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Decoupled diversity patterns in microbial geographic distributions on the arid area (the Loess Plateau)

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ABSTRACT

Soil microbes are essential to biogeochemical cycling, soil organic matter decomposition and climate regulation in terrestrial ecosystems. The biogeography of soil bacteria and fungi lags behind in animals and plants, especially in arid areas with alkaline conditions. Understanding the biogeographic of soil microbes and the interactions with environmental factors will provide new insights into the ecosystem functions and services droved by soil bacteria and fungi. Therefore, we chose 48 dryland sites from two transects (north-south and east-west transects) on the Loess Plateau (an arid area) to determine soil bacterial and fungal diversity and community compositions in response to environmental factors and geographic distance. The results showed that soil organic carbon enhanced soil fungal diversity rather than soil bacterial diversity, while soil bacterial diversity was not affected by the environmental factors on the Loess Plateau. The significant associations between the abundance of main bacteria and fungi and soil pH, suggesting that soil pH was the predominant factor affecting soil microbial community structure. In the alkaline soils (pH = 7.4–9.1), soil bacterial community compositions were limited by soil pH, while soil fungal community composition was less sensitive in response to the alterations in soil pH, revealing soil fungi has a wider optimal pH range than bacteria. Compered to historical contingencies, local environment mainly controlled the geography of bacteria and fungi in soils. On the Loess Plateau, soil microbial communities diverge most by soil pH, especially for soil bacteria. These results provide a well understanding of soil microbial geography and associated biogeochemical cycling in arid areas with higher soil pH.

1. Introduction

Soil harbors diverse and abundant microbes regulating ecosystem function and stabilizing terrestrial ecosystem (Van Der Heijden et al., 2008). Thus, understanding the spatial patterns of soil microbes and clarifying the underlying drivers is critical for ecosystem functioning and service (Hazard et al., 2013). Up to date, although some efforts to explore the microbial geography has been conducted by many authors (Cui et al., 2019; Liu et al., 2020; Zeng et al., 2019), the underlying mechanism of the biogeography patterns of microbial diversity still need to better understand (Bardgett and van der Putten, 2014; Liu et al., 2020), especially in arid/semi-arid areas. Various biotic and abiotic factors impact the distributions of soil bacterial and fungal diversity and community compositions, mainly including contemporary environmental conditions (.i.e., climate, soil properties and plant community) and historical contingencies (geographic distance) (Ge et al., 2008; Martiny et al., 2006; Wu et al., 2013). However, the observational studies reached contradictory conclusions and showed that the relative contributions of contemporary environmental conditions and historical contingencies in regulating soil microbial geography depending on the spatial scales.

Alterations in land uses, climate (temperature, precipitation), edaphic properties (pH, organic matter, available nutrients), latitude, elevation, and plant community (diversity, net primary production and ecological stoichiometry) were main direct or indirect affecting factors in soil microbes (Cui et al., 2018; Liu et al., 2018; Maestre et al., 2015; Morrissey et al., 2014; Wang et al., 2015; Xiong et al., 2012; Zeng et al., 2017). A larger spatial scale study of soil microbial biogeography would provide a well understanding of terrestrial ecosystem functions and services. To date, a large body study of research has revealed that soil microbes exhibit distinct biogeography patterns in comparison with animals and plants (Caporaso et al., 2011; Lauber et al., 2009; Lindström and Langenheder, 2012; Liu et al., 2014; Tian et al., 2018), and there have been inconsistent conclusions in soil microbial

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geography. These different patterns of soil microbial geography for bacteria and fungi may be explained by the differences of spatial scale, climate and local conditions (Martiny et al., 2011). Although some studies have assessed the geography of soil microbes, the knowledge of soil microbial geography is still limited, especially the underlying factors and the interactions between these biotic and abiotic factors (Fierer and Jackson, 2006). Soil moisture has been considered as the dominant factor resulting in variations in plant compositions, soil processes and nutrient availability, which might directly or indirectly alter soil microbial community structure (Cui et al., 2020; Lladó et al., 2018).

Therefore, two transects (west-east and north-south transects) of the Loess Plateau (China) were chosen to assess the spatial patterns of soil microbes in an arid area. In this area, climate, edaphic factors, and geographic distance strongly varied from north to south or from west to east. Since 1999, vegetation restoration was widely performed to prevent soil erosion, improve plant coverage and enhance ecosystem functioning (Zhou et al., 2016). The obvious changes in plants and soils might be the driving forces of soil microbial diversity. Therefore, we hypothesize that (1) soil bacterial and fungal diversity exhibit graphical patterns; (2) soil bacteria are more sensitive to soil pH and available nutrients than fungi, as soil fungi had a wider optimum pH; (3) contemporary environmental conditions contributed more variation since the “Grain for Green” project. The “Grain for Green” project was performed to conduct large scale reforestation and the conversion of land types, which has resulted in great changes in soils and plants and subsequently may lead to changes in soil microbial compositions via above-ground plant or climate changes.

2. Materials and methods

2.1. Study site description and soil sampling

We chose 48 dryland sites from two transects on the Loess Plateau (China) as sampling sites (Fig. 1). In this region, mean annual temperature (MAT) varied from 7.61 to 13.08 °C, while the mean annual precipitation (MAP) ranged from 372 to 585 mm (Table S1). Loessial (Genetic Soil Classification of China) soils is the main soil type, and Entisols (U.S.A. taxonomy) (Zeng et al., 2016). The vegetation types included forests, grass lands, shrub lands, apple orchard and crop lands.

Soil sampling was performed in July 2016. In each site, we collected the latitudes, longitudes, height, land uses and other terrain factors. We conducted three randomly plots (20 × 20 m) for soil sampling. We collected 20 surface soil cores (0–20 cm soil layers) randomly in each plot to format a sample. After removing roots, stones and plant litters, each soil sample divided into different parts based on the specific uses. An approximate 10 g fresh soil was stored at −80 °C for the analysis of soil fungi and bacteria. An approximate 100 g air-dried soil was stored at room temperature for the measurement of edaphic characteristics, including soil pH, electricity conductivity (EC), organic carbon (SOC), nitrate nitrogen (NO3N), total nitrogen (TN), microbial biomass carbon (SMBC), ammonium nitrogen (NH4N), available phosphorus (AVP) and total phosphorus (TP).

2.2. The analysis of edaphic properties and climate factors

Soil properties were determined by the previous studies with the general methods. The details were listed in the previous study (Zeng et al., 2019; Liu et al., 2018). MAP and MAT of each site were collected from China Meteorological Data Service Center (http://data.cma.cn). The details were listed in supporting materials.

2.3. Soil DNA extraction, amplification and sequencing

The PowerSoil kit (MoBio Laboratories, Carlsbad, CA, USA) was used to extract DNA according to the manufacturer's instructions. An aliquot of DNA was used as a template for amplification. The amplification libraries were assessed by the primers 338F and 806R for hypervariable V3-V4 regions of 16S rRNA genes (Caporaso et al., 2011). The ITS1 variable region was amplified using the primer sets ITS3 and ITS4 (Fujita et al., 2001). The details of PCRs were conducted based on the supporting information. The Illumina MiSeq platform was used to sequence.

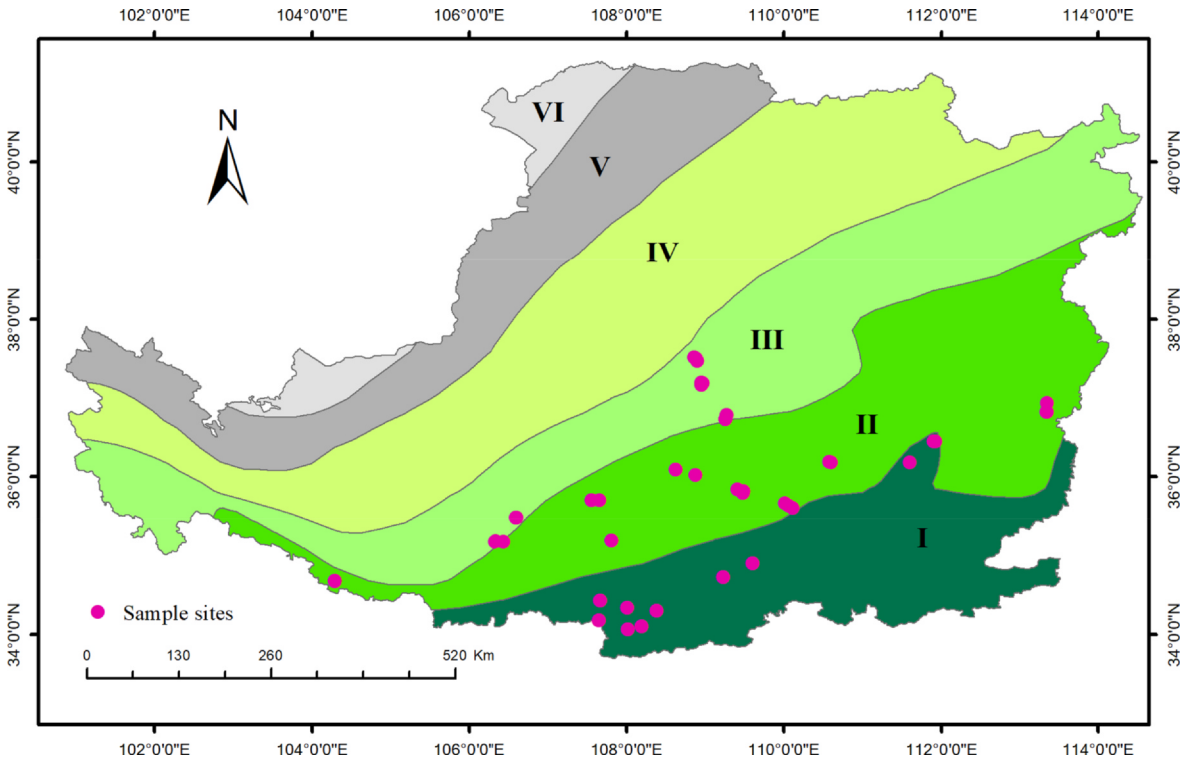

Fig. 1. The sample sites (n = 48) in the Loess Plateau. I, Broadleaved forest; II, Forest steppe; III, Steppe; IV, Desert-steppe; V, Steppe-desert; VI, Desert.

2.4. Analysis of sequencing data

Initial sequence processing for both bacterial 16S rRNA and fungal ITS genes were conducted by QIIME (version 1.17). After quality filtering and normalizing (28204 and 27,000 for 16S rRNA and ITS, respectively), the sequences were clustered into operational taxonomic units (OTUs) at a 97% similarity using uparse (version 7.1 http://drive5.com/uparse/) (Edgar et al., 2011). For 16S RNA OTUs, UCLUST was used to assign taxonomy with the Greengenes database (Version 13_850). For ITS OTUs, BLAST was used to assign taxonomy with the UNITE database.

2.5. Statistical analysis

The associations between soil bacterial and fungal diversity and environmental factors were determined by the Pearson correlation analyses in SPSS 25.0 (IBM Corporation, Armonk, NY, USA). Nonmetric multidimensional scaling (NMDS) ordinations were used to assess soil microbial community structure in R 3.6 with vegan package (Oksanen et al., 2013). The mantel test was conducted to determine the associations between microbial community structure and each environmental variable in R 3.6. The distance decay analysis was used to determine the associations between the distance of soil bacterial or fungal community (based on Bray-Curtis distance) and distance of geographic distance and environmental factors (based on Euclidean distance). Multiple regression was used to assess the contribution of each factor to the variations in soil bacterial and fungal structure in R 3.6. The contribution of each factor was expressed by the relative importance (RI) using the relaimpo package (Grömping, 2007; Reinhart et al., 2016).

Structural Equation Modeling (SEM) was used to assess the direct and indirect effects of environmental factors on soil fungal and bacterial diversity and community structure. The community structure was represented by the NMDS1 of NMDS analysis. The value of χ^2 and the root mean square error of approximation were used to determine the fit of the model. The standardized effects were used to express the influences of each variable on soil bacterial and fungal community structure and diversity based on SEM. The SEM was conducted in Amos 20.0 (IBM SPSS).

3. Results

3.1. Variations in soil bacterial and fungal diversity

The observed bacterial Shannon diversity index ranged from 8.4 to 10.49, while phylotype richness (OTUs) varied from 1401 to 2716. All the detected environmental factors had no significant associations with soil bacterial α-diversity indices.

The soil fungal phylotype richness varied from 163 to 907, and the fungal Shannon diversity ranged from 3.28 to 7.7. Soil fungal Shannon diversity ($p < 0.05$) and phylotype richness ($p < 0.05$) significantly increased with increases in SOC and TN (Table 1). Soil fungal phylotype richness was significantly correlated with height and NH4N and soil pH. Among these environmental factors, SOC was emerged as the most important factor in determining the fungal Shannon diversity index (RI = 0.85), followed by soil pH (RI = 0.15) (Table 2), demonstrating that SOC drives the geographic pattern of soil fungal diversity.

3.2. Soil microbial community compositions on the Loess Plateau

Five bacterial phyla were dominant in all soils (with an average relative abundance of > 4%, n = 48), including Actinobacteria (36.0%), Proteobacteria (26.1%), Acidobacteria (11.8%), Chloroflexi (12.8%), and Gemmatimonadetes (4.8%) (Fig. 2), accounting for 91% of the total sequences. In addition, Nitrospirae, Bacteroidetes, Verrucomicrobia and Firmicutes were also detected in almost all soils, with a lower relative abundance (< 2%). The Proteobacteria taxa were dominated by Alphaproteobacteria (16.2%), followed by Betaproteobacteria (4.3%), Deltaproteobacteria (3.0%) and Gammaproteobacteria (2.6%). Among Acidobacteria populations, Subgroup_6 was the most abundant class with a relative abundance of 5.5%; Blastocatellia was the next most abundant class (2.8%). At the class level, Actinobacteria (17.3%), Thermoleophilia (9.9%) and Acidimicrobiia (5.3%) were most abundant among the Actinobacteria phyla.

On the Loess Plateau, Ascomycota (56.3%), Basidiomycota (30.2%) and Zygomycota (3.3%) were the dominant fungal phyla (Fig. 2). Anthophyta, Cercozoa, Rozellomycota and Glomeromycota were also found in almost soils (relative abundance < 1%). Agaricomycetes (Basidiomycota, 24.9%), Sordariomycetes (Ascomycota, 22.8%), Eurotiomycetes (Ascomycota, 7.5%), Dothideomycetes (Ascomycota, 7.3%), Leotiomycetes (Ascomycota, 4.5%), Tremellomycetes (Basidiomycota, 2.5%), Pezizomycetes (Ascomycota, 2.0%), Wallemiomycetes (Basidiomycota, 2.1%), Archaeorhizomycetes (Ascomycota, 1.5%) and Lecanoromycetes (Ascomycota, 1.1%) were main classes (relative abundance > 1%), which accounted for 75% of the total relative abundance.

Table 1
The Pearson correlations between microbial diversity and environmental factors.

Variables	Bacteria		Fungi	
	Shannon	OTUs	Shannon	OTUs
MAP	0.262	0.156	0.074	0.074
MAT	0.010	−0.123	−0.103	−0.193
Height	−0.083	0.133	0.122	0.257
SOC	0.128	0.242	0.420**	0.545**
TN	0.136	0.248	0.428**	0.527**
TP	0.265	0.176	0.167	0.087
pH	0.068	−0.102	−0.11	−0.271
EC	0.035	0.025	−0.112	−0.017
NO3N	0.100	0.059	0.033	−0.017
NH4N	0.053	0.158	0.253	0.369**
AVP	0.152	0.186	−0.03	−0.025
C:N	0.077	0.042	0.081	0.195

MAP, mean annual precipitation; MAT, mean annual temperature; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; EC, electricity conductivity; NO3N, nitrate nitrogen; NH4N, ammonia nitrogen; AVP, available phosphorus; C:N, the ratio of SOC to TN. *indicates significant correlations at the level of 0.05; ** indicates significant correlations at the level of 0.01.

Table 2
The effects of environmental factors on soil fungal diversity on the Loess Plateau using a multiple regression model (R^2 = 0.2352, F = 6.92, p = 0.002397).

Variables	Estimate	t	P	IR
(Intercept)	3.17	2.390	0.021	
pH	0.283	1.860	0.069	0.15
SOC	0.0384	3.623	0.0007	0.85

IR, the relative importance of each factor based on the multiple regression model. SOC, soil organic carbon.

3.3. Microbial community structure on the Loess Plateau

Soil samples were clearly separated at the pH gradient in the NMDS plot (Fig. 3A and B), indicating that the microbial community structure was strongly impacted by soil pH. Climate factors and soil properties were considered using the correlation analysis with the ordination score of the first axis of the nonmetric dimensional scaling (NMDS1) ordination. The correlations showed that height ($r = 0.446$, $p < 0.01$), soil pH ($r = -0.884$, $p < 0.01$), NH4N ($r = 0.733$, $p < 0.01$), TN ($r = 0.705$, $p < 0.01$) and SOC ($r = 0.727$, $p < 0.01$) significantly affected the soil bacterial community structure. Similarly, for soil fungi,

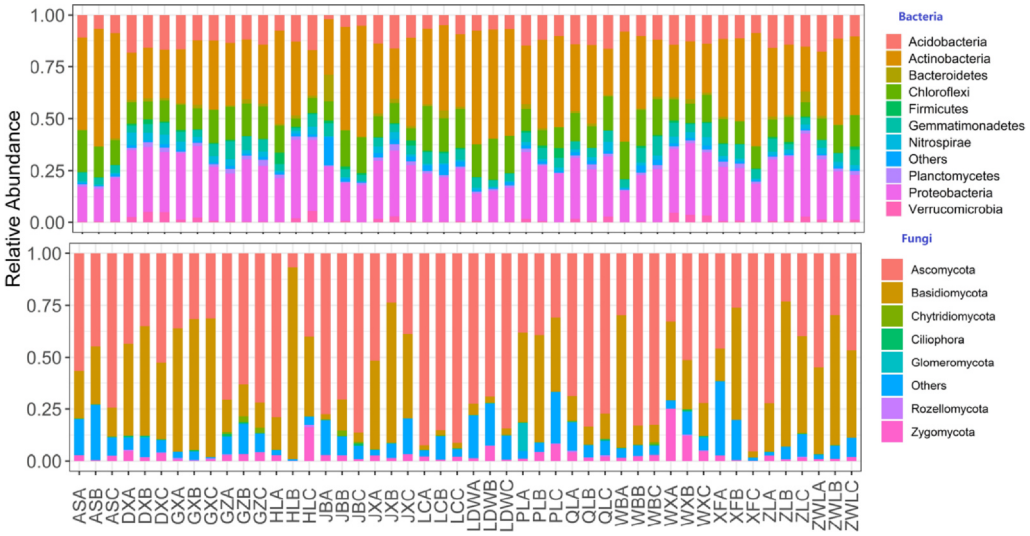

Fig. 2. The distributions of soil microbial community compositions at the level of phylum on the Loess Plateau.

the regression analysis demonstrated that pH ($r = -0.701$, $p < 0.001$), NH4N ($r = 0.618$, $p < 0.001$), SOC ($r = 0.558$, $p < 0.001$), TN ($r = 0.521$, $p < 0.001$), height ($r = 0.479$, $p < 0.001$), C:N ($r = 0.343$, $p < 0.05$) and TP ($r = -0.299$, $p < 0.05$) were significantly correlated with NMDS1 (Table 3).

We used the Mantel test to evaluate the effects of each environmental variable on soil bacterial and fungal community structure. The results showed that pH ($r = 0.579$, $p = 0.001$), NH4N ($r = 0.317$, $p = 0.001$), MAP ($r = 0.301$, $p = 0.001$), SOC ($r = 0.289$, $p = 0.001$), TN ($r = 0.254$, $p = 0.001$), TP ($r = 0.131$, $p = 0.029$), EC ($r = 0.119$, $p = 0.032$), height ($r = 0.156$, $p = 0.003$), AVP ($r = 0.147$, $p = 0.024$), C:N ($r = 0.148$, $p = 0.007$) and MAT ($r = 0.109$, $p = 0.025$) significantly impacted soil bacterial community structure (Fig. 3C). Similarly, the soil fungal community structure was strongly influenced by soil pH ($r = 0.277$, $p = 0.001$), NH4N ($r = 0.154$, $p = 0.003$), MAP ($r = 0.141$, $p = 0.008$) and C:N ($r = 0.091$, $p = 0.025$) (Fig. 3C).

Environmental factors had significant associations with the relative abundances of soil bacterial and fungal community compositions (Fig. 4). Soil pH significantly promoted the increase in soil Actinobacteria ($r = 0.64$, $p < 0.0001$) and Chloroflexi ($r = 0.46$, $p = 0.001$), while the relative abundance of soil Verrucomicrobia ($r = -0.71$, $p < 0.0001$), Proteobacteria ($r = -0.7$, $p < 0.0001$), Nitrospirae ($r = -0.68$, $p < 0.0001$) and Acidobacteria ($r = -0.64$, $p < 0.0001$) were negatively correlated with soil pH (Fig. 4). Oppositely, soil TN, NH4N and SOC enhanced the relative abundance of Acidobacteria, Proteobacteria, Nitrospirae and Verrucomicrobia. The soil main fungal phyla (Ascomycota, Basidiomycota, Zygomycota, Rozellomycota and Chytridiomycota) also had significant correlations with soil pH, TN and NH4N (Fig. 4). Soil pH was positively significantly correlated with the relative abundance of Ascomycota ($r = 0.43$, $p = 0.0022$), while soil pH was negatively significantly correlated with the relative abundance of Basidiomycota ($r = -0.49$, $p = 0.00048$) (Fig. 4).

3.4. Accounting for microbial community structure drivers between geographic distance and environmental factors

The distance decay analysis showed that geographic distance and environmental factors significantly affected soil bacterial and fungal

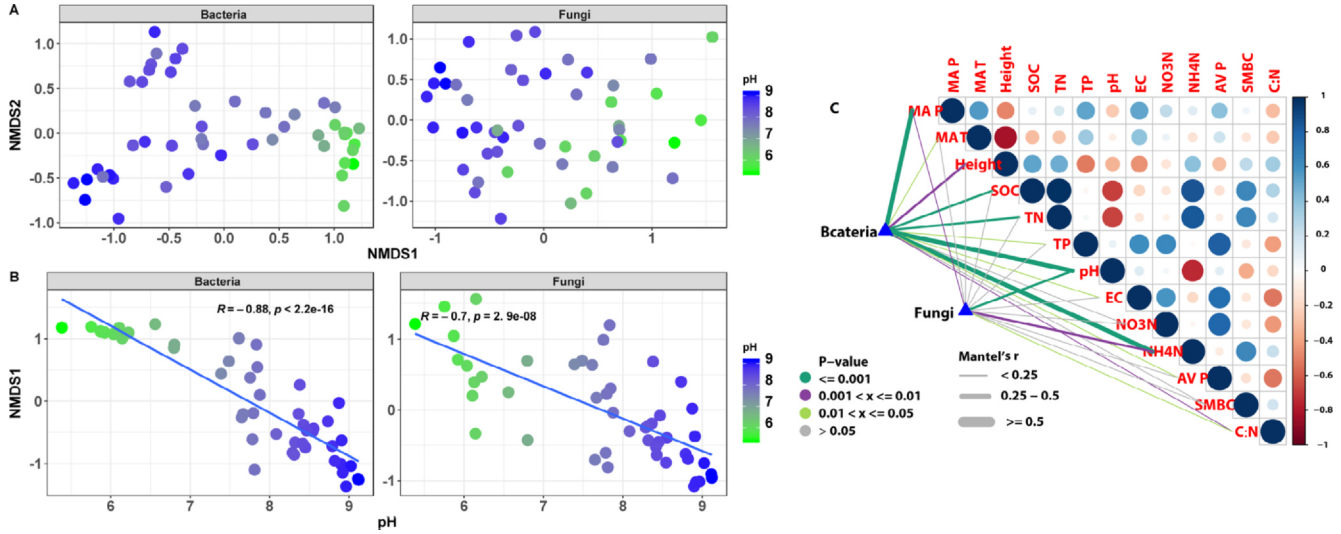

Fig. 3. The NMDS plots and mantel test of soil bacteria and fungi with environmental factors on the Loess Plateau. MAP, mean annual precipitation; MAT, mean annual temperature; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; EC, electricity conductivity; NO3N, nitrate nitrogen; NH4N, ammonia nitrogen; AVP, available phosphorus; SMBC, soil microbial biomass carbon; C:N, the ratio of SOC to TN.

Table 3
Pearson correlations between the ordination score of the first two axes of NMDS and environmental factors.

Variables	Bacteria		Fungi	
	$NMDS_1$	$NMDS_2$	$NMDS_1$	$NMDS_2$
MAP	0.231	0.314*	0.117	−0.155
MAT	−0.045	0.171	−0.141	−0.019
Height	0.446**	−0.197	0.479**	−0.069
SOC	0.727**	−0.019	0.558**	−0.27
TN	0.705**	0.023	0.521**	−0.267
TP	−0.22	0.513**	−0.298*	−0.383**
pH	−0.884**	0.1	−0.701**	0.218
EC	−0.274	0.420**	−0.279	−0.172
NO3N	−0.174	0.396**	−0.176	−0.246
NH4N	0.733**	−0.064	0.619**	−0.133
AVP	−0.246	0.559**	−0.214	−0.330*

*indicates significant correlations at the level of 0.05; ** indicates significant correlations at the level of 0.01. MAP, mean annual precipitation; MAT, mean annual temperature; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; EC, electricity conductivity; NO3N, nitrate nitrogen; NH4N, ammonia nitrogen; AVP, available phosphorus.

community (Fig. 5). These regression results indicated that geographic distance ($r_{bacteria}$ = 0.3174, r_{fungi} = 0.2597) and environmental factors ($r_{bacteria}$ = 0.2467, r_{fungi} = 0.1659) were significantly associated with soil microbial structure.

The mantel test also indicated that geographic distance and local environmental factors were positively correlated with the community structure of bacteria and fungi (Table 4). The partial mantel test showed that when controlling for the effect of environmental factors, the associations between microbial community similarity and geographic distance was not significant (bacteria: r = 0.06928, p = 0.091; fungi: r = 0.07688, p = 0.076); when controlling for geographic distance, the associations between soil microbial community similarity and contemporary environment were still significant ($p < 0.001$), suggesting that contemporary environment (expressed by the local environmental factors) controls the shifts of soil microbial community.

In order to the quantify the potential of each environmental factor in shaping soil microbial community structure, we used multiple regression models to assess the contribution of main environmental factors. The proportion of variance explained by the model was 87.32%, and the results showed that soil pH (RI = 0.60) was the best factor altering the soil bacterial structure, followed by SMBC (RI = 0.12), Height (RI = 0.13), EC (RI = 0.06) and MAP (0.09) (Table 5). The multiple regression model showed that these environmental factors explained 67.2% of the variations in the soil fungal community structure. Soil pH (RI = 0.38) contributed the most to the variations of soil fungal community, followed by SOC (RI = 0.15), SMBC (RI = 0.11), TN (RI = 0.13) and Height (RI = 0.18) (Table 5).

The integrated responses of climate and edaphic properties were investigated using the SEM model, which can reveal effects of environmental factors on soil microbial community compositions and diversity. SEM indicated that soil pH, SOC, MAT and MAP have direct and indirect effects on soil microbial structure and diversity (Fig. 6). Soil pH and SOC directly impacted soil bacterial structure, while MAT through affecting SOC impacted soil bacterial structure. In addition to direct effects, soil pH could also soil bacterial community structure via influencing SOC. For fungal diversity, SOC had the most important effects, followed by soil pH. In addition, soil pH and MAT significantly impacted SOC, resulting in an indirect effect on soil fungal diversity. Soil pH directly and significantly affected the community structure of soil bacteria and fungi. SOC, MAP and MAT had poor effects on the soil microbial community structure.

4. Discussion

Generally, soils had similar bacterial phyla. The most dominant bacterial phyla in almost soil were Proteobacteria, Actinobacteria, Acidobacteria, Chloroflexi and Gemmatimonadetes (Fig. 2), which are common occurred in soils regardless of land uses or ecosystem types (Nemergut et al., 2011; Xia et al., 2016; Zeng et al., 2019). On the Loess Plateau, Ascomycota was the most dominant fungal communities, followed by Basidiomycota, Zygomycota, Chytridiomycota, and Glomeromycota (Fig. 2), which is in line with the global geographic patterns

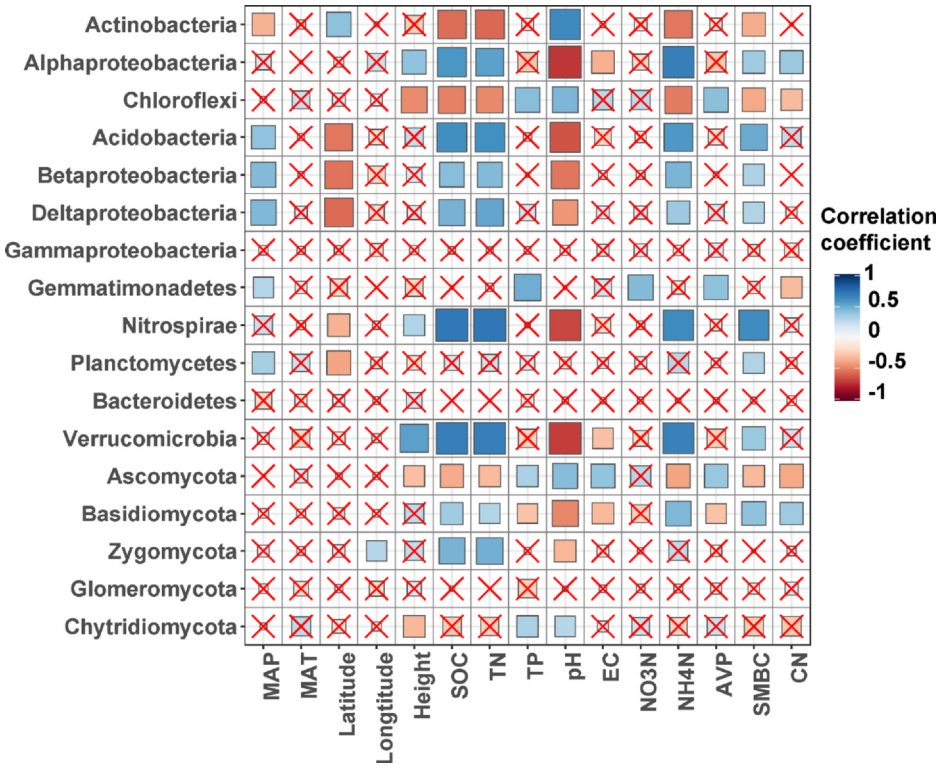

Fig. 4. The Pearson correlations between main bacteria and fungi phyla and environmental factors. MAP, mean annual precipitation; MAT, mean annual temperature; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; EC, electricity conductivity; NO3N, nitrate nitrogen; NH4N, ammonia nitrogen; AVP, available phosphorus; SMBC, soil microbial biomass carbon; CN, the ratio of SOC to TN.

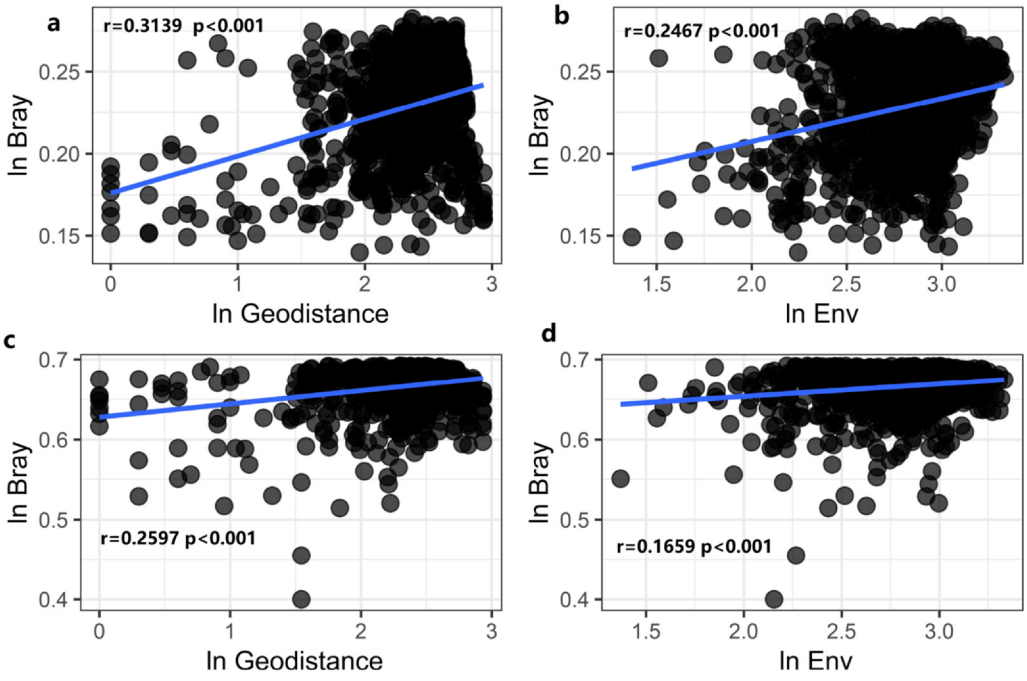

Fig. 5. The correlations between environmental factors and geographic distance and microbial community structure (a and b represent soil bacteria; c and d represent soil fungi) based on distance similarity on the Loess Plateau. Bray represents Bray-curtis similarity; Env represents environmental similarity based on Euclidean distance.

Table 4
The associations between soil microbial community structure and geographic distance and environmental distance with mantel test or partial mantel test.

Type	Factors	Control for	r	p
Bacteria	Environmental factors	Geodistance	0.1887	0.001
	Geodistance	Environmental factors	0.06928	0.091
	Environmental factors		0.2163	0.002
	Geodistance		0.1278	0.011
Fungi	Environmental factors	Geodistance	0.1397	0.001
	Geodistance	Environmental factors	0.07688	0.076
	Environmental factors		0.1485	0.001
	Geodistance		0.09214	0.039

Table 5
The effects of environmental factors on soil microbial structure on the Loess Plateau based on the multiple regression models.

Type	Variables	Estimate	t value	p	RI
Bacteria	(Intercept)	1.347	1.289	0.204	
	pH	−0.518	−9.322	0.000	0.60
	EC	−0.001	−2.920	0.006	0.06
	SMBC	0.001	2.531	0.015	0.12
	MAP	0.004	3.238	0.002	0.09
	Height	0.000	2.951	0.005	0.13
Fungi	(Intercept)	−0.407	−0.281	0.780	
	pH	−0.350	−4.062	0.000	0.38
	SOC	0.065	2.000	0.052	0.15
	SMBC	0.001	2.453	0.019	0.11
	TN	−1.015	−2.487	0.017	0.13
	MAP	0.004	2.492	0.017	0.05
	Height	0.001	3.481	0.001	0.18

MAP, mean annual precipitation; SOC, soil organic carbon; TN, total nitrogen; EC, electricity conductivity; SMBC, soil biomass carbon; RI, relative importance.

(Tedersoo et al., 2014). Our findings showed that a higher dominance of Ascomycota (56%) than a global survey (31%) (Tedersoo et al., 2014). In our study, almost soils were alkaline, which was different many studies conducted in acid soils. We speculate that Ascomycota were the most dominant phyla in arid or semiarid areas.

Soil pH affected the distributions of main phyla of soil bacteria and fungi, including Ascomycota, Basidiomycota, Zygomycota, Glomeromycota, Chytridiomycota, Ciliophora, Rozellomycota, Actinobacteria, Alphaproteobacteria, Betaproteobacteria, Deltaproteobacteria, Acidobacteria, Chloroflexi, Nitrospirae, Thermoleophilia and Verrucomicrobia. These strong associations suggest that soil pH was the main factor controlling the spatial patterns of soil bacteria and fungi on the Loess Plateau. Similarly, Liu et al. (2014) found that black soil pH was significantly correlated with the relative abundance of Alphaproteobacteria and Chloroflexi. Rousk et al. (2010) reported that pH was defined as the critical factor altering soil bacterial community compositions (Rousk et al., 2010). These studies concluded that soil microbial communities were shaped by soil pH.

To quantify the contributions of climate and soil properties on the variations of soil bacteria and fungi, we used multiple regression models to assess the superior predictors. Our models showed that soil organic carbon was the best predictor of soil fungal Shannon diversity index with a relative importance of 0.85, while all the environmental factors had no significant effects on soil bacterial diversity. For microbial community structure, soil pH had the strongest effects on soil bacterial and fungal community structure on the Loess Plateau, which is in consistent with previous studies in soils (Glassman et al., 2017; Zhalnina et al., 2015). In addition, soil pH, MAP and soil organic carbon had strong effects on the soil bacterial community structure in our study.

SEM can be used to assess the indirect and direct effects of environmental factors on soil microbial community structure and diversity. The results from SEM showed that MAT can directly affect SOC and sequentially influence soil bacterial and fungal Shannon diversity. However, the direct effects of MAP and MAT on soil fungal Shannon diversity are not significant. SOC was the best predictor of soil fungal diversity, followed by soil pH. Other factors had no strong effects on soil fungal Shannon diversity. Soil pH had significant effects on SOC, resulting in indirect effects on fungal Shannon diversity. For bacterial Shannon diversity, SOC and pH were the main affecting factors. Other factors, such as MAT, had stronger indirect effects on SOC and pH and sequentially influenced soil bacterial Shannon diversity. Soil pH and SOC had similar impacts on the soil bacterial Shannon diversity as the soil fungal Shannon diversity, and the affecting degree was much poorer than soil fungal diversity.

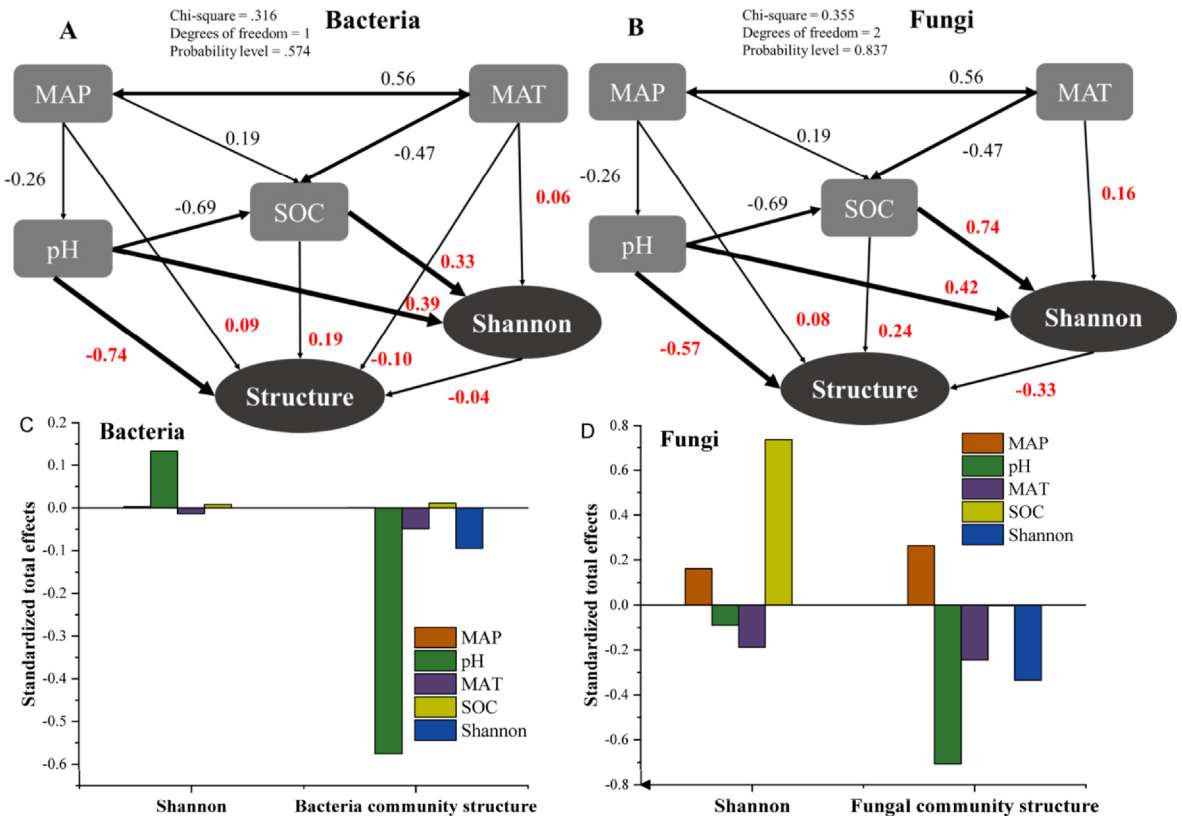

Fig. 6. SEMs fitted to the diversity and structure of soil bacteria (A) and fungi (B) and standardized total effects (direct plus indirect effects) derived from them (C and D). MAP, mean annual precipitation; MAT, mean annual temperature; SOC, soil organic carbon; Shannon, soil microbial Shannon index.

The SEM also highlighted the critical roles of pH and SOC in driving the diversity of soil bacteria and fungi on the Loess Plateau. First, soil pH can directly impact the growth of soil bacteria and fungi. Because soil bacteria and fungi have different optimal pH ranges (Rousk et al., 2010), which mainly determined the diversity and compositions of bacteria and fungi in soils. Soil pH could impact the availability of SOC which indirectly influenced soil microbial diversity and community structure. In our models, we also found that SOC directly influenced soil microbial diversity. These results suggest that soil C was the limited factor of soil bacteria and fungi on the Loess Plateau and align with previous studies (Siciliano et al., 2014; Tian et al., 2018). However, most previous studies showed that soil bacterial diversity was determined by soil pH regardless of land uses, soil types and ecosystem types (Lauber et al., 2009; Zeng et al., 2019). These discrepancies are likely linked to the high pH values (with a mean value of 7.73) found at our study sites (5.38–9.12), and most soils (73%) were alkaline (pH $>$ 7.3). In previous studies (soil pH ranged from 3.5 to 6.5), soil bacterial diversity linearly increased with soil pH in the acid soils (Lauber et al., 2009). The roles of pH shaping bacterial community structure is more important than that impacting soil fungal community structure. Consistent with previous studies suggested that the critical roles of soil pH in driving soil fungal diversity patterns (Fierer and Jackson, 2006; Lauber et al., 2009).

In addition, TN and SOC significantly affected the compositions of soil bacteria. The Mantel test also indicated that TN ($r = 0.257$, $p < 0.01$) and SOC ($r = 0.289$, $p < 0.01$) significantly impacted the soil bacterial community. When controlling for SOC and TN, the associations between soil pH and main bacterial phyla and classes remained significant ($r_{Alphaproteobacteria} = -0.578$, $P = 0.0001$; $r_{Actinobacteria} = 0.434$, $P = 0.003$; $r_{Verrumicrobia} = -0.449$, $P = 0.002$; $r_{Acidobacteria} = -0.381$, $P = 0.009$; $r_{\beta\text{-}Proteobacteria} = -0.384$, $P = 0.008$; $r_{Nitrospirae} = -0.383$, $P = 0.009$; $r_{Thermoleophilia} = 0.348$, $P = 0.018$), demonstrating the predominant roles of soil pH contributing the alterations of bacterial composition (Rousk et al., 2010). At alkaline conditions (pH $>$ 7.3, n = 35), soil pH still affected soil bacterial taxa, including Actinobacteria ($r = 0.49$, $p = 0.0031$), Acidobacteria ($r = -0.62$, $p < 0.0001$), Proteobacteria ($r = -0.64$, $p < 0.001$), Chloroflexi ($r = 0.58$, $p = 0.0002$), Nitrospirae ($r = -0.47$, $p = 0.0047$) and Verrucomicrobia ($r = -0.43$, $p = 0.011$) (Fig. S1). In the acidic soils, the main bacterial phyla were not impacted by soil pH, as demonstrated by the correlations between soil pH and their relative abundances (Fig. S1).

Soil fungal diversity was influenced by soil pH, which is similar with a study conducted in the global drylands highlighting a negative association between fungal richness and soil pH (Tedersoo et al., 2014). Soil pH also impacted most fungal phyla. For example, the relative abundance of Ascomycota, Rozellomycota and Chytridiomycota increased concomitantly with soil pH, while the relative abundance of Zygomycota and Basidiomycota declined with soil pH. The relationships between soil main fungal phyla and SOC were opposite those of soil pH. In acidic soils, the correlations between soil pH and the main fungal phyla were not significant, while in alkaline soils, just the relative abundance of Basidiomycota ($r = -0.46$, $p = 0.0054$) was significantly correlated with soil pH. Compared with soil bacteria, the effects of soil pH in the alkaline soils become poor. These results may have been associated with the wide optimum pH range of many fungal taxa. However, soil pH just affected the compositions of soil bacteria rather than soil bacterial diversity because of the life strategies of different bacterial taxa. In our study, most soils (73%) were alkaline, and the distribution patterns of soil bacteria were strongly impacted by soil pH, which may fill up the knowledge of microbial geography inhabiting alkaline and arid soils.

5. Conclusions

This study is an attempt to understand spatial patterns of soil

bacteria and fungi on the Loess Plateau, which is represented a typical arid area of China. Our study reveals that environmental factors exhibited no influence on soil bacterial α-diversity, while soil organic carbon enhance soil fungal α-diversity. Soil microbial community structure in this region was mainly controlled by soil pH, especially for soil bacteria. Compared with local environmental profiles, geographic distances played less important roles in shaping soil microbial community structure. This finding highlighted the critical roles of environmental conditions in shaping soil fungi and bacteria. On the Loess Plateau, the program of "Green for Grain" project might be the underlying effects on soil bacterial and fungal spatial patterns. These results fill up the knowledge gap of soil microbial geography in the arid and semiarid areas with alkaline conditions.

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

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