Plant Biomass and Soil Nutrients Mainly Explain the Variation of Soil Microbial Communities During Secondary Succession on the Loess Plateau

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Abstract
Soil microorganisms play an important role in the circulation of materials and nutrients between plants and soil ecosystems, but the drivers of microbial community composition and diversity remain uncertain in different vegetation restoration patterns. We studied soil physicochemical properties (i.e., soil moisture, bulk density, pH, soil nutrients, available nutrients), plant characteristics (i.e., Shannon index \([H_{Plant}]\) and Richness index \([S_{Plant}]\), litter biomass \([LB]\), and fine root biomass \([FRB]\)), and microbial variables (biomass, enzyme activity, diversity, and composition of bacterial and fungal communities) in different plant succession patterns (Robinia pseudoacacia [MF], Caragana korshinskii [SF], and grassland [GL]) on the Loess Plateau. The herb communities, soil microbial biomass, and enzyme activities were strongly affected by vegetation restoration, and soil bacterial and fungal communities were significantly different from each other at the sites. Correlation analysis showed that LB and FRB were significantly positively correlated with the Chao index of soil bacteria, soil microbial biomass, enzyme activities, Proteobacteria, Zygomycota, and Cercozoa, while negatively correlated with Actinobacteria and Basidiomycota. In addition, soil water content (SW), pH, and nutrients have important effects on the bacterial and fungal diversities, as well as Acidobacteria, Proteobacteria, Actinobacteria, Nitrospirae, Zygomycota, and microbial biomass. Furthermore, plant characteristics and soil properties modulated the composition and diversity of soil microorganisms, respectively. Overall, the relative contribution of vegetation and soil to the diversity and composition of soil bacterial and fungal communities illustrated that plant characteristics and soil properties may synergistically modulate soil microbial communities, and the composition and diversity of soil bacterial and fungal communities mainly depend on plant biomass and soil nutrients.

Keywords Vegetation restoration patterns · Soil bacteria and fungi · Plant characteristics · Soil properties

Introduction
Plant secondary succession is an effective way to improve soil conditions and promote ecosystem restoration [1, 2]. Changes in plant community characteristics and soil physicochemical properties may drive changes in microbial communities among different succession styles [3]. For one thing, the succession of undergrowth vegetation, the decomposition of litter, and changes of rhizosphere carbon inputs drive growth and activity of soil microbes [4]. And for another, changes in soil properties such as pH, moisture, clay content, C, N, and phosphorus availability have significant effects on soil microbial communities under different land types [5, 6]. Conversely, as the main driving force of ecosystem processes, soil microorganisms complete the decomposition of soil organic matter and plant litter, and mediate the nutrient cycle of plant-soil ecosystems [7]. Therefore, understanding the coupling relationships among plant characteristics, soil properties, and microbial communities among different succession styles provides insight into the adaptation and response mechanisms of soil microorganisms in plant and soil ecosystems.

The change of soil microbial community caused by plant succession is a complex process, which is regulated by many biotic and abiotic factors [1, 8]. Recent research has explored how environmental changes (such as plant diversity,
underground vegetation characteristics, pH, soil nutrients, and soil moisture) affect soil microbial communities on a local scale, however the results are equivocal [9, 10]. Some studies indicated that plant diversity was predicted to promote the diversity of soil microorganisms by increasing the diversity of available nutrient pools and physical microhabitats, and by providing diverse plant hosts for symbiotic and pathogenic microorganisms [11]. Previous studies have also revealed that increased in vegetation coverage changed soil moisture and solar radiation, which in turn drives the diversity of soil microbial communities [1, 12]. Furthermore, abiotic factors such as soil nutrients and humidity have also proven to be key factors in building microbial communities [13]. Some studies indicated that lower soil nutrient availability may promote fungal growth in soil, as fungi have a competitive advantage related to nitrogen and phosphorus absorption [14, 15], while other studies indicated that bacteria can adjust their lifestyle (r- or k-strategists) to change community composition to adapt to nutritional levels [1, 16]. In addition, the shifts in the diversity and composition of soil microorganisms drive variables in microbial biomass and extracellular enzyme synthesis, which affect soil mineralization and nutrient availability [17, 18]. For instance, β-1,4-glucosidase (BG), β-1,4-N-acetylglucosaminidase (NAG), leucine aminopeptidase (LAP), and acid or alkaline phosphatase (ALP) have been increasingly used to indicate nutrient limitation and microbial nutrient demand [19]. Therefore, the relative contribution of vegetation factors and soil properties in determining microbial communities remain unclear, especially under distinct vegetation succession patterns.

The Loess Hilly Region of China is severely affected by soil erosion and desertification, which has accelerated the fragmentation and degradation of the ecosystem [20, 21]. To change these conditions, the Chinese government has taken various measures to repair the ecosystem and counteract soil erosion since 1950s [22]. These measures include the Grain to Green Project, which have increased vegetation coverage and improved soil erosion on the Loess Plateau [22, 23]. Notably, most of the farmland and pastures were afforested or abandoned [19]. The effects of different vegetation restoration styles on soil physical and chemical properties, microbial dynamics, and plant characteristics have been observed [24, 25]. For example, Zhang et al. [1] found that the diversity of bacterial communities was modulated by soil nutrients and plant biomass during the grassland succession. Liu et al. [12] clarified that the response of microbial communities to soil phosphorus was strong in Robinia pseudoacacia plantations. However, information on the links between them is still scarce, especially among different plant succession patterns. This information is critical to understanding the driving mechanisms of soil microbial communities and the proper management and protection of fragile ecosystems.

To illustrate the changes in the dominant factors affecting soil microbial communities in the hilly and gully regions of Loess Plateau, we studied soil physicochemical properties, plant characteristics, and microbial variables (biomass, enzyme activity, diversity and composition of bacterial and fungal communities) in different plant succession patterns. For one thing, some studies have found that soil fungal communities were sensitive to plant characteristics, while bacterial communities responded strongly to soil nutrients [11, 24]. We proposed the first hypothesis that the diversity and composition of soil bacterial and fungal communities responded differently to soil properties and vegetation characteristics, which is attributed to survival strategies of bacterial and fungal communities. And for another, some studies have found that plant biomass, soil nutrients, and microbial diversity were significantly different during different land use patterns [6, 7]. We proposed the second hypothesis that there is the strong correlation between vegetation characteristics and soil microbial diversities. Therefore, the objectives of the study were to (i) describe the differences in soil properties, vegetation communities, and microbial characteristics under different plant succession patterns; (ii) explore whether soil properties and vegetation characteristics have different effects on fungal and bacterial diversity; and (iii) determine the main driving factors for the composition and diversity of soil microbial communities under different succession patterns.

Materials and Methods

Study Area and Experimental Design

The study was carried out in Wuliwan watershed, located in the Loess Plateau region of Shaanxi Province (36°51′–36°53′ N, 109°20′–109°22′ E). The region is characterized by annual average precipitation of 510 mm, rainfall mainly occurring from July to September, the annual average temperature of 8.8 °C, 2415 h of sunshine, and 157 days of frost-free period each year. The soil is mainly composed of Calcielsols with typical loose and soft texture (judged by the Food and Agriculture Organization of the United Nations). Some farmland was abandoned or used to plant plantations in 1989. Robinia pseudoacacia and Caragana korshinskii are the main tree species in the artificial planting area, used because of their drought tolerance and water conservation. Some abandoned farmlands have gradually replaced by natural grasslands.

The experiment was conducted in July 2018, which coincided with the growing season in the forest area. Three types of land use were selected, namely Robinia pseudoacacia (macrophanerophytes forest, MF), Caragana korshinskii (shrub forest, SF), and grassland (GL) with similar geographical features and soil types. Each type of land use was represented by three independent replicate sites. All selected sites...
were located at similar gradients, slope aspects, elevations, and the main crops of maize were alternately planted at these sites before afforestation (Table 1). Three 20 m × 20 m plots were established in each site.

**Sampling and Vegetation Investigation**

After removing the litter layer and other debris, soil samples of the 0–10 cm profile were collected from 10 points arranged in the S shape using a soil auger (5 cm in diameter). The 10 soil samples from each point were homogenized to create the final soil samples, which were then sieved through a 2 mm mesh to remove roots and other debris. A portion of each soil sample was immediately shipped to the lab to determine soil water content. A set of subsamples were stored at −80 °C for DNA extraction, and the remaining soil subsamples were air dried and stored at room temperature to assess soil chemistry and pH.

Plant characteristics were measured in six 1 × 1 m quadrats were randomly arranged in each plot. Six 1 m × 1 m sample quadrats were created in each plot to assess plant diversity, biomass and coverage of the herb layer as well as biomass of the litter layer. In each quadrat, the name and number of the undergrowth plant species were recorded, and the coverage of that was measured. Plant coverage (HC) was calculated as the average percentage of ground surface covered by the shadow of the foliage in each quadrat. Above-ground parts of all plants in each quadrat were collected by shearing, dried to constant weight at 75 °C, and above-ground biomass (HB) was calculated. The calculation formulas of Shannon-Wiener diversity index (HPlant) and Margalef richness index (SPlant) for each sample are as follows [26]:

$$H_{Plant} = -\sum_{i=1}^{S} p_i \ln p_i$$

(1)

$$S_{Plant} = \frac{S-1}{\ln(N)}$$

(2)

where $S$ is the species number in a plot; $N$ is the sum of all species in a plot; $N_i$ is the number of the species “$i$” in a plot; $p_i$ is the density proportion of species “$i$” in a plot ($P_i=N_i/N$; $\ln=$natural log.

The litter layer samples were collected from each study site using nine spatially independent subsamples from litter traps without understory vegetation. The litter was dried to constant weight at 75 °C to obtain litter biomass (LB). While other measurement methods were performed, fine-root (<2mm diameter) samples were collected at the 0–10 cm depth with a 9-cm diameter stainless steel drill in each plot, and these samples also matched the plant quadrats. The roots were separated from the soil, washed repeatedly with water, then dried in an oven at 60 °C for 48 hours and the fine root biomass (FRB) was weighed.

**Analysis of Soil Properties**

Soil pH was measured with a pH meter after shaking the soil–water (1:5 w/v) suspension for 30 min. Soil bulk density (SBD) was obtained by calculating the ratio of soil mass to total volume of the core (g·cm$^{-3}$) after oven-drying to a constant weight at 105 °C [27]. Soil water content (SWC) was determined by oven drying the secondary samples to constant mass at 105 °C. The content of soil clay (Clay) was determined by a laser particle-size analyzer (Mastersizer, UK). Soil organic carbon (SOC) was determined by the K$_2$Cr$_2$O$_7$ oxidation method, and the soil N and P contents were determined by the Kjeldahl and colorimetric method, respectively [27]. Soil dissolved organic carbon (DOC) was analyzed using the TOC analyzer (TOC-L CPH, Shimadzu, Japan). Ammonia nitrogen (NH$_4$$^+$-N, SAN) and nitrate nitrogen (NO$_3^-$-N, SNN) of soil were measured using an AA3 continuous flow analysis system (AA3, Germany) and 1mol L$^{-1}$ KCl extraction. Soil total phosphorus (STP) was determined colorimetrically after wet digestion with HClO$_4$-H$_2$SO$_4$ [22]. Soil available phosphorus (SAP) was measured using the spectrophotometer (Mapada corporation, China) with a

| Sites | Gradient (°) | Slope aspect (°) | Altitude (m) | Understory vegetation |
|-------|--------------|------------------|--------------|-----------------------|
| GL    | 30           | 103              | 1250–1260    | *L. floribunda* B.  |
|       |              |                  |              | *T. vulgare* N.      |
| SF    | 20           | 317              | 1250–1260    | *P. heterophylla* B. |
|       |              |                  |              | *D. indicum* (L.) D. M. |
| MF    | 40           | 303              | 1270–1280    | *Dendranthema indicum* (L.) Des Moul.|
|       |              |                  |              | *P. sphondyloides* T. |
|       |              |                  |              | *P. heterophylla* B. |

Note: *L. floribunda* B., *Lespedeza floribunda* Bunge; *T. vulgare* N., *Tripolium vulgare* Nees; *P. sphondyloides* T., *Poa sphondyloides* Trin.; *P. heterophylla* B., *Patrinia heterophylla* Bunge; *D. indicum* (L.) D. M., *Dendranthema indicum* (L.) Des Moul; GL, grassland; SF, Caragana korshinskii; MF, Robinia pseudoacacia
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The activities of carbon-acquiring enzymes (BG), nitrogen-acquiring enzymes (LAP and NAG), and phosphorus-acquiring enzymes (ALP) was determined using the modified standard fluorometric techniques [28]. The four types of soil enzyme activity were measured using a 96-well plate with three replicate wells for each sample per assay. The analysis included 3 replicate wells for each blank, negative control, and quenched standard [19]. One gram of fresh soil was homogenized in 125 mL of sodium acetate buffer (pH = 8.5) to extract ecological enzymes. Then, the 200 μL soil suspension and 50 μL of 200 μmol L⁻¹ fluorometric substrate were added to the microplate. The fluorometric substrates of BG, LAP, NAG and AP were 4-MUB-β-D-glucoside, 4-MUB-N-acetyl-β-D-glucosaminide, L-leucine-7-amido-4-methylcoumarin and 4-MUB-phosphate, respectively. In addition, 4-methylumbelliferone (MUB) or 7-amino-4-methylcoumarin (AMC) was used as the standard substance. After the microplate was incubated for 4 hours at 25 °C in the dark, 10 μL of 0.5 mol L⁻¹ NaOH was added to each well to stop the reaction. Finally, the fluorometric values were measured using the microplate reader (Tecan Infinite M200 Pro Plex, Austria).

### Soil DNA Extraction and PCR Amplification

Soil DNA was extracted with an E.Z.N.A soil DNA kit (Omega Bio-tek, Inc., Norcross, GA, USA) and electrophoresed on 1.0% agarose to check the quality and size of DNA. The extracted soil DNA was stored at −80 °C until PCR amplification and analysis. The 16S V3V4 (target fragment length 480 bp) and ITS1 (target fragment length 250 bp) regions in soil bacteria and fungi were amplified by PCR and sequenced. Soil bacterial 16S rRNA targeted the V4 region by using primers 338F (5′-ACTCCTACGGGAGGCAGCA-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′) [29]. The fungal ITS-1 region was amplified by using primers ITS5F (5′-GGAAGTAAAAGTCGTAACAAGG-3′) and ITS1R (5′-GCTGCGTTCTTTCATCGATGC-3′) [30]. Soil bacterial 16S rRNA amplification samples were denatured at 95 °C for 3 min, and then amplified by 27 cycles of 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 45 s, which was followed by extension at 72 °C for 10 min. PCR of the rRNA subunit was conducted in 25 μL reaction mixtures containing 0.5 μL of 30 μL of each of 1-1 primers. The fungal ITS-1 amplification samples were denatured at 95 °C for 2 min and then amplified by 30 cycles of 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 30 s, which was then followed by a final extension at 72 °C for 5 min. Three independent PCR assays were performed for each DNA sample to obtain replicates. Gene copy number was calculated by the standard curve method. The standard curve was generated by using 10-fold-diluted series of plasmids containing each target gene. Finally, a total of the PCR products was achieved and an equal amount of PCR product from each sample was then transferred into the clean tubes and sequenced using Illumina’s MiSeq platform at the Major Biological Institute, Shanghai, China.

### Sequence Data Processing

The DNA data of soil samples amplified by PCR was demultiplexed and mass filtered. Sequence analysis was performed using USEARCH v5.2.32 after QIIME standard processing [29]. Similar sequences with less than 3% dissimilarity were clustered to eliminate data noise. Combining clustering molecules with 97% similarity, 16S rRNA and ITS rRNA operational taxa were selected for classification. Finally, the complete data were stored in the National Biotechnology Information Center (NCBI) Sequence Read Archive (SRA) database under the accession numbers of SRP243825 and SRP243837.

### Statistical Analyses

Taxonomic alpha diversity was based on the diversity of soil microbial communities in individual samples, using the Chao index (S_Bacteria and S_Fungi) that reflected the richness of the community and the Shannon index (H_Bacteria and H_Fungi) that took the uniformity of the community into account, was determined using MOTHUR software (version v.1.30.1). These indicators can accurately reflect the richness and uniformity of bacterial and fungi communities. A one-way analysis of variance (ANOVA) and multiple significant differences (p < 0.05) were used to assess the changes in soil properties (SW, Clay, SB, pH, SOC, DOC, STN, SAN, SNN, STP, and SAP), plant characteristics (HC, HB, LB, FRB, H_plan and S_plan) and soil microbial community diversity and composition using SPSS 20.0 (SPSS Inc. Chicago, USA). The data for this analysis were normalized via log-transformation. Principal component analysis (PCA) methods were used to assess soil microbial clusters across different land uses using the Vegan package in R. Pearson correlation analysis were used to assess the relationships between dominant microflora, microbial community diversity and environmental variables (plant characteristics and soil properties) using SPSS 20.0 (SPSS Inc. Chicago, USA). Redundancy analysis was used to identify the contributions of plant characteristics and soil properties on soil bacteria and fungi using the Vegan package in R. Partial least squares path models (PLS-SM) analysis was used to evaluate the direct and indirect effects of plant characteristics and soil properties on soil microbial communities using the Vegan package in R.
Results

Variation in Vegetation Characteristics

The composition, diversity, coverage, and biomass of herb communities were strongly affected by land use from abandoned farmland (Tables 1 and 2). The significant increase in canopy closure from grassland (GL) to shrub forest (SF) and thence to macrophanerophyte forest (MF) resulted in population classification changed from shady plants to light plants. The light plants such as Lespedeza floribunda B. and Tripolium vulgare N. were the dominant species in GL. The Dendranthema indicum and Patrinia heterophylla B. were gradually becoming the dominant species to replace the xerophytic species in SF. The shady plants such as Poa sphondylodes T. increased significantly in MF. The LB, FRB, and $H_{\text{Plant}}$ of undergrowth plant community increased significantly from GL to MF. The herb coverage (HC) of SF was 51.75% and 97.72% higher than that of GL and MF, respectively. In addition, the herb biomass (HB) and $S_{\text{Plant}}$ of SF were the largest compared to the other two land uses.

Variation in Soil Properties

The SOC, STN, DOC, SNN, SW, and Clay were significantly different among different secondary succession patterns (Table 3). The contents of SW and SAN were greater in MF sites, relative to GL and SF sites. Compared with GL sites, Clay, STN and SNN contents were higher in SF and MF sites, while SBD was inverted. Furthermore, compared with the GL sites, the SOC contents increased by 14.89% and 17.80% in the SF and MF sites, respectively; the DOC contents increased by 75.42% and 102.76% in the SF and MF sites, respectively; the SAP contents decreased by 4.06% and 6.69% in the SF and MF sites, respectively. In addition, STP and pH did not differ significantly among different land use patterns.

Variation in Microbial Indexes

Soil Microbial Biomass and Enzyme Activities

Soil microbial biomass and enzyme activities significantly differed among different secondary succession patterns (Table 4). Compared with GL, MBC, MBN, MBP, BG, NAG+LAP, and ALP increased by 2.22, 2.02, 1.84, 1.28, 1.08, and 1.51 times after the artificial secondary succession, respectively, and those of MF were the largest. In addition, MBC, MBN, BG, and ALP showed significant differences between grassland and afforestation. Notably, the MBP and NAG+LAP value was the highest in MF than that of GL and SF.

Table 2 The vegetation characteristics in the three land types

| Land types | HC (%)  | HB (kg·m$^{-2}$) | LB (kg·m$^{-2}$) | FRB (kg·m$^{-2}$) | $H_{\text{Plant}}$ | $S_{\text{Plant}}$ |
|------------|---------|-----------------|-----------------|------------------|-------------------|-----------------|
| GL         | 53.33±5.88b | 0.29±0.04ab    | 0.12±0.01c     | 0.13±0.01c       | 2.54±0.13b       | 4.51±0.10b     |
| SF         | 80.93±4.30a | 0.40±0.06a     | 0.31±0.01b     | 0.16±0.01b       | 2.50±0.04b       | 4.78±0.06a     |
| MF         | 40.93±4.04b | 0.22±0.01b     | 0.51±0.01a     | 0.18±0.01a       | 2.68±0.11a       | 4.67±0.33ab    |

The values are mean ± standard error. Different letters indicate significant differences ($p<0.05$) among different land use types based on a one-way ANOVA followed by an LSD test.

HC, herb coverage; HB, herb biomass; LB, litter biomass; FRB, fine root biomass; $H_{\text{Plant}}$, Shannon-Wiener diversity index; $S_{\text{Plant}}$, Margalef richness index; GL, grassland; SF, Caragana korshinskii; MF, Robinia pseudoacacia
Diversity and Composition of Microbial Communities

The $H_{\text{Bacteria}}$ was the lowest at SF than that at GL and MF sites (Fig. 1a). The $S_{\text{Bacteria}}$ of GL, SF, and MF were $2.52 \times 10^3$, $2.98 \times 10^3$, and $3.33 \times 10^3$, respectively. Compared with MF, $S_{\text{Fungi}}$ decreased by 11.72 and 10.15% at GL and SF, respectively (Fig. 1b).

The soil bacteria was dominated by Actinobacteria (24.40%) and Acidobacteria (27.78%), followed by Proteobacteria (20.39%), Chloroflexi (11.94%), Gemmatimonadetes (8.87%), and Nitrospira (2.86%) (Fig. 2a). The relative abundance of Actinobacteria was the lowest in the GL than that in the SF and MF. The relative abundance of Proteobacteria was greatest in MF compared to the other three land uses. However, the relative abundance of Acidobacteria showed different changes, and that of GL (35.75%) was higher relative to SF (26.59%) and MF (21.01%). In addition, Ascomycota (40.11%), Basidiomycota (17.09%), Zygomycota (6.64%), and Cercozoa (1.09%) dominated the fungal community composition in all sites (Fig. 2b). Compared with GL, the relative abundance of Ascomycota increased by 1.60 and 1.70 times in SF and MF, respectively. The relative abundance of Basidiomycota increased significantly from GL to MF. The relative abundances of Zygomycota and Cercozoa were higher in MF compared to those in the other land uses.

The PCA method, employed to assess the variations in community composition and structure among the sites, and soil microbial communities differ significantly at each land use (Fig. 3). The analysis reinforces the view that the soil bacterial and fungal communities were significantly different from each other at the sites of the three land uses.

Relationships Between Plant Characteristics, Soil Variables, and Microbial Communities

Plant characteristics significantly affected the diversity of soil bacteria (Figs. 4 and 5). The LB and FRB were significantly positively correlated with $S_{\text{Bacteria}}$, soil microbial biomass carbon (MBC, MBN, and MBP), and enzyme activity (Fig. 4). LB and FRB were significantly positively correlated with Actinobacteria, Proteobacteria, Zygomycota, and Cercozoa, while negatively correlated with Acidobacteria and Basidiomycota (Fig. 5).

Soil properties have important effects on the diversity and composition of soil microorganisms (Figs. 4 and 5). $S_{\text{Bacteria}}$, soil microbial biomass, and enzyme activity were significantly positively correlated with SW, Clay, SOC, STN, DOC, SAN, and SNN, while these variables negatively correlated with SBD and SAP (Figs. 4 and S1). In addition, Acidobacteria showed significant negative correlation with SW, Clay,

### Table 4 The soil microbial biomass and enzyme activity in the three land types

| Land types | MBC (mg kg$^{-1}$) | MBN (mg kg$^{-1}$) | MBP (mg kg$^{-1}$) | BG (nmol g$^{-1}$ h$^{-1}$) | NAG+LAP (nmol g$^{-1}$ h$^{-1}$) | ALP (nmol g$^{-1}$ h$^{-1}$) |
|------------|-------------------|-------------------|-------------------|------------------|-----------------|------------------|
| GL         | 157.57±6.33c      | 28.26±1.53c       | 8.60±0.31b        | 51.47±1.10c      | 69.30±1.37b     | 72.28±1.36c      |
| SF         | 248.56±5.21b      | 43.15±0.87b       | 9.80±0.35b        | 59.11±0.52b      | 71.13±1.36b     | 87.91±1.32b      |
| MF         | 449.10±2.51a      | 71.15±0.78a       | 21.87±0.35a       | 72.86±1.08a      | 78.81±0.78a     | 130.07±2.71a     |

The values are mean± standard error. Different letters indicate significant differences ($p<0.05$) among different land use types based on a one-way ANOVA followed by an LSD test.

MBC, soil microbial biomass carbon; MBN, soil microbial nitrogen; MBP, soil microbial phosphorus; BG, β-1,4-glucosidase; NAG, β-1,4-N-acetylglucosaminidase; LAP, leucine aminopeptidase; ALP, alkaline phosphatase; GL, grassland; SF, Caragana korshinskii; MF, Robinia pseudoacacia.
SOC, STN, DOC, SAN, and SNN, and positive correlation with SBD and SAP, but Proteobacteria and Actinobacteria had the inverse relationship with these properties (Fig. 5). SW, DOC, and SAN were significantly negatively correlated with Basidiomycota and positively correlated with Zygomycota and Cercozoa.

The responses of soil bacterial and fungal communities to plant characteristics and soil properties were heterogeneous (Figs. 6 and 7). The contributions of plant and soil can explain 76.95% of soil bacterial diversity and 90.64% of bacterial composition (Figs. 6a and 7a), in which the effect of plant characteristics on diversity was more intense. The relative effects of HB, HC, SPlant, and HPlant on the diversity of soil bacteria were 10.84, 10.43, 10.30, and 10.19%, respectively, which were more significant than other variables (Fig. 6a). The contributions of plant and soil can explain 88.14% of the diversity of soil fungi and 71.39% of the composition of fungi (Figs. 6b and 7b). The effect of soil properties on composition was slightly higher than the effect of plant properties. The relative effects of LB, SAN, and SW on the composition of soil fungal communities were 6.71, 6.41, and 6.25%, respectively, which were more significant than other variables (Fig. 7b). According to the PLS-PM analysis, we found that restoration patterns significantly regulated plant characteristics (HC, HB, LB, and FRB) and soil properties (SW, pH, SOC, STN, and SNN) (Fig. 8). Notably, soil properties significantly affected the diversity of soil bacterial and fungal communities, and plant characteristics were closely related to the dominant phyla of soil microbial communities.

Discussion

Effects of Vegetation Characteristic Variables on Soil Microbial Properties

In this study, litter and fine root biomass significantly affected the diversity of soil bacterial communities, which confirmed our first hypothesis. Simultaneously, the effects of HB, HC, SPlant, and HPlant on the diversity of soil bacteria were more significant than other variables (Fig. 6a). These results were consistent with the findings by Zhang et al. [1] who observed...
that plant diversity was significantly correlated with the diversity of bacterial communities. The correlations may be attributed to the fact that the increase of vegetation communities in secondary succession accelerated the accumulation of litter and root biomass and provided adequate C resources and nutrients for microbial growth [8]. Litter decomposition and root exudates provide energy and nutrient sources for the soil community and improve soil alkaline environment caused by organic acids and humic acids for soil microbial growth [31]. Furthermore, with greater quantity and quality of litter materials and fine root biomass, afforestation generates more organic matter and other resources for soil microbes than grassland (Table 2), leading to more abundant decomposers and supporting a more biodiverse microbial community [32, 33]. In addition, we found that LB and FRB were significantly positively correlated with soil microbial biomass, and enzyme activity (Fig. S1). Previous studies showed that the soil microbial biomass, C, N, and P acquisition enzymes are significantly higher in vegetations with greater biomass of root systems [34, 35]. Besides, Peng and Wang [36] also revealed that extracellular enzymes reflected nutrient requirements of microorganisms and the supply of nutrients in the environment. However, we found that there was no significant relationship between soil fungal diversity and plant characteristics (Fig. 4). This discrepancy might be due to the deficiency of co-linked environmental control factors and direct functional associations between plant and soil fungi in our survey region [31]. Therefore, plant characteristics could explain differences in the diversity of soil bacterial communities under different vegetation succession patterns.

Our study found that LB and FRB were significantly positively correlated with Proteobacteria, Actinobacteria, Zygomycota, and Cercozoa, but negatively correlated with Acidobacteria and Basidiomycota (Fig. 5). Simultaneously, the effect of LB on the composition of soil fungi was most significant than other variables (Fig. 7b). These results can be explained by litter decomposition and root exudates provide C resources and nutrients for soil microorganisms, which modulate the composition and growth of soil microbial communities [10]. Furthermore, some studies have demonstrated that bacteria communities are associated with soil carbon and nitrogen cycling [22]. Proteobacteria is commonly used as copiotrophic bacteria, due to its extracellular membrane consists of lipopolysaccharide that was involved in carbon conversion [37]. Metabolism in Acidobacteria was affected by light intensity, and these
groups were generally regarded as oligotrophic bacteria in previous studies [8]. We found that LB and FRB were significantly positively correlated with the relative abundance of Actinobacteria (Fig. 5), which was attributed to the increase of organic matter enhances the metabolic efficiency of Actinobacteria [38]. Considering the N2-fixing capacity of leguminous plants such as *Robinia pseudoacacia* and *Caragana korshinskii*, the combination of N2-fixing microorganisms and mycorrhizas was stronger [22]. In addition, some studies have confirmed that soil fungal communities are modulated by rotten detritus, litter, and rhizosphere [24]. Previous studies identified that strains of Zygomyctota are involved in symbiotic mycorrhizas with plants and aid in the decomposition of plant residues and litter [31]. In contrast, overly dense herbs and litter may inhibit the growth of Basidiomycota [39, 40]. Furthermore, the significant correlation between vegetation characteristics (LB and FRB) and the abundance of dominant phyla of soil bacteria and fungi emphasized that plant biomass plays an important role in the succession of microorganisms [8]. Therefore, we inferred from these results that plant characteristics differentially affect the composition and growth of soil microbial communities mainly through litter and fine root biomass.

### Effects of Soil Variables on Soil Microbial Properties

The development of plant community is fundamental for soil restoration, and it strongly influences the dynamics of soil physicochemical properties [41]. Furthermore, changes in microbial community diversity are sensitive to changes of soil environment, such as changes in soil moisture, density, and nutrients [1]. This study observed the effects of soil properties on the diversity of soil bacteria after afforestation, we found that *S*<sub>Bacteria</sub> and microbial biomass were significantly positively correlated with SOC, Clay, STN, DOC, SAN, and SNN, and negatively correlated with SBD and SAP (Figs. 4 and S1). Besides, the richness index of soil bacteria and soil nutrients in afforestation were higher than in abandoned soil (Table 3 and Fig. 1). In the same area where this study was conducted, Ren et al. [22] have revealed that the increase in organic input from litters and rhizomes promoted the utilization of C resources and nutrients by microorganisms. In

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**Fig. 6** Effects of vegetation characteristics and soil physicochemical properties on the diversity of soil bacteria (a) and fungi (b). HC, herb coverage; HB, herb biomass; LB, litter biomass; FRB, fine root biomass; SWC, soil water content; SBD, soil bulk density; SOC, soil organic carbon; STN, soil total nitrogen; STP, soil total phosphorus; DOC, soil dissolved organic carbon; SAN, soil ammonia nitrogen; SNN, soil nitrate nitrogen; SAP, soil available phosphorus

**Fig. 7** Effects of vegetation characteristics and soil physicochemical properties on the composition of soil bacteria (a) and fungi (b). HC, herb coverage; HB, herb biomass; LB, litter biomass; FRB, fine root biomass; SWC, soil water content; SBD, soil bulk density; SOC, soil organic carbon; STN, soil total nitrogen; STP, soil total phosphorus; DOC, soil dissolved organic carbon; SAN, soil ammonia nitrogen; SNN, soil nitrate nitrogen; SAP, soil available phosphorus
general, the increase of root growth and soil porosity after afforestation enhance root exudates accumulation and soil aeration, which is conducive to improving microbial metabolism and diversity [42, 43]. Thus, the increase in soil fungal diversity and biomass were consistent with the decrease in bulk density among vegetation restoration. Moreover, microbial community diversity and biomass with vegetation restoration were influenced by soil nitrate N, which is considered the preferred source of N for microbes [44, 45]. Barak et al. [46] also found that the increase of soil nitrate N after fertilization is paralleled by the accumulation of H⁺. Furthermore, the growth rate hypothesis emphasizes that the growth of soil microbes is related to the need for P for r-RNA synthesis, prompting the microbial community to enter soil [22, 47]. However, the low SAP observed may limit the absorption of P by microbes [8]. In contrast, the correlation between soil bacterial diversity and soil properties was inconsistent with fungi (Fig. 4). This result may be related to excessive Acidobacteria in abandoned grassland [1]. Allison and Vitousek [48] found that soil ALP activity was inversely related to soil P availability, and soil N cycling can promote the increase of NAG and LAP activities. Our results also found that the response characteristics of microbial biomass to soil physicochemical properties were consistent with the regularity of enzyme activity (Fig. S1). The result implied that any modification of environmental factors to the microbial community can be reflected in the level of enzyme activities (C-acquiring, N-acquiring, and P-acquiring enzymes) [25, 49].

We found that the composition of soil bacterial and fungal communities responded differently to soil factors (Figs. 5, 7, and 8). Our results showed that Acidobacteria was significantly negatively correlated with Clay, SOC, STN, STP, DOC, SAN, and SNN, and positively correlated with SBD and SAP, but Proteobacteria and Actinobacteria were reversed (Fig. 5). In general, copiotroph and oligotroph were often regarded as a measure about soil environment of ecosystems [8, 12]. Proteobacteria associated with the enrichment of carbon pool is regarded as copiotrophs [12]. Zhang et al. [26] have revealed that the input of soil organic C was beneficial to the accumulation of N content at low N level. Therefore, increases in the abundance of Proteobacterial flora can promote the accumulation of soil N. Conversely, Acidobacteria may be richer in nutrient-poor soil environments and likely act as oligotrophs [1]. And the reduction of soil pH provides an optimal living environment for microorganisms, which was conducive to the use of soil carbon resources and nutrients by copiotrophs [8]. Moreover, Actinobacteria was positively correlated with SOC, DOC, STN, SAN, and SNN, implying that Actinobacteria is sensitive to the accumulation and decomposition of organic matter, and the increase of soil

**Fig. 8** Partial least squares path models (PLS-PM) of the drivers of soil bacterial and fungal community. Path analysis results for direct and indirect effects of restoration patterns, soil properties and plant characteristics on the diversity and composition of soil bacterial and fungal community. Numbers on arrows are path coefficients indicating a positive (positive number) or negative effect (negative number). $H_{\text{Bacteria}}$ and $S_{\text{Bacteria}}$, the Shannon and Chao index of soil bacteria; $H_{\text{Fungi}}$ and $S_{\text{Fungi}}$, the Shannon and Chao index of soil fungi; SW, soil water content; SOC, soil organic carbon; STN, soil total nitrogen; SNN, soil nitrate nitrogen; SAP, soil available phosphorus; HC, herb coverage; HB, herb biomass; LB, litter biomass; FRB, fine root biomass
nutrients enhances the metabolism level of Actinobacteria in different restoration patterns [8, 12]. Besides, DOC and SAN were significantly negatively correlated with Basidiomycota and positively correlated with Zygomycota and Cercozoa (Fig. 5). Prescott et al. [10] found that soil C and N dynamics can affect fungal community composition because Zygomycota metabolize the organic substrates of rhizodeposition. The abundance of Basidiomycota decreased significantly with afforestation, which is inconsistent with Liu’s [12] conclusions, revealing that Basidiomycota is linked to litter biomass and soil nutrients. This result may be attributed to indirect interference from other environmental factors in this area [11]. Overall, the regulation of soil microbial diversity by soil properties emphasized that the enrichment of dominant species for soil bacteria and fungi in nutrient-rich soil.

In addition, our study found that SW was significantly positively correlated with $S_{\text{Bacteria}}$, $S_{\text{Fungi}}$, Proteobacteria, Actinobacteria, Zygomycota, and Cercozoa, but negatively correlated with Acidobacteria and Basidiomycota (Figs. 4 and 5). Generally, soil moisture is an important factor driving changes in soil microbial respiration and soil nutrients, which can affect soil microbial communities [47]. Previous studies have clarified that the increase of soil moisture enhances the activity of microorganisms after afforestation [42], and the leaching loss of SAP is also closely related to the soil water contents [8]. In addition, Zhong et al. [2] also found that the increase in soil moisture enhanced the metabolic efficiency of soil microorganisms on organic matter in semi-arid ecosystems. Thus, the results of our study implied that the soil water contents significantly affected the microbial community, which was mainly reflected in the soil nutrient level.

**Conclusions**

Altogether, these results indicated that plant characteristics and soil factors were significantly varied under different vegetation restoration patterns. Additionally, we explored the relationship between vegetation and soil variables and soil microbial diversity and composition under different restoration patterns, and the results of this study provide evidence for differences in the diversity and composition of soil microbial communities in different vegetation restoration. The relative contribution of vegetation and soil to bacterial and fungal communities illustrated that plant characteristics and soil properties may synergistically modulate the diversity and composition of soil microbial communities, and soil bacterial and fungal communities are affected by plant biomass and soil nutrients. Overall, this study provides important guidance for understanding the driving mechanisms of soil microbial communities and the strategy of plantation management and protection in the ecologically fragile areas.

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**Author’s Contribution** MPX, XHH and JYJ conceived and designed the experiments; MPX and CJR performed the experiments and processed the samples; MPX wrote a first version of the manuscript, and YFZ and GHY substantially contributed to the last version of the manuscript.

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**Data Availability** Some or all data, models, or code generated or used during the study are available from the corresponding author by request.

**Declarations**

**Conflict of Interest** The authors declare no competing interests.

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