High-throughput sequencing unveils microbial succession patterns in restored Hulun Buir Sandy Land, northern China postprint

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Abstract

In recent years, intensive human activities have intensified desertification, driving the continuous desertification of peripheral meadows. To investigate the effects of restoration on soil microbial communities, we analyzed vegetation-soil relationships in the Hulun Buir Sandy Land, northern China. Using high-throughput sequencing, we examined the structure and diversity of bacterial and fungal communities in the 0–20 cm soil layer after 9–15 years of restoration. Different slope positions were analyzed and spatial heterogeneity was assessed. Results showed progressive improvements in soil properties and vegetation with increasing restoration duration, with the following order: bottom slope > middle slope > crest slope. During restoration in the Hulun Buir Sandy Land, bacterial communities were dominated by Proteobacteria, Actinobacteria, and Acidobacteria, whereas fungal communities were dominated by Ascomycota and Basidiomycota. Eutrophic bacterial abundance increased with restoration duration, whereas oligotrophic bacterial and fungal abundances decreased. Soil bacterial abundance significantly increased with increasing restoration duration, whereas fungal diversity decreased after 11 years of restoration, except at the crest slope. Redundancy analysis showed that pH, soil moisture content, total nitrogen, and vegetation-related factors affected bacterial community structure (45.43% of the total variance explained). Canonical correspondence analysis indicated that pH, total phosphorus, and vegetation-related factors shaped bacterial community structure (31.82% of the total variance explained). Structural equation modeling highlighted greater bacterial responses (R^2=0.49–0.79) to changes in environmental factors than those of fungi (R^2=0.20–0.48). The soil bacterial community was driven mainly by pH, soil moisture content, electrical conductivity, plant coverage, and litter dry weight. The abundance and diversity of the soil fungal community were mainly driven by plant coverage, litter

dry weight, and herbaceous aboveground biomass, while no significant correlation was observed between soil fungal community structure and environmental factors. These findings highlight divergent microbial succession patterns and environmental sensitivities during sandy grassland restoration.

Full Text

Preamble

High-throughput sequencing unveils microbial succession patterns in restored Hulun Buir Sandy Land, northern China

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Abstract: Intensive human activities have accelerated desertification in recent years, driving the continual expansion of deserts into peripheral meadows. To investigate the effects of restoration on soil microbial communities, we analyzed vegetation-soil relationships in the Hulun Buir Sandy Land of northern China. Using high-throughput sequencing, we examined the structure and diversity of bacterial and fungal communities within the 0–20 cm soil layer after 9–15 years of restoration, assessing spatial heterogeneity across different slope positions. The results showed progressive improvements in soil properties and vegetation with increasing restoration duration, following the pattern: bottom slope > middle slope > crest slope. During restoration, bacterial communities were dominated by Proteobacteria, Actinobacteria, and Acidobacteria, whereas fungal communities were dominated by Ascomycota and Basidiomycota. Eutrophic bacterial abundance increased with restoration duration, whereas oligotrophic bacterial and fungal abundance decreased. Soil bacterial abundance increased significantly with restoration duration, whereas fungal diversity decreased after 11 years of restoration, except at the crest slope. Redundancy analysis showed that pH, soil moisture content, total nitrogen, and vegetation-related factors explained 45.43% of the total variance in bacterial community structure.

Canonical correspondence analysis indicated that pH, total phosphorus, and vegetation-related factors shaped the fungal community structure, explaining 31.82% of the total variance. Structural equation modeling revealed stronger bacterial responses ($R^2 = 0.49–0.79$) to environmental changes than fungal responses ($R^2 = 0.20–0.48$). The soil bacterial community was driven mainly by pH, soil moisture content, electrical conductivity, plant coverage, and litter dry weight. Fungal abundance and diversity were primarily driven by plant coverage, litter dry weight, and herbaceous aboveground biomass, while no significant correlation was observed between soil fungal community structure and environmental factors. These findings highlight divergent microbial succession patterns and environmental sensitivities during sandy grassland restoration.

Keywords: revegetation; soil microbes; high-throughput sequencing; sandy grassland; dunes

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1 Introduction

Sandy desertification, characterized by sandstorm activity resulting from unbalanced human–land relationships, arises from intensive human activities in arid, semi-arid, and certain sub-humid areas and represents a form of desertification (Wang et al., 2004). In 2024, most countries worldwide committed to prioritizing land restoration and drought resilience within their national policies and international cooperation frameworks (United Nations Convention to Combat Desertification (UNCCD), 2024). Consequently, desertification has become a significant global environmental issue, with land restoration emerging as a key focus of international research (Keesstra et al., 2018).

China has made substantial efforts to combat desertification and achieved remarkable success (Anon, 2022). According to the Sixth National Desertification Monitoring Report, the area of desertified land in China decreased to 1.69×10^6 km^2 by 2019, representing a net reduction of 33,352 km^2 since 2014 (National Forestry and Grassland Administration, 2022). Hulun Buir, located in northern China, serves as a vital component of the northern ecological safeguard (Zhang et al., 2021). While the overall desertified land area in China is decreasing, some areas continue to deteriorate. In recent years, human activities have exerted increasing pressure on the Hulun Buir Sandy Land, one of China' s largest sandy lands (Li et al., 2018), driving its continuous expansion into adjacent grasslands (Na et al., 2019a; Gou et al., 2021) and resulting in a 32.20% reduction in grassland area from 2021 to 2022 (Hulun Buir City Bureau of Statistics, 2023).

Soil microbes are highly sensitive to environmental changes (Chen et al., 2015; Ling et al., 2017; Chen et al., 2021) and, as important functional groups in soil (He et al., 2007), play crucial roles in shaping ecological processes. They actively participate in organic matter decomposition (Hu et al., 2022), drive nutrient cycling (Zhang et al., 2014; Li et al., 2016), regulate ecosystem functions (van der Putten et al., 2013), and contribute to carbon sequestration in sandy lands (Zhou et al., 2025). Extensive research worldwide has focused on soil microbes in restored areas within semi-arid sandy lands. Enclosure management can increase microbial diversity in desertified grasslands (Qiao et al., 2024). As vegetation coverage increases in restored sandy lands, nutrient limitation shifts from nitrogen to phosphorus, which can be indirectly alleviated by microbes through organic matter mineralization and regulation of soil stoichiometric balance (Yao et al., 2025). The increasing dominance of shrub communities also significantly influences soil microbial community structure (Hu et al., 2021; Lan et al., 2021; Zhang et al., 2023b), enhancing microbial functions related to nutrient cycling in desertified grasslands (Ma et al., 2022).

During ecosystem restoration, microbial communities encounter nutrient limitations. Phosphorus directly constrains microbial survival strategies (Li et al., 2025) and serves as a key driver of rhizosphere microbes (Bi et al., 2022). The supply of carbon and nitrogen affects microbial network complexity (Huang et al., 2025). Efficient vegetation restoration may intensify microbial nutrient competition, resulting in exacerbated nutrient limitation and reduced diversity (Yu et al., 2023). In semi-arid dune ecosystems, active dunes, semi-fixed dunes, fixed dunes, and lowland meadows constitute the landscape (Zhao et al., 2000), with highly mobile active dunes being prioritized for restoration (Wang et al., 2023). However, due to the topographic structure of active dunes, differences in slope aspect and position may significantly influence the distribution of shrub communities (Nunes et al., 2019). Previous studies in forest lands have confirmed that microtopography mediates the community assembly of prokaryotes in soil (Lv et al., 2023) and the co-utilization of phosphorus by plants and microbes through rhizosphere processes (Qiu et al., 2023). Although revegetation is common during sand dune restoration in desertified areas, few studies have investigated the impacts of sand dune microtopography on soil microorganisms throughout ecosystem restoration processes, which are critical for effective restoration.

To address these knowledge gaps, we compared surface soil bacterial and fungal community structure and diversity across four restoration periods (9, 11, 13, and 15 years) and three slope positions (bottom slope, middle slope, and crest slope) in the Hulun Buir Sandy Land. Our previous study at the site revealed that different restoration durations affect plant community characteristics (Hao et al., 2023). Based on these findings, we hypothesize that artificial shrub restoration in sandy lands drives divergent succession trajectories between bacterial and fungal communities, which are mediated by slope position-modulated soil property gradients (Liu et al., 2020), and that long-term restoration vegetation might alter microbial divergence (Zhou et al., 2017; Hu et al., 2021).

2.1 Study area

The Hulun Buir Sandy Land is located in northern China and encompasses three sand belts (Chen et al., 2023). The study area is situated at the center of the middle sand belt, within the Ganzhuer Sandy Land (47°59 –48°43 N, 117°55 – 119°22 E; Fig. 1 [Figure 1: see original paper]) in New Barag Left Banner, Hulun Buir City, Inner Mongolia Autonomous Region, China. Since 2005, active dunes (formerly grasslands) in the study area have been restored annually through a combination of fencing and replanting native drought-tolerant plants, resulting in changes in dune types and shrub proliferation in the restoration areas (Hao et al., 2023). This region has a temperate semi-arid continental climate, with a mean annual temperature of 0.3°C and extreme temperatures ranging from –47.8°C to 39.5°C. Average annual precipitation is 287 mm, concentrated in July and August. The predominant prevailing wind direction is northwest (Zhou et al., 2019). Before desertification control measures were implemented, the study area was dominated by active dunes. Since 2005, artificial revegetation has been conducted annually, primarily through mixed planting of shrubs and grasses supplemented with a small number of *Pinus sylvestris* var. *mongolica* Litv., followed by independent fencing for natural regeneration.

Fig. 1 Location of sampling plots under different restoration years and slope positions. B, bottom slope; M, middle slope; C, crest slope. The abbreviations are the same in the following figures.

2.2 Experimental design and sampling

This study employed a space-for-time substitution approach. In August 2021, we selected plots that had been revegetated and fenced for 9, 11, 13, and 15 years. The 9-year plot was a grass-shrub mixed area, while the 11-, 13-, and 15-year plots were shrub-dominated areas. In each plot, five parallel transects were established along the direction of revegetation patterns, with intervals of more than 50 m. Each transect was located on the windward slope of the dunes (western slope), more than 20 m away from the fence. Differences in slope gradient among transects were less than five degrees. We established three sampling points at each slope position—bottom slope (B), middle slope (M), and crest slope (C)—resulting in a total of 60 sampling points (Fig. 1).

2.3 Aboveground vegetation sampling

Based on actual vegetation growth conditions, one herbaceous quadrat (1 m × 1 m) and one shrub quadrat (5 m × 5 m) were established at each sampling point. In each quadrat, we investigated plant community composition and recorded species richness, coverage, and height, as well as total vegetation coverage. Additionally, diameter at breast height and crown width were recorded in shrub quadrats. Aboveground portions in herbaceous quadrats were harvested, and litter was collected separately. Samples were oven-dried at 65.0°C to constant weight to determine herbaceous aboveground biomass and litter dry weight. Data from shrub quadrats were input into corresponding biomass models to calculate shrub aboveground biomass (Tong et al., 2018; Guo et al., 2022).

2.4 Soil sample collection

After harvesting herbaceous quadrats, a cylindrical tool (3 cm in diameter) was used to collect soil cores from each corner and the center of the quadrat at two depths (0–10 and 10–20 cm). The cores from each layer were pooled into two corresponding soil samples per sampling point, yielding 120 samples from the 60 sampling points. Each soil sample was divided into two portions. One portion was temporarily stored in a low-temperature insulated box (4.0°C), returned to the laboratory, and stored at -80.0°C before high-throughput deoxyribonucleic acid (DNA) sequencing. The other portion was air-dried and sieved for soil property analysis.

2.5 Analyses of soil properties and high-throughput DNA sequencing

Soil properties were analyzed following protocols from *Soil and Agricultural Chemistry Analysis* (Bao, 2000) for soil moisture content, soil bulk density, pH, electrical conductivity (EC), total carbon (TC), total nitrogen (TN), total phosphorus (TP), and total potassium (TK). Genomic DNA was extracted using the hexadecyltrimethylammonium bromide (CTAB) method.

For bacterial 16S ribosomal RNA (rRNA) gene V3–V4 region amplification, primers (5 -CCTAYGGGRBGCASCAG-3) and (5 -GGACTACNNGGGTATCTAAT-3) were used for polymerase chain reaction (PCR). For fungal ribosomal DNA internal transcribed spacer-1 (ITS1) region amplification, primers ITS5-1737F (5 -GGAAGTAAAAGTCGTAACAAGG-3) and ITS2-2043R (5 -GCTGCGTTCTTCATCGATGG-3) were employed. For 16S rRNA V3–V4 PCR products, equal-concentration mixing was performed based on product concentration, followed by purification using the Qiagen Gel Extraction Kit (Qiagen, Düsseldorf, Germany) through 2.00% agarose gel electrophoresis in 1×TAE (tris-acetate-EDTA) buffer. Library construction was conducted using the TruSeq® DNA PCR-Free Sample Preparation Kit (Illumina Inc., San Diego, USA). Following qualification through Qubit quantification and library detection, sequencing was performed on the NovaSeq 6000 high-throughput sequencing platform to obtain raw data for bacterial operational taxonomic units (OTUs). For ITS rDNA PCR products, a small-fragment library was established via paired-end sequencing following pooling proportions. The library was quantified using the QuantiFluor™-ST blue fluorescence quantification system. Purification and recovery were performed with the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, USA). Library concentration was preliminarily assessed via Nanodrop, and library fragments were analyzed using the Agilent 2100 system. Precise quantification was achieved through quantitative PCR (qPCR). Finally, sequencing was conducted with the MiSeq® Reagent Kit v3 (Illumina Inc., San Diego, USA) on an Illumina high-throughput sequencing platform to obtain raw data for fungal OTUs.

2.6 Meteorological data

Precipitation data were obtained from the Loess Plateau Subcenter, National Earth System Science Data Center, and National Science and Technology Infrastructure of China (http://loess.geodata.cn) (Peng et al., 2019). Administrative district data were obtained from the National Catalog Service for Geographic Information (http://www.webmap.cn). Annual precipitation data for New Barag Left Banner from 2006 to 2021 were compiled, and the average annual precipitation during the first year of restoration (PRE) was calculated accordingly.

2.7 Data analysis

Raw high-throughput DNA sequencing data were subjected to bioinformatics analysis following the Quantitative Insights Into Microbial Ecology (QIIME) 2 Framework (Q2F) with customized program scripts (https://docs.qiime2.org/2019.1/).

Alpha diversity of soil microbial communities was characterized using the Chao1, Shannon, and Pielou indices, representing community abundance, diversity, and evenness, respectively. Variations in microbial alpha diversity indices among groups and differences in soil properties, vegetation factors, and absolute abundance of dominant bacterial phyla were analyzed using one-way analysis of variance (ANOVA) followed by Duncan’ s test. All ANOVA tests were performed and visualized using R software.

Microbial community structural variations across groups were visualized via nonmetric multidimensional scaling (NMDS) based on the Bray-Curtis metric. To explore environmental drivers of microbial communities, redundancy analysis (RDA) and canonical correspondence analysis (CCA) were conducted at the genus level. Alpha diversity analysis, NMDS ordination, RDA, and CCA were performed using R v.4.2.3 for Windows with the Picante (Kembel et al., 2010) and Vegan (Dixon, 2003) packages (functions: diversity, metaMDS, decorana, rda, cca), and plots were generated with ggplot2. Spearman' s correlation analysis was conducted in R v.4.2.3 using the corr.test function in the psych package, with plots generated using pheatmap. Structural equation modeling (SEM) was performed in R v.4.2.3.

3.1 Soil and aboveground vegetation properties

Soil and aboveground vegetation properties changed significantly with increasing restoration duration and slope position (Fig. 2 [Figure 2: see original paper]). Soil pH became more alkaline over time, while abiotic factors—including EC, soil moisture content (SMC), TC, TN, TP, and TK—generally increased, with or without a sudden increase between the 9- and 11-year plots, and were greater in bottom slope (B) plots than in middle slope (M) plots, which in turn exceeded crest slope (C) plots. In contrast, biological factors—including litter dry weight (MA), herbaceous aboveground biomass (HBM), shrub aboveground biomass (SBM), and total vegetation coverage (PC)—gradually increased over time.

Fig. 2 Soil and aboveground vegetation properties under different restoration years and slope positions. (a) pH; (b) EC (electrical conductivity); (c) soil bulk density; (d) SMC (soil moisture content); (e) TC (total carbon); (f) TN (total nitrogen); (g) TP (total phosphorus); (h) TK (total potassium); (i) MA (litter dry weight); (j) HBM (herbaceous aboveground biomass); (k) SBM (shrub aboveground biomass); (l) PC (total vegetation coverage). Uppercase letters denote significant differences among restoration years for the same slope position at $P < 0.050$. Lowercase letters denote significant differences among slope positions for the same restoration year at $P < 0.050$. Bars represent standard errors. Abbreviations are the same in subsequent figures.

3.2 Soil microbial community components

Bacterial community composition at the phylum level changed significantly with restoration duration and slope position (Fig. 3a [Figure 3: see original paper]; Table 1). Proteobacteria, Actinobacteria, and Acidobacteria dominated the soil bacterial community, constituting approximately 75.00% of the total composition. The relative abundance of Proteobacteria in the 11-, 13-, and 15-year plots decreased significantly compared with the 9-year plot ($P < 0.050$; Table 1) and was greater in B plots than in M plots, which exceeded C plots. Actinobacteria and Acidobacteria exhibited the opposite trend. Ascomycota and Basidiomycota were the dominant fungal phyla (Fig. 3b), constituting approximately 88.00% of the total soil fungal composition.

Fig. 3 Phylogenetic classification of microbial communities at the phylum level under different restoration years and slope positions. (a) Bacteria; (b) fungi.

Table 1 Post hoc Tukey test results of one-way ANOVA on the absolute abundance of dominant bacterial phyla

Restoration year (a)	Actinobacteria	Proteobacteria	Acidobacteria
9	a	a	a
11	b	b	b
13	b	b	b
15	b	b	b
Slope position			
Bottom	a	a	a
Middle	b	b	b
Crest	c	c	c

Note: Different lowercase letters within the same column denote significant differences among restoration years and slope positions at $P < 0.050$.

3.3 Alpha diversity of soil microbial community

Changes in soil microbial alpha diversity indices among slope positions were much smaller than those among restoration years (Fig. 4 [Figure 4: see original paper]). Among slope positions, significant differences were observed only when the Chao1 index was relatively high. For bacteria, alpha diversity indices in B plots were significantly greater than those in M and C plots ($P < 0.050$), while for fungi, indices in M plots exceeded those in C plots ($P < 0.050$). With increasing restoration duration, the bacterial Chao1 index increased significantly ($P < 0.050$). Shannon and Pielou indices differed significantly when the grass-shrub mixed plot (9 years) transitioned to a shrub plot (11 years) ($P < 0.050$). This transformation also affected soil fungal alpha diversity indices, which decreased after the transition across restoration years, except at the crest slope ($P > 0.050$).

Spearman' s correlation analysis revealed that soil bacterial alpha diversity indices were significantly negatively correlated with PRE ($P < 0.001$; Fig. 5 [Figure 5: see original paper]) and positively correlated with PC ($P < 0.050$). Bacterial community abundance showed greater sensitivity than diversity and evenness, as the abundance index was significantly positively correlated with EC, SMC, TK, MA, HBM, and SBM ($P < 0.050$). In contrast, fungal indices showed the opposite trend and were more sensitive in terms of diversity and evenness, which were negatively correlated with environmental factors ($P < 0.050$).

Fig. 4 Alpha diversity indices of soil microbial community under different restoration years and slope positions. (a) Bacterial Chao1 index; (b) bacterial Shannon index; (c) bacterial Pielou index; (d) fungal Chao1 index; (e) fungal Shannon index; (f) fungal Pielou index. Uppercase letters indicate significant differences among restoration years at the same slope position at $P < 0.050$; lowercase letters indicate significant differences among slope positions at the same restoration year at $P < 0.050$. Bars represent standard errors.

Fig. 5 Relationships between microbial community alpha diversity and environmental factors. (a) Bacteria; (b) fungi. PRE, average annual precipitation during the first year of restoration; , *$P < 0.050$;* ***, $P < 0.010$;*** , $P < 0.001$.

3.4 Soil microbial community structure

Overall differences in soil microbial community structure were visualized through NMDS (Fig. 6 [Figure 6: see original paper]). Soil bacterial community structure (stress = 0.1550) gradually changed with increasing restoration duration, showing a trend toward intergroup separation and intragroup aggregation (Fig. 6a). After 13 and 15 years of restoration, bacterial community structures in M and C plots separated from those in B plots. In contrast, soil fungal community structure (stress = 0.0759) showed a trend toward intergroup aggregation and intragroup separation with increasing restoration duration, with no apparent pattern among slope positions (Fig. 6b).

Fig. 6 Two-dimensional nonmetric multidimensional scaling (NMDS) ordination of microbial communities under different restoration years and slope positions at the genus level. (a) Bacteria; (b) fungi.

Redundancy analysis (RDA) explored correlations between soil bacterial community structure at the genus level and environmental factors. The Monte Carlo permutation test revealed that the RDA model was significant ($P = 0.001$), explaining 45.43% of the total variation in bacterial community structure (Fig. 7 [Figure 7: see original paper]), with the first two axes being significant ($P < 0.050$). Results indicated that bacterial community structure in the Hulun Buir Sandy Land was driven primarily by pH, SMC, TN, MA, HBM, SBM, PC, and PRE ($P < 0.050$).

Fig. 7 Redundancy analysis (RDA) results for environmental factors and soil bacterial community composition at the genus level.

Canonical correspondence analysis (CCA) explored correlations between soil fungal community structure at the genus level and environmental factors. The Monte Carlo permutation test showed that the CCA model was significant ($P = 0.025$), explaining 31.82% of the total variation in fungal community structure (Fig. 8 [Figure 8: see original paper]), but neither axis was significant ($P > 0.050$), indicating limited practical explanatory power of the first two axes.

Results suggested that fungal community structure was driven primarily by pH, TP, MA, SBM, PC, and PRE ($P < 0.050$).

Fig. 8 Canonical correspondence analysis (CCA) of environmental factors and soil fungal community composition at the genus level.

Structural equation modeling (SEM) revealed distinct environmental sensitivity patterns in bacterial and fungal communities (Fig. 9 [Figure 9: see original paper]). Compared with fungal community structure ($R^2 = 0.20$), abundance ($R^2 = 0.48$), and diversity ($R^2 = 0.33$), bacterial community structure ($R^2 = 0.49$), abundance ($R^2 = 0.79$), and diversity ($R^2 = 0.69$) exhibited stronger responses to environmental changes. Bacterial community structure was significantly negatively correlated with MA and bacterial abundance ($P < 0.050$). Bacterial abundance was significantly negatively correlated with PC ($P < 0.050$). Bacterial diversity and evenness were significantly negatively correlated with SMC, pH, and MA ($P < 0.050$) and positively correlated with EC and bacterial abundance ($P < 0.050$). Fungal community structure was not significantly correlated with any measured environmental factors ($P > 0.050$). Fungal abundance was significantly positively correlated with pH, MA, and bacterial diversity and evenness ($P < 0.050$). Fungal diversity and evenness were significantly negatively correlated with fungal abundance ($P < 0.050$) and positively correlated with EC and HBM ($P < 0.050$).

Fig. 9 Structural equation modeling (SEM) of microbial communities and environmental factors.

4.1 Succession of soil microbial community

Soil moisture content, nutrients, and biological factors increased with restoration duration (Fig. 2). The increases in *Caragana microphylla* Lam. coverage and biomass may contribute to soil amelioration, accompanied by increased litter and herbaceous biomass. The enhancement of vegetation community biomass, soil organic carbon, and soil total nitrogen is facilitated by *C. microphylla* during vegetation restoration (Zhu and Li, 2024).

Dominant bacterial phyla included Proteobacteria, Actinobacteria, and Acidobacteria (Fig. 3a), whereas dominant fungal phyla included Ascomycota and Basidiomycota (Fig. 3b). These phyla are commonly dominant in surface soils of sandy lands in semi-arid (Ding et al., 2021; Tian et al., 2023) and arid areas (Liu et al., 2018; An et al., 2023), as well as in the rhizosphere microbial communities of three *Caragana* species in arid and semi-arid regions of northern China (Na et al., 2018).

Soil bacterial community composition at the phylum level changed significantly over time (Fig. 3a; Table 1). Ascomycota and Basidiomycota, as important soil decomposers, consistently dominated the fungal community (Fig. 3b) (Muggia et al., 2020; He et al., 2022). When the grass-shrub mixed plot (9 years) transitioned to a shrub plot (11 years), despite increased soil nutrients, the abundance of Proteobacteria (eutrophic, gram-negative bacteria) decreased, whereas the abundance of Actinobacteria and Acidobacteria (oligotrophic, gram-positive bacteria) increased (Figs. 2 and 3a; Table 1). Dominant bacterial phyla abundance remained relatively stable during the shrub period (11–15 years) (Fig. 6a). Different vegetation types in the Hulun Buir Sandy Land can cause significant differences in soil bacterial abundance (Yan and Feng, 2020). Additionally, during shrub encroachment in Inner Mongolia grasslands, the transition from grass-shrub mixed to shrub-dominated plots may decrease gram-negative bacteria and increase Actinobacteria and gram-positive bacteria (Zhou et al., 2017; Hu et al., 2021).

Alpha diversity indices of the soil microbial community were significantly impacted by the transformation of aboveground vegetation types and restoration duration (Fig. 4). Soil bacterial community abundance increased over time, whereas diversity and evenness indices first increased significantly and then remained stable. This pattern reflects rapid bacterial community shifts following vegetation restoration, with different taxa responding at varying rates and directions (Yao et al., 2018; Hu et al., 2019). Soil fungal community alpha diversity indices generally decreased over time (Han et al., 2024) and changed in abundance when aboveground vegetation type shifted (Zhang et al., 2023a). Both results indicate that vegetation type transformation influenced soil microbial communities, improving soil properties and increasing aboveground biomass (Fig. 2) while decreasing fungal diversity but increasing bacterial abundance with stable diversity and evenness (Fig. 4). The increased biomass associated with *C. microphylla* expansion improved soil conditions (Zhu and Li, 2024), reduced wind and sunlight impacts on the soil surface (Liu et al., 2013), and provided favorable conditions for surface soil microbial reproduction, leading to increased bacterial abundance (Fig. 4). Improved soil nutrients during grassland restoration might simultaneously increase eutrophic bacterial abundance while decreasing oligotrophic bacterial and fungal abundance, thereby affecting microbial community structure (Fig. 3a) (Li et al., 2023). This compositional shift may be amplified by potential bacterial-fungal antagonistic interactions (Bahram et al., 2018). If such interactions exist, they might explain the significantly positive correlation between most environmental factors and bacterial abundance and the significantly negative correlation with fungal diversity indices (Fig. 5), indicating that positive environmental changes during restoration promoted variations in microbial community structure and diversity.

4.2 Impact of terrain on soil microbial community

Significant differences among slope positions were observed only for microbial community abundance and only when abundance was relatively high (Fig. 4). Bacterial abundance was greater in B plots than in M and C plots, whereas fungal abundance was greater in M plots than in C plots. Several factors may explain these patterns. First, although soil nutrients and moisture accumulate downhill, they are extremely deficient in desertified areas (Nielsen and Ball, 2015). Therefore, at initial restoration stages, topographic differences in dunes might negligibly affect nutrient and moisture distribution, leading to nonsignificant differences among slope positions. Second, as shrub communities developed, aboveground vegetation effectively intercepted and consumed more precipitation (Alamusa et al., 2024), and soil water-holding capacity increased accordingly (Gao et al., 2021), which could enhance upward transport of soil nutrients (Liu et al., 2022). These hydrological changes might alter nutrient and moisture distribution patterns in dunes, potentially providing more nutrients to soil microbial communities and affecting their distribution (Nielsen and Ball, 2015; Na et al., 2019b). Additionally, sampling points at the foot of slopes were adjacent to lowland meadows, which have better environmental conditions than dunes, such as greater seedling density, soil nutrient levels, and moisture content (Yan and Li, 2017), resulting in higher soil microbial diversity (Han et al., 2024). Therefore, as upward water transport increased, lowland meadows might serve as nutrient sources for dunes, with nearby slope bottoms receiving the greatest nutrient supply, thereby increasing bacterial abundance at the foot of slopes while reducing fungal abundance.

4.3 Driving factors of soil microbial community

In this study, the soil bacterial community was affected mainly by water- and litter-related factors, whereas fungal community structure was influenced primarily by aboveground vegetation (Fig. 9). Bacterial community abundance and fungal community diversity and evenness showed broader environmental correlations than bacterial diversity/evenness and fungal abundance (Fig. 5). Bacterial community structure was more sensitive to environmental changes than fungal community structure (Fig. 9) (Ding et al., 2020). In semi-arid ecosystems, soil moisture variation strongly affects soil microbes (Wang et al., 2017). Soil bacteria preferentially decompose carbon sources with low C:N ratios (e.g., soil organic matter), whereas fungi preferentially decompose carbon sources with high C:N ratios (e.g., litter) (Waring et al., 2013). This functional divergence is particularly evident in lignin processing, as bacteria are limited in ligninolytic enzyme production (Vicuña, 1988). Ascomycota (hydrocarbon utilizers) and Basidiomycota (lignin degraders) predominated in the fungal community (Fig. 3b) and possess documented enzymatic systems for lignin decomposition (Lundell et al., 2010; Bugg et al., 2011). These findings explain the opposite responses of bacterial and fungal communities to litter (Fig. 9). Vegetation composition influenced litter decomposition by attracting different fungal communities (Meng et al., 2024). Moreover, the abundance of Actinobacteria, a bacterial phylum relatively closely associated with lignin decomposition, increased significantly with shrub biomass (Table 1; Fig. 2). Collectively, litter-derived carbon availability likely created microbial selection pressures that ultimately shaped community structure and diversity.

4.4 Evaluation of ecological restoration effects

The Hulun Buir Sandy Land exhibits characteristics of a bistable ecosystem with potential alternative states of grasslands and shrublands (He et al., 2015), as relatively high vegetation coverage and aboveground biomass were maintained after restoration (Fig. 2) (Hao et al., 2023). A shrubland-grassland-forest transition pattern of dominant vegetation exists from arid to humid areas (Qu et al., 2025). Therefore, in previously desertified areas like the study site, shrublands may demonstrate a competitive advantage in maintaining stability. In sandy grassland restoration, it is essential to consider not only wind-break and sand-fixation functions but also ecosystem productivity and multifunctionality. Perennial grasslands affected by shrub encroachment have traditionally been considered typical indicators of desertification in certain areas (Huenneke et al., 2002). After shrub encroachment, improved environmental conditions and unique microbial composition at the soil surface may form a positive feedback loop for shrub encroachment, rendering it irreversible (Lan et al., 2021). However, recent research suggests that shrub encroachment represents a natural successional process rather than degradation, with one study demonstrating an 8.00% increase in ecosystem multifunctionality following encroachment (Ding and Eldridge, 2024). Restoration efforts might struggle to revert to more productive grasslands without artificial intervention (Zhao et al., 2022). Furthermore, bacterial succession reflects progressive soil nutrient enrichment and shrub establishment, while fungal succession indicates vegetation transition from grass-shrub mixtures to shrub dominance, demonstrating steady environmental improvement (Figs. 2 and 4). Therefore, for shrublands restored to a moderate ecological threshold, adopting alternative management strategies may represent more sustainable land-use pathways, as opposed to traditional approaches employing mechanical, chemical, or biological interventions to eradicate shrubs for grassland restoration (Eldridge et al., 2013; Wang et al., 2018).

5 Conclusions

This study analyzed variations in surface soil bacterial and fungal community structure and diversity across four restoration periods (9, 11, 13, and 15 years) and different slope positions in the Hulun Buir Sandy Land using high-throughput sequencing, focusing on vegetation-soil relationships. Dominant bacterial phyla were Proteobacteria, Actinobacteria, and Acidobacteria, while dominant fungal phyla were Ascomycota and Basidiomycota. Bacterial community succession, characterized by increased eutrophic bacterial abundance and decreased oligotrophic bacterial abundance, reflected progressive soil nutrient accumulation and shrub establishment. Fungal community succession, characterized by decreased fungal abundance, signaled a transition in aboveground vegetation from grass-shrub mixed to shrub-dominated plots. The bacterial community was affected primarily by pH, SMC, EC, PC, and MA. Slope-specific microbial patterns, particularly increased bacterial abundance at the slope bottom, highlighted spatially heterogeneous recovery processes linked to water and nutrient redistribution. Fungal abundance and diversity were affected mainly by vegetation-related factors. Our results enhance understanding of above- and belowground community changes following restoration. Future research should prioritize long-term monitoring of microbial dynamics to identify irreversible recovery thresholds and develop prediction models integrating metagenomic data with ecosystem functions, ultimately guiding sustainable restoration strategies for the Hulun Buir Sandy Land.

Conflict of interest

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

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