Velasco et al., 2017). However, our understanding of bacterial community variation along successional sequences of biocrusts remains limited (Zhang, 2014; Liu et al., 2017). Studies of this knowledge gap could improve our understanding of biocrust functions in the process of ecological restoration of sandy deserts (Bowker, 2007; Winkler et al., 2018; Letendre et al., 2019), and are critical to predicting desert ecosystem responses under climate change scenarios (Weber et al., 2016).

Recent advances in molecular techniques have enabled studies of the microorganisms which flourish in barren soils (McHugh et al., 2017). Microbial communities vary with environmental variables across a geographical scale, which is systematically heterogeneous but not cosmopolitan (Green and Bohannan, 2006). Environmental filtering and dispersal limitation are two of the most fundamental mechanisms shaping the geographical pattern of microbial communities (Green and Bohannan, 2006). The geographical pattern of bacterial communities is largely determined by dispersal limitation, which is demonstrated by a distance-decay relationship in many studies (Martiny et al., 2011). Besides of the dispersal limitation, increasing geographical distance is usually accompanied with increasing environmental differences, which increasingly enhance community differences as species are selected from local taxa pool based on their niche preferences (Bell, 2010). Growing evidence supports the relative importance of environmental filtering in explaining geographical patterns of microbial communities (Bell, 2010), including soil pH (Chu et al., 2010; Rousk et al., 2010), soil texture and carbon content (Fierer and Jackson, 2006), soil organic carbon quality (Lauber et al., 2008), and aridity (Maestre et al., 2015). The discrepancies among studies may be partly due to differences in ecosystem categories (Angel et al., 2010; Bell, 2010; Bachar et al., 2012), microbial groups and taxa (Angel et al., 2010; Dvořák et al., 2012), and inconsistent sampling or sequencing methodologies (Jones et al., 2009; Dvořák et al., 2012). Environmental variables shaping microbial communities differ in terms of the geographical scale (Bell, 2010; Nemergut et al., 2011). For instance, bacterial and fungal communities are determined by environmental filtering at a local scale (Pasternak et al., 2013) and by dispersal limitation at the continental scale (Green and Bohannan, 2006).

Biocrusts usually show sequential development, with thickness and cover usually increasing and the dominant taxa shifting from cyanobacteria and algae to lichen and moss with improved soil properties at local scale (Li et al., 2012; Su et al., 2013a, b; Zhang et al., 2016). Therefore, it is reasonable to infer that soil matrix and biocrust development may be a potential filter to microbial communities at a local scale. The relative cover of early successional biocrusts (cyanobacterial crusts) versus late successional biocrusts (moss crust) generally decreases with increasing precipitation at the geographical scale (Li et al., 2017). Soil organic carbon and nutrient contents, as well as microbial biomass in moss crusts are much higher than those in cyanobacterial crusts, moreover, microbial communities vary with the succession of biocrusts at local scale (Housman et al., 2006 & 2007; Li et al., 2010). Microbial communities in biocrusts have been investigated with respect to limited regions and specific taxa (Garcia-Pichel et al., 2003; Chamizo et al., 2012; Blay et al., 2017; Li et al., 2017). However, it remains unclear how microbial communities in biocrusts differ at geographical scale.

Here, we conducted two independent experiments to investigate the variation and the factors driving bacterial communities in biocrusts. In the first experiment, we examined soil bacterial communities from cyanobacterial-lichen and moss crusts in five desert habitats stretching 2000 km in northern China, and evaluated the relative importance of environmental factors and biocrust development versus geographic distance to a distance–decay relationship. In the second experiment, we examined soil bacterial communities at slope scale, this experiment combining the first experiment explored the effects of the sampling scale on the spatial pattern. We addressed the following two hypotheses: (1) soil and biocrust traits would regulate the geographical pattern of bacterial communities, and the rate of distance decay (the slope of the distance–decay curve) would be different between two successional biocrusts, since soil attributes and biocrust properties exhibited a sequential variation pattern along the precipitation gradient at landscape scale; (2) environmental variables would contribute more to the microbial variation at slope scale than that at landscape scale due to the substantial successional process of biocrusts in micro-habitats along the sand dune slope.

2. Materials and methods

2.1. Study site description

For experiment I, the study sites were distributed in five desert habitats of northern China (Fig. 1A, Table S1) where biocrusts were well developed and played key ecological functions (Su et al., 2013a, b; Zhao et al., 2014; Li et al., 2017). The annual precipitation ranged from 75 mm in the center of the Gurbantunggut Desert, in northwestern China, to 559 mm in the Loess Plateau, in the middle of northern China. The aridity index ranged from 0.04 to 0.28 (Table S1). Detailed climatic, soil and vegetation properties have been described in previous studies (Zhao et al., 2010; Su et al., 2013a, b; Li et al., 2017).

For experiment II, the study site was located at the center of the Gurbantunggut Desert (45.43N, 87.41E) in northwestern China. The mean annual precipitation is 75 mm, and the mean potential annual evaporation is 1844 mm. The mean annual temperature is 7.5 °C. Vegetation is dominated by *Haloxylon persicum* Bunge ex Boiss. Et Buhse at the top and upslope of sand dunes, *H. ammodendron* (C.A. Meyer) Bunge and *Ephedra distachya* L. at the downslope and lowland. Besides shrubs and semi-shrubs, ephemerals and ephemeroids boom in spring and early summer, reaching a cover of 40%. This region is characterized with south-north fixed and semi-fixed sand dunes, with a slope gradient of 12–23°. The vertical height of the sand dunes is in the range of 7–10 m, the slope length is in the range of 15–50 m, the inter-dune width between two adjacent sand dunes usually reaches 100–220 m (Wang et al., 2012a,b). From the top to the lowland of a typical sand dune, the type of biocrusts were cyanobacterial and physical crusts on the top and the upland of a sanddune, cyanobacterial-algal crusts on the upland and midland of a sanddune, cyanobacterial-lichen crusts on the lowland and the inter-dune between two sand dunes, moreover, moss crusts were sparsely distributed on the lowland and inter-dunes (Fig. 1B).

2.2. Geographical location and climate data

The latitude, longitude, and altitude were determined using a GPS (Magellan GPS315, Magellan, Santa Clara, CA, USA). Mean annual precipitation (MAP) and mean annual temperature (MAT) were calculated from the WorldClim database (http://www.worldclim.org/) using ArcGIS 10.0 Spatial Analysis tool (SERI, Redlands, CA, USA) based on the geographical coordinates (Hijmans et al., 2005). Aridity index was calculated as the mean annual precipitation dividing mean annual evaporation.

2.3. Soil sampling, biocrust development index and soil microbial biomass measurements

Microbial community of biocrusts varies widely even at the millimeter scale (Grondin and Johansen, 1993; Wheeler et al., 1993). To gauge the diversity and capture the heterogeneity of each habitat, three 10,000 m^2 plots with a distance of 1–2 km between plots were set up in

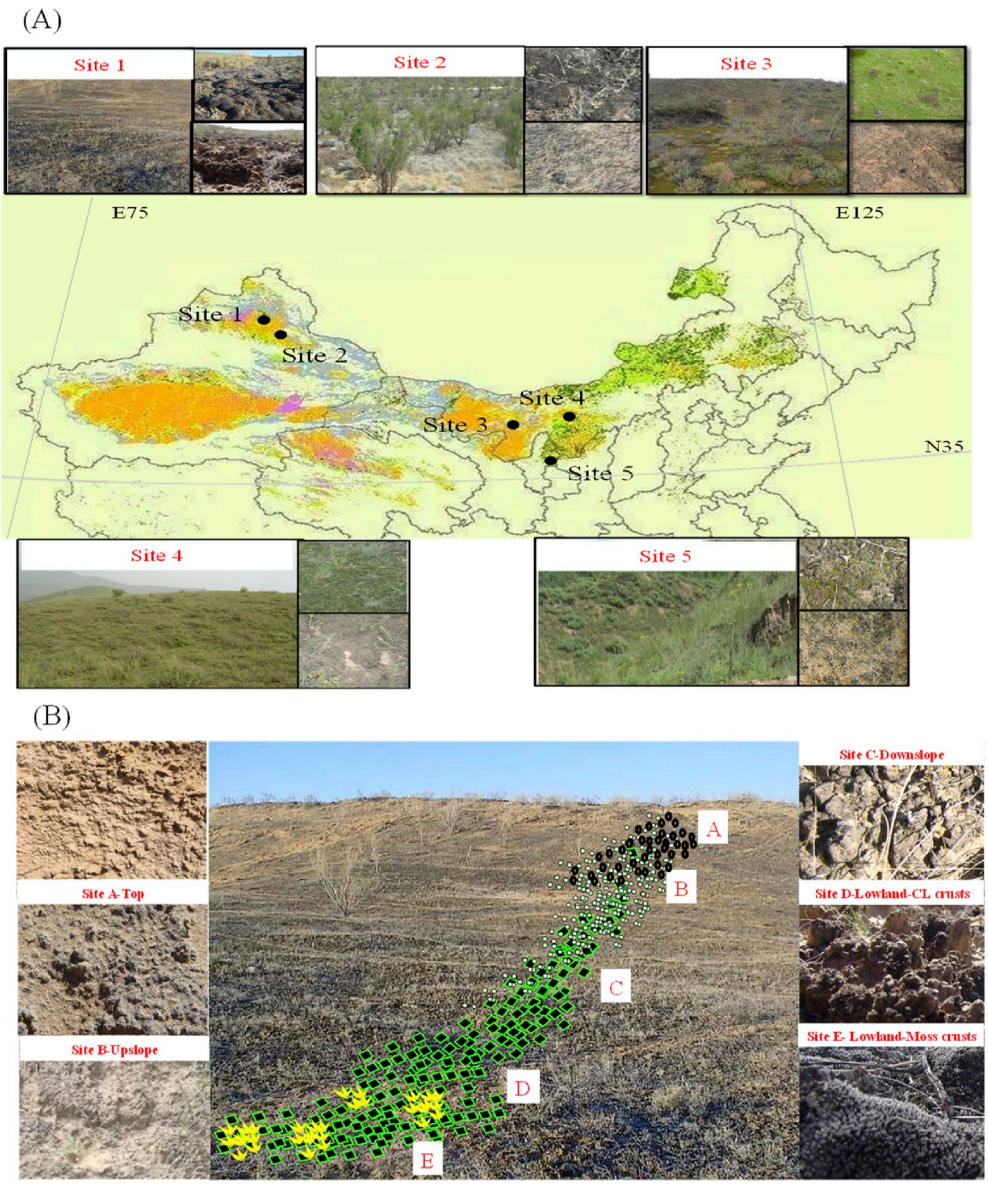

Fig. 1. Sampling site locations of the study. A) shows the distribution of sampling sites in northern China for experiment I. Site1 and Site2 were in the center and southern margin of Gurbantunggut Desert with MAP of 75 mm and 147 mm. Site 3 lied in the southern margin of Tengger Desert with a MAP of 186 mm, Site 4 lied in the Mu Us Desert with a MAP of 393 mm and Site 5 lied in the Loess Plateau with a MAP of 559 mm. B) shows the distribution of sampling sites and the spatial pattern of dominant biocrusts in a typical sand dune in the southeastern Gurbantunggut Desert in experiment II. Brown dots with black circles indicated physical crusts, light green dots indicate cyanobacterial crusts, dark solid squares with green border indicate cyanobacterial, algal and lichen mixed crusts, and yellow symbols indicate moss crusts. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

each habitat for experiment I, five individual samples (cyanobacterial-lichen crusts and moss crusts) were collected from each plot and mixed as a composite sample. There were three replicates for each biocrust in a region. For experiment II, three typical sand dunes were selected, and five locations (top, upslope, downslope, lowland with cyanobacterial-lichen crusts and lowland with moss crusts) were set up along the windward slope in each sand dune (biocrusts colonized windward slope). In each location, five individual samples were collected and mixed as a composite sample, in total three replicates for each location. Bacterial communities primarily inhabit the top millimeter or centimeters in dryland soils where the majority of the sequestered carbon, nutrients and living biota reside (Li et al., 2015; Liu et al., 2019). Considering the maximum thickness of biocrusts in our study and the common sampling depth in arid and semiarid regions (Steven et al., 2014; Wang et al., 2015a, 2017; Liu et al., 2017), the top 0–5 cm of biocrusts and sub-soil were collected intact by pushing a sterile soil core (5 cm in diameter, 5 cm in depth) into the soil and then sliding a flat metal sheet under it to remove the intact core. The collected samples were preserved in an ice box, taken to the laboratory and immediately sieved (1 mm sieve) to remove stones, plant roots, and moss. Samples were divided into two parts, one was air-dried for soil property analysis and the other was stored at −80 °C for bacterial community analysis. Specifically, nucleic acids were extracted from homogenized crust samples within 2 weeks of collection.

The development of biocrusts was generally visually assessed at a small scale using different standards (Belnap et al., 2008; Chamizo et al., 2012; Lan et al., 2013). In our study, the cover of moss exceeding 85% was regarded as a moss crust; similarly, the coverage of lichen and cyanobacteria over 85% was a cyanobacterial-lichen crust (Lan et al., 2013). The cover of biocrusts was measured using a point sampling frame (2.5 cm × 2.5 cm grid; 169 points per 30 cm × 30 cm quadrat, Li et al., 2010). For thickness measurement, we lifted cyanobacterial-lichen crusts up with tweezers, and gently shook them until no soil fell from the biocrusts, and then measured the crust thickness with a vernier caliper. Moss rhizoids are critical to the crust thickness; no consensus has been reached in terms of how to measure the thickness of moss crusts. Here, moss stem and rhizoid length was included in the thickness.

Soil microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) were estimated using a chloroform fumigation extraction method (Brookes, 1985). Paired 20-g fresh soil samples that were either unfumigated or fumigated with alcohol-free $CHCl_3$ for 24 h were

extracted with 0.5 M K_2SO_4 (1:2.5 v/v). C and N were analyzed using a TOC analyzer (multi N/C 3100, Jena, Germany). The efficiency factors for MBC ($K_c = 0.38$ (Vance et al., 1987),) and MBN ($K_n = 0.54$ (Brookes et al., 1985),) were used to calculate the respective biomass.

The chlorophyll *a* content of cyanobacterial-lichen crusts and the stem and leaf of moss in biocrusts were analyzed by extraction with 98% ethanol at 4 °C for 24h and measured by absorption at 649 nm and 665 nm using a spectrophotometer (UV-1700 PharmaSpec, Kyoto, Japan, Li et al., 2001).

2.4. Soil property measurements

Soil organic carbon, total nitrogen, total phosphorus, total potassium, total salt, soil bulk density, soil silt and clay content, soil pH, and electrical conductivity were used to represent the basic soil properties in our study. The soil organic carbon (SOC) content was determined using the dichromate oxidation method (Nelson and Sommers, 1982). The total nitrogen (TN) content was measured using a Kjeltec System 1026 Distilling Unit (Tecator AB, Hganაs, Sweden). Soil total phosphorus and potassium contents were measured using the methods described by Olsenard and Sommers (1982). Total soil salt content was analyzed using the methods described by the Nanjing Institute of Soil Research, Chinese Academy of Sciences (1980). Soil bulk density was measured using a cutting ring (5 cm in inner diameter and 5 cm in depth), calculated as soil weight after oven-dried at 105 °C for 48h dividing the volume of the cutting ring. The soil particle size was analyzed using the pipette method (Loveland and Walley, 2001). The soil pH and electrical conductivity were determined in a 1:5 ratio soil:water suspension using a calibrated pH meter (Mettler Toledo FE28, Zurich, Switzerland) and electrical device (Mettler Toledo FE20, Zurich, Switzerland). Soil mass water content was measured monthly from May to September and calculated as soil volumetric water content.

2.5. DNA extraction and Illumina MiSeq sequencing of bacterial communities

DNA extraction was performed following the manufacturer's protocol using the MOBIO Power Soil DNA Isolation Kit (CAT: 12,888–100, MO BIO Laboratories, Carlsbad, CA, USA). For MiSeq sequencing, the universal forward and reverse primers 515F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′), respectively, were used to amplify the V4 hypervariable region of the 16S rRNA gene. A unique 12 bp barcode was added at the 5′ end of the reverse primer, and each sample had its own unique barcode. The resulting PCR product was approximately 281 bp. The PCR mixture (25 μl) contained 1x PCR buffer, 1.5 mM $MgCl_2$, deoxynucleoside triphosphate at 0.4 mM, each primer at 1.0 μM, 0.5 U ExTaq (TaKaRa, Dalian), and 10 ng of soil genomic DNA. The PCR amplification program included an initial denaturation at 98 °C for 1 min, followed by 30 cycles of 98 °C for 10 s, 50 °C for 30 s, and 72 °C for 30 s, with a final extension at 72 °C for 5 min. The PCR products were purified using the GeneJET™ Gel Extraction Kit (Thermo Scientific, Massachusetts, USA). All purified PCR products were mixed at equal molar amounts for library construction using the TruSeq DNA kit and sequenced using an Illumina MiSeq platform (Illumina Inc., San Diego, CA, USA) at the Novogene Bioinformatics Technology Co., Ltd. (Beijing, China).

Sequence processing, clustering, taxonomic assignments, and biodiversity calculations were performed with the QIIME (V1.7.0, http://qiime.org/index.html, Caporaso et al., 2010). First, sequences were de-multiplexed and the primer and barcode sequences were removed. The sequences with high quality (length > 260 bp, without ambiguous 'N' bases, and an average base quality score > 30) were used for downstream analyses. Operational taxonomic units (OTUs) were generated by an open-reference OTU picking protocol, where the sequences were clustered against the GreenGene Database, with a 97% similarity cutoff. Taxonomic assignments were performed against the SILVA (SSU115) 16S rRNA database using a confidence threshold of 70% (Jörg, 2007; McDonald et al., 2012). The raw reads were deposited in the NCBI Sequence Read Archive database (accession number: SRP229704).

2.6. Statistical analysis

The differences in soil properties, biocrust attributes, MBC, MBN, bacterial richness, α-diversity, and phylogenetic diversity among sampling sites were all analyzed by one-way ANOVA. Correlation between alpha-diversity, phylogenetic diversity and richness with climate, soil and biocrust properties were analyzed by SPSS software (SPSS 13.0 for Windows, SPSS Inc., Chicago, IL, USA). The other statistical analyses were conducted using the program R v.3.5.1 (R Development Core Team, 2018). The non-metric multidimensional scaling (NMDS) was conducted with the "metaMDS" (Minchin, 1987) and the multiple response permutation procedure using 'mrpp' was used to test the bacterial community composition differences among sampling sites. Monte Carlo permutation test (permutest) and "envfit" functions (Legendre et al., 2011) were used to test the significant environmental variables during NMDS analysis. The "Bray–Curtis" dissimilarity matrix for the bacterial community composition and the "Euclidean" dissimilarity matrices for geographic distance, soil and biocrust variables were constructed with the "vegdis" function (Oksanen et al., 2016). The significant PCNM vectors constructed with the "pcnm" (Borcard and Legendre, 2002) and environmental variables were used as explanatory variables in NMDS for variation partition analysis with "varpart" function (Peres-Neto et al., 2006). BioEnv procedure was performed to select the environmental variables which were further used to construct environmental distance matrix (Clarke and Ainsworth, 1993). Mantel tests with 999 permutations (Legendre and Legendre, 2012) were used to examine the correlation (Pearson's rank correlation) between geographic, soil variables, biocrust properties and bacterial community distance. Moreover, linear regression was used to examine the relationship between the geographic distance and similarity in bacterial composition among samples. Arrhenius (log–log) function was used to investigate the species-geographic distance relationship in the form: $\ln(Ss) = \text{constant} - 2z \ln(D)$, where Ss is the pairwise similarity in bacterial community composition, D is the geographic distance and z is a measure of the species turnover rate across distance. A one-sample *t*-test between the original slope and a mean of bootstrapped slopes by random pairing of the original set (permuted 999 times) was performed for testing the significance of z values (Zhou et al., 2008).

3. Results

3.1. Biocrust and soil properties

At the landscape scale, the thickness and cover of cyanobacterial-lichen crusts decreased from hyper-arid (S1) to semi-arid habitat (S5) (Table 1), the cover of moss crusts was significantly higher in semi-arid than in hyper-arid habitat, and the thickness showed no consistent pattern across five habitats (Table 1). Biocrust thickness and cover increased significantly with their development from the top to the lowland of the sand dunes (Table 1), consistently, MBC and MBN also increased significantly (Table 1).

Soil properties differed significantly among the sampling sites at both the landscape and slope scales (Table S2, all $P < 0.05$). Soil organic carbon, total nitrogen, soil silt and clay content increased, soil bulk density and pH decreased with precipitation increase at landscape scale (Table S2). At the slope scale, soil organic carbon and total nitrogen, soil silt and clay contents all increased, soil bulk density and pH decreased from the top to the lowland of sand dunes (Table S2).

Table 1
Biocrust properties comprising thickness (mm), cover (%) and Chl a content (μg cm^{-2}) of crusts layer and soil microbial biomass carbon (MBC, mg kg^{-1}) and nitrogen (MBN, mg kg^{-1}) contents at 0–5 cm soil layer. Values are mean ± SE (n = 3). S1–S5 indicated five sampling desert habitats as demonstrated in Fig. 1, with annual mean precipitation denoted in brackets. Different small letters indicate significant difference between sampling habitats at landscape scale and between sampling location at sand dune scale.

Site	Thickness (mm)	Cover (%)	Chl a (μg cm^{-2})	MBC (mg kg^{-1})	MBN (mg kg^{-1})
Geographical scale					
Cyanobcterial-lichen crusts					
S1 (75 mm)	1.77 ± 0.09a	68.33 ± 1.67a	3.55 ± 0.34a	313.15 ± 23.04a	28.76 ± 1.77a
S2 (147 mm)	1.23 ± 0.09b	44.33 ± 2.96b	2.56 ± 0.35b	234.71 ± 73.19 ab	29.32 ± 9.55a
S3 (186 mm)	0.90 ± 0.06c	38.33 ± 1.67c	1.70 ± 0.23c	193.62 ± 28.70b	24.92 ± 5.33a
S4 (393 mm)	0.83 ± 0.09c	35.00 ± 2.89c	1.28 ± 0.20cd	336.64 ± 50.17a	31.07 ± 13.91a
S5 (559 mm)	0.70 ± 0.06c	25.00 ± 2.89d	1.16 ± 0.14d	384.47 ± 37.62c	36.50 ± 3.44a
Moss crusts					
S1 (75 mm)	22.87 ± 1.36a	5.67 ± 0.67a	41.23 ± 3.50a	424.40 ± 79.08a	36.98 ± 4.63a
S2 (147 mm)	15.73 ± 1.45b	2.60 ± 0.70b	26.20 ± 2.89b	365.07 ± 35.28 ab	25.80 ± 6.71a
S3 (186 mm)	17.40 ± 1.19b	8.33 ± 2.03c	35.90 ± 3.10 ab	335.05 ± 30.74b	45.98 ± 17.94a
S4 (393 mm)	21.83 ± 1.45a	9.00 ± 1.00c	26.60 ± 2.90b	461.56 ± 85.63a	45.00 ± 7.64a
S5 (559 mm)	18.30 ± 1.34 ab	10.67 ± 2.33c	35.85 ± 3.17 ab	537.41 ± 75.37a	84.07 ± 37.67b
Sand dune scale					
Top	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	42.78 ± 15.61a	9.66 ± 5.84a
Upslope	0.83 ± 0.09b	29.00 ± 2.08b	0.52 ± 0.07b	148.50 ± 9.35b	8.81 ± 0.71b
Downslope	1.30 ± 0.06c	42.33 ± 1.45c	1.38 ± 0.21c	231.73 ± 36.44c	19.60 ± 6.61a
Lowland-CL crusts	1.77 ± 0.09d	68.33 ± 1.67d	3.55 ± 0.34d	313.1 ± 23.04d	28.76 ± 1.77c
Lowland-Moss crusts	22.87 ± 1.36e	85.67 ± 4.67e	41.23 ± 3.50e	424.40 ± 79.08d	36.98 ± 4.63b

3.2. The composition and richness of bacterial communities in biocrusts at landscape scale

In total, 45 libraries of bacterial 16S rRNA were constructed and a total of 203,952,000 V4 region gene sequences were obtained. From the sequence data, 14,307 operational taxonomic units (OTUs) were annotated at 97% similarity. In total, 37 phyla were retrieved at genetic distances of 3% (Fig. S1), 18 phyla were observed with the relative abundance of the total bacterial communities higher than 1% in our study (Fig. 2). The dominant phyla were Actinobacteria (~27.4%), Proteobacteria (~24.98%), Bacteroidetes (~11.25%), Acidobacteria (~6.14%), Cyanobacteria (~4.70%) and Chloroflexi (~4.76%), they together accounted for more than 75% of the bacterial sequences (Fig. 2).

Bacterial α-diversity, phylogenetic diversity and Shannon index showed no consistent varying pattern in five habitats along the precipitation gradient (Table 2). Crust thickness positively affected richness and Shannon diversity in both two biocrusts (Table S3). Bacterial α-diversity and richness in moss crusts were higher than those in cyanobacterial-lichen crusts (Table 2, $P < 0.05$). The shared OTUs of the five habitats took up nearly one third of the total bacterial OTUs (Fig. S2). The relative abundance of Bacteroidetes, Cyanobacteria and Proteobacteria in cyanobacterial-lichen crusts were highest in the semi-humid habitat with highest precipitation (Table S4). In contrast, Actinobacteria and Firmicutes were negatively related with MAP (Table S4). In moss crusts, the relative abundance of Planctomycetes, Proteobacteria and Verrucomicrobi were positively related with precipitation (Table S4).

3.3. Bacterial community structure and β-diversity at the landscape scale

Bacterial community structure in cyanobacterial-lichen crusts did not change regularly with precipitation, bacterial communities in sites 1 and 2 (MAP<150 mm) were clustered together, and sites 3–5 (MAP: 186–559 mm) were clustered as another group (Fig. 3A). MAP, SOC, TP and soil clay content were significantly correlated with bacterial community structure in cyanobacterial-lichen crusts (Table 3, $P < 0.05$), biocrust properties, including thickness, cover and Chl a also impacted bacterial community composition in cyanobacterial-lichen crusts at the landscape scale (Table 3, $P < 0.05$). Soil bacterial communities in moss crusts were similar at thelandscape scale (Fig. 3B), MAP, TN, TP, and bulk density were correlated with bacterial communities in moss crusts (Table 3, $P < 0.05$), while biocrust thickness and cover exerted no significant impacts on bacterial communities across the landscape scale (Table 3, $P < 0.05$).

3.4. Relationships between bacterial community similarity and environmental and geographic distance

Geographic distance, soil and biocrust properties as a whole were significantly related with bacterial community composition in cyanobacterial-lichen crusts (Table 4, r = 0.79, $P = 0.002$). Soil properties were significantly related with bacterial community composition when controlling geographic distance and biocrust properties (Table 4, r = 0.32, $P = 0.002$), while biocrust properties were not related with bacterial communities when controlling geographic distance and soil properties (Table 4, $P > 0.05$).

A significant distance–decay relationship was observed for microbial communities in cyanobacterial-lichen crusts (Fig. 4, $r^2 = 0.39$, $P < 0.001$), with an estimated z-value of 0.01 of the whole community (Table 5). The slopes differed among the first dominant 10 phyla, with the highest slope of 0.11 for Firmicutes and the lowest of 0.0005 for Armatimonadetes (Table 5). Bacterial community dissimilarity increased significantly with the dissimilarity of soil (Fig. 4, $r^2 = 0.42$, $P < 0.001$) and biocrust properties (Fig. 4, $r^2 = 0.07$, $P = 0.007$). Geographic distance explained 15.4% variation of bacterial community variations among habitats, and environmental variables explained 22.8% variation (Fig. 5A).

Soil properties were significantly related with bacterial communities in moss crusts when controlling the geographic distance and biocrust variables (Table 4, r = 0.33, $P = 0.024$). Bacterial community dissimilarity increased with geographical distance (Fig. 4, $r^2 = 0.16$, $P < 0.001$), z-value of bacterial communities as a whole was 0.0045, and differed in terms of the phylum (Table 5). Bacterial community dissimilarity also increased with the dissimilarity of soil properties (Fig. 4, $r^2 = 0.22$, $P < 0.001$). Geographic distance explained 9.7% of the variation in bacterial community differences among sampling sites, and environmental variables explained 13.3% of the variation (Fig. 5B).

3.5. Bacterial community structure and β-diversity at the slope scale

Bacterial community composition differed significantly among slope locations (Fig. 6, $P < 0.001$, MRPP). Bacterial communities in cyanobacterial-lichen crusts among the upslope, downslope and lowland were similar and clustered together, while they were separated from that at the top of the sand dune and lowland dominated by moss crusts (Fig. 6). Of all soil properties, SOC, TN, clay content, and soil pH were significantly correlated with bacterial community composition (Table 3, $P < 0.05$). Biocrust thickness and Chl a content were significantly related with bacterial community composition (Table 3, $P < 0.05$).

Spatial, soil and biocrust distances together were significantly correlated with bacterial community composition (Table 4, r = 0.75, P

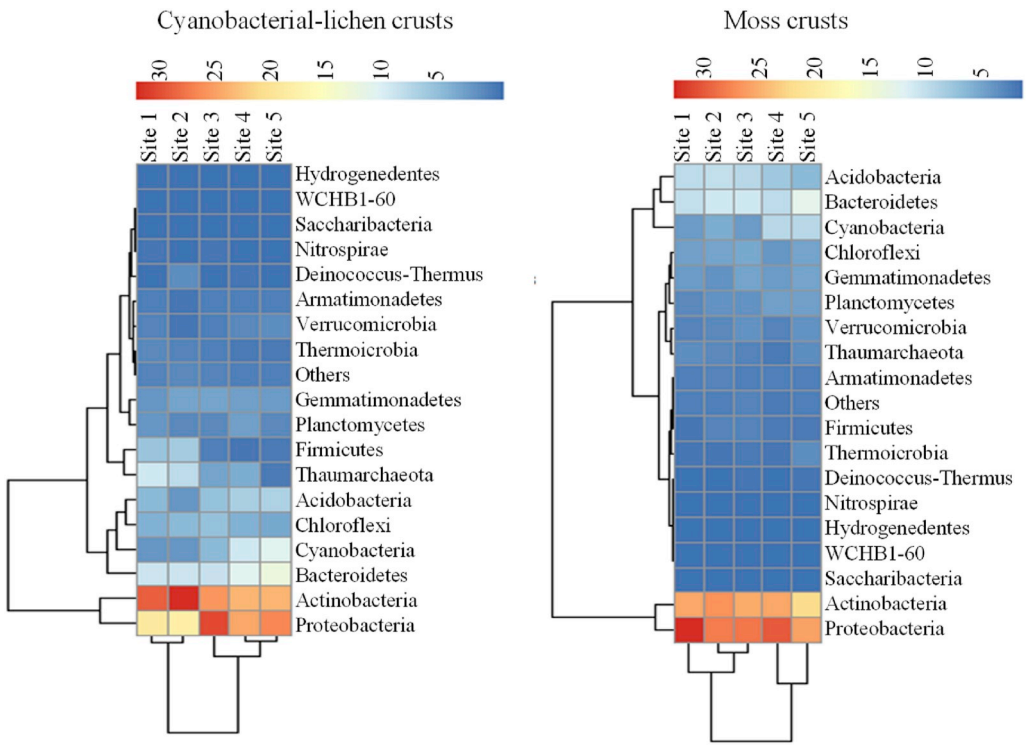

Fig. 2. Relative abundance of bacterial communities at phylum level in cyanobacterial-lichen crusts and moss crusts at the five desert habitats at landscape scale. Only 18 phyla, found at a relative abundance greater than 1%, were included by name, all other phyla were grouped into "others", completing the count to 100% of the number of identified phyla.

Table 2
Bacterial richness, α-diversity, and phylogenetic diversity for cyanobacterial-lichen crusts and moss crusts at landscape scale, and at slope scale. Values are means ± SE (n = 3). S1–S5 indicated five sampling desert habitats as demonstrated in Fig. 1, with annual mean precipitation denoted in brackets. In landscape scale, values are from three replications, each replication was a composite sample from five individual samples. At slope scale, values are from three replications which were collected in three typical sand dunes, each replication was a composite sample from five individual samples. Different small letters indicated significant differences between sampling sites at $P < 0.05$ level.

Site	Richness			Alpha-diversity		Phylogenetic diversity
	Observed species	Chao1	ACE	Shannon	Simpson	
Landscape scale						
Cyanobcterial-lichen crusts						
S1 (75 mm)	3720.67 ± 42.65a	4876.34 ± 60.17a	5104.65 ± 76.85a	9.56 ± 0.08a	1.00 ± 0.00a	272.44 ± 1.21a
S2 (147 mm)	3769.67 ± 71.34a	5001.13 ± 74.53a	5321.78 ± 67.41a	9.48 ± 0.06a	0.99 ± 0.00a	272.24 ± 7.30a
S3 (186 mm)	3338.33 ± 47.03b	4241.01 ± 48.10b	4458.85 ± 70.97b	9.45 ± 0.09b	0.98 ± 0.01b	250.46 ± 2.58b
S4 (393 mm)	3538.33 ± 328.63 ab	4587.18 ± 573.79 ab	4798.74 ± 601.49b	9.08 ± 0.41c	0.99 ± 0.00a	265.46 ± 16.71a
S5 (559 mm)	3740.33 ± 98.96a	5006.15 ± 249.52a	5184.62 ± 246.59 ab	9.36 ± 0.20b	0.99 ± 0.01a	276.48 ± 10.86a
Moss crusts						
S1 (75 mm)	4191.33 ± 310.32 ab	5489.98 ± 508.29a	5848.51 ± 485.97 ab	10.08 ± 0.20a	1.00 ± 0.00a	308.47 ± 20.41a
S2 (147 mm)	3920.67 ± 128.68a	5087.46 ± 395.61b	5394.94 ± 355.48a	9.87 ± 0.11 ab	1.00 ± 0.00a	285.18 ± 9.81a
S3 (186 mm)	3903.33 ± 98.56a	4961.80 ± 264.47b	5260.90 ± 251.57a	9.72 ± 0.05b	0.99 ± 0.00b	283.79 ± 3.00a
S4 (393 mm)	4451.33 ± 80.62b	5943.72 ± 102.75c	6232.60 ± 50.08b	10.28 ± 0.05a	1.00 ± 0.00a	318.92 ± 5.21a
S5 (559 mm)	3771.67 ± 83.72a	5162.53 ± 176.50 ab	5318.73 ± 142.43a	9.52 ± 0.38c	0.99 ± 0.01b	275.71 ± 3.46a
Slope scale						
Top	1856.33 ± 54.82a	2392.98 ± 30.77a	2467.64 ± 3.16a	7.27 ± 0.31a	0.96 ± 0.02a	164.78 ± 4.18a
Upslope	3012.00 ± 71.63b	4083.07 ± 182.25b	4297.55 ± 138.87b	8.44 ± 0.04b	0.98 ± 0.01b	241.15 ± 3.12b
Downslope	3351.00 ± 340.84bc	4605.42 ± 378.01c	4773.90 ± 429.03bc	9.07 ± 0.49c	0.99 ± 0.01b	251.46 ± 20.04b
Lowland-CL crusts	3720.67 ± 42.65c	4876.34 ± 60.17c	5104.65 ± 76.85c	9.56 ± 0.08d	0.99 ± 0.00b	272.44 ± 1.21bc
Lowland-Moss crusts	4191.33 ± 310.32c	5489.98 ± 508.29c	5848.51 ± 485.97d	10.08 ± 0.20e	1.00 ± 0.00b	308.47 ± 20.41c

= 0.001). Soil (Table 4, r = 0.41, $P = 0.001$) and biocrust (Table 4, r = 0.58, $P = 0.001$) variables were both significantly correlated with bacterial community composition. Bacterial community dissimilarity increased linearly with the spatial distance (Fig. 7, $r^2 = 0.23$, $P < 0.001$), with an estimated z-value of 0.0605 when all OTUs were pooled as a whole (Table S6); moreover, bacterial community dissimilarity also increased linearly with the dissimilarity of both soil properties (Fig. 7, $r^2 = 0.28$, $P < 0.001$) and biocrust properties (Fig. 7, $r^2 = 0.33$, $P < 0.001$). Spatial distance explained 16.0% of the variation, and environmental variables explained 19.2% of the variation in bacterial community differences at the slope scale (Fig. S3).

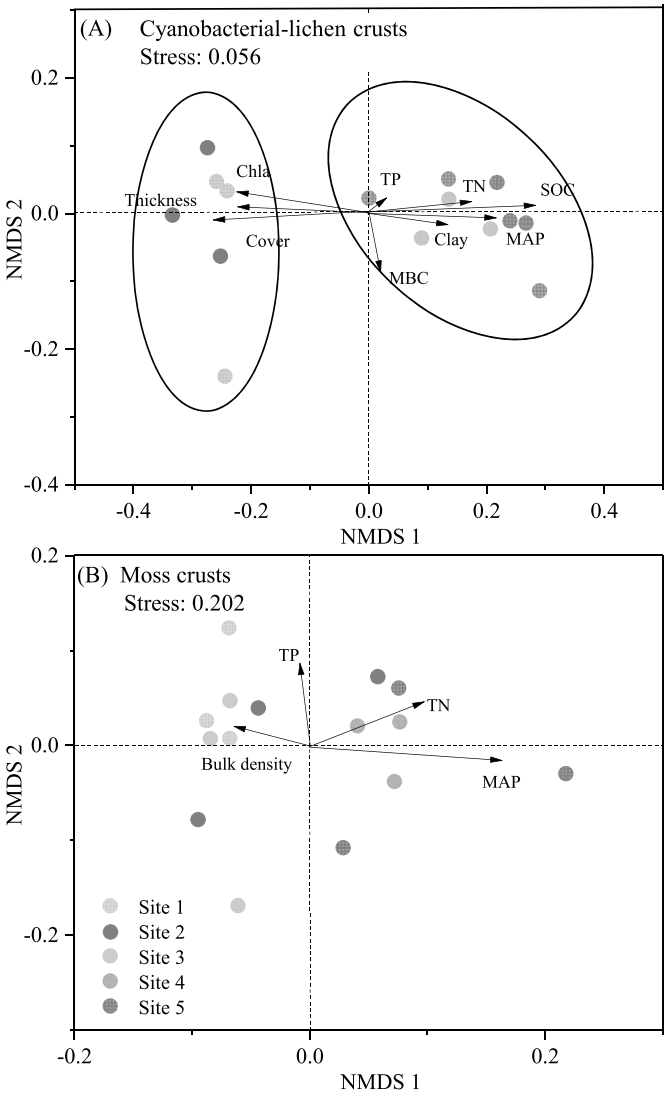

Fig. 3. Non-metric multidimensional scaling (NMDS) analysis on bacterial community composition in cyanobacterial-lichen crusts and moss crusts at five desert habitats at landscape scale. The stress was 0.056 and 0.202 for cyanobacterial-lichen crusts and moss crusts. Vector direction represents the average direction of environmental gradients. Vector length is proportional to the magnitude of correlation between the environmental parameter and bacterial community composition. Manually drawn ellipses indicate no difference of bacterial community composition between sampling regions within the same ellipse. The label represents five sampling regions at the landscape scale as shown in Fig. 1.

4. Discussion

4.1. Soil bacterial community composition and its influencing factors in desert ecosystems

The main bacterial phyla in biocrusts were Actinomycetes, Proteobacteria, Bacteroidetes, Acidobacteria, Cyanobacteria and Chloroflexi in our study. This is consistent with the dominant phyla in an adjacent grassland ecosystem (Wang et al., 2017) and in the Gurbantunggut desert in northwestern China (Liu et al., 2019). However, the dominant phyla showed inconsistent patterns with precipitation change across five habitats at the landscape scale. The relative abundance of Actinomycetes is related to soil pH (Lauber et al., 2009; Jones et al., 2009), but it was negatively correlated with precipitation and independent of soil pH in our study, suggesting the relative abundance of Actinomycetes is

Table 3
Associations of bacterial community composition with climate, soil and biocrust parameters at landscape scale for cyanobacterial-lichen crusts and moss crusts, and for biocrusts development at slope scale. MAP, mean annual precipitation; MAT, mean annual temperature; SOC, soil organic carbon content; TN, soil total nitrogen; TP, soil total phosphorus; TK, soil total potassium; EC, electrical conductivity; SVWC, soil volumetric water content; Chl a, chlorophyll *a* content; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen.

Parameters	Landscape scale				Slope scale	
	Cyanobacterial-lichen crusts		Moss crusts			
	r^2	*P*	r^2	*P*	r^2	*P*
Climatic variables						
MAP	0.5509	**0.005**	0.3433	**0.034**	-	–
MAT	0.023	0.842	0.1005	0.576	-	–
Soil properties						
SOC	0.7379	**0.003**	0.1160	0.447	0.5305	**0.018**
TN	0.3356	**0.056**	0.4215	**0.042**	0.4349	**0.046**
Bulk density	0.1411	0.395	0.4248	**0.042**	0.263	0.230
Silt	0.2852	0.110	0.1503	0.401	0.3092	0.130
Clay	0.4449	**0.020**	0.2932	0.109	0.3997	**0.047**
TP	0.4413	**0.036**	0.4469	**0.049**	0.2373	0.253
TK	0.0435	0.764	0.1175	0.482	0.0573	0.676
Total salt	0.0410	0.758	0.0842	0.740	0.093	0.379
pH	0.0579	0.687	0.0694	0.614	0.4198	**0.041**
EC	0.0357	0.732	0.2563	0.156	0.2407	0.172
SVWC	–	–	–	–	0.2844	0.109
Biocrust properties						
Thickness	0.4769	**0.039**	0.3589	0.094	0.6293	**0.010**
Cover	0.5606	**0.003**	0.0944	0.600	0.2345	0.201
Chl a	0.5099	**0.005**	0.3237	0.115	0.5048	**0.033**
MBC	0.6537	**0.002**	0.0219	0.866	0.0949	0.529
MBN	0.0407	0.792	0.2752	0.143	0.1361	0.454

Table 4
Influence of geographic distance, soil traits and biocrust development on microbial community composition. Mantel and partial Mantel test were used and statistical significance was tested based on 999 permutations.

Effects of	Controlling for	Mantel statistic R	Mantel statistic P
Landscape scale			
Cyanobcterial-lichen crusts			
Geographic, soil and biocrust distances		0.7932	**0.002**
Geographic distance		0.5705	**0.001**
Soil variables		0.4229	**0.001**
Biocrust variables		0.3576	**0.001**
Geographic distance	Soil and biocrust variables	0.1374	0.082
Soil variables	Geographic and biocrust properties	0.3225	**0.002**
Biocrust variables	Geographic and soil properties	−0.0505	0.655
Moss crusts		0.4955	**0.001**
Geographic, soil and BSC distances			
Geographic distance		0.1747	**0.045**
Biocrust variables		0.0958	0.276
Soil variables		0.2791	**0.034**
Geographic distance	Soil and biocrust variables	0.0727	0.164
Soil variables	Geographic and biocrust properties	0.3289	**0.024**
Biocrust variables	Geographic and soil properties	−0.105	0.835
Slope scale			
Spatial, soil and biocrust distances		0.7462	**0.001**
Spatial distance		0.2466	**0.037**
Soil variables		0.4678	**0.001**
Biocrust variables		0.5947	**0.001**
Spatial distance	Soil and biocrust variables	0.2626	0.059
Soil variables	Spatial and biocrust properties	0.4171	**0.001**
Biocrust variables	Spatial and soil properties	0.5787	**0.001**

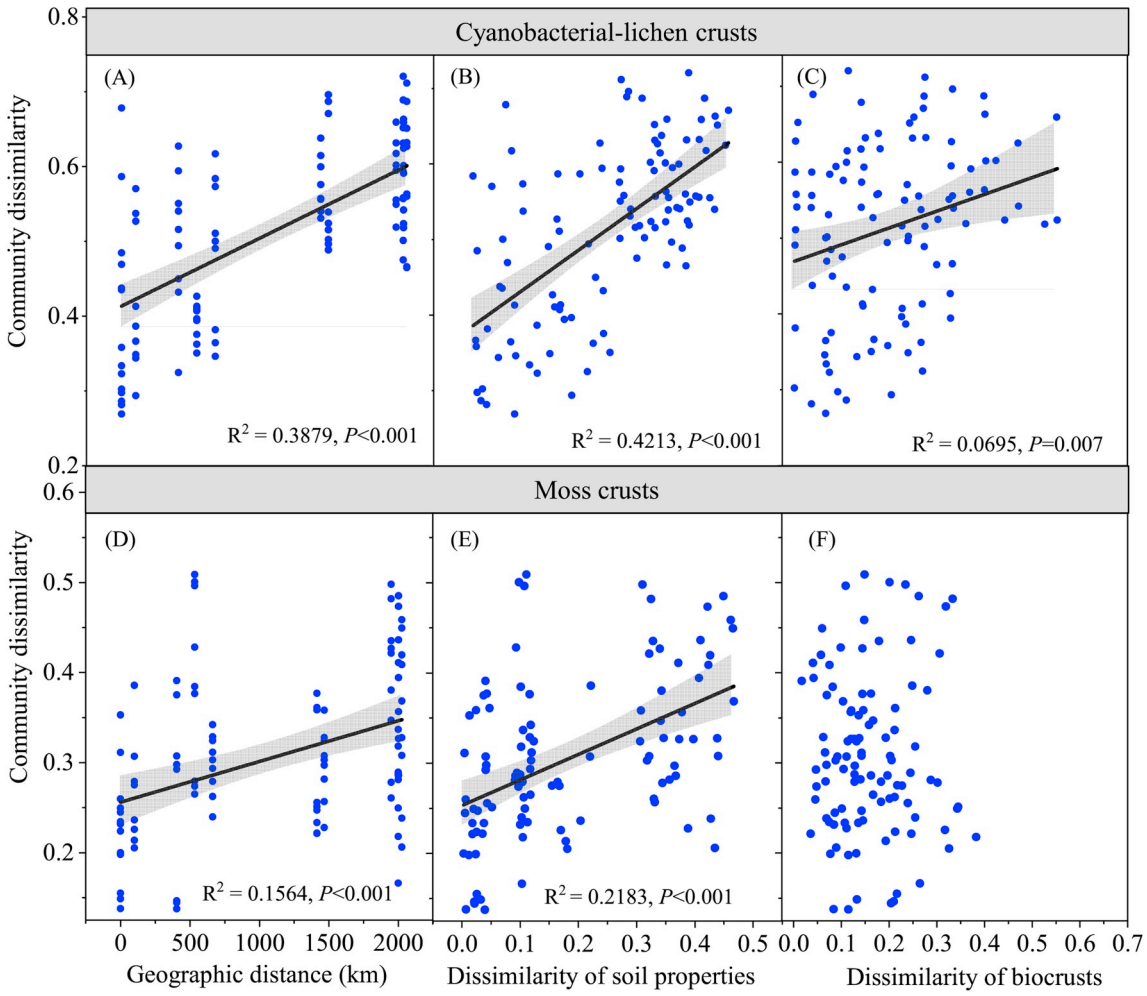

Fig. 4. Distance-decay relationship and the correlation of bacterial community dissimilarity with dissimilarity of soil properties and dissimilarity of biocrust properties for bacterial communities in cyanobacterial-lichen crusts and moss crusts at landscape scale. Each circle represents the pairwise similarity of a microbial community (Bray-Curtis index).

Table 5
Summary statistics of the distance-decay relationship for the dominant bacterial phyla in cyanobacterial-lichen and moss crusts at landscape and slope scales.

	Landscape scale			Slope scale		
	z	t	P-value	z	t	P-value
Cyanobacterial-lichen crusts						
All OTUs	0.0100	−4.732	<0.001	0.0605	−6.365	<0.001
Acidobacteria	0.0250	−2.755	0.007	0.0835	−5.03	<0.001
Actinobacteria	0.0205	−2.643	0.010	0.0555	−4.69	<0.001
Armatimonadetes	0.0005	0.135	0.893	0.0360	−3.381	0.001
Bacteroidetes	0.0200	−2.845	0.005	0.0425	−2.573	0.012
Chloroflexi	0.0105	−1.115	0.267	0.0220	−2.358	0.020
Cyanobacteria	0.0995	−2.799	0.006	0.1515	−2.48	0.015
Firmicutes	0.1125	−3.204	0.002	0.0870	−7.755	0.007
Planctomycetes	0.0065	0.038	0.704	0.0495	−3.329	0.001
Proteobacteria	0.0090	−1.978	0.051	0.0590	−5.898	<0.001
Verrucomicrobia	0.0335	−2.263	0.026	0.0815	−3.416	0.001
Moss crusts						
All OTUs	0.0045	−3.509	0.001			
Acidobacteria	0.0270	−2.745	0.007			
Actinobacteria	0.0110	−3.072	0.003			
Armatimonadetes	0.0380	−3.675	<0.001			
Bacteroidetes	0.0175	−4.999	<0.001			
Chloroflexi	0.0260	−4.975	<0.001			
Cyanobacteria	0.0325	−3.005	0.003			
Firmicutes	0.0500	−2.656	0.009			
Planctomycetes	0.0360	−2.543	0.013			
Proteobacteria	0.0155	−3.839	<0.001			
Verrucomicrobi	0.0240	−3.900	<0.001			

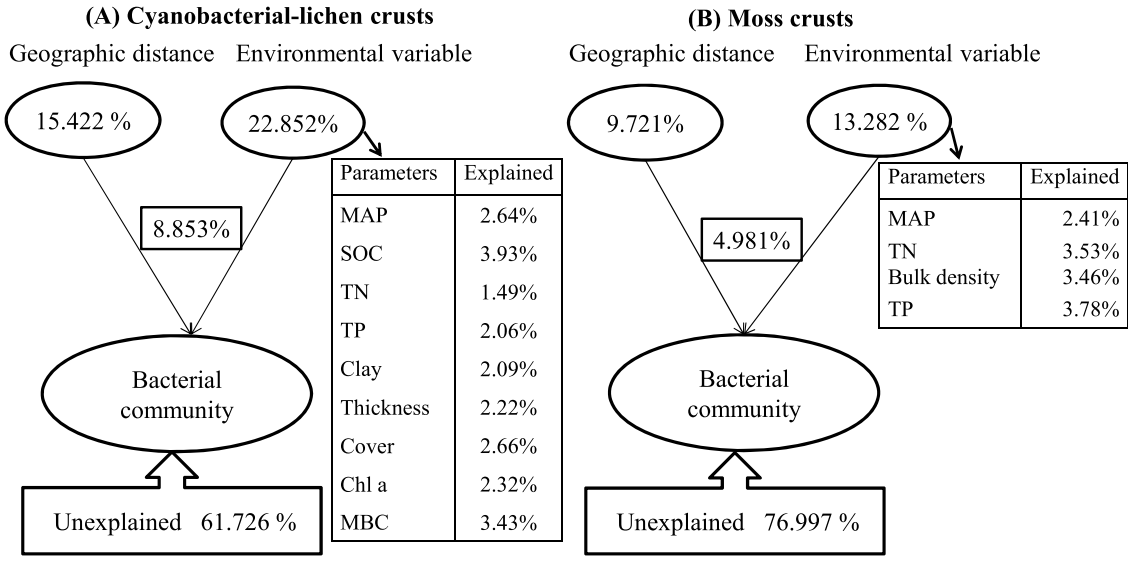

Fig. 5. Variation partition analysis of the effects of geographic distance and environmental variables on bacterial communities in cyanobacterial-lichen crusts and moss crusts.

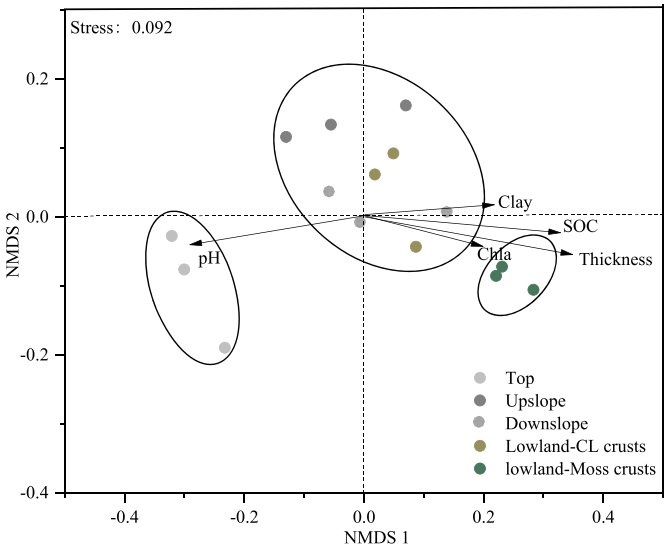

Fig. 6. Non-metric multidimensional scaling (NMDS) analysis on bacterial community composition at the slope scale. Manually drawn ellipses indicate no difference of bacterial community composition between sampling locations along the sand dune slope within the same ellipse. The label represents five sampling locations from the top to the lowland of the sand dune as shown in Fig. 1.

higher in drier regions. This result is consistent with studies conducted in other desert ecosystems (Pointing et al., 2009; Rego et al., 2019). The relative abundance of Proteobacteria and Acidobacteria increased with precipitation in cyanobacterial-lichen crusts while decreasing in moss crusts. Acidobacteria belong to oligotrophic bacteria and are negatively correlated with soil carbon availability (Jones et al., 2009; Männistö et al., 2013; Kielak et al., 2016). Soil organic carbon and nitrogen content in moss crusts were ca. two times those in cyanobacterial-lichen crusts, this can explain the lower relative abundance of Acidobacteria in moss crusts. Proteobacteria and Bacteroidetes, especially β-Proteobacteria, belong to copiotrophic bacteria, their relative abundance increases with soil available carbon (Fierer et al., 2007). Cyanobacteria showed a higher relative abundance in our study as compared with other regions, this may be caused by the development of biocrusts. The relative abundance of Cyanobacteria was positively related with precipitation in cyanobacterial-lichen crusts, this is of great significance to the ecological functions of biocrusts since a large number of species in Cyanobacteria are photoautotrophic species or participate in N fixation (Maier et al., 2018).

Many studies have demonstrated that water availability positively influences vegetation production, plant diversity and abundance (Soininen et al., 2007). Bacterial community diversity was also largely influenced by water availability in some previous studies (Clark et al., 2009; Angel et al., 2010). However, bacterial α-diversity and richness were not influenced by precipitation at the landscape scale in our study. This may be related to the following causes. Firstly, the responses of bacterial community diversity might not change consistently in a linear manner with precipitation, and a response threshold might exist. This can be evidenced by an aridity threshold for microbial metabolism (Hou et al., 2019) and N transformation (Wang et al., 2014) along a gradient of precipitation. Biocrusts exhibited a better development as demonstrated by thickness and cover in more arid deserts (MAP<200 mm), suggesting the development and succession of cyanobacterial-lichen crusts were not always positively related with the improved soil nutrients and increasing precipitation (Büdel, 2003). Secondly, considering the microbial acclimation to drought (Crowther and Bradford, 2013; Makhalanyane et al., 2015), a large number of bacteria would be shared among different desert habitats, as demonstrated by the high shared OTUs in our study. In addition, although the sampling depth of 5 cm was chosen based on our investigation and many previous studies in northern China (Lan et al., 2013; Su et al., 2013a; Zhang et al., 2016; Li et al., 2017), it was quite deep especially for cyanobacterial-lichen crusts in less arid habitats. This may be partly responsible for the similar bacterial α-diversity, because the sub-soil composition is less likely to vary compared to the very top surface.

Our study demonstrated that the impacts of environmental factors on soil bacterial communities were dependent on spatial scale, this is in line with some previous studies (Ettema and Wardle, 2002; Franklin and Mills, 2003; Fierer et al., 2009). Biocrust thickness was the most important factor controlling bacterial α-diversity at the slope scale, meanwhile, soil organic carbon content and clay content, which are closely related with the colonization of biocrusts, were also fundamental to bacterial community pattern at slope scale. Similar patterns were also observed in some restoration experiments in sandy deserts, showing increasing microbial biomass and chlorophyll with increasing biocrust

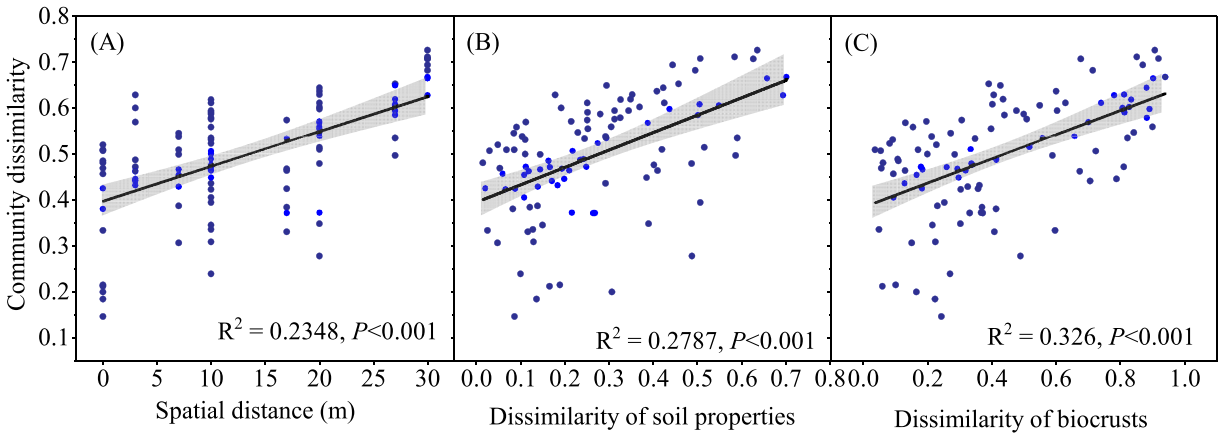

Fig. 7. Distance-decay relationship (A) and the correlation of bacterial community dissimilarity of biocrusts with dissimilarity of soil properties (B) and dissimilarity of biocrust properties (C) at sand dune slope scale. Each circle represents the pairwise similarity of a microbial community (Bray-Curtis index).

thickness along restoration processes (Rao et al., 2009; Li et al., 2010, 2014).

Soil pH is regarded as the most important determinant for bacterial communities at the landscape scale (Fierer and Jackson, 2006; Lauber et al., 2009; Plassart et al., 2019). However, it had no impacts in our study. This may be caused by the narrow variation of soil pH (7.74–8.51) and similar soil taxa, which were grey desert soil and sierozem across the five habitats in our study.

Bacterial α-diversity in moss crusts was significantly higher than that in cyanobacterial-lichen crusts within the same habitat. This result suggests that moss crusts can provide more favorable resources and protection for soil bacterial communities due to their higher dust capture, water and nutrient retention (Maier et al., 2018). Moreover, moss crusts exhibit later successional stage as compared with cyanobacterial-lichen crusts (Belnap et al., 2008; Chamizo et al., 2012; Lan et al., 2013), this result also suggests that the development and succession of biocrusts influence soil bacterial communities. Biocrusts exhibit sequential development from the top to the lowland along sand dune slope, our study demonstrates that bacterial diversity and richness are positively related with the index of biocrust development (thickness) at slope scale. This result suggests that the development of biocrusts increase with soil bacterial diversity and this is critical to the improvement of soil nutrients in bare soils (Lan et al., 2013; Su et al., 2013a).

4.2. The influences of biocrust development on the spatial pattern of bacterial communities

Bacterial community similarity was significantly correlated with geographic, soil and biocrust distances as a whole for both moss and cyanobacterial-lichen crusts, and was independent of geographic distance when soil and biocrust variables were controlled. This result indicates that the geographical variation of bacterial community composition in biocrusts was caused by the soil heterogeneity among sampling habitats.

Soil microbes usually exhibit strong adaptation to the fluctuation of ambient environment, and the dispersal limitation impacts on soil microbes are very weak (Bailey et al., 2018). Soil microbial assemblage is largely dependent on habitat, environmental filtering always exerts a profound impact on the geographical pattern of bacterial communities (Bell et al., 2009; Andrew et al., 2012; Bachar et al., 2012). In our study, geographic distance only explained 15.4% and environmental variables only explained 22.8% of the variation of bacterial communities in cyanobacterial-lichen crusts, therein, SOC played key roles in constructing bacterial communities. Soil texture and nutrient content generally improve persistently with the development and succession of biocrusts (Li et al., 2002 & 2003), which favors microbial inhabitation and growth. Besides, many studies have shown that environmental variables are the primary determinants for geographical variation of soil bacterial communities (Fierer and Jackson, 2006; Lauber et al., 2009). Different from cyanobacterial-lichen crusts, geographic distance and environmental variables explained 9.7% and 13.3% bacterial communities of the variation in moss crusts, while they explained 16.0% and 19.2% of the variation at slope scale. The relative importance of geographic distance and environmental filtering on bacterial communities differs among studies, the spatial scale is considered to be an important factor determining their relative importance (Jenkins et al., 2007; Martiny et al., 2011; Prevost-Boure et al., 2014). Dispersal limitation exerts stronger impacts on large body-size organisms at large landscape scales (Jenkins et al., 2007; Bailey et al., 2018), while environmental variables are more important to small body-size organisms since they are more dependent on living habitats (Bailey et al., 2018).

Soil bacterial communities exhibited significant distance-decay relationships at both slope and landscape scales in our study. This distance-decay relationship was stronger at slope scale as suggested by the higher z-value. Meanwhile, biocrust development and environmental variables also exerted profound impacts on bacterial community similarity. In our study, the distance-decay rates ranged from 0.01 in cyanobacterial-lichen crusts at landscape scale and 0.065 at slope scale; they were in the range of previous studies (Horner-Devine et al., 2004). The distance-decay rate was 0.0045 in moss crusts, combining with the similar MBC and MBN among five habitats, this result suggests that bacterial communities in moss crusts are very consistent across different habitats. Moss crusts generally dwell in soils under shrub canopies at lowland (Yin et al., 2017), soil moisture and nutrients are higher than adjacent soils due to “fertilization island” effects (Su et al., 2013b; Zhao et al., 2014; Li et al., 2017). Caution should be taken to explain the similar bacterial community patterns of moss crusts at landscape scale.

More importantly, the distance-decay rate was dependent on the spatial scale. Steeper slope at slope scale suggests a faster turnover rate of bacterial communities than that at the landscape scale. The heterogeneities of soil attributes and biocrust development were determined by the slope location. At the landscape scale, samples were collected at lowland, therefore, topography exerted negligible impacts on soil attributes and bacterial communities. This result suggests that the spatial pattern of soil bacterial communities is partly regulated by biotic factors, including biocrust development. When biocrust development and environmental variables were controlled, geographic distance had no significant impacts on bacterial community similarity. This result demonstrates that environmental variables (soil texture and biocrust development) are more important than geographic distance to soil bacterial communities. The dominant phyla of Actinobacteria, Bacteroidetes, and Acidobacteria showed larger distance-decay rates as

indicated by the higher z-values, this suggests that bacterial community dissimilarity among habitats was mainly originated from the discrepancies of Actinobacteria, Bacteroidetes, and Acidobacteria. At the slope scale, Cyanobacteria showed the highest z value, suggesting Cyanobacteria are the most important phylum for bacterial community turnover rate. The 61.7% unexplained variation of bacterial communities may be caused by two reasons. Firstly, the lack of auto-correlation of measured parameters in desert ecosystems increased the unexplained variation (Martiny et al., 2011); secondly, some inner stochastic processes, including drift and some accidental historical events (Hawkes et al., 2017), which were beyond the scope of our projection may also have contributed to the large unexplained variation.

5. Conclusion

Bacterial community similarity showed obvious distance-decay relationships with geographic distance at both landscape and slope scales. The slope of the distance-decay relationship for cyanobacterial-lichen crusts was larger than that for moss crusts. The bacterial community structure in cyanobacterial-lichen crusts differed profoundly, whereas it was similar in moss crusts among the habitats in northern China. Bacterial communities varied sequentially with the development and succession of biocrusts at the slope scale. Variation partition analysis showed that environmental variables exhibited larger explanation for bacterial community differences than geographic distance, suggesting weaker influences of dispersal limitation on the bacterial community structure in biocrusts. Our study demonstrates that the succession of biocrusts profoundly alters bacterial community patterns at the landscape scale, and soil attributes, influenced by the regional environment and biocrust development, are the dominant factors driving bacterial community pattern in biocrusts.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2020.107721.

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