Diversity of soil bacterial and fungal communities in artificial forests of the sandy-hilly region of Northwest China (Postprint)

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Abstract

Soil erosion is a serious issue in the sandy-hilly region of Shanxi Province, Northwest China. There has been gradual improvement due to vegetation restoration, but soil microbial community characteristics in different vegetation plantation types have not been widely investigated. To address this, we analyzed soil bacterial and fungal community structures, diversity, and microbial and soil environmental factors in Caragana korshinskii Kom., Populus tomentosa Carr., Populus simonii Carr., Salix matsudana Koidz, and Pinus tabulaeformis Carr. forests. There were no significant differences in the dominant bacterial community compositions among the five forest types. The alpha diversity of the bacteria and fungi communities showed that ACE (abundance-based coverage estimator), Chao1, and Shannon indices in C. korshinskii forest were significantly higher than those in the other four forest types ($P<0.05$). Soil organic matter, total nitrogen, and urease had a greater impact on bacterial community composition, while total nitrogen, β-glucosidase, and urease had a greater impact on fungal community composition. The relative abundance of beneficial and pathogenic microorganisms was similar across all forest types. Based on microbial community composition, diversity, and soil fertility, we ranked the plantations from most to least suitable as follows: C. korshinskii, S. matsudana, P. tabulaeformis, P. tomentosa, and P. simonii.

Full Text

Preamble

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Diversity of Soil Bacteria and Fungi Communities in Artificial Forests of the Sandy-Hilly Region of Northwest China

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Abstract: Soil erosion is a serious issue in the sandy-hilly region of Shanxi Province, Northwest China. Although vegetation restoration has led to gradual improvement, soil microbial community characteristics in different plantation types remain poorly understood. To address this knowledge gap, we analyzed soil bacterial and fungal community structures, diversity, and associated microbial and soil environmental factors in *Caragana korshinskii* Kom., *Populus tomentosa* Carr., *Populus simonii* Carr., *Salix matsudana* Koidz, and *Pinus tabulaeformis* Carr. forests. No significant differences were observed in the dominant bacterial community compositions among the five forest types. Alpha diversity analysis of bacterial and fungal communities revealed that ACE (abundance-based coverage estimator), Chao1, and Shannon indices in *C. korshinskii* forest were significantly higher than those in the other four forest types ($P < 0.05$). Soil organic matter, total nitrogen, and urease activity exerted greater influence on bacterial community composition, while total nitrogen, β-glucosidase, and urease had stronger effects on fungal community composition. The relative abundance of beneficial and pathogenic microorganisms was similar across all forest types. Based on microbial community composition, diversity, and soil fertility, we ranked the plantations from most to least suitable as follows: *C. korshinskii*, *S. matsudana*, *P. tabulaeformis*, *P. tomentosa*, and *P. simonii*.

Keywords: microbial community composition; artificial forest; bacteria; fungi; diversity; sandy-hilly region

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Introduction

Soil microorganisms play critical roles in nutrient cycling, soil structural formation, and plant interactions—functions that are essential for reestablishing soil microbial function and biodiversity during ecosystem restoration (Fu et al., 2008; Cui, 2021). However, anthropogenic activities (e.g., afforestation) and climate change can directly or indirectly affect soil physicochemical properties (Yang et al., 2017), thereby altering the structure and function of soil microbial communities (Dong and Zheng, 2009; Ge et al., 2013; Sun et al., 2013; Huang et al., 2019; Zhao et al., 2020). These changes subsequently influence plant productivity by regulating the availability of plant nutrients (Wu et al., 2008; Zhao et al., 2018). In arid and semi-arid regions, soil microbes play a vital role in ecosystem protection and in maintaining stable productivity of plant communities. In recent decades, the area of degraded land in China has tended to increase in response to global climate change and intensified anthropogenic activities. Consequently, artificial vegetation has become the most rapid and effective means to improve the ecological environment (He et al., 2005; Zhao et al., 2018). China is now reported to have planted approximately one-third of the world's total area of artificial forests (Zhang and Gao, 2000). In recent years, the effects of artificial afforestation on soil physicochemical properties and microbial communities have received increasing attention and become a research hotspot in ecological studies.

Previous studies have examined the effects of artificial forest plantations on the structure and diversity of soil microbial communities and physicochemical properties. For instance, Zhao et al. (2020) studied the effects of artificial *Pinus massoniana* Lamb. forests of different ages on soil microbial community structures and metabolic functional diversity, finding that forest age had a significant effect on soil microbial community structure. Yu et al. (2015) investigated the effects of artificial sea buckthorn forests of different ages in a hilly loess region on soil microbial community structure and soil nutrient characteristics, revealing that total phospholipid fatty acid content and total bacterial content reached their maximum in mature forests, while total fungi peaked in middle-aged forests and then decreased slightly in mature forests. Wu et al. (2015) found that soil nutrient content is closely related to the functional diversity of soil microorganisms, and that declines in soil nutrient content inevitably reduce microbial diversity. Collectively, these studies have shown that artificial forest plantations have significant effects on soil microbial community structures and diversity. However, these studies mainly focused on the impact of planting single plant species on soil microorganism communities. The impacts of different plant species plantations on microorganisms are relatively rare, and only a few studies provide direct comparisons and analyses of the diversity of soil bacterial and fungi communities in different artificial forests.

The sandy-hilly region of Shanxi Province, Northwest China is a typical agriculture-pasture interlaced zone, where soil erosion, land degradation, and blown-sand activities are severe (Wang et al., 2018). To achieve wind prevention, people planted sand-fixation artificial forests in this region since the 1980s. The planted shrub species are mainly the drought-tolerant and barrenness-tolerant *Caragana korshinskii* Kom. (Liang et al., 2019), and the planted arbor species mainly include *P. tomentosa*, *P. simonii*, *S. matsudana*, and *P. tabulaeformis*. A succession of ecological restoration and construction projects have clearly improved vegetation cover and alleviated soil erosion and water loss in the sandy-hilly region. Previous studies on artificial forests in this region have mainly focused on their effects on soil moisture (Zhao et al., 2004; Guo and Shao, 2010; Xu et al., 2021), soil nutrients (Chang and Yue, 2008; Zhang et al., 2011; Yu et al., 2021), and understory herbaceous plants (Zhao et al., 2011; Shu et al., 2021). Wang and Li (1989) and Liang et al. (2014) investigated the characteristics of soil moisture content in artificial *C. korshinskii* forests of different ages in the sandy-hilly region, showing that soil moisture content tends to decrease with increasing forest age. Liu et al. (2022) researched the vegetation communities and soil properties of 50-year-old artificial *C. korshinskii* forests and found that with increasing age, soil organic carbon, pH value, and rapidly available soil nitrogen and potassium tended to increase, while soil moisture content, salinity, and rapidly available soil phosphorus tended to decrease. Additionally, the improvement in soil environment brings about a significant increase in the variety and quantity of herbaceous plants, as well as changes in dominant species. The understory herbaceous plant species were found to be most abundant in 30-year-old artificial *C. korshinskii* forests (Cui et al., 2018). However, relatively few studies have focused on characterizing the soil bacterial and fungal communities in different artificial forests in the sandy-hilly region. In this study, we comparatively analyzed the main artificial *C. korshinskii*, *P. tomentosa*, *P. simonii*, *S. matsudana*, and *P. tabulaeformis* plantations in the sandy-hilly region based on soil bacterial and fungal community composition and diversity, and the relationship between soil microorganisms and soil environmental factors. The objective of this study was to provide a scientific basis for the maintenance and cultivation of soil fertility, the conservation of soil microbial diversity, and comprehensive ecological governance for the agriculture-pasture interlaced zone of Shanxi Province, Northwest China.

2.1 Study Area

The study area was located in Shizuitou Village, Xinzhou City, Shanxi Province, China (38°44 –39°17 N, 111°28 –113°00 E; 1200–1400 m a.s.l.). The region is dominated by a temperate continental monsoon climate, with frequent sandstorms in spring and most rainfall occurring from June to September. The average annual wind speed is 2.8 m/s, annual precipitation is approximately 400 mm, annual evaporation is 1913 mm, and daily mean temperature is 4.1°C–5.5°C. The main soil type is loess-like light chestnut brown soil, with a loose texture, high porosity, and low fertility. The main artificial arbor species planted in the sandy-hilly region include *P. simonii*, *P. tomentosa*, *S. matsudana*, and *P. tabulaeformis*, while the main shrub species is *C. korshinskii* and the understory herbaceous plants include *Bothriochloa ischaemum* (L.) Keng, *Artemisia* spp., and *Agriophyllum squarrosum* (L.) Moq. The morphological characteristics of the arbor and shrub species are presented in Table 1 .

Table 1 Morphological characteristics of dominant plant species

Indicator	*Caragana korshinskii*	*Populus tomentosa*	*Populus simonii*	*Salix matsudana*	*Pinus tabulaeformis*
Plant height (m)	$0.42 \pm 0.02d$	$2.21 \pm 0.03d$	$5.50 \pm 0.60c$	$3.10 \pm 0.33b$	$5.17 \pm 0.55a$
Crown breadth (m)	$0.21 \pm 0.02c$	$5.67 \pm 0.50c$	$12.33 \pm 0.33a$	$2.43 \pm 0.04b$	$2.86 \pm 0.07b$
Stem diameter (cm)	$0.40 \pm 0.01c$	$7.12 \pm 0.25b$	$3.18 \pm 0.54b$	$2.33 \pm 0.10b$	$13.78 \pm 0.40a$

Note: Different lowercase letters within the same row indicate significant differences among different artificial forests at $P < 0.05$ level. Values are mean±SD.

2.2 Collecting and Pretreating Soil Samples

Soil samples were collected from two depths (0–10 and 10–20 cm) under the canopy in five artificial forests (*C. korshinskii*, *P. tomentosa*, *P. simonii*, *S. matsudana*, and *P. tabulaeformis*) from July to October 2019. A hand auger was used for sampling. The sample plots were located on flat land between hills with similar site conditions (i.e., soil matrix, vegetation, and climate). Natural recovery land with *Artemisia dalailamae* Krasch. as the dominant species was selected as a control (CK). We used a nested experimental design to randomly select three sampling sites with similar slope degree (4°–8°) and aspect (south) for each artificial forest. The slope positions of the sampling sites were located at the top-slope, mid-slope, and down-slope of each artificial forest, separated by at least 200 m. Then, three 20 m$×$20 m quadrats, separated by at least 25 m, were established at each sampling site. At each quadrat, a 3-m-wide and 20-m-long transect was set up, and five soil samples were collected under and between the artificial forest along the transect, then pooled to form two composite samples for each quadrat. For each artificial forest, 18 soil samples were collected, yielding a total of 108 soil samples. Each sample was divided into two sub-samples: one was stored at −20°C for soil DNA extraction and enzyme activity analysis, and the other was air-dried for soil physicochemical analysis (Zhang et al., 2018).

2.3 Determining Soil Physical-Chemical Properties and Enzyme Activity

The determination methods used for the physical, chemical, and biological properties of the soil are described in Table 2 .

Table 2 Determination methods used for various soil indices

Indicator	Determination method
Soil physical property	
Soil water	STEPS soil five-parameter analyzer (COMBI 5000, Berlin, Germany)
Soil chemical properties	
Organic matter	Potassium dichromate oxidation-oil bath heating method (Xi et al., 2015)
Total nitrogen	Semi-micro Kjeldahl method
Total phosphorus	Sodium hydroxide alkali melting-molybdenum antimony anti-colorimetric method
Soil biological properties	
β-glucosidase	Colorimetric method of nitrophenol (Xu et al., 2018)
Alkaline phosphatase	Colorimetric method of phenyl disodium phosphate (Liu et al., 2019)
Urease	Sodium phenol-sodium hypochlorite colorimetric method
Soil microorganism	Illumina MiSeq high-throughput sequencing was conducted by Beijing Baimaike Biological Co., Ltd., Beijing, China

2.4 Soil Sample DNA Extraction and High-Throughput Sequencing

Three duplicate soil samples collected at depths of 0–10 and 10–20 cm from different artificial forests were mixed. Then, 0.5 g was taken from the mixed samples for DNA (deoxyribonucleic acid) extraction using a Power Soil DNA Isolation Kit according to the manufacturer's instructions. For the extracted genomic DNA, the 16S rDNA V3-V4 bacterial regions were amplified using the forward primer 5 -ACTCCTACGGGAGGCAGCA-3 and reverse primer 5 -GGACTACHVGGGTWTCTAAT-3 , and the ITS-ITS1 fungal regions were amplified using the forward primer 5 -CTTGGTCATTTAGAGGAAGTAA-3 and reverse primer 5 -GCTGCGTTCTTCATCGATGC-3 . PCR amplification based on primer sequences was performed under the following reaction conditions: pre-denaturation at 95°C for 5 min, denaturation at 95°C for 1 min, annealing at 50°C for 1 min, extension at 72°C for 1 min for 15 cycles, then final extension at 72°C for 7 min, and storage at 4°C. The amplification products were subjected to 2% agarose gel electrophoresis. Finally, the amplification products were subjected to Illumina MiSeq high-throughput sequencing and analysis. The sequencing and bioinformatic services for this study were provided by Beijing Biomarker Technologies Co., Ltd., Beijing, China.

2.5 Data Processing and Analysis

Operational taxonomic unit (OTU) analysis was conducted for the microbial communities. First, sequences were processed using QIIME2 (quantitative insights into microbial ecology) software by performing the following steps: (1) eliminating sequences <50 bp in length and reads with sequence tail quality <20; (2) filtering low-complexity sequences to remove sequences in non-amplified regions from the pre-processed sequences; and (3) identifying and removing chimeras using UCHIME v.8.1. The qualified sequences were then subjected to OTU clustering at the 97% similarity level using USEARCH v.10.0, and bacterial and fungal sequences were comparatively analyzed using the Silva (http://www.arb-silva.de/) and Unite (Release v.8.0, https://unite.ut.ee/) databases, respectively. Finally, the 97% similarity level was used as a threshold to classify the OTUs. Microbial community diversity was analyzed using bacterial and fungal alpha diversity indices (including community richness indices ACE and Chao1, and Shannon diversity index) for the soil samples using QIIME2.

2.6 Statistical Analysis

One-way analysis of variance (ANOVA) was conducted using SPSS v.21.0 to determine differences in soil physicochemical properties and soil enzyme activity at the same soil depth between different sample plots, with statistical significance indicated at $P < 0.05$. Redundancy analysis (RDA) was conducted using Canoco v.4.0 to examine relationships between soil physicochemical properties, enzyme activity, and microbial diversity. Graphs of dominant species composition and diversity indices at each taxonomic level were generated using Origin v.9.0. Correlations between bacterial and fungal community diversities and environmental factors were assessed using R v.4.1.0.

3.1.1 Dominant Microbial Communities at the Phylum Level

Among soil microorganisms in the five artificial forests, eight bacterial phyla had abundances >1%: Proteobacteria, Acidobacteria, Actinobacteria, Chloroflexi, Gemmatimonadetes, Bacteroidetes, Verrucomicrobia, and Rokubacteria. At the phylum level, there were no significant differences in the dominant bacterial community compositions among the five artificial forests, while microorganisms from four phyla (Proteobacteria, Acidobacteria, Actinobacteria, and Chloroflexi) constituted the dominant bacterial communities, with collective relative abundances of approximately 79.9%–83.4%. The relative abundance of Proteobacteria was the highest (28.2%–36.9%), followed by Acidobacteria (17.8%–22.5%), Actinobacteria (15.0%–21.0%), and Chloroflexi (8.2%–13.9%; Fig. 1 [Figure 1: see original paper]). Relative abundances of the bacterial communities were significantly different among the five artificial forests. The descending order for Proteobacteria in the five artificial forests was as follows: *P. tomentosa*, *C. korshinskii*, *S. matsudana*, *P. tabulaeformis*, and *P. simonii*; values for *P. tomentosa* and *C. korshinskii* were significantly higher than those for *S. matsudana*, *P. tabulaeformis*, and *P. simonii.* The relative abundance of Acidobacteria in descending order was as follows: *C. korshinskii*, *P. simonii*, *S. matsudana*, *P. tomentosa*, and *P. tabulaeformis*; values for *C. korshinskii* and *P. simonii* were not significantly different but were significantly higher than that for *P. tabulaeformis.* The descending order for Actinobacteria was as follows: *S. matsudana*, *P. simonii*, *P. tabulaeformis*, *C. korshinskii*, and *P. tomentosa*; values for *P. simonii*, *S. matsudana*, and *P. tabulaeformis* were significantly higher than that for *P. tomentosa.* The descending order for Chloroflexi was as follows: *P. tabulaeformis*, *P. simonii*, *S. matsudana*, *P. tomentosa*, and *C. korshinskii*; values for *P. simonii*, *S. matsudana*, and *P. tabulaeformis* were significantly higher than that for *C. korshinskii* (Fig. 1a).

In the five artificial forests, the fungal phyla Ascomycota, Basidiomycota, Mortierellomycota, Glomeromycota, Chytridiomycota, Zoopagomycota, Olpidiomycota, and Kickxellomycota had relative abundance values >1%. The Ascomycota, Basidiomycota, and Mortierellomycota phyla constituted the dominant fungal communities, with collective relative abundances of approximately 66.0%–99.1%. The highest value was for Ascomycota (23.8%–75.7%), followed by Basidiomycota (5.9%–70.5%), and Mortierellomycota (0.4%–14.5%). The species composition and relative abundances of the fungal communities were significantly different among the five artificial forests. In the artificial forest of *P. tabulaeformis*, the relative abundance of Basidiomycota was the highest, followed by Ascomycota. In *C. korshinskii*, *P. tomentosa*, *P. simonii*, and *S. matsudana* forests, the relative abundance of Ascomycota was the highest. In *C. korshinskii*, the relative abundance of Mortierellomycota was also quite high. The relative abundance of Ascomycota in the five artificial forests in descending order was as follows: *P. tomentosa*, *S. matsudana*, *P. simonii*, *C. korshinskii*, and *P. tabulaeformis.* Its relative abundance was significantly higher in *P. tomentosa* forest compared with those of *C. korshinskii* and *P. tabulaeformis.* The relative abundance of Basidiomycota in descending order was as follows: *P. tabulaeformis*, *P. simonii*, *S. matsudana*, *C. korshinskii*, and *P. tomentosa.* Its relative abundance was significantly higher in the artificial forest of *P. tabulaeformis* than in the other four artificial forests. The relative abundance of Mortierellomycota in descending order was as follows: *C. korshinskii*, *S.*

matsudana, *P. tabulaeformis*, *P. tomentosa*, and *P. simonii*; the value for *C. korshinskii* was significantly higher than those of the other four forests (Fig. 1b).

3.1.2 Dominant Microbial Communities at the Class Level

The dominant bacterial classes of the five artificial forests, including Alphaproteobacteria, Gammaproteobacteria, subgroup_6, and Acidimicrobiia, were not significantly different, while the relative abundances of dominant microbial communities were significantly different ($P < 0.05$; Fig. 1c [Figure 1: see original paper]). The relative abundance of Alphaproteobacteria in descending order was as follows: *P. tomentosa*, *C. korshinskii*, *P. tabulaeformis*, *P. simonii*, and *S. matsudana*; the value for *P. tomentosa* was significantly higher than those of *P. tabulaeformis* and *S. matsudana.* The relative abundance of Gammaproteobacteria in descending order was as follows: *C. korshinskii*, *S. matsudana*, *P. tomentosa*, *P. simonii*, and *P. tabulaeformis*; values for *C. korshinskii* and *S. matsudana* were significantly higher than that of *P. tabulaeformis.* The relative abundance of subgroup_6 in descending order was as follows: *C. korshinskii*, *P. simonii*, *S. matsudana*, *P. tomentosa*, and *P. tabulaeformis*; the value for *C. korshinskii* was significantly higher than those of the other four forests. The relative abundance of Acidimicrobiia in descending order was as follows: *S. matsudana*, *P. tabulaeformis*, *P. simonii*, *P. tomentosa*, and *C. korshinskii*; the value for *S. matsudana* was significantly higher than those of the other four forests.

At the class level, the dominant fungal classes of the five artificial forests showed significant differences in the soils ($P < 0.05$). In *C. korshinskii*, the dominant fungal communities were Sordariomycetes, Agaricomycetes, and Mortierellomycetes, whereas in *P. tomentosa* and *P. simonii*, Sordariomycetes and Agaricomycetes were the dominant communities. In *S. matsudana*, the dominant fungal communities were Sordariomycetes, Agaricomycetes, and Eurotiomycetes, while in *P. tabulaeformis*, Sordariomycetes were dominant (Fig. 1d [Figure 1: see original paper]). The relative abundance of Sordariomycetes in the five artificial forests in descending order was as follows: *S. matsudana*, *P. simonii*, *P. tomentosa*, *C. korshinskii*, and *P. tabulaeformis*, while for Agaricomycetes the descending order was as follows: *P. tabulaeformis*, *P. simonii*, *S. matsudana*, *C. korshinskii*, and *P. tomentosa.* The relative abundance of Dothideomycetes in descending order was as follows: *C. korshinskii*, *S. matsudana*, *P. tabulaeformis*, *P. tomentosa*, and *P. simonii*; while that of Mortierellomycetes was *C. korshinskii*, *S. matsudana*, *P. tabulaeformis*, *P. tomentosa*, and *P. simonii.*

3.1.3 Dominant Microbial Communities at the Family Level

At the family level, the compositions of Sphingomonadaceae, uncultured_c_subgroup_6, Gemmatimonadaceae, and Clostridiaceae, which were the dominant bacterial communities of the five artificial forests, did not show significant differences in the soils. However, the relative abundance of the dominant bacterial families was significantly different among the five artificial forests ($P < 0.05$; Table 3). The relative abundance of Sphingomonadaceae in descending order was as follows: *P. tomentosa*, *C. korshinskii*, *P. tabulaeformis*, *S. matsudana*, and *P. simonii.* The relative abundance of uncultured_c_subgroup_6 in descending order was as follows: *C. korshinskii*, *P. simonii*, *S. matsudana*, *P. tomentosa*, and *P. tabulaeformis*; the value for *C. korshinskii* was significantly higher than those of the other forests. The relative abundance of Gemmatimonadaceae in descending order was *P. tabulaeformis*, *C. korshinskii*, *S. matsudana*, *P. simonii*, and *P. tomentosa*; the value for *P. tabulaeformis* was significantly higher than those in the other four forests. The relative abundance of Pyrinomonadaceae in descending order was as follows: *P. tomentosa*, *P. simonii*, *P. tabulaeformis*, *C. korshinskii*, and *S. matsudana*; the value for *P. tomentosa* forest was significantly higher than those of the other four forests.

The dominant fungal families of the five artificial forests were significantly different in the soils ($P < 0.05$; Table 3). In *C. korshinskii*, the dominant fungal families included Inocybaceae, Mortierellaceae, and Chaetomiaceae; in *P. tomentosa*, they were Inocybaceae and Cortinariaceae; in *P. simonii*, they were Inocybaceae, Sordariaceae, and Thelephoraceae; in *S. matsudana*, they were Inocybaceae, Cortinariaceae, and Eurotiaceae; and in *P. tabulaeformis*, they were Inocybaceae and Thelephoraceae. The relative abundance of Inocybaceae in descending order was as follows: *P. tabulaeformis*, *P. simonii*, *C. korshinskii*, *S. matsudana*, and *P. tomentosa*; the value for *P. tabulaeformis* was significantly higher compared with those of the other four forests. The relative abundance of Cortinariaceae in descending order was as follows: *S. matsudana*, *P. tomentosa*, *P. simonii*, *C. korshinskii*, and *P. tabulaeformis*; the value for *C. korshinskii* was significantly higher compared with those of the other four forests. The relative abundance of Mortierellaceae in descending order was as follows: *C. korshinskii*, *S. matsudana*, *P. tabulaeformis*, *P. tomentosa*, and *P. simonii*; the value for *C. korshinskii* was significantly higher compared with those of the other four forests. The relative abundance of Chaetomiaceae in descending order was as follows: *C. korshinskii*, *S. matsudana*, *P. tabulaeformis*, *P. tomentosa*, and *P. simonii*; the value for *C. korshinskii* was significantly higher compared with those of the other four forests.

Table 3 Dominant families and relative abundances of soil bacterial and fungal communities in different artificial forests

Community	Classification	Relative abundances (%)				
		Caragana korshinskii	*Populus tomentosa*	*Populus simonii*	*Salix matsudana*	*Pinus tabulaeformis*
Bacteria	Sphingomonadaceae	14.3 ± 2.5*a*	9.3± 1.2*ab*	11.9± 2.4*ab*	5.7± 1.4*b*	10.1± 0.3*a*
	Uncultured_c_subgroup_6	9.5 ± 0.4*ab*	8.1± 0.4*c*	10.0± 0.2*ab*	6.1± 1.1*b*	9.1± 0.2*b*
	Gemmatimonadaceae	8.3 ± 0.5*bc*	6.4± 0.5*c*	7.1± 0.4*bc*	7.9± 0.8*bc*	10.4± 1.4*a*
	Pyrinomonadaceae	4.8 ± 0.3*ab*	6.1± 0.9*a*	4.8± 0.6*ab*	4.3± 0.5*ab*	7.0± 1.6*b*
	Nitrosomonadaceae	2.6 ± 0.4*ab*	2.4± 0.5*b*	3.4± 0.5*ab*	4.7± 0.5*ab*	3.3± 0.5*ab*
	Uncultured_o_IMCC26256	2.3 ± 0.2*cd*	1.8± 0.1*d*	2.2± 0.1*cd*	3.3± 0.4*a*	2.1± 0.0*cd*
	Uncultured_c_KD4-96	1.6 ± 0.1*c*	2.9± 0.5*ab*	4.1± 0.5*a*	2.6± 0.2*bc*	4.1± 0.0*a*
Fungi	Inocybaceae	3.8 ± 2.1*bc*	11.6± 3.5*bc*	19.4± 1.8*b*	12.3± 3.0*bc*	39.8± 4.4*a*
	Cortinariaceae	17.1 ± 9.4*b*	0.0± 0.0*b*	0.1± 0.0*b*	7.8± 4.8*ab*	5.3± 2.2*ab*
	Mortierellaceae	14.9 ± 6.6*a*	0.7± 0.2*b*	0.4± 0.1*b*	11.9± 5.0*a*	0.5± 0.1*b*
	Chaetomiaceae	13.3 ± 2.3*a*	0.1± 0.0*b*	0.1± 0.0*b*	2.3± 0.6*b*	1.0± 0.3*b*
	Thelephoraceae	0.2 ± 0.1*c*	3.0± 0.8*c*	6.9± 1.3*b*	2.3± 0.6*b*	3.2± 0.6*c*
	Eurotiaceae	0.0 ± 0.0*b*	2.3± 1.5*b*	13.5± 6.3*a*	4.9± 3.1*ab*	0.0± 0.0*b*
	Nectriaceae	0.1 ± 0.0*b*	0.2± 0.1*c*	1.7± 0.2*bc*	1.0± 0.3*c*	1.7± 0.1*b*

Note: OTU, operational taxonomic unit. Different lowercase letters within the same row indicate significant differences among different artificial forests at $P < 0.05$ level. Values are mean±SD.

3.1.4 Dominant Microbial Communities at the Genus Level

At the genus level, the five artificial forests did not show significant differences in the dominant bacterial genera ($P > 0.05$). The dominant bacterial genera were uncultured_c_subgroup_6, *Sphingomonas*, uncultured_bacterium_f_Gemmatimonadaceae, and RB41.

The dominant fungal genera of the five artificial forests showed significant differences in the soils ($P < 0.05$; Fig. 2 [Figure 2: see original paper]). At the natural recovery plot (CK), *Mortierella* and *Chaetomium* were the dominant genera, whereas *Inocybe* and *Mortierella* were the dominant genera in *C. korshinskii*. In *P. tomentosa*, *P. simonii*, and *S. matsudana*, *Inocybe* and *Cortinarius* were the dominant genera; *Inocybe* and *Tricholoma* were the dominant genera in *P. tabulaeformis* (Fig. 2b). In *P. tabulaeformis*, *Inocybe* was significantly higher than those of the other four forests. In *C. korshinskii*, *Mortierella* and *Cladosporium* were significantly higher than those of the other four forests.

3.2 Alpha Diversity of Soil Microbial Communities

Eligible sequences were subjected to OTU clustering based on 97% similarity. The alpha diversity of soil bacterial and fungal communities in the five forests is shown in Figure 3 [Figure 3: see original paper]. ACE and Chao1 indices are used to measure species richness, with higher values indicating greater richness. The Shannon index measures community diversity, with higher values indicating greater diversity. Alpha diversity of soil microbial communities was significantly different among the five artificial forests ($P < 0.05$). ACE and Chao1 indices of soil bacterial communities in descending order were as follows: *C. korshinskii*, *S. matsudana*, *P. tabulaeformis*, *P. simonii*, and *P. tomentosa*. ACE and Chao1 indices of soil bacterial communities were significantly higher in *C. korshinskii* compared with those of the other four forests ($P < 0.05$), but were not significantly different among the other forests (Figs. 3a and 3b). Shannon index for soil bacterial communities in descending order was as follows: *C. korshinskii*, *S. matsudana*, *P. simonii*, *P. tabulaeformis*, and *P. tomentosa*. Specifically, the Shannon index of soil bacterial communities was significantly higher in *C. korshinskii* than in the other four forests (Fig. 3c).

ACE index for soil fungal communities in descending order was as follows: *C. korshinskii*, *S. matsudana*, *P. tomentosa*, *P. tabulaeformis*, and *P. simonii*; the value for *C. korshinskii* was significantly higher than those of the other four forests ($P < 0.05$), which were not significantly different (Fig. 3d). Chao1 index of soil fungal communities in descending order was as follows: *C. korshinskii*, *S. matsudana*, *P. tabulaeformis*, *P. tomentosa*, and *P. simonii*; the value for *C. korshinskii* was significantly higher than those of the other four forests (Fig. 3e). Shannon indices for soil fungal communities in descending order were as follows: *C. korshinskii*, *P. tabulaeformis*, *S. matsudana*, *P. simonii*, and *P. tomentosa*; the value for *C. korshinskii* was significantly higher than those of the other four forests (Fig. 3f). Overall, the richness and diversity of soil bacterial and fungal communities were highest in *C. korshinskii*, followed by *S. matsudana*, and relatively low in *P. tomentosa* and *P. simonii*.

3.3 Beta Diversity of Soil Microbial Communities

For the five artificial forests, inter-group differences in bacterial and fungal communities were greater than intra-group differences ($R^2 = 0.246$ and $R^2 = 0.809$, respectively), and these differences were significant ($P < 0.05$; Fig. 4 [Figure 4: see original paper]). Differences in beta diversity for bacterial communities between *C. korshinskii* and *P. tomentosa* forests were more significant than those among *P. simonii*, *S. matsudana*, and *P. tabulaeformis*, with only slight differences in bacterial community beta diversity among *P. simonii*, *S. matsudana*, and *P. tabulaeformis* (Fig. 4a). Differences in beta diversity for fungal communities between *C. korshinskii* and *P. tomentosa* were more significant than those between *S. matsudana* and *P. tabulaeformis*, with only slight differences between *S. matsudana* and *P. tabulaeformis* (Fig. 4b).

3.4 Soil Physical-Chemical Properties

Soil physicochemical properties such as soil moisture, total nitrogen, and total phosphorus were significantly affected by the five artificial forests. At the 0–10 cm depth, soil moisture content in descending order was as follows: *P. tomentosa*, *P. simonii*, CK, *P. tabulaeformis*, *S. matsudana*, and *C. korshinskii*. At the 10–20 cm depth, soil moisture content in descending order was as follows: CK, *P. tomentosa*, *P. tabulaeformis*, *S. matsudana*, *P. simonii*, and *C. korshinskii*. Soil moisture content was significantly lower in *C. korshinskii* compared with that in *P. tomentosa* at both 0–10 and 10–20 cm depths ($P < 0.05$; Fig. 5a [Figure 5: see original paper]). At the 0–10 cm depth, soil total nitrogen content was significantly affected by the five artificial forests. Soil total nitrogen contents in *P. tomentosa*, *P. simonii*, and *S. matsudana* were significantly higher than those in *C. korshinskii* and *P. tabulaeformis*, reaching the lowest value in *C. korshinskii*. At the 10–20 cm depth, soil total nitrogen content was not significantly different among the five artificial forests (Fig. 5b). At both 0–10 and 10–20 cm depths, soil organic matter content was not significantly affected by the five artificial forests. However, soil organic matter content of the five forests was significantly lower than that of CK (Fig. 5c). At the 0–10 cm depth, soil total phosphorus content was significantly affected by the five artificial forests. Soil total phosphorus contents in *P. tomentosa* and *P. simonii* were significantly higher than those in *C. korshinskii* and *P. tabulaeformis*, with maximum and minimum values found in *P. simonii* and *P. tabulaeformis*, respectively. At the 10–20 cm depth, soil total phosphorus content was not significantly affected by the five artificial forests (Fig. 5d).

3.5 Soil Enzyme Activity

Soil β-glucosidase and urease activities were significantly affected by the five artificial forests ($P < 0.05$). At the 0–10 cm depth, soil β-glucosidase was not significantly affected; however, values were all higher than CK. The lowest and highest β-glucosidase activities were obtained in CK and *S. matsudana*, respectively. At the 10–20 cm depth, soil β-glucosidase was significantly affected by the five artificial forests. Values in descending order were as follows: *P. tomentosa*, *S. matsudana*, *P. tabulaeformis*, *P. simonii*, and *C. korshinskii*. β-glucosidase in *P. tomentosa* and *S. matsudana* was significantly higher than that in *C. korshinskii*, *P. simonii*, and *P. tabulaeformis* (Fig. 6a [Figure 6: see original paper]). Soil urease activity was significantly affected by the five artificial forests at both 0–10 and 10–20 cm soil depths. At the 0–10 cm depth, urease activity in descending order was as follows: CK, *S. matsudana*, *C. korshinskii*, *P. simonii*, *P. tabulaeformis*, and *P. tomentosa*. At the 10–20 cm depth, the descending order of urease activity was as follows: CK, *C. korshinskii*, *S. matsudana*, *P. simonii*, *P. tomentosa*, and *P. tabulaeformis* (Fig. 6b). Alkaline phosphatase activity was not significantly affected by the five artificial forests at either 0–10 or 10–20 cm depths; however, values were significantly lower than CK (Fig. 6c). Overall, soil β-glucosidase activity was higher than those of alkaline phosphatase and urease. Planting artificial forests can improve soil β-glucosidase activity.

3.6 Effects of Environmental Factors

The correlation matrix between bacterial community diversity indices and environmental factors showed that soil bacterial diversity was correlated with soil environmental factors. For soil bacterial communities, ACE index was very significantly and positively correlated with Chao1 and Shannon indices, and significantly and negatively correlated with total nitrogen content. Chao1 index was significantly and negatively correlated with soil moisture content, and very significantly and negatively correlated with total nitrogen content (Table 4). The correlation matrix between fungal community diversity indices and environmental factors showed that ACE index of soil fungal communities was significantly and negatively correlated with total phosphorus content and alkaline phosphatase activity. Shannon index was very significantly and positively correlated with urease activity (Table 5). Overall, soil moisture content and total nitrogen content were identified as key environmental factors affecting bacterial community abundance and diversity, whereas total phosphorus content, alkaline phosphatase, and urease activities were identified as important environmental factors affecting fungal community abundance and diversity.

To examine correlations between microbial community composition and soil environmental factors, we conducted RDA analysis using genus-level microbial communities as response variables and soil physical, chemical, and biological properties as environmental explanatory variables. RDA results between bacterial community structure and soil environmental factors showed that the cumulative explanatory power of the first and second axes for bacterial communities was 67.6% and 88.8%, respectively. The main environmental factors affecting bacterial community structures included total phosphorus content, organic matter content, and urease activity. Dominant bacterial genera including uncultured_c_subgroup_6, *Sphingomonas*, and uncultured_bacterium_f_Gemmatimonadaceae in the five forests were positively correlated with soil total phosphorus content, organic matter content, and urease activity (Fig. 7a [Figure 7: see original paper]).

For soil fungal communities, the cumulative explanatory power of the first and second axes was 53.9% and 84.5%, respectively. The main environmental factors affecting fungal community structures included total nitrogen content, organic matter content, β-glucosidase activity, and urease activity (Fig. 7b). Dominant fungal genera including *Inocybe*, *Mortierella*, and *Cladosporium* in *C. korshinskii* were significantly correlated with organic matter content, urease activity, and β-glucosidase activity. Dominant fungal genera including *Inocybe*, *Cortinarius*, and *Penicillium* in *P. tomentosa* and *S. matsudana* were significantly correlated with total nitrogen content. Dominant fungal genera including *Inocybe*, *Cortinarius*, and *Tomentella* in *P. simonii* were correlated with β-glucosidase activity. Dominant fungal genera including *Inocybe*, *Tricholoma*, and *Tomentella* in *P. tabulaeformis* were significantly correlated with β-glucosidase activity.

4.1 Effects of Different Artificial Forests on Soil Microbial Community Composition

This study showed that the dominant bacterial phyla in the artificial *C. korshinskii*, *P. tomentosa*, *P. simonii*, *S. matsudana*, and *P. tabulaeformis* forests were Proteobacteria, Acidobacteria, Actinobacteria, and Chloroflexi, and their relative abundance levels differed significantly among the five forests ($P < 0.05$). These results are consistent with the findings of Wang et al. (2019), who investigated the effects of different vegetation types on soil microorganisms in the Chinese Loess Plateau. Specifically, Proteobacteria, Chloroflexi, Acidobacteria, and Actinobacteria had the highest relative abundances in *P. tomentosa*, *P. tabulaeformis*, *C. korshinskii*, and *S. matsudana* forests, respectively. The dominant fungal phyla included Ascomycota, Basidiomycota, and Mortierellomycota, consistent with the conclusions of Huang et al. (2018) for soil microorganisms in arid and semi-arid regions. Basidiomycota had the highest abundance in *P. tabulaeformis*, followed by Ascomycota. In the other four forests, the relative abundance of Ascomycota was highest, whereas that of Mortierellomycota was relatively high in *C. korshinskii*. Due to differences in ground vegetation, dry branches, fallen leaves, and root exudates varied among the five artificial forests and changed the soil physicochemical properties. Consequently, the composition and relative abundance of soil microbial communities also differed among the five artificial forests (Zhang et al., 2002; Wu et al., 2008).

The dominant bacterial genera in the five artificial forests were not significantly different and included uncultured_c_subgroup_6, *Sphingomonas*, uncultured_f_Gemmatimonadaceae, and RB41. In contrast, the dominant fungal genera differed in composition among different artificial forests and included *Inocybe*, *Mortierella*, *Cortinarius*, *Tricholoma*, and *Penicillium.* These results showed that different artificial forests affected fungal communities more significantly than bacterial communities and that bacterial communities were relatively stable across the five artificial forests. These results differ from those of Deng et al. (2020) and Wang et al. (2020). Deng et al. (2020) investigated the composition and functional characteristics of soil fungal communities in different artificial forests in a windy and sandy region of northwestern Liaoning Province, showing that the dominant fungal genera in the region included *Guehomyces*, *Mortierella*, and *Penicillium.* In contrast, Wang et al. (2020) studied soil microorganisms in lilac shrubs in the Helan Mountains, showing that the dominant bacterial genera included *Sphingomonas*, RB41, *Lysobacter*, and H16, and that the dominant fungal genera included *Clonostachys*, *Saccharomycopsis*, *Fusarium*, and *Mortierella.* These differences may reflect heterogeneity in habitat conditions (e.g., climate, soil, vegetation, and landform). Microbial communities can thus respond differently to environmental factors under different land use and vegetation conditions, resulting in changes to both their number and composition.

Soil microorganisms can promote plant growth by regulating nutrient supply and metabolism, while some pathogenic microorganisms can cause plant decline or death (Ning et al., 2022). Among the microbial communities, certain bacterial (e.g., *Sphingomonas* and uncultured_f_Gemmatimonadaceae) and fungal genera (e.g., *Inocybe*, *Mortierella*, *Chaetomium*, and *Tomentella*) can promote plant growth. Specifically, *Cortinarius* and *Tricholoma* are important ectomycorrhizal fungi that can promote forest growth, improve forest stress resistance, and increase afforestation survival and forest productivity. Consequently, these are vital for maintaining the stability of forest ecosystems (Li et al., 2018; Wang et al., 2021). *Inocybe*, *Mortierella*, and *Penicillium* play important roles in the cycling of carbon, nitrogen, and phosphorus in the soil (Peng et al., 2019; Zhang et al., 2019). Significant changes in the dominant bacterial and fungal species showed that the relative abundance of *Cladosporium* was highest in *C. korshinskii* (Fig. 8 [Figure 8: see original paper]). *Cladosporium* is a common genus of endophytic fungi, and most are saprophytic, but some cause secondary plant infections that can produce leaf spot, leaf mold, fruit rot, stem rot, textile decay, and wood decay, leading to serious losses in agricultural products. A few *Cladosporium* fungi can also cause human and animal diseases (Jiao et al., 2019). Some studies have argued that artificial sand-fixing *C. korshinskii* forests are characterized by strong adaptability, drought and barren tolerance, and rapid growth at early and middle planting stages, but face problems such as growth slowdown, premature senescence, and pest and disease damage approximately 30 years after planting. In the future, adverse influences of pathogenic microorganisms (e.g., *Cladosporium*) on the growth of *C. korshinskii* in northwestern Shanxi Province will need to be considered. Overall, the relative abundance of beneficial microorganisms (e.g., *Inocybe*, *Mortierella*, *Chaetomium*, and *Tomentella*) was highest in *P. tabulaeformis*, followed by *C. korshinskii*, and lowest in *P. tomentosa*.

4.2 Effects of Different Forest Types on Soil Microbial Community Diversity

Previous studies have shown that land use patterns can affect soil physicochemical properties through vegetation diversity and heterogeneity and different management measures, which subsequently affect the diversity and composition of soil microorganisms (Guo, 2017; Deng et al., 2020). This study found that alpha diversity of soil bacterial and fungal communities was highest in *C. korshinskii*, followed by *S. matsudana*, but relatively low in *P. tomentosa* and *P. simonii*. This may be due to the following factors: (1) *C. korshinskii*, as a leguminous shrub species, hosts a large number of rhizobia on its roots that can fix atmospheric nitrogen and increase soil nitrogen content; and (2) *C. korshinskii* has luxuriant branches and leaves, and when they fall, they can increase soil organic matter and total nitrogen, thus improving soil fertility (Niu et al., 2003). Consequently, increased soil nutrient content can enhance the abundance and diversity of soil microorganisms (Niu et al., 2003). The abundance and diversity of soil bacterial and fungal communities were relatively low in *P. tomentosa* and *P. simonii*, primarily because their dry branches and fallen leaves contain large quantities of slowly decomposable organic matter (e.g., lignin and cellulose) (Yang et al., 2007), which results in low soil nutrient content and consequently low soil microorganism abundance and diversity.

This study also found that differences in beta diversity for bacterial communities between *C. korshinskii* and *P. tomentosa* were more significant than those among *P. simonii*, *S. matsudana*, and *P. tabulaeformis*, with only slight differences in bacterial community beta diversity among *P. simonii*, *S. matsudana*, and *P. tabulaeformis*. Differences in beta diversity for fungal communities among *C. korshinskii*, *P. tomentosa*, and *P. simonii* were more significant than that between *S. matsudana* and *P. tabulaeformis*, with only slight differences between *S. matsudana* and *P. tabulaeformis*. These results showed that *C. korshinskii* forest exhibited significant differences but low similarities in species diversity compared with the other four forests. This may be due to: (1) with increasing planting age, soil environment improves, and the variety and quantity of herbaceous plants increase significantly (Liu et al., 2022); and (2) *C. korshinskii* has a well-developed root system, which positively affects the diversity of soil microbial communities. In contrast, *P. simonii*, *S. matsudana*, and *P. tabulaeformis* do not have well-developed rootlets, and their artificial forests have relatively few herbaceous plants, dry branches, and fallen leaves on the soil surface, thus producing a smaller effect on soil microorganisms.

4.3 Correlation Between Soil Microorganisms and Soil Environmental Factors

Soil physicochemical properties are usually strongly correlated with the structure and diversity of rhizospheric microbial communities. This study found that soil moisture and total nitrogen contents were key environmental factors affecting the abundance and diversity of soil bacterial communities in Shanxi Province, while total phosphorus content, alkaline phosphatase activity, and urease activity were important environmental factors affecting fungal community abundance and diversity. These results differ somewhat from the conclusions of Liu et al. (2013) and Dai et al. (2017). Dai et al. (2017) found that soil bacterial community diversity has a positive and significant correlation with soil nutrient content (e.g., organic matter content). However, Liu et al. (2013) found that soil bacterial diversity is positively correlated with soil total nitrogen, total phosphorus, and soil organic matter content, but negatively correlated with soil pH. These discrepancies may be due to differences in environmental conditions across regions, indicating that soil microbial community diversity is not driven by a single factor but is related to a diverse and complex array of environmental factors.

RDA results showed that dominant bacterial species are significantly affected by soil total phosphorus content, soil organic matter content, and urease activity, while dominant fungal species are significantly affected by soil total nitrogen content, soil organic matter content, β-glucosidase activity, and urease activity. Evidently, soil nutrient content and enzyme activity are important regulatory factors for soil microorganisms. The dominant fungal species compositions differed among the five artificial forests because essential nutrients varied across microbial species, and the environmental factors affecting soil microorganisms were somewhat different among the five forests.

5 Conclusions

In the sandy-hilly region examined in this study, planting artificial forests significantly affected the composition and diversity of soil bacterial and fungal communities. Furthermore, soil nutrient content and enzyme activity levels were important driving factors for changes in soil microbial composition and diversity. Overall, artificial *C. korshinskii* forest had the highest abundance and diversity levels for soil bacterial and fungal communities, soil nutrient content, enzyme activity, and relative abundance of beneficial microorganisms. *P. tomentosa* forest had high soil nutrient content and enzyme activity levels but low abundance and diversity of soil microorganisms, whereas *P. simonii* had low abundance and diversity of soil microorganisms, soil nutrient content, and enzyme activity. From a microbiological perspective, the most suitable plant species for this sandy-hilly region was *C. korshinskii*, followed by *S. matsudana* and *P. tabulaeformis*. In contrast, neither *P. tomentosa* nor *P. simonii* were beneficial for increasing soil microbial abundance and diversity in Shanxi Province. *C. korshinskii* forest also had increased soil fertility and a higher abundance of certain pathogenic microorganisms compared with the other four artificial forests.

The long-

Note: Figure translations are in progress. See original paper for figures.