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# Soil saprophytic fungi could be used as an important ecological indicator for land management in desert steppe

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ABSTRACT

Soil microbes are among the most complex and diverse communities on Earth, actively participating in biogeochemical cycles while responding positively to environmental changes. Saprophytic fungi are important factors in soil carbon cycle, and the response and driving factors in grassland to forestland and grassland to farmland conversion in desert steppe are still poorly understood. Therefore, we analyzed the soil microbial community structure and saprophytic fungal communities in grasslands, shrub lands, and farmlands in typical desert grassland areas of northwest China. It was found that the cultivation of desert steppe plants/crops increased the proportion of silt in soil aggregates while decreasing soil salinity and increasing soil total carbon, nitrogen, and organic matter content. Proteobacteria, Actinobacteriota and Ascomycota were the dominant phyla in desert steppe soils, with Proteobacteria, Gemmatimonadota and Mucoromycota were more responsive to soil environment changes. The co-occurrence network relationship further characterized the process of niche sharing/competition between bacteria and fungi. The complexity of the co-occurrence network was deepened by land use, and fungi occupied more of the niche in shrub planting than in desert steppe and maize planting. Network relationships further characterized the process of niche sharing/competition between bacteria and fungi, and land use deepened the complexity of the co-occurrence network, with soil fungi occupying more ecological niches in shrub cultivation than in grassland and maize cultivation. In addition, saprophytic fungi are the main functional fungi in bacterial-fungal co-occurrence networks and are influenced by soil properties. Random forest analysis further explained the importance of saprophytic fungi in response to environmental changes in desert steppes. The enrichment of soil saprophytic fungi had an obvious correlation with soil aggregate stability, soil physical properties, and soil nutrients, especially in the background of shrub forestation in desert steppes. This study further highlights afforestation as one of the ways to benefit land management in desert steppes, while emphasizing the importance of saprophytic fungi as ecosystem indicators.

## 1. Introduction

The desert steppe ecosystem is located in arid and semiarid areas of northern China, with harsh natural conditions (annual average precipitation<200 mm), a simple vegetation community structure, and a fragile ecological environment that is extremely sensitive to climate change and human activities (Wang et al., 2017a; Liu et al., 2019). Competition for land for grain and grass is becoming increasingly serious in the region, and economic development requires the expansion of arable land to meet food demands (Miao et al., 2009). The conversion of grassland to arable land has led to shortages of water and soil nutrients. Groundwater is often used as a supplement. This, together with the application of large amounts of fertilizers, has broken the regional pattern of water use and material balance, exacerbating soil mineralization in the area (Zeng et al., 2017).

Moreover, the conversion of grassland to farmland has negative effects on soil health, including changes in soil physical properties, loss of soil nutrients, and decline in soil microbial diversity (Qiu et al., 2012;

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Alem and Pavlis, 2014). Soil microorganisms are essential for plant growth and survival because of the availability of soil water and nutrient resources, which increases plant access to resources in desert steppe ecosystems (Pointing and Belnap, 2012; Naylor and Coleman-Derr, 2018). Simultaneously, soil microorganisms change soil properties by interacting with plants (van der Putten et al., 2013). In particular, human disturbance changed the direction and intensity of plant secretions and litter input to the soil, with negative effects on plant-soil feedbacks (Wen et al., 2020).

Not all grassland conversions have negative effects on desert grassland ecosystems, such as afforestation. Afforestation greatly improves soil conditions and promotes land development, especially in degraded ecosystems with extremely poor environments (Zheng, 2006; Zhao et al., 2015). In the process of desert grassland afforestation, the aboveground and belowground components of the ecosystem are closely linked, and their interactions greatly influence the structure and function of the ecosystem (Zhang et al., 2016). Afforestation can increase soil organic carbon stocks by reducing the rate of soil carbon decomposition and increasing the availability of soil nitrogen by reducing the concentration of inorganic nitrogen and the rate of net nitrogen mineralization (Cheng et al., 2013; Deng et al., 2016). Moreover, afforestation has enhanced the relationship between soil microbes and improved the soil microbial diversity (Arévalo-Gardini et al., 2020; Strukelj et al., 2021). For example, differences in plant litter can affect soil physicochemical properties, especially the accumulation of soil organic matter (SOM) (Li et al., 2022). Moreover, the effect on the soil microbial community was more pronounced (Barberán et al., 2015; Georgiou et al., 2017).

It is well known that soil fungi play a key role in the decomposition of plant litter, especially saprophytic fungi are involved in the decomposition pathways of complex macromolecules such as lignin (Berg and McClaugherty, 2014; Schmidt et al., 2019). Therefore, changes in soil chemical properties and physical structures caused by plant type differences (land use differences) drive the composition of the saprophytic fungi community. The differences in SOM make it possible for soil saprophytic fungal communities to have more ecological niches to utilize the more abundant SOM and redistribute it to plants in the

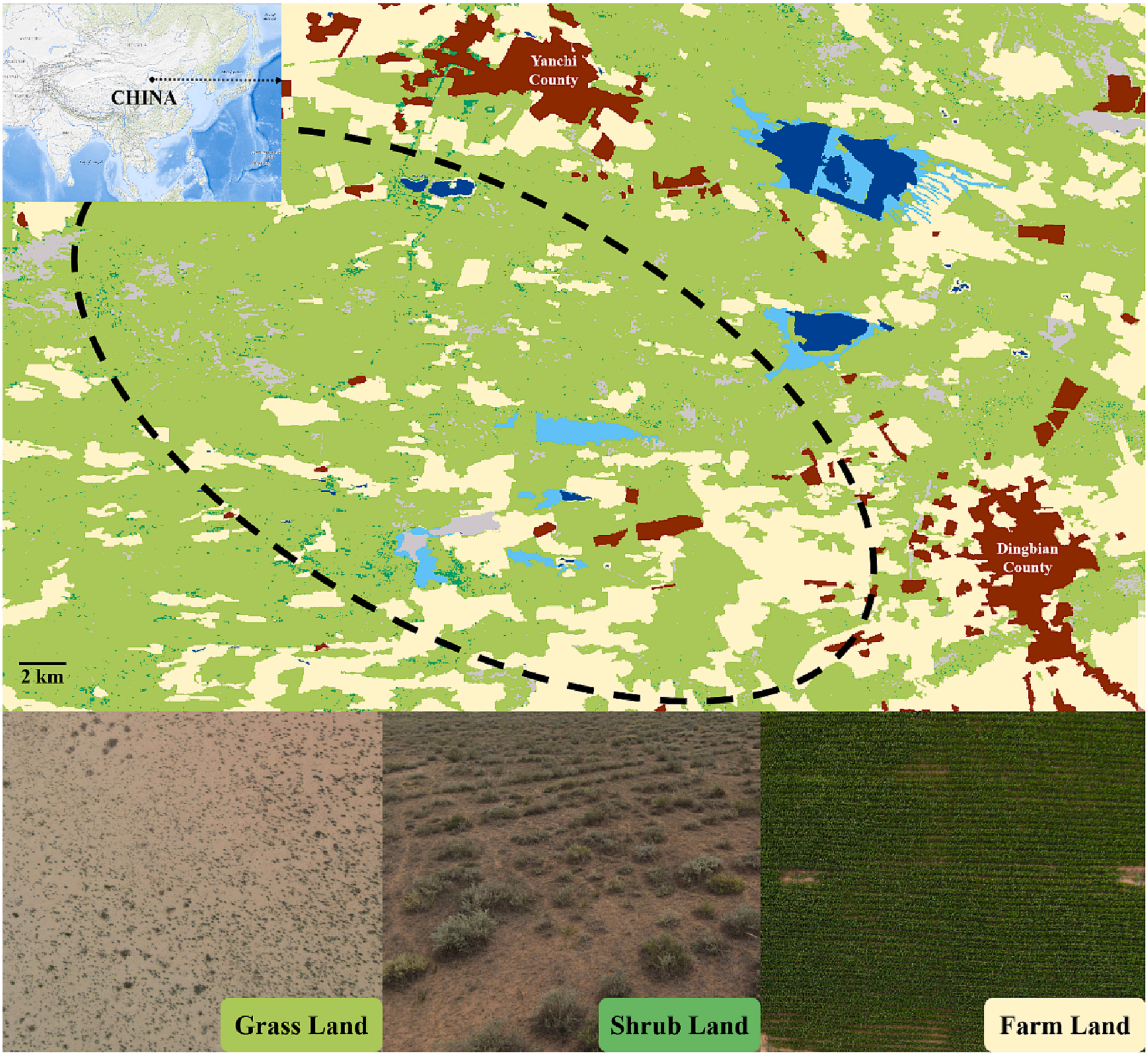

**Fig. 1.** Sampling sites in different land management in Yanchi County, Northwest China.

mycelium (Frey et al., 2000; Fontaine et al., 2011). However, little is known about whether soil saprophytic fungal community structure change in desert steppe was driven by soil characteristics. Therefore, the differences in soil nutrient inputs from different land management types in the desert steppe provide an opportunity for our study. Our study focused on desert steppe in the central arid zone of China and investigated the soil saprophytic fungal community structure change and the driving factors under different land management practices in desert grasslands, artificial shrublands, and farmland. We proposed the following hypotheses: (1) different land management in desert grasslands drive functional fungal taxa to niche occupation (2) soil saprophytic fungal communities may be indicative of land management in desert grasslands.

## 2. Materials and methods

### *2.1. Study area*

This study area is located near Yanchi County, Ningxia, and Dingbian County, Shannxi (E107°22′, N37°39′), which is an agroforestry-desert transition zone with an area of approximately 10 $km^2$ and an annual precipitation of<200 mm, which is a typical desert grassland ecosystem. To improve the ecological barrier function of the area, the local government planted large areas of shrubs to prevent desertification (Zhu et al., 2014). In the study area, grassland (*Sophora alopecuroides* sample plot, GL), shrub land (*Caragana korshinskii* sample plot, SL), and farmland (*Zea mays* sample plot, FL) were used. *C. korshinskii* have been planted for more than 8 years, and *Z. mays* has been planted for more than 5 years (Fig. 1).

### *2.2. Soil sample collection*

The sampling period was August 2021, and the study area was divided into three sample areas (GL, SL, and FL). Twelve sample squares (5 × 5) were set in each sampling area, and five soil samples were randomly taken from each square and mixed into one soil sample as a representative of one sample square (Pan et al., 2021). A total of thirty-six soil samples were collected from the three sample plots of GL, SL and FL. At the same time, soil under the plant canopy was avoided plant roots and excess litter was removed. The obtained samples were placed in sterile centrifuge tubes and cryogenic refrigerators were used as containers. After all the samples were brought back to the laboratory, they were ground under sterile conditions at a low temperature and divided into two parts after screening. One part was used for the extraction of soil DNA and the other was used to measure soil physicochemical properties.

### *2.3. Soil properties analysis*

Soil agglomerates were transferred to aggregate analyzer (DIK-2012) after soaking the soil using deionized water referring to the method of Wu et al. (2021), and the analyzed soil samples were divided into clay (<0.002 mm), silt (0.002–0.05 mm) and sand (0.05–2.0 mm) (Qi et al., 2018). Then, the soil samples were naturally dried, and the soil pH (with a water–soil ratio of 1:5) and electrical conductivity (EC) were measured using the method described by Bao (2000). And soil total carbon (TC), total nitrogen (TN), and total phosphorus (TP) contents were analyzed by atomic absorption spectrometry (Bettinelli et al., 2000). Soil total organic carbon (TOC)was determined by the method described by Bao (2000).

### *2.4. Soil microorganism analysis*

We extracted DNA from thirty-six soil samples by CTAB (Cetyltrimethyl ammonium bromide) method and amplified the V3-4 gene region of soil bacteria after qualified gel electrophoresis detection with primers 341F (5′ -CCTA YGGG RBGC ASCA G-3′) and 806R (5′ -GGAC TACN NGGG TATC TAAT-3′). We also amplified the ITS1-2 gene region of soil fungi using the primers ITS1 (5′ -CTTG GTCA TTTA GAGG AAGT AA-3′) and ITS2 (5′ -GCTG CGTT CTTC ATCG ATGC-3′) (Claesson et al. 2009; Cheng et al. 2022). After primer amplification and sequencing using the Illumina NovaSeq PE250 platform, an average of 71,031 bacterial tags and 70,815 fungal tags were obtained for each soil sample, and an average of 70,129 bacterial and 69,120 fungal valid data were obtained for each soil sample after quality control. Bacterial and fungal operational taxonomic units (OTUs) of 36 soil samples were clustered based on 97% identity, and 12,010 bacterial OTUs and 4,099 fungal OTUs were obtained (Edgar et al. 2011). We further annotated the OTUs using species annotation databases selected from Silva138 (bacteria) and UNITE (fungi) (Kõljalg et al. 2005; Yilmaz et al. 2014). The raw data of bacteria and fungi from thirty-six soil samples were deposited in the NCBI sequence read archive database (PRJNA866674 and PRJNA866692).

### *2.5. Data analysis*

After obtaining the sequencing data, we used QIIME (V1.9.1) to calculate the alpha diversity indices of the bacterial and fungal communities of the thirty-six soil samples, including the number of operational taxonomic units (OTUs), diversity index (Shannon), and richness index (ACE) (Caporaso et al. 2012). Spearman correlation analysis was performed for the soil physicochemical properties and alpha diversity of bacteria and fungi (Pan et al. 2022). We then calculated the beta diversity using the Bray-Curtis distance matrix (Legendre and Anderson, 1999), and the effects of the Bray-Curtis dissimilarity index and environmental factors on community composition (Kang et al., 2022).

The relative abundance of the bacterial and fungal phyla for each of GL, SL and FL plots were averaged and presented. Co-occurrence network is a convenient tool for evaluating microbial interactions. We calculated all Spearman correlation coefficients ($R>|0.9|$ and $p < 0.01$) of OTUs between bacteria and fungi in three sample plots (GL, SL, and FL), which were displayed using the Cytoscape software (3.7.1) (Pan et al., 2022). Metrics such as the number of nodes, edges, modules, and the average path length in the network were also obtained from this analysis (Kang et al., 2022).

Saprophytic fungi are divided into seven major groups, saprotroph, symbiotroph, pathotroph, saprotroph-symbiotroph, pathotroph-symbiotroph, pathotroph-saprotroph and pathogen-saprotroph-symbiotroph (Nguyen et al., 2016). The RDA ranking of the saprophytic fungi were analyzed. We further analyzed the contribution of environmental factors to saprophytic fungi based on correlation and random forest models, constructed a phylogenetic tree of saprotrophic fungi, and selected soil physicochemical indicators for Spearman correlation tests with the relative abundance of saprotrophic fungi (Schliep, 2011; Jiao et al., 2022). The above analysis was implemented in the R software, and all indicators in this study were described by one-way analysis with Duncan's multiple range test for significant differences between groups ($p < 0.05$).

## 3. Results

### *3.1. Soil microbial diversity and the influencing factors in desert steppe*

The clay particles in soil aggregates were higher in FL than SL and GL plot under different land management conditions, obviously ($p < 0.05$). And silt particles were higher in SL and FL plots than in GL plots ($p < 0.05$). Similarly, soil TS content was reduced in SL and FL plots compared to GL plots, but pH had no significant effect. In addition, soil TC, TN, and SOM contents were significantly higher in SL and FL plots than GL plot ($p < 0.05$) (Table 1).

Land management changed the number of OTUs, soil bacterial diversity and richness; while the alpha diversity index of soil bacteria in FL

**Table 1**
Physicochemical characterization in different land management.

| | GL | SL | FL |
|---|---|---|---|
| Clay | 1.94 ± 0.19b | 2.65 ± 0.1b | 3.62 ± 0.36a |
| Silt | 15.41 ± 1.96b | 23.52 ± 2.41a | 24.78 ± 1.53a |
| Sand | 82.65 ± 2.13a | 73.83 ± 2.56b | 71.60 ± 1.77b |
| pH | 9.01 ± 0.06a | 8.86 ± 0.08a | 8.81 ± 0.07a |
| SWC | 11.76 ± 1.27b | 14.48 ± 1.37b | 23.36 ± 1.15a |
| TS | 0.40 ± 0.06a | 0.29 ± 0.03ab | 0.25 ± 0.007b |
| TC | 7.37 ± 0.51b | 10.44 ± 0.76a | 11.87 ± 0.70a |
| SOM | 6.14 ± 0.76b | 8.88 ± 1.27a | 8.35 ± 0.54a |
| TN | 0.26 ± 0.03b | 0.38 ± 0.05a | 0.41 ± 0.02a |
| TP | 0.19 ± 0.01b | 0.22 ± 0.01b | 0.34 ± 0.03a |

plot were all higher than GL plot ($p < 0.05$). The OTUs of soil fungi in SL plots were higher than those in GL and FL plots, but the changes in soil fungal diversity and richness were not obvious in response to different land management practices. The number of OTUs of soil fungi in the SL plot was higher than that in GL and FL plots, but the changes in soil fungal diversity and richness were not significant ($p < 0.05$) (Fig. 2A). Compared with the other two plots, soil bacterial and fungal community aggregation increased in the FL plot, while soil fungal community aggregation was also higher in the SL sample plot (Fig. 2B). Soil physicochemical properties had a significant effect on soil bacterial community diversity and NMDS1 in the three sample plots, where sand, pH, and TS showed negative correlations ($p < 0.05$) (Fig. 2C).

We further analyzed the relationship between soil microbial Bray-Curits dissimilarity and soil factors, and found that soil bacterial and fungal community assembly were affected by soil factors. Whereas silt, sand, TS, TC and SOM were significantly correlated with Bray-Curits dissimilarity ($p < 0.05$) (Fig. S1).

### 3.2. Soil microbial community composition and network relationships in desert steppe

Among the bacterial communities, Proteobacteria, Actinobacteriota, Acidobacteriota, Chloroflexi, and Firmicutes were the dominant phyla in all three plots. Compared with the GL plot (36.1%), the relative abundance of Proteobacteria decreased in SL (27.4%) and FL (15.9%) plots, while Actinobacteriota decreased in SL plot (15.4%), but increased in the FL plot (25.7%). And the relative abundance of Ascomycota and Basidiomycota in SL (45.8% and 5.1%) and FL (61.9% and 9.6%) plots increased, while the relative abundance of Mortierellomycota was high in the SL plot (12.5%) (Fig. 3A). Random forest analysis further showed that Proteobacteria, Gemmatimonadota and Mucoromycota all explained the effects of soil factors on microbial communities to varying degrees (Fig. S2).

By constructing the co-occurrence network, we found that the relative abundance of bacteria in the SL plot was lower than that in the GL and FL plots, whereas the relative abundance of fungi in the GL plot was the lowest, followed by that in the SL plot and the highest in the FL plot (Fig. 3B). Soil bacterial-fungal co-occurrence network relationships were more complex in GL and FL plots than in FL plot. The numbers of nodes, edges, and modules were 306, 388, and 414 in the GL plot; 456, 653, and 394 in the SL plot; and 564, 554, and 848 in the FL plot, respectively (Table 2). It is noteworthy that the interactions between fungi and bacteria, as well as the interactions between fungi, were more prominent in the SL plot (Fig. 3C).

### 3.3. Soil functional fungi distribution and influencing factors in desert steppe

In the bacterial-fungal co-occurrence network analysis, we found that the number of fungal nodes in the network was higher than in SL plot than in GL and FL plots (Fig. 4A). Combined with the fungal functional analysis, the soil saprophytic fungi had a higher frequency of

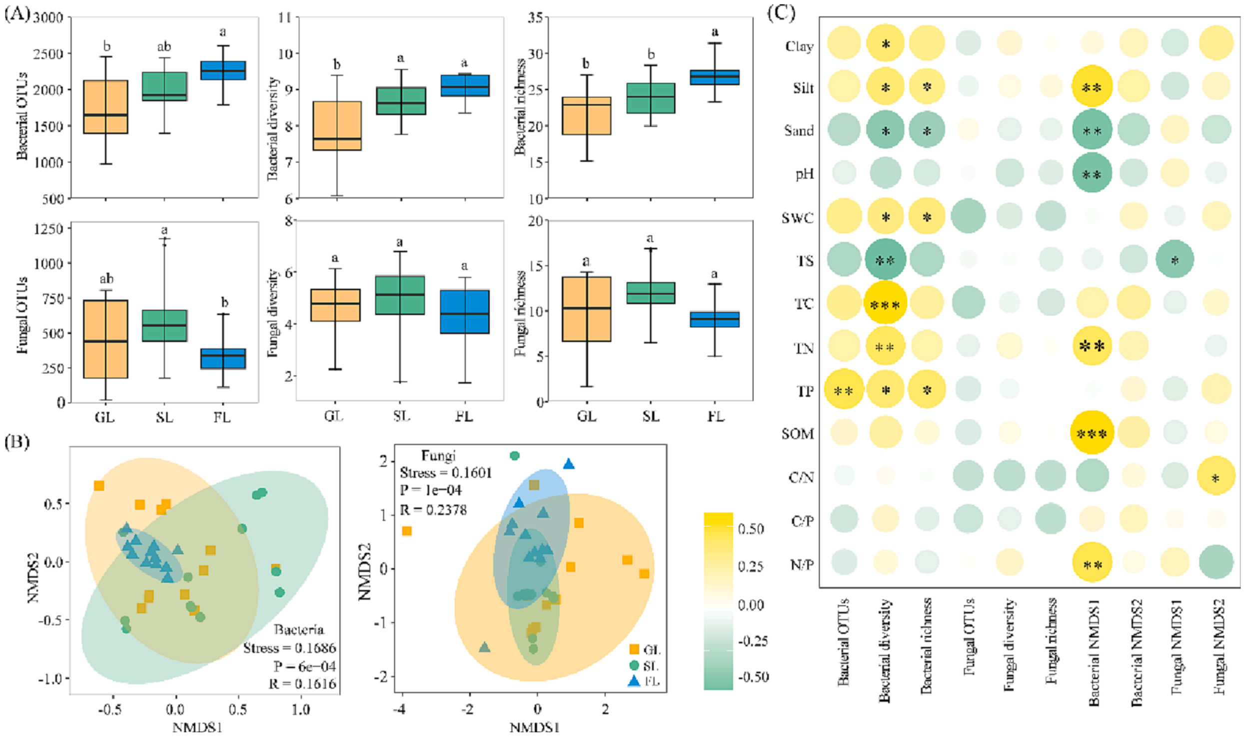

**Fig. 2.** Alpha diversity index (A) and non-metric multidimensional scale ordering (B) of bacteria and fungi, and the correlation between soil physicochemical properties and alpha diversity indices (C) in different land management. Bacterial diversity: Shannon index of bacteria; Bacterial richness: ACE index of bacteria; Fungal diversity: Shannon index of fungi; Fungal diversity: Shannon index of fungi. GL: grass land sample plot; SL: shrub land sample plot; FL: farm land sample plot. (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

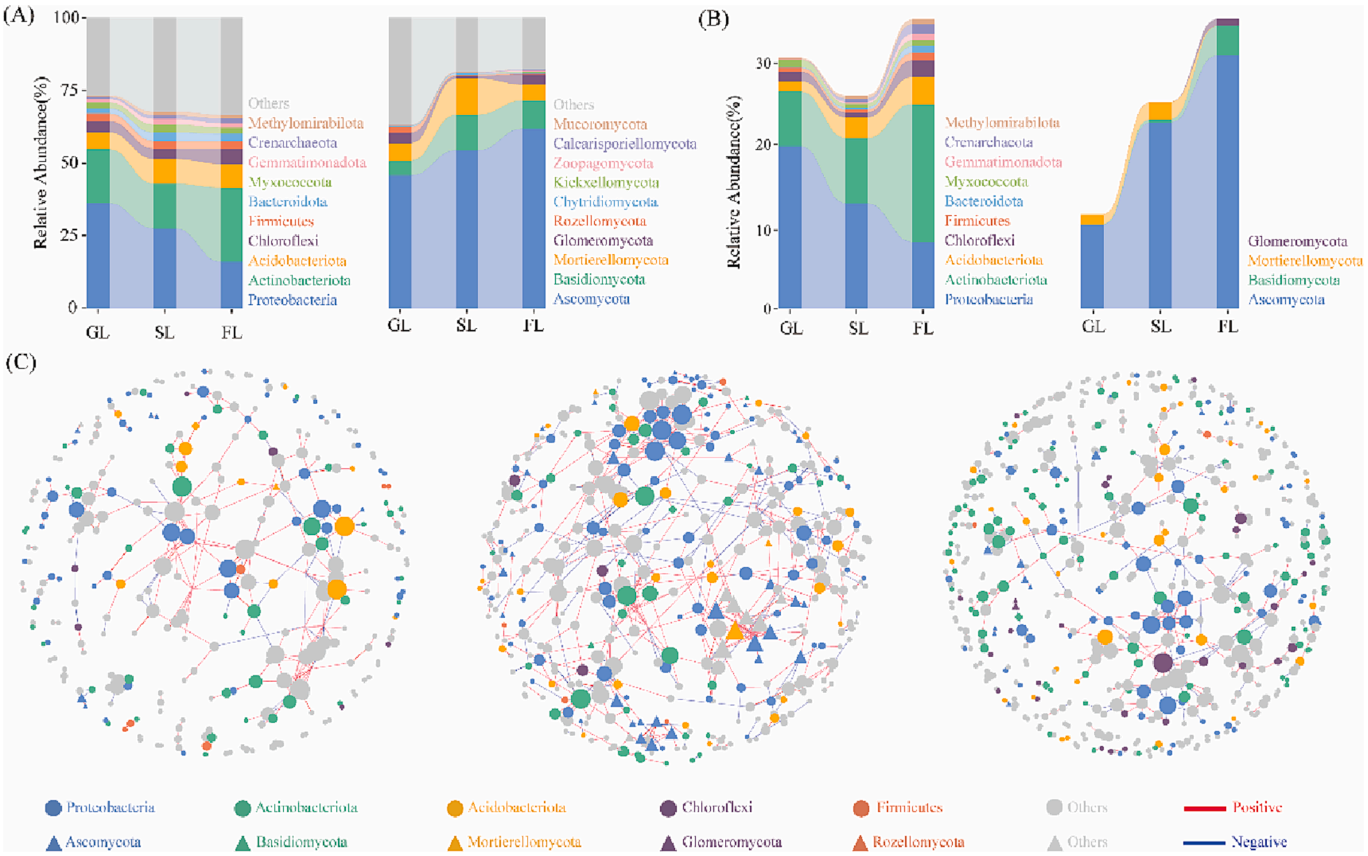

**Fig. 3.** The alluvial of the top 10 phyla of bacteria and fungi (A), and the phyla of bacteria and fungi in co-occurrence networks (B), and the co-occurrence network of soil bacterial and fungal (C) in different land management. The color and shape of the nodes indicate different bacteria and fungi.

**Table 2**
Network topological features in different land management.

| | GL | SL | FL |
|---|---|---|---|
| Total Nodes | 306 | 456 | 564 |
| Total edges | 388 | 653 | 554 |
| Positive edges | 310 | 472 | 365 |
| Negative edges | 78 | 181 | 189 |
| Number of modules | 414 | 394 | 848 |
| Modularity | 0.8169 | 0.8795 | 0.9343 |
| Average path length | 6.2057 | 9.8452 | 7.6610 |
| Graph diameter | 18.4261 | 25.6939 | 18.3796 |
| Graph density | 0.0018 | 0.0021 | 0.0007 |
| Clustering coefficient | 0.3605 | 0.3769 | 0.2948 |
| Betweenness centralization | 0.0180 | 0.0429 | 0.0077 |
| Degree centralization | 0.0151 | 0.0145 | 0.0064 |

occurrence in the three networks (Fig. 4B). The distribution of functional fungal groups also differed among the three plots, with predominant pathotroph-saprotroph and saprotroph (Fig. 4C). Further analysis of the interrelationships between saprophytic fungi and environmental factors by RDA revealed that soil clay, silt, TC, TN, and SOM were strongly correlated, while pathotroph and saprotroph had more obvious pointers to the above soil factors, and the pointers of saprotroph were more prominent ($p < 0.05$) (Fig. 4D).

### *3.4. Soil functional fungi distribution and influencing factors in desert steppe*

Based on random forest analysis, we further found that there were different explained variations of soil saprophytic fungi for environmental factors, with the highest rate of 32.72% for saprotroph (Fig. 5A). Among the most important environmental factors for saprotroph were sand, pH, TS (negative effect), silt, TN, and N/P (positive effect). According to the evolutionary relationship of the saprotroph taxa (top 200 OTU), most members belonged to Ascomycota, followed by Mortierellomycota and Basidiomycota. Among the environmental factors, sand and pH were negatively correlated, while TC, TN, and SOM were positively correlated (Fig. 5B).

### *3.5. Soil saprophytic fungi in desert steppe respond differently to land management*

No significant correlation between soil saprophytic fungi and soil physicochemical characteristics in GL and FL plots; whereas pH and TS were negatively correlated with the relative abundance of saprophytic fungi, and TC, TN, and TP showed significant positive correlations in SL plot ($p < 0.05$) (Fig. 6A). Combining the above results, we further indicate that the enrichment of soil saprophytic fungi has a more significant correlation with the stability of soil aggregates, soil physical properties, and increase in soil nutrients. In addition, bacterial-fungal interactions and the enrichment of functional fungal taxa also influence the enrichment of soil saprophytic fungi. These results were particularly evident in the background of afforestation in the desert steppe (Fig. 6B).

## 4. Discussion

### *4.1. Soil microbial community diversity and assembly were driven by soil characteristics in desert steppe*

In recent decades, grassland conversion has become widespread globally, and most of them have been planted in crops (Tang et al., 2022). According to statistics, 4.8% of China's total grassland area

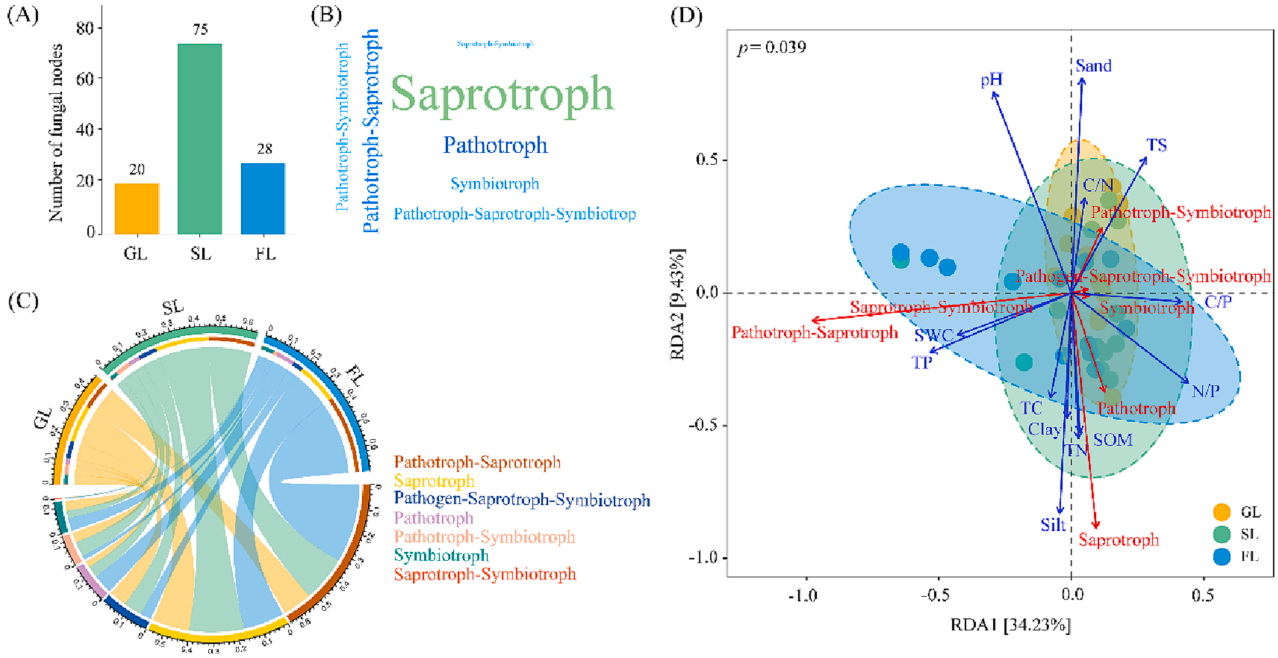

**Fig. 4.** Soil saprophytic fungi in different land management. (A) The number of fungal nodes in the network. (B) Word frequency graph of functional fungi. (C) The relative properties abundance of functional fungi. (D) RDA analysis of functional fungi and soil physicochemical.

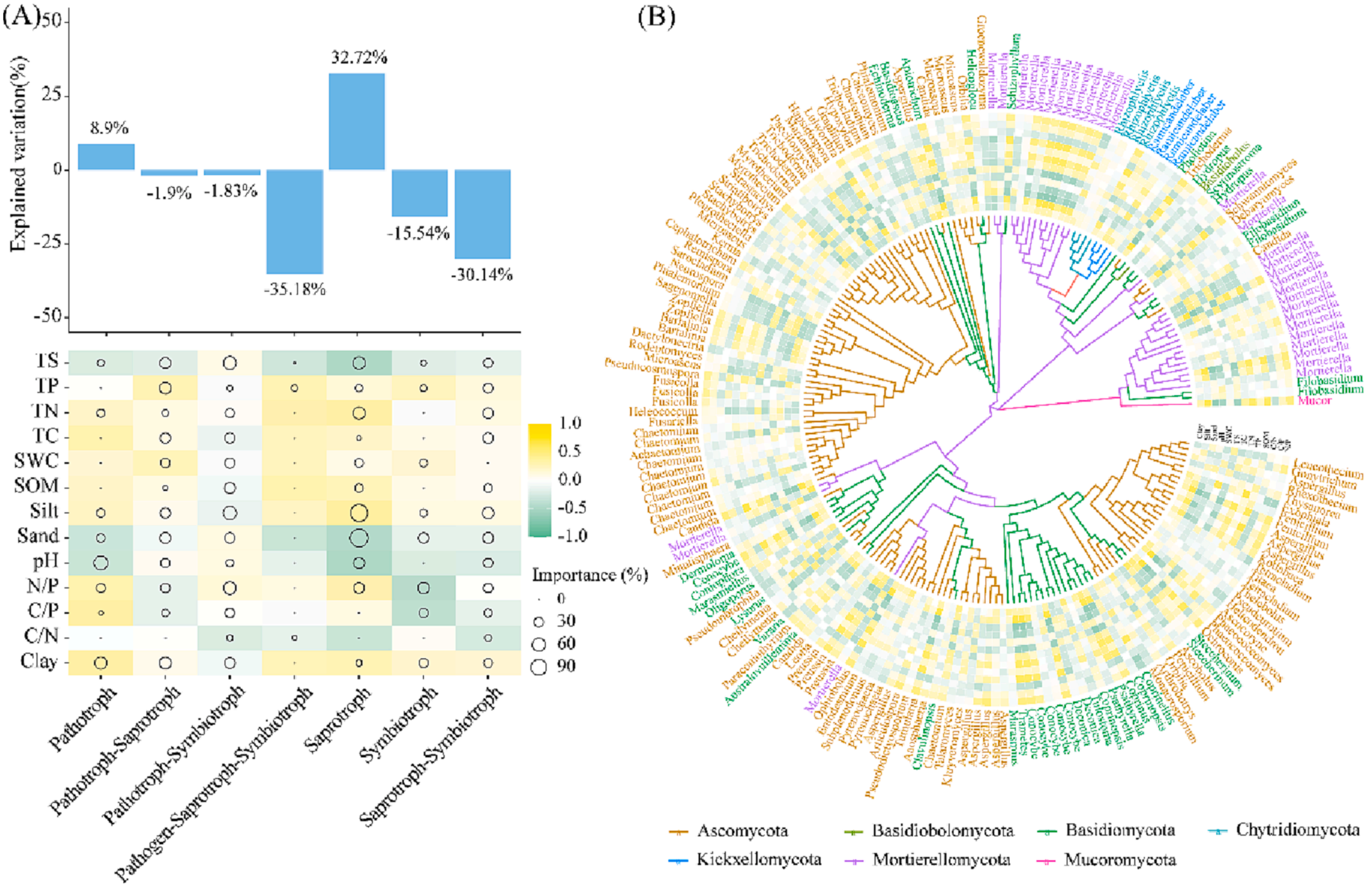

**Fig. 5.** Drivers of soil saprophytic fungi in different land management. (A) Contribution of environmental factors to saprophytic fungi based on correlation and random forest models. (B) Phylogenetic distribution of soil saprophytic fungi.

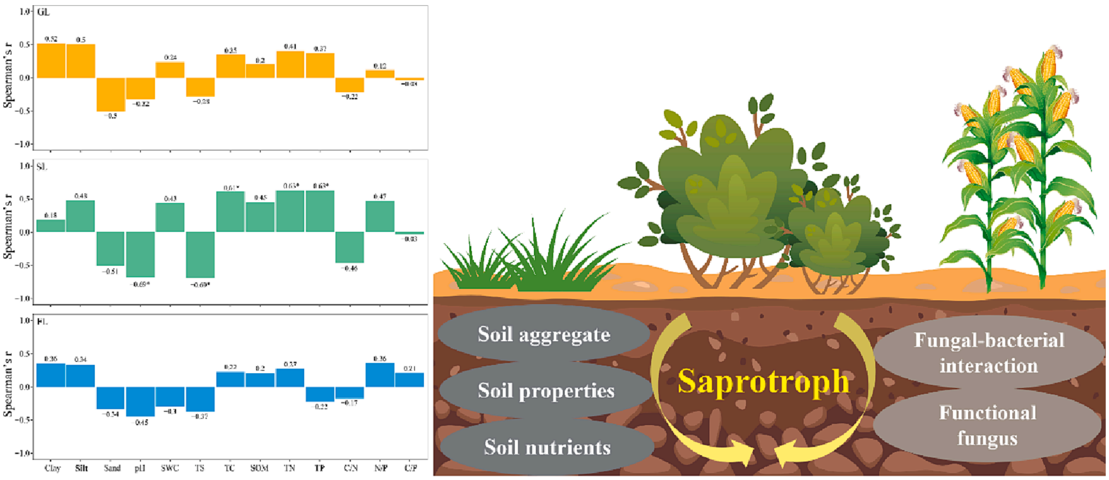

**Fig. 6.** Correlation between soil saprotroph fungi and soil physical structure and chemical properties, and ecology indicators of soil saprotroph fungi in different land management. (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

(approximately 1.9 × $10^5$ $km^2$) was converted to arable land, and this phenomenon mainly occurred in the agro-pastoral ecotone in northern China (Fan et al., 2000). This study was conducted in northwestern China, which is a typical desert steppe ecosystem. However, the conversion of grassland to arable land is common in regions where corn has been cultivated for five years. Our study is similar to the results of previous studies in that desert steppe soil aggregates were dominated by large and medium agglomerates (Lu et al., 2022). Previous studies have further confirmed that land use or conversion increases the proportion of soil microaggregates and medium aggregates (Dong et al., 2016). We found that both *C. korshinskii* and *Z. mays* cultivation increased the proportion of clay and silt.

Due to the extremely low soil water content and lack of organic carbon and nutrients, the desert steppe was transformed into farmland through irrigation, cultivation, and fertilization, which greatly changed the composition of the soil and the accumulation of chemical substances (Huang et al., 2020). It has been found that nitrogen application lowered soil pH compared to unmanaged desert areas (Wang et al., 2016; Gao et al., 2022), and this study confirmed these findings that planting maize lowered soil pH (Table 1). In this study, the soil water, TC, and TN contents of the FL sample plots were significantly higher than those of the DS sample plots. This was largely attributed to water and nutrient inputs from irrigation, manure, fertilizer, and crop straw, which improved soil fertility after land reclamation; specifically, significant TC and TN enrichment had especially strong impacts (Rodríguez Martín et al., 2019; Su et al., 2020).

To prevent the degradation of ecosystems and reduce the harm caused by desertification, introduced shrubs have been widely planted to address the increasingly serious problem of land degradation (Yang et al., 2019; Liu et al., 2021). Our studies showed that, *C. korshinskii* was planted (individuals more than 8 years of age) in large quantities as protective forests in the desert steppe-agro pastoral ecotone, which belonged to the "Three Northern Protective Forest Development Program" (Li et al., 2012). Afforestation in desert steppe means that seasonal plants are replaced by long-growing plants; therefore, it changes the composition and characteristics of plants, as well as soil physicochemical properties (Peichl et al., 2012; Guo et al., 2022). Our results suggest that the soil water content of the SL plots was apparently higher than that of the GL plots because afforestation increased the plant coverage of the desert steppe, not only providing habitat for ephemeral plants but also reducing soil water dissipation. Desert shrub afforestation can increase soil TC and SOM content and increase SOM input due to plant stubble and litter (Liu et al., 2020). First, it reduces soil carbon decomposition to increase soil TC storage (Cheng et al., 2013). In addition, the higher TN content in SL plots further highlights the advantages of afforestation. Plants can increase soil nitrogen availability by reducing the soil inorganic nitrogen concentration and net nitrogen mineralization (Deng et al., 2016). Many studies have confirmed the important role of afforestation in ecological restoration, especially in arid and stone desertification areas (Ebrahimi et al., 2019; Chen et al., 2020).

### 4.2. *Afforestation of desert steppe increased the ecological niche occupation by saprophytic fungi*

In this study, the introduction of an additional water supply and fertilization in the FL plots increased the effectiveness of soil moisture and nutrients and maintained microbial diversity, and the OTU number and bacterial diversity were higher than those in the other sample plots (Fig. 2A), indicating that water shortage is an important factor affecting the microbial diversity in the desert steppe (Köberl et al., 2011). We found that changes in the bacterial community composition and ecosystem diversity are sensitive to the environment (Cheng et al., 2018; Wu et al., 2021). In addition, the number of OTUs and fungal diversity did not differ significantly among the three sampling sites (Fig. 2B), which supports a previous conclusion that fungal communities are less sensitive than bacterial communities in arid areas (de Vries et al., 2018). Moreover, the soil bacterial diversity was more sensitive to land management practices than the fungal community in the desert steppe (Fig. 2). It was further confirmed that the construction of protective forests resulted in significant changes in soil physicochemical properties but not necessarily in microbial community diversity (Li et al., 2015; Li et al., 2018).

The soil physicochemical properties altered by the introduction of desert steppe plants or crops further changed the soil microbial community structures. Proteobacteria are the most widely distributed and diverse microorganisms on Earth in terms of morphology, physiology, and metabolism (Spain et al., 2009). In the desert steppe, Proteobacteria was the most dominant phylum, with a high relative abundance in the GL plots (Fig. 3A). In general, the metabolic activity of Proteobacteria in soil plays a key role in carbon metabolism and amino acid synthesis (He et al., 2020). We speculated that the decrease in the relative abundance of Proteobacteria with changes in land use practices may be influenced by soil heterogeneity. It was further shown that water enrichment in agricultural land is beneficial for the accumulation of Bacteroidetes (Fierer et al., 2007). However, the increase in the relative abundance of Actinobacteriota under shrub and maize cultivation was mainly caused by the positive role of soil bacteria in regulating soil organic carbon content and agglomerate stability (Lan et al., 2022). In addition, Basidiomycota and Ascomycota are usually dominant in high salinity or cultivated soils (Rousk et al., 2010). Ascomycota was the dominant fungi in all samples, followed by Basidiomycota (Fig. 3C), indicating that Ascomycota were more competitive than Basidiomycota. Our results further suggest that different land management practices affect the soil microbial community structure in desert steppes. Acidobacteriota, Chloroflexi, Firmicutes, and Ascomycota suggests that specific microbial taxa can be used as predictors of soil multifunctionality in desert steppe (Cheng et al., 2018).

Niche overlap/differentiation or competition among microorganisms plays an important role in the formation of co-occurrence network in soil microbe (Li et al., 2020; Zhang et al., 2021). Changes in land management altered soil bacterial-fungal network relationships. Both shrub and maize cultivation increased the number of nodes in the network, with the difference that shrub cultivation increased the bacterial-fungal community relationships in the network. We speculate that the complex co-occurrence network of soil bacteria and fungi in desert steppe afforestation was more resistant to external environmental interference. This is similar to the results of Yu et al. (2021) and Ding et al. (2022). Moreover, we found that afforestation increased SOC and TN content, along with the enrichment of functional fungi (saprophytic fungi), which might improve the conversion and utilization of soil nutrients. Specifically, differences in the organic matter entering the soil make it possible for soil saprophytic fungal communities to have more ecological niches (Frey et al., 2000; Fontaine et al., 2011). Our results further confirmed that more fungal nodes appeared in the bacterial-fungal network after shrub cultivation. Furthermore, soil bacterial and fungal networks in natural ecosystems are more complex, while this finding may be related to greater niche sharing and microbial interactions due to plant cover (Qiu et al., 2022). This supports our first hypothesis that different land management in desert steppe drive niche occupation by functional fungi. In addition, studies on forest, grassland, farmland, and desert ecosystems have confirmed that stable ecosystems have more complex networks to maintain the stability of soil ecosystem structures and functions (Toju et al., 2018). Therefore, the more complex network relationships of soil bacteria in the SL plots further suggest that desert plants are more likely to select microorganisms with a strong ability to adapt to harsh environments, and that such microorganisms are salt tolerant and resistant to dehydration. Such host selection and microbial boarding selection mechanisms render microbial networks highly stable when subjected to stressful environments (Ushio et al., 2013). It can be seen that microorganisms will avoid anthropogenic disturbance through ecological niche competition to maintain the function of soil ecosystem (Yao et al., 2018).

### 4.3. *Saprophytic fungi can be used as an ecological indicator of land management in desert steppe*

Shrub cultivation in the desert steppe increased the number of soil fungal OTUs and fungal nodes in co-occurrence network, largely increasing the number of saprophytic fungal taxa. This is due to the enrichment of functional soil microbial taxa caused by changes in soil physicochemical properties (Liu et al., 2020). Saprophytic fungi are important agents in soil carbon cycling and are regulated by soil physicochemical properties (Shahzad et al., 2015). We further found that soil aggregates such as silt and sand equally affected the aggregation of saprophytic fungal taxa. Much of this is attributable to the effect of soil aggregate stability on soil moisture and pH, which affects the soil microbial community structures and functions. (Ning et al., 2021). In particular, the accumulation of SOM and TN directly influenced the aggregation of saprophytic fungal taxa. In addition, different soil aggregates affect the nutrient requirements of the soil biomes. In our study, the increase in the proportion of clay and silt in the SL plot had a positive effect on the accumulation of SOM and TN and was one of the reasons for the aggregation of saprophytic fungal taxa in the SL plot (Wang et al., 2017b).

More importantly, the diversity of soil organic matter inputs increased due to vegetation cover differences (shrub planting may increase the occupation of ecological niches of short-lived plants in the plant community), which in turn increased the opportunities and space occupied by the ecological niches of saprophytic fungi (Meier et al. 2008). The development of saprophytic fungal lineages is also correlated with soil physicochemical properties, and the coupling of saprophytic fungal taxa with soil properties is not the only evidence of enhanced plant-fungal interactions (Peay et al., 2013; Zong et al., 2021). This also supports our second hypothesis that soil saprophytic fungal communities may be indicative of land management in desert steppe. In our study, enrichment of saprophytic fungi was more closely related to soil environment changes in the shrub cultivation plots.

The role of saprophytic fungi in grazing and mowing has been highlighted in grassland management (Bai et al., 2022). In sustainable agricultural development, soil saprophytic fungi also respond positively to land management (Moreno et al., 2021). Our study further highlights the changes in soil physicochemical properties as a result of differences in land management, and emphasizes that desert steppe afforestation may be one of the ways to benefit land management, while soil microbial communities respond more positively to environmental heterogeneity, especially saprophytic fungi.

## 5. Conclusion

Facing an increasingly serious land crisis, the proper management and development of limited land resources is a long-term and difficult task for researchers. Soil microbial community structure and function respond positively to environmental changes. In our study, the conversion process of grassland–forestland and grassland-cropland in desert steppe increased the proportion of silt in soil aggregates, while reducing salinity and increasing the content of soil TC, TN, and SOM. Changes in soil physical properties had a more pronounced effect on bacterial diversity and richness, as well as significantly affect the assembly of bacterial and fungal communities. Proteobacteria, Actinobacteriota and Ascomycota were the dominant phyla in desert steppe soils, with Proteobacteria, Gemmatimonadota and Mucoromycota were more responsive to soil environment changes. The co-occurrence network relationship further characterized the process of niche sharing/competition between bacteria and fungi. The complexity of the co-occurrence network was deepened by land use, and fungi occupied more of the niche in shrub planting than in desert steppe and maize planting. Network relationships further characterized the process of niche sharing/competition between bacteria and fungi, and land use deepened the complexity of the co-occurrence network, with soil fungi occupying more ecological niches in shrub cultivation than in grassland and maize cultivation. In addition, saprophytic fungi are the main functional fungi in bacterial-fungal co-occurrence networks and are influenced by soil properties. Random forest analysis further explained the importance of saprophytic fungi in response to environmental changes in desert steppes. The enrichment of soil saprophytic fungi had more obvious correlation characteristics on soil aggregates stability, soil physical properties, and soil nutrients, especially in the background of shrub forestation in desert steppes. This study further highlights the importance of saprophytic fungi as indicators of ecosystems.

## CRediT authorship contribution statement

**Peng Kang:** Conceptualization, Methodology, Data curation, Writing – original draft, Writing – review & editing. **Yaqing Pan:** Conceptualization, Investigation, Methodology, Data curation, Formal analysis. **Yichao Ran:** Investigation, Methodology, Data curation. **Weina Li:** Investigation, Formal analysis. **Mingxin Shao:** Investigation. **Yaqi Zhang:** Investigation, Methodology. **Qiubo Ji:** Investigation. **Xiaodong Ding:** Conceptualization, Funding acquisition, Project administration.

## 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.

## Data availability

No data was used for the research described in the article.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110224.

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