



Land Use Types Drive the Distinct Patterns of Bacterial and Fungal Communities in Soils from the Semi-arid Area

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Abstract

Land types and ways of utilization significantly influence soil microbial communities in arid and semi-arid regions, which are vital for nutrient cycling and ecosystem functionality. In this study, the soil bacterial and fungal communities of five land types, including natural grasslands, farmlands, artificial grasslands, uncultivated lands, and riverbeds in the semi-arid lower reaches of the Heihe River, China, were investigated. Farmlands exhibited the highest bacterial Chao1 richness and Shannon diversity, while uncultivated soils had the lowest bacterial Chao1 richness. Fungal diversity was highest in uncultivated soils compared to farmlands. Principal coordinate analysis (PCoA) showed distinct microbial community structures across land types, with *Actinobacteria*, *Proteobacteria*, *Firmicutes*, and *Chloroflexi* dominating bacterial communities, and *Ascomycota* and *Basidiomycota* dominating fungal communities. Life history strategies revealed distinct patterns between bacterial and fungal communities within farmland soils and artificial grassland soils. Microbial community assembly in natural grasslands was primarily deterministic, with limited stochastic influence, while farmlands exhibited mixed assembly processes. Co-occurrence network analysis showed more stable and cooperative microbial networks in natural grasslands, while farmland networks were more competitive and reliant on key species. These findings provide important insights into the role of land use in shaping microbial diversity and ecosystem function, offering guidance for sustainable land management in semi-arid oasis regions.

Keywords Farmland · Life history strategy · Assembly mechanism · Co-occurrence network · Semi-arid region

Introduction

Microbial communities play an essential role in maintaining the multifunctions of soil ecosystem, such as nutrient cycling, organic matter decomposition, and soil formation [1, 2]. The composition, biogeographic patterns, and the assembly processes of microbial communities are the research focus of microbial ecology from different spatial scales, such as global [3] and local levels [4]. At a large scale, climate, soil pH, and

available carbon are usually the main factors shaping the composition of soil bacterial and fungal communities [5, 6]. Under the same climatic zone, anthropogenic factors, especially the land use types, significantly alter the composition and function of soil microbial communities [7].

Arid and semi-arid regions, accounting for 40% of the Earth's total land area, play a crucial role in providing food for humans and influencing global climate patterns. However, these areas face serious challenges, including nutrient-deficient soils, water scarcity, and declining soil quality [8]. Vegetation has a significant impact on the structure and function of soil microbial communities in the semi-arid and arid regions [9, 10]. In the semi-arid regions, such as Inner Mongolia, China, grassland has been the dominant land use type, followed by woodland, uncultivated land, sandy land, and farmland. Grassland accounted for more than 45% of the total land area, while farmland exhibited an increasing trend from 1980 to 2015 [11]. Among these land use types, natural grasslands have been identified as the most effective model for vegetation restoration in arid and semi-arid areas [12]. The differences in the composition of

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microbial communities between the farmland and grassland in the semi-arid region have been studied [13]. Generally, there is a gradient of human activities moving outward from riverbeds to farmlands, progressing through riverbed soils, uncultivated areas, natural grasslands, artificial grasslands, and finally farmlands. However, a comprehensive understanding of how these different land use types affect both soil bacterial and fungal communities in semi-arid regions remains limited.

Microbial community assembly processes and life history strategies play pivotal roles in shaping microbial biogeography and determining how microbial communities respond to environmental changes, particularly under the stress of human activities. Assembly processes, including deterministic and stochastic factors, influence the distribution and composition of microbial communities across diverse ecosystems [14]. At the regional scale, deterministic and stochastic processes dominated the community of bacterial communities in the soils from farmland and grassland, respectively [13]. However, at the local scale, stochastic processes dominated the community assembly of bacterial communities under different soil salt intensities in arid and semi-arid regions [15]. Hence, more studies are still needed to understand the assembly process of microbial communities, including bacteria and fungi, in extreme environments.

Assembly processes are also closely linked to the life history strategies of microorganisms, which can range from opportunistic (r-strategists) to more conservative (K-strategists) approaches, depending on resource availability and environmental stability [16]. Anthropogenic disturbance, such as agricultural activities, can disrupt the natural assembly processes of microbial communities, resulting in changes in community structures. For instance, intensive farming practices often introduce sustained inputs of nutrients and organic matter into the soil, which can subsequently shift the life history and dynamics of microorganisms [17]. A shift from r- to K-strategists was found due to the greater SOC stability and recalcitrance in semi-arid orchards with cover crops [18].

The Heihe River is the second largest inland river in China, with its watershed characterized by a semi-arid to arid climate and limited precipitation [19]. The region encompasses diverse land use types, including natural grasslands, farmlands, riverbeds, and artificial grasslands, which are likely to shape distinct soil microbial communities. Therefore, this study aims to elucidate how different land use types influence the composition, life-history strategies, and assembly processes of soil microbial communities in a semi-arid environment. Specifically, we compared the diversity and composition of bacterial and fungal communities across various land types, and investigated the life history strategies (r/K) and community assembly mechanisms that govern their distribution. Furthermore, we constructed and analyzed integrating co-occurrence networks that include

both bacterial and fungal taxa in farmland and natural grassland soils, in order to assess the complexity, cooperation, and stability of microbial interactions under contrasting levels of anthropogenic disturbance. By combining multiple ecological perspectives, community diversity, assembly rules, life-history traits, and cross-kingdom interaction networks, our study would provide a more comprehensive understanding of how land use shapes microbial ecology in semi-arid soils. These insights are essential for guiding sustainable land management and conservation in fragile dryland ecosystems.

Materials and Methods

Studied Region and Samples Collected

The Heihe River, located in northwestern China, is the country's second-largest inland river and is characterized by a semi-arid climate with limited summer rainfall. Its basin supports diverse ecosystems, including desert steppe, riparian forests, and agricultural lands. The Ejina Oasis in the lower reaches of the Heihe River Basin was selected as the study area. In this region, grassland constitutes the dominant land use type, followed by farmland. Notably, the farmland area expanded from 95.65 km² in 2000 to 137.33 km² in 2020 [20]. Grasslands were categorized as natural or artificial based on the level of anthropogenic disturbance. Artificial grassland is established for pasture or ecological restoration and is periodically managed through irrigation and other interventions. In contrast, natural grassland experiences minimal human interference. Farmland is actively managed, characterized by regular fertilization and irrigation. Uncultivated land refers to abandoned or naturally recovering areas without direct management, whereas the riverbed is primarily shaped by the hydrological dynamics of the Heihe River, with minimal direct human influence. In this study, 59 sampling sites were set based on the main land use types of this region: farmland (12), natural grassland (26), uncultivated land (6), riverbed (9), and artificial grassland (6) (Fig. 1). At each site, a bulk soil sample from the surface layer (0–10 cm) was collected by combining five subsamples, which were then mixed thoroughly and transported to the laboratory for analysis.

Soil Physicochemical Factors

Fifteen edaphic physicochemical factors, including pH, water content, electric conductivity, water-soluble salt, carbon content, substitutive potassium, substitutive sodium, organic matter, total nitrogen, total potassium, total phosphorus, hydrolyzed nitrogen, available phosphorus, and available potassium, were investigated in the soils across different landscape types, according to the previous methods in our work [4].

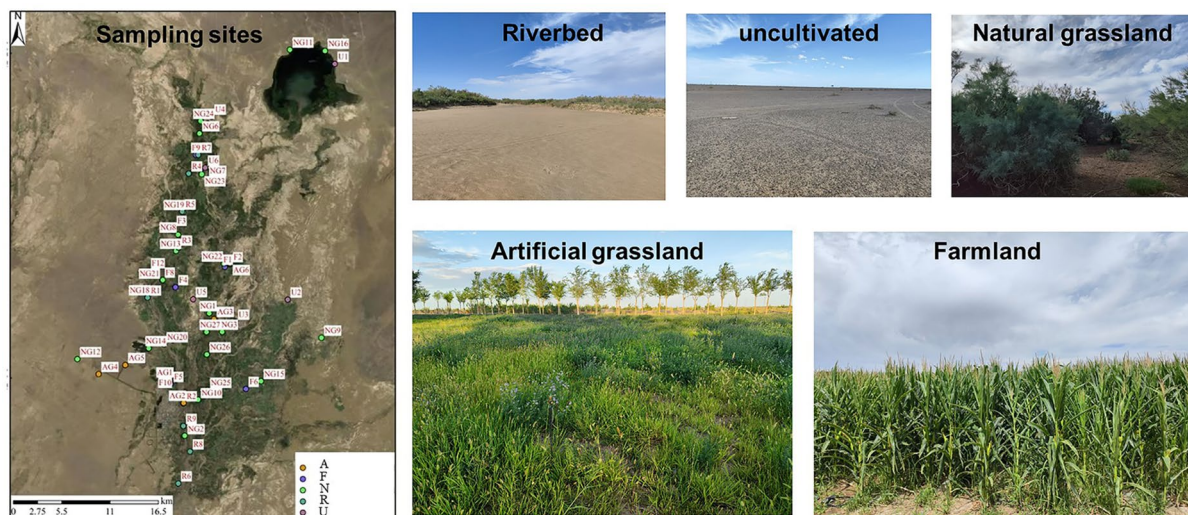


Fig. 1 Distribution of sampling sites and dominant land use types in the semi-arid landscape of Ejinaqi along the lower Heihe River Basin

DNA Extraction, Sequencing, and Annotation

DNA extraction from soil samples was carried out using the QIAGEN DNeasy PowerMax Soil Kit according to the protocol. The quality and quantity of extracted soil DNA were assessed using gel electrophoresis and NanoDrop™ 2000/2000c spectrophotometers to ensure purity. High-throughput sequencing was then performed using the Illumina platform (www.biomarker.com.cn), targeting the V3–V4 region of the 16S rRNA gene (338 F/806R) for bacterial communities and the ITS1 region (ITS1 F/ITS2) for fungal communities. Raw sequencing data were processed using bioinformatics pipelines, which included quality filtering, demultiplexing, and the removal of chimeric sequences. Taxonomic classification was conducted using reference databases such as SILVA [21] for bacteria and UNITE [22] for fungi, allowing for the annotation of sequences at different taxonomic levels. Detailed information could be found in the previous studies [23–25]. All the sequencing data in this study were uploaded in the NCBI SRA Database (accession number: PRJNA1233915).

Statistical Analysis

The diversity, composition, life strategies, assembly process, and co-occurrence network analysis of bacterial and fungal communities in soils across different land use types were all performed and visualized in the R environment (version 4.2.1). Pairwise Wilcoxon rank-sum tests were performed to assess differences in the relative abundance of the top 10 bacterial and fungal phyla among different land use types. The unique and shared amplicon sequence variants (ASVs)

of microbial communities, Chao1, Shannon diversity indices, and composition of microbial communities were calculated with the Vegan package [26]. Principal coordinate analysis (PCoA) of bacterial and fungal communities was performed based on Bray–Curtis distances of ASVs and validated using a permutational multivariate analysis of variance (PERMANOVA) test. The microbial life-history strategy ratios ($K:r$) for bacterial and fungal communities were calculated as follows: (*Actinobacteriota* + *Acidobacteriota* + *Chloroflexi*) to (*Proteobacteria* + *Bacteroidota* + *Firmicutes*) for bacteria ($B_{K:r}$), and *Basidiomycota* to (*Ascomycota* + *Mortierellomycota*) for fungi ($F_{K:r}$), respectively [27]. The neutral model developed by Sloan [28] was performed to investigate the assembly process of bacterial and fungal communities in soils of main land use types. The package “hmisc” was used to calculate the Spearman correlation of ASVs, and strong correlations ($|r| \geq 0.7$ and $P < 0.05$) were selected for the construction and analysis of the co-occurrence network [29]. The co-occurrence network of microbial communities and their topological parameters were visualized and calculated with the igraph Package. A significance threshold of $P < 0.05$ was applied for all statistical analyses, and the main R code in this study is available online at: <https://doi.org/https://doi.org/10.5281/zenodo.15055161>.

Results

The Analysis of Soil Physiochemical Parameters

Among the 15 parameters, temperature, water content, electrical conductivity, water-soluble salt, and hydrolyzed nitrogen did not show any significant difference across various land types

(Table 1). Riverbed soil had a higher pH (9.11), compared to natural grassland (8.77) and farmland (8.57). Farmland soil exhibited a higher carbon content (2.51%), substitutive potassium (0.64 cmol/kg), organic matter (9.91 g/kg), total nitrogen (0.61 g/kg), total phosphorus (0.73 g/kg), total potassium (19.95 g/kg), and available phosphorus (69.07 mg/kg). Natural grassland had a relatively higher carbon content (1.94%), substitutive potassium (0.71 cmol/kg), total nitrogen (0.57 g/kg), organic matter (11.03 g/kg), and available potassium (569.96 mg/kg).

The Diversity Index of Bacterial and Fungal Communities

A total of 25,496 and 6602 ASVs were obtained for bacteria and fungi, respectively. However, only 83 and 162 ASVs for bacteria and fungi were shared across all soil types, respectively. Natural grassland had the highest number of unique ASVs in both bacteria (8951) and fungi (2358) (Fig. S1, supplementary materials). Figure 2 shows the Chao1 richness and Shannon diversity index of soil bacterial communities across all land types. Uncultivated soil had the lowest average Chao1 richness (638), which was significantly lower than other land types ($P < 0.05$). The Chao1 index of natural grassland (894) was significantly lower than artificial grassland (1166) and farmland (1190) ($P < 0.05$) (Fig. 2A). The Shannon diversity of natural grassland (5.75) was also significantly lower than that of artificial grassland (6.22) and farmland (6.32) ($P < 0.05$). There were no significant differences in Shannon diversity of soil bacteria between natural grassland (5.75) and uncultivated land (5.52) ($P > 0.05$). It should also be noted that there were no significant differences in Chao1 richness and Shannon diversity of soil bacteria between artificial grassland

and farmland ($P > 0.05$). There were no significant differences in Chao1 index of fungal communities in soils across all five land types ($P > 0.05$) (Fig. 2B). The Shannon index of fungal communities in natural grassland (3.30) and farmland (3.62) was significantly lower than that of uncultivated land (4.54) and riverbed soils (4.38) ($P < 0.05$) (Fig. 2B).

The Composition of Bacterial and Fungal Communities

Across the five land use types, the bacterial communities at the phylum level were predominantly composed of *Actinobacteria* (18.13–23.63%), *Proteobacteria* (20.41–25.32%), *Firmicutes* (7.20–12.77%), and *Chloroflexi* (6.49–12.78%) (Fig. S2 A). Among the top 10 most abundant bacterial phyla, the relative abundances of *Proteobacteria*, *Firmicutes*, *Myxococcota*, and *Desulfobacteria* did not differ significantly across the five land use types ($P > 0.05$, Fig. 3). In contrast, *Actinobacteria* were significantly more abundant in natural grassland soils compared to riverbed soils, while *Chloroflexi* and *Acidobacteria* showed significantly higher relative abundances in farmland soils than in uncultivated and natural grassland soils ($P < 0.05$).

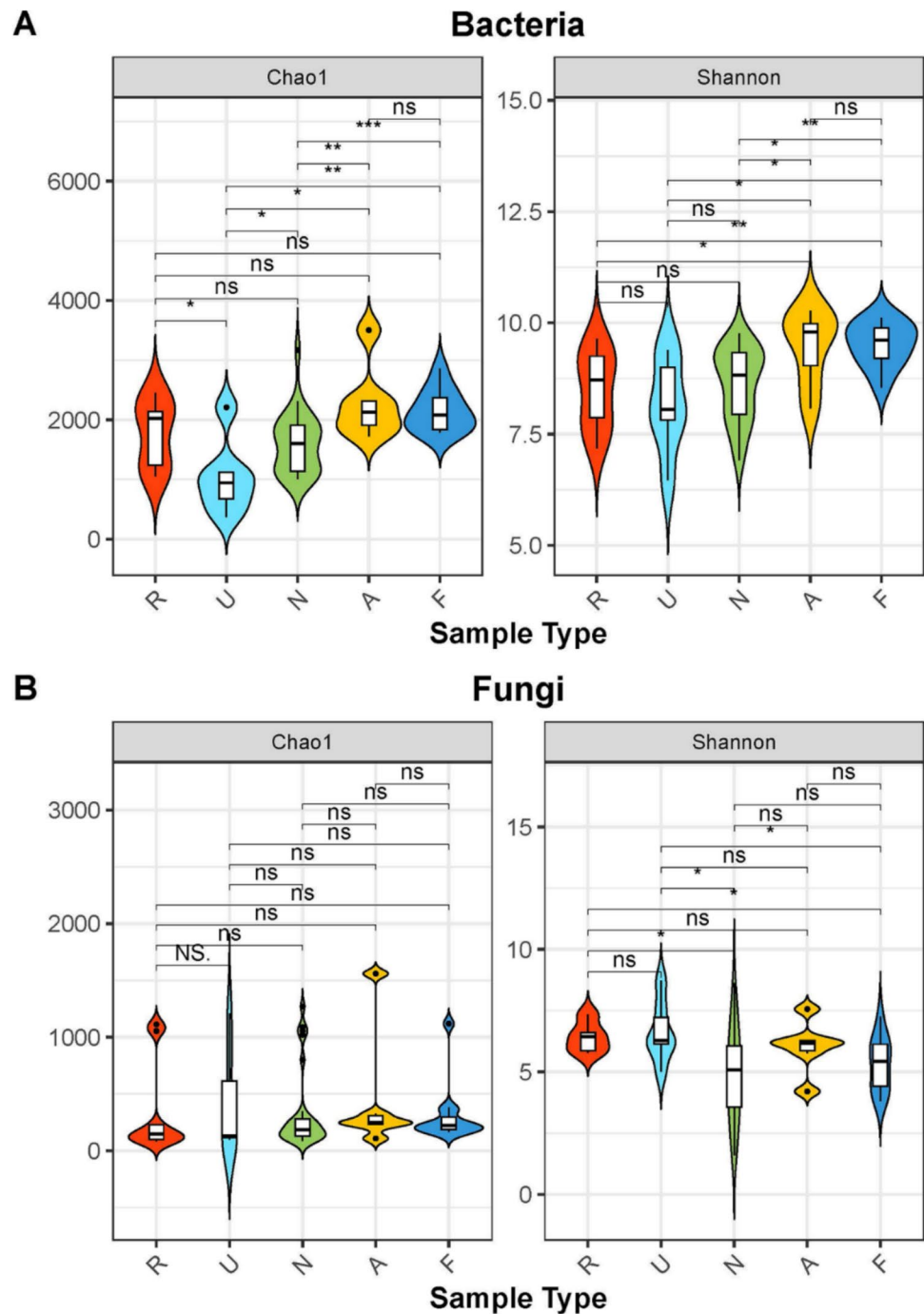
Ascomycota dominated the fungal communities across all soil types, accounting for 57.04–70.15% of the total relative abundance, followed by *Basidiomycota*, which ranged from 14.72 to 18.34% (Fig. S2B). The relative abundance of *Ascomycota* was significantly higher in natural grassland soils than in riverbed soils ($P < 0.05$, Fig. S3), whereas no significant differences were observed in the abundance of *Basidiomycota* across the five land use types. In addition, *Olpidiomycota* exhibited a higher relative abundance in farmland soils compared to natural

Table 1 The physiochemical parameters in soils across five land types

Factors [†]	Artificial grassland	Farmland	Natural grassland	Riverbed	Uncultivated land
Temperature (°C)	35.72 ± 0.92a	35.15 ± 6.66a	32.09 ± 5.32a	34.96 ± 4.57a	33.75 ± 4.01a
Water content (cm ³ /cm ³)	0.06 ± 0.08a	0.20 ± 0.06a	0.07 ± 0.19a	0.01 ± 0.02a	0.22 ± 0.38a
Electrical conductivity (µm/cm)	12.33 ± 13.23a	48.27 ± 29.75a	21.41 ± 56.81a	4.00 ± 3.00a	58.17 ± 88.00a
pH	8.85 ± 0.27ab	8.57 ± 0.19b	8.77 ± 0.25b	9.11 ± 0.11a	8.75 ± 0.51ab
Water-soluble salt (mg/g)	13.23 ± 29.32a	5.66 ± 3.57a	35.01 ± 47.42a	0.95 ± 0.46a	49.78 ± 62.58a
Carbon content (%)	1.75 ± 0.63ab	2.51 ± 0.73a	1.94 ± 0.72ab	1.61 ± 0.59b	1.63 ± 0.61ab
Substitutive potassium (cmol/kg)	0.49 ± 0.60ab	0.64 ± 0.29a	0.71 ± 0.41a	0.09 ± 0.02b	0.63 ± 0.73ab
Substitution sodium (cmol/kg)	3.30 ± 7.26ab	0.84 ± 0.43b	5.05 ± 6.77b	0.20 ± 0.05b	18.56 ± 30.08a
Organic matter (g/kg)	7.07 ± 2.94ab	9.91 ± 2.58a	11.03 ± 7.00a	1.56 ± 0.29b	5.95 ± 5.45ab
Total nitrogen (g/kg)	0.34 ± 0.23ab	0.61 ± 0.15a	0.57 ± 0.38a	0.05 ± 0.01b	0.36 ± 0.41ab
Total phosphorus (g/kg)	0.50 ± 0.17bc	0.73 ± 0.12a	0.50 ± 0.10b	0.35 ± 0.02c	0.45 ± 0.12bc
Total potassium (g/kg)	18.53 ± 2.16a	19.95 ± 1.08a	18.50 ± 1.26a	16.09 ± 0.96b	18.38 ± 2.82a
Hydrolyzed nitrogen (mg/kg)	78.43 ± 74.97a	142.15 ± 117.94a	103.33 ± 162.25a	10.86 ± 4.31a	162.78 ± 265.66a
Available phosphorus (mg/kg)	22.21 ± 23.08b	69.07 ± 40.66a	20.21 ± 13.78b	0.94 ± 0.33b	9.42 ± 6.68b
Available potassium (mg/kg)	411.42 ± 676.92ab	285.27 ± 114.90ab	569.96 ± 469.22a	44.73 ± 10.21b	374.00 ± 468.70ab

[†] Average ± SD, different letters indicate significance between land use types via Tukey's post-hoc test for pairwise comparisons

Fig. 2 Chao1 richness and Shannon diversity indices of soil bacterial (A) and fungal (B) communities across five land use types (riverbed (R), uncultivated land (U), natural grassland (N), artificial grassland (A), and farmland (F)). *Significant at $P < 0.05$ level; ns, not significant



grassland soils (Fig. S3). PCoA further revealed that the composition of both bacterial and fungal communities varied markedly with land use type (Fig. 4A and B), confirmed by the PERMANOVA test ($P < 0.05$).

The Life History Strategies of Bacterial and Fungal Communities

For bacterial communities, the $B_{K:r}$ ratio was significantly higher in farmland and artificial grassland compared to

natural grassland and uncultivated land ($P < 0.05$), indicating a shift toward K -strategists (e.g., *Actinobacteriota*, *Acidobacteriota*, *Chloroflexi*) in human-managed soils (Fig. 4C). In contrast, fungal communities displayed a different pattern. The $F_{K:r}$ ratio was highest in uncultivated land, significantly greater than in both farmland and artificial grassland ($P < 0.05$), suggesting that fungal K -strategists (e.g., *Basidiomycota*) were more dominant in less disturbed, low input environments (Fig. 4D). However, unlike bacteria, fungal $F_{K:r}$ ratios in natural grasslands did not differ

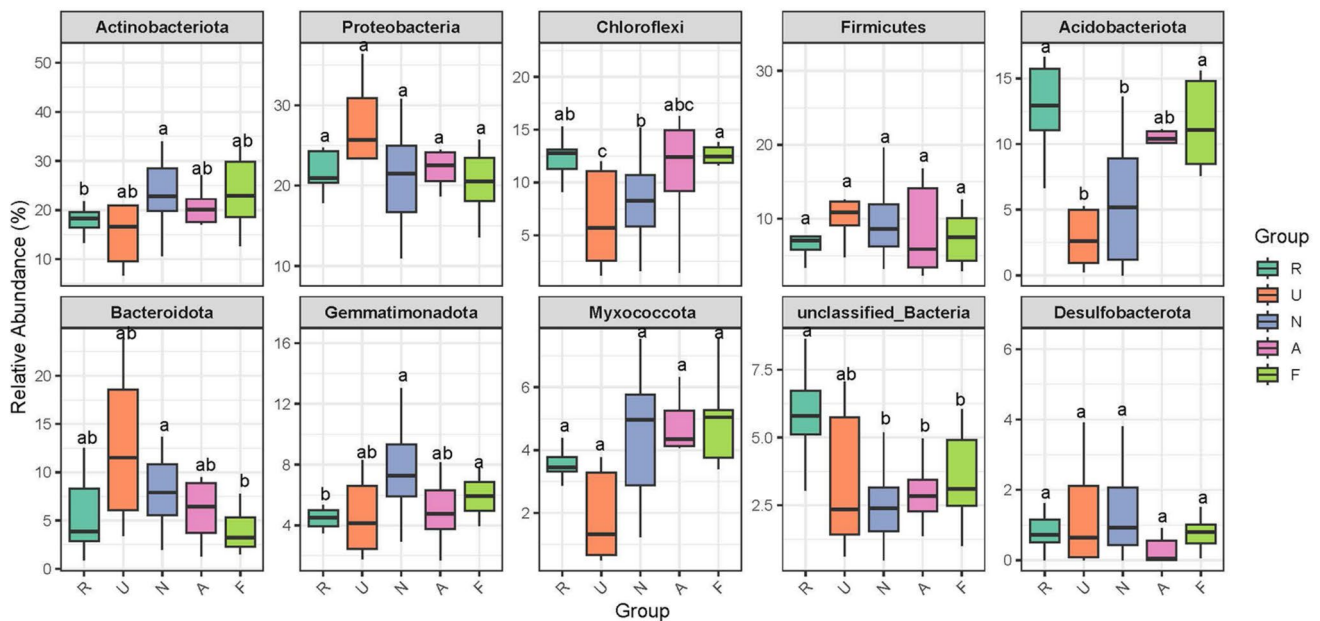


Fig. 3 Differential composition of the soil bacterial community at the phylum level across five land use types via Wilcoxon tests (R, riverbed; U, uncultivated land; N, natural grassland; A, artificial grass-

land; F, farmland; different letters indicate significance between land use types via Wilcoxon tests for pairwise comparisons)

significantly from most other land types, highlighting that fungal life-history responses may be less sensitive to land use changes than bacterial ones.

The Assembly Process of Soil Microbial Communities of Main Land Types

The soil bacterial communities of natural grasslands and farmlands partially followed the neutral model. The closer R^2 is to 1, the more it indicates that stochastic processes dominate. For the farmland soils, a relatively high R^2 value (0.45) was observed, indicating that both deterministic and stochastic processes appeared to play significant roles in shaping bacterial communities in farmland soils (Fig. 5A). In contrast, for natural grassland soils, a low R^2 value (0.13) and a small value (0.0022) were observed, suggesting that bacterial communities are primarily shaped by deterministic processes, limitedly influenced by immigration (Fig. 5B). The results from the DDR model also confirmed this result. Bacterial communities in farmland exhibited a significantly steeper positive slope in the distance decay relationship, indicating that community dissimilarity increased with geographic distance (Fig. 5C). In contrast, no significant distance decay relationship was observed for fungal communities in farmland, suggesting that geographic distance had a limited effect on fungal community dissimilarity in farmland (Fig. 5D). For natural grassland, both bacterial and fungal communities exhibited significantly positive distance decay relationships, although the slopes were relatively low (Fig. 5C and D). The Mantel test

also confirmed that the bacterial community in grassland soils was more influenced by the soil physiochemical parameters (salt concentration, total potassium, and available potassium), while there was no significant Mantel correlation between bacterial communities in farmland soils and the 15 tested factors (Fig. S4). As for soil fungal communities in both natural grasslands and farmland, negative R^2 values were obtained, indicating that these communities do not fit the neutral model (Fig. S5). The Mantel tests also found that the soil fungal communities in farmland and natural grassland were influenced by three (organic matter, total phosphorus, and total nitrogen) and four (water content, electric conductivity, total potassium, and available potassium) physiochemical parameters, respectively (Fig. S4). This implies that deterministic processes are the dominant factors driving the assembly of fungal communities.

Co-occurrence Network of Soil Microbial Communities of Main Land Types

Co-occurrence networks comprising both bacterial and fungal ASVs were constructed for natural grassland and farmland soils based on strong Spearman correlations ($|r| > 0.7$, $P < 0.05$). The farmland network included 624 nodes and 8135 edges, while the natural grassland network consisted of 684 nodes and 2278 edges (Fig. 6A and B). Farmland soils exhibited significantly higher average degree and closeness centrality ($P < 0.05$), indicating a more complex and densely connected microbial network (Fig. S6). In both land

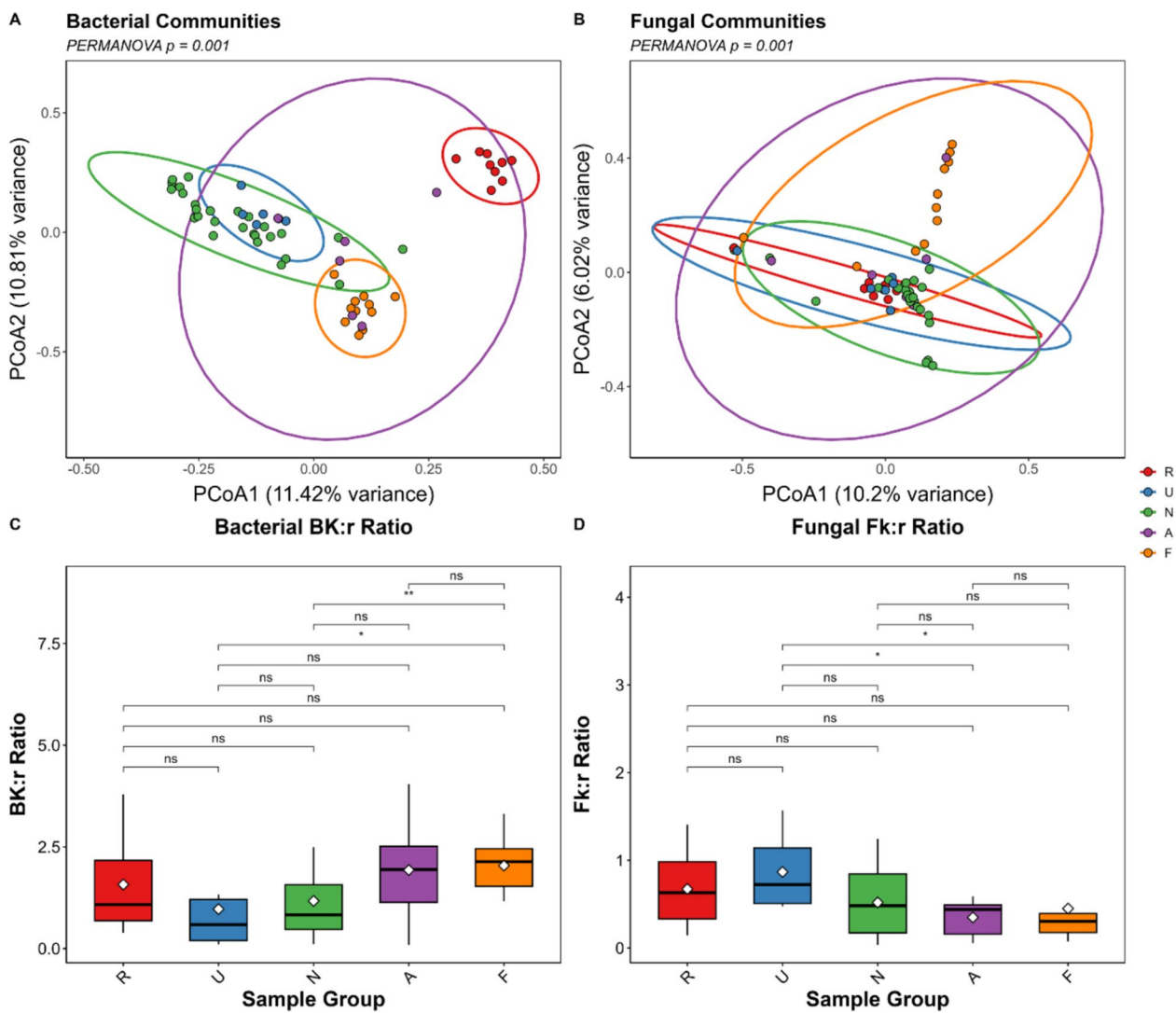


Fig. 4 Principal coordinates analysis (PCoA) of soil bacterial (A) and fungal (B) communities, along with the life history strategy ratios of bacterial ($B_{K:r}$, C) and fungal ($F_{K:r}$, D) communities across five land

use types (R, riverbed; U, uncultivated land; N, natural grassland; A, artificial grassland; F, farmland)

types, bacterial taxa dominated the networks, accounting for 89.9% of nodes in farmland and 88.7% in natural grassland soils (Fig. S7 A). A notable distinction was observed in the proportion of negative correlations: 36.6% in farmland versus only 0.2% in natural grassland. In farmland soils, 30.8% of the negative interactions occurred within bacterial communities. Additionally, interactions between bacterial and fungal communities were more diverse in farmland, with 7.4% positive and 5.6% negative correlations, compared to only 5.8% positive correlations in natural grassland. These findings suggest that microbial interactions in natural grassland soils are predominantly cooperative, particularly within bacterial taxa, whereas farmland soils exhibit a more complex pattern of cooperative and competitive relationships, likely shaped by anthropogenic disturbance (Fig. S7B).

To elucidate the ecological roles of microbial taxa within the co-occurrence networks, network topology was examined using Zi-Pi plots, which categorize nodes into peripherals, connectors, module hubs, and network hubs based on their within-module (Zi) and among-module (Pi) connectivity (Fig. 6C and D). Connectors and hubs are considered keystone taxa, contributing to intra- and inter-module stability and overall network cohesion. In the farmland network, a total of 228 ASVs were identified as connectors (202 bacterial and 26 fungal ASVs), along with two module hubs and three network hubs, all of which were bacteria (Fig. S7 C). These keystone taxa were predominantly composed of *Actinobacteriota* (24.89%), *Chloroflexi* (17.60%), *Proteobacteria* (17.17%), and *Ascomycota* (9.87%), highlighting the central role of these groups in maintaining network structure under agricultural conditions.

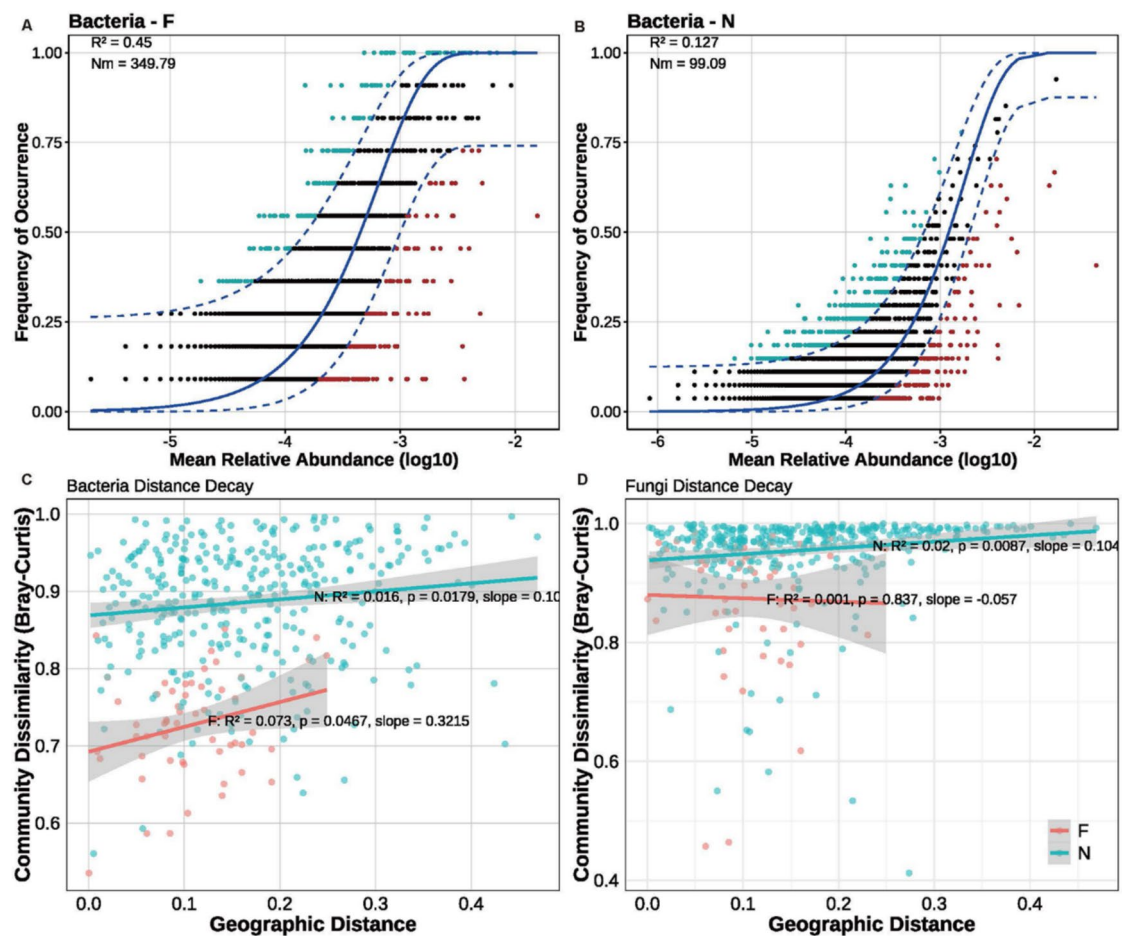


Fig. 5 Fitted neutral model of soil bacterial communities (ASVs) in farmland (A) and natural grassland (B), and distance-decay relationships between community dissimilarity and geographic distance for bacterial (C) and fungal (D) communities (N, natural grassland; F, farmland)

In contrast, the natural grassland network featured only 14 connector ASVs and eight module hubs, all bacterial. Keystone taxa in grassland soils were mainly from *Actinobacteriota* and *Proteobacteria*, each accounting for 22.73% (Fig. S7D). Network stability analysis further supported the structural differences between land types. The farmland network exhibited a significantly steeper decline in natural connectivity (slope = -0.45) compared to the grassland network (slope = -0.17), indicating a higher vulnerability to species loss. In contrast, the gentler slope in the grassland network suggests greater structural robustness and a stronger ability to maintain connectivity under environmental disturbance (Fig. S8).

Discussion

In this study, we found the strong influence of land use types on soil microbial communities in arid and semi-arid regions along the lower reaches of the Heihe River, the second largest inland river of China. Our results indicate significant

variations in microbial diversity, community composition, assembly processes, life history strategies, and network structures in soils across different land use types. Besides, bacterial and fungal communities exhibit distinct patterns in response to agricultural practices. Human-developed land, including farmland and artificial grassland, increased the diversity of bacterial communities. However, the bacterial community in farmlands showed a more sensitive and unstable co-occurrence network compared to natural grasslands.

Natural grassland was the dominant land use type in the study region and harbored the highest number of unique bacterial and fungal ASVs among all land types, suggesting its potential role as a critical reservoir of microbial diversity in arid ecosystems. Notably, farmland areas have been steadily expanding in the region and are characterized by elevated levels of organic matter and nutrients, such as available phosphorus (69.07 mg/kg), which may further influence microbial composition and ecosystem functioning. In this study, the soil bacterial communities of farmland have been found to exhibit lower β -diversity compared to natural grassland (Fig. 4A). For

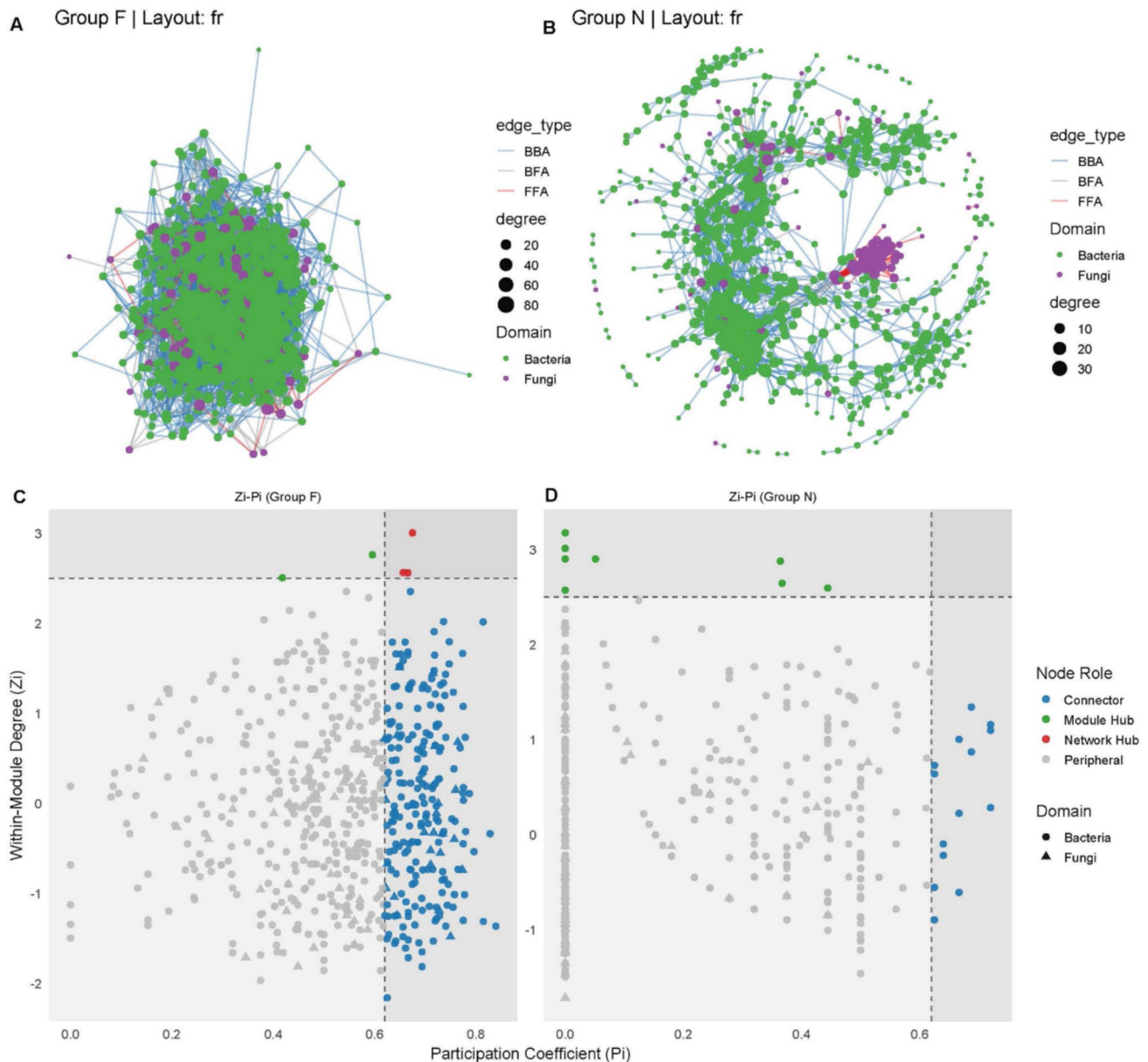


Fig. 6 Co-occurrence networks (**A, B**) and Zi-Pi plots (**C, D**) of soil microbial communities in farmland (**A, C**) and natural grassland (**B, D**) (F, farmland; N, natural grassland; BBA, bacteria-bacteria association; FFA, fungi-fungi association; BFA, bacteria-fungi association)

α -diversity of bacterial communities, farmland and artificial grassland soils had higher Chao1 and Shannon indices compared to other land types (riverbed, uncultivated land, and natural grassland) without human disturbance (Fig. 2A). A similar trend was also found between cropland soil and grassland soil in arid northwest China [30]. There was no obvious difference among all land types on Chao1 richness of fungal communities, but vegetation-free riverbed and uncultivated land had higher Shannon diversity of fungal communities compared to farmland and artificial grassland soils (Fig. 2). A similar trend was also observed for the uncultivated land and farmland/artificial land in desertified areas [31] and typical steppes [32].

At the phylum level, *Actinobacteria*, *Proteobacteria*, *Firmicutes*, and *Chloroflexi* dominated the bacterial communities across all land use types, consistent with findings from the semi-arid Chaco region, Argentina [33], and the desert-oasis ecotone in Xinjiang, China [34]. However, significant variations in the relative abundance of these phyla were observed among five land use types (Fig. 3). *Acidobacteriota* and *Chloroflexi* were less abundant in natural grassland soils compared to farmland soils, reflecting the influence of agricultural practices on shaping soil bacterial community composition. In semi-arid, arid, and hyper-arid regions of northwestern China, *Firmicutes* demonstrated a

greater ability to survive in resource-limited hyper-arid environments, while *Acidobacteriota* and *Chloroflexi* exhibited an opposite trend, thriving less under these conditions [35]. Fungal communities were dominated by *Ascomycota*, followed by *Basidiomycota*, across all land use types, which were similar to the results observed from soils in the Loess Plateau [36] and northwestern China [35]. *Ascomycota* were more abundant in artificial grasslands, natural grasslands, and farmlands (Fig. S3).

Life history strategies of microorganisms influence their metabolic potential and adaptability to environmental stress, particularly in semi-arid and arid ecosystems [3]. *Proteobacteria*, *Bacteroidota*, and *Firmicutes* are commonly considered typical r-strategists, whereas *Actinobacteriota*, *Acidobacteriota*, and *Chloroflexi* are generally classified as K-strategists. For fungal communities, *Basidiomycota* are identified as K-strategists, while *Ascomycota* and *Mortierellomycota* are classified as r-strategists. The ratios of K:r used in this research are in line with previous studies [27, 37, 38], providing a useful proxy to assess microbial ecological strategies under different land use conditions. It has been found that microbial communities in semi-arid soil ecosystems tend to favor K-strategists, as these organisms adapt to arid conditions by developing diverse functions [39].

Our results revealed distinct patterns for bacterial and fungal communities. For bacteria, $B_{K:r}$ ratios were significantly higher in farmland and artificial grassland than in natural grassland and uncultivated land ($P < 0.05$), suggesting a relative dominance of K-strategists in human-managed soils (Fig. 4C). This pattern may reflect selective pressures such as frequent physical disturbances (e.g., tillage), episodic nutrient fluctuations, and localized resource limitations typical in agricultural environments, which can favor stress-tolerant and metabolically efficient taxa [40, 41]. In contrast, fungal $F_{K:r}$ ratios were highest in uncultivated soils, significantly greater than that in farmland and artificial grassland ($P < 0.05$), indicating that r-strategist fungi, such as *Ascomycota*, were less prevalent in less-disturbed environments (Fig. 4D and Fig. S3). However, it is important to acknowledge the limitations of this classification method. The assignment of microbial taxa into r- or K-strategists based solely on broad taxonomic ranks (e.g., phylum or class) may oversimplify the true ecological strategies of microbial communities. Within a single phylum, such as *Proteobacteria*, there can be substantial functional and ecological diversity, with members exhibiting a wide range of life-history traits [42]. Therefore, while the K:r ratio provides a useful heuristic, it should be interpreted with caution and ideally supplemented with functional gene or trait-based analyses in future studies. In particular, integrating measurements of ecosystem functions, such as carbon mineralization, nutrient cycling, and denitrification, will be essential to clarify the ecological implications of microbial life-history strategies.

The bacterial and fungal communities of natural grassland soils exhibited different assembly patterns from farmland. Our results suggested that the assembly mechanism of bacteria in farmland soils was governed by a combination of stochastic and deterministic processes, whereas deterministic processes dominated in natural grasslands (Fig. 5). Stochastic and deterministic processes were also found to contribute most equally to the community assembly of bacteria in farmland soils from arid and semi-arid areas [13]. Deterministic processes were found to dominate the community assembly process of the soil microbes in three main Chinese grassland regions [43] and temperate grasslands [44]. Fungal communities were also found to be dominated by deterministic processes in soils from both farmland and natural grassland in arid regions. Nutrients were the main factors driving the fungal community structure in farmland and natural grassland soils (Fig. S4). In the local floodplain ecosystem, the assembly of both bacterial and fungal communities of farmland soils was also mainly dominated by deterministic processes at a local scale, which supports our results [45].

The construction of co-occurrence networks revealed pronounced differences in microbial interaction patterns between farmland and natural grassland soils. Natural grassland networks were characterized by looser connectivity and a predominance of positive correlations, especially within bacterial communities (Fig. 6B and Fig. S7B), indicating more cooperative interactions and greater structural stability [46]. In contrast, farmland networks showed higher complexity (more nodes and edges), a greater proportion of negative correlations (36.6%), and stronger bacterial-bacterial competition (Fig. 6A and Fig. S7B), reflecting increased ecological stress under intensive management [47, 48]. Similar results were also found in the soil from temperate grassland; agricultural disturbance generally increases the complexity of species interactions [49]. Although both networks were dominated by bacterial taxa (> 88% of nodes), interactions between bacteria and fungi were relatively limited—particularly in natural grassland, where only 5.8% of edges linked the two kingdoms. Farmland exhibited more inter-kingdom interactions, but these included both positive and negative correlations, suggesting less stable cross-kingdom relationships under disturbance [45]. Zi-Pi analysis further showed that the farmland network depended on a greater number of keystone taxa (233 ASVs, including fungal ones), whereas the natural grassland network had fewer keystone species, all bacterial (Fig. 6C and D).

Network stability analysis based on node removal further verified that natural grassland networks are more robust (Fig. S8), maintaining functionality despite species loss, while farmland networks are more sensitive, likely due to intensive management in a semi-arid farmland [50]. These results suggest that agricultural practices not only reshape microbial diversity and composition but also lead to more competitively structured networks.

Conclusions

In this study, we found significant influence of land use types on soil microbial communities in the arid desert area of the lower reaches of Heihe River Basin. Different land use practices affect microbial diversity, community composition, and assembly processes. Natural grasslands emerge as key reservoirs of microbial diversity, promoting resilience and stability through predominantly positive interactions. In contrast, farmlands show not only increased microbial diversity but also higher sensitivity to environmental disturbances, with more competitive interactions. The deterministic processes that dominated natural grassland soils contribute to their stability, while farmlands exhibited a combination of stochastic and deterministic assembly processes. These findings highlight the importance of careful land use management in arid ecosystems to preserve microbial diversity and maintain ecosystem functionality, thereby contributing to conservation efforts and sustainable practices in these fragile regions. While this study provides a comprehensive overview of bacterial and fungal communities across different land use types, it does not account for seasonal variations. Given that seasonal fluctuations in soil chemistry and microbial activity play a crucial role in shaping microbial community dynamics, future research should explore these temporal changes to gain a more complete understanding of microbial responses in semi-arid environments.

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Data Availability All the sequencing data in this study were upload in the NCBI SRA Database (Accession number: PRJNA1233915).

Declarations

Competing interests The authors declare no competing interests.

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