BMC Microbiology

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Analysis of soil microbial community structure changes in the drainage field of the Shengli coalfield based on high-throughput sequencing

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Abstract

Background The study of soil environment in drainage fields is important for environmental management and ecological restoration, and there is currently a knowledge gap in understanding the impact of soil microbial communities in the Shengli coalfield drainage fields and the corresponding ecological effects. To investigate the changes in rhizosphere soil microbial communities of different dominant plants after years of restoration, this study examines the improvement effects of different dominant plants on the soil environment.

Results This study is based on high-throughput sequencing to restore the slope of coal mine spoil after 15 years as the sampling site. The rhizosphere soil of five dominant plants was selected for microbial community analysis, and functional prediction of the microbial community was conducted. The dominant plants selected included Erect Milkvetch (*Astragalus adsurgens*), Lemongrass (*Caragana korshinskii*), Alfalfa *(Medicago sativa*), Phyllanthus pinnatifida *(Elymus dahuricus*), and Brassica Rapa (*Brassica campestris*). The results showed that after 15 years of restoration, the soil physicochemical properties in the Phyllanthus pinnatifida group were better than those in the other groups overall, but some of them were inferior to those in the lemon-stripped mallard group. Abundant saprophytic fungal communities were found in different dominant plant groups, mainly belonging to the phyla Ascomycota and Basidiomycota, resulting in significantly higher organic matter content in the dominant plant groups compared to the CK group. The bacterial communities were dominated by the phyla Actinobacteriota, Proteobacteria, Chloroflexi, and Firmicutes. Among these microbial phyla, the Phyllanthus pinnatifida group had higher abundance, which is beneficial for vegetation colonization. Redundancy analysis showed that soil pH was significantly correlated with microbial communities. Organic matter content and pH are the main factors influencing the composition of soil microbial communities, significantly affecting the composition of microorganisms in different groups. After years of restoration, the environment of the Shengli Coalfield's spoil heap has been greatly improved.

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Conclusions The planting of various beneficial plants has resulted in significant improvements to the soil microbial community and physicochemical properties, with Phyllanthus pinnatifida having the most positive impact. This lays the foundation for the subsequent restoration of the slope of the spoil heap.

Keywords Coal mine, Different dominant plants, Rhizosphere soil, Microbial community characteristics, Functional prediction

Introduction

In recent years, coal mining and utilization have had a significant impact on the soil environment [1]. As a large amount of waste dumping area is generated during coal mining, the soil environmental characteristics of the drainage site are significantly different from those of conventional farmland or natural habitats [2, 3]. The construction and management of drainage sites are important to mitigate the negative impact of coal mines on the surrounding soil ecology [4]. The soil microbial community, as one of the most sensitive and responsive components of the soil ecosystem, may have a significant response to changes in the soil environment of the drainage site. Therefore, an in-depth study of the soil microbial community structure of the drainage site can provide a scientific basis for the environmental management and ecological restoration of the drainage site.

The study of soil microbial communities has become an important area of research in contemporary environmental science [5, 6]. As an important component of soil ecosystems, soil microbial communities play a key role in soil ecological functions, nutrient cycling, plant growth, and ecosystem stability [7]. Therefore, an in-depth understanding of the structure and changes in soil microbial communities is important for maintaining soil ecosystem health as well as environmental management.

The Shengli coalfield is one of China's important coal resource extraction areas, and the study of soil environmental conditions in its drainage field is particularly important [8]. However, currently, there is relatively limited research on the changes in soil microbial community structure in the drainage field of the Shengli coalfield, leading to a knowledge gap in understanding the impact of the drainage field on soil microbial communities and their ecological effects. Therefore, this study aims to apply high-throughput sequencing technology to systematically analyze the composition and changes in the root-associated soil microbial communities of different dominant plants in the drainage field of the Shengli coalfield to reveal the mechanisms by which plants influence the soil microbial community structure and provide a scientific basis for the environmental management and ecological restoration of the Shengli coalfield drainage field.

This study collected rhizosphere soil samples of different dominant plants in the Shengli coalfield, analyzed the soil microbial community using high-throughput sequencing technology, and compared it with the surrounding natural soil. By comparison and analysis, this study aims to explore the diversity, abundance, and structural changes in soil microbial communities in the spoil heap soil of the Shengli coalfield and analyze the impact of different dominant plants on soil microbial communities.

Results and analysis

Analysis of soil physicochemical properties

The analysis of the soil physicochemical properties of the different dominant plants showed that the soil organic matter content and Avail-K (AK) content of the control group (CK) group were significantly lower than those of the dominant plants ($P<0.05$); the Olsen-P (OP) content of the *Lemongrass* (NT) rhizosphere soil was significantly higher than that of the other dominant plants ($P<0.05$), while the Alkali-N (AN) content was not significant among the different dominant plants ($P>0.05$), the soil pH value of the CK group was significantly higher than that of the dominant plants ($P<0.05$), and the soil showed strong alkalinity. Among them, the pH of the Phyllanthus pinnatifida (PJC) rhizosphere soil is the lowest, the content of soil organic matter (SOM) and OP is lower than that of Lemongrass (NT), but other indicators are better than NT. Considering comprehensively, PJC is better for improving the physicochemical environment of mine soil (Table 1).

Analysis of different dominant plant rhizosphere soil microbial Otus

The sequencing results (Table 2) showed that after double-ended sequence assembly and filtering with parameters evaluated at 97% similarity, a total of 252,565 optimized sequences of bacteria in the rhizosphere soil of different dominant plants were obtained, with an average of 17,427,583 optimized sequence bases and an average optimized sequence length of 414 bp. For fungi, a total of 256,303 optimized sequences were obtained, with an average of 10,227,331 optimized sequence bases and an average optimized sequence length of 239 bp. The results of OTU clustering analysis showed that a total of 18,534 bacterial OTUs and 5652 fungal OTUs were obtained after

Table 1 Physicochemical properties of soil between the roots of different dominant plants

Sample	SOM(g/kg)	AN(g/kg)	OP(mg/kg)	AK(mg/kg)	pH
SDW	5.02 ± 0.12 c	15.23 ± 4.33 a	3.07 ± 0.79 b	173.73 ± 1.92 d	9.09 ± 0.03 b
ZHMX	9.67 ± 0.27 b	18.14 ± 7.71 a	4.60 ± 0.60 b	348.60 ± 4.29 a	8.54 ± 0.01 c
PJC	11.21 ± 1.10 ab	24.89 ± 7.25 a	9.13 ± 1.05 b	283.03 ± 4.74 c	8.16 ± 0.02 e
NT	12.93 ± 0.32 a	22.31 ± 7.37 a	31.13 ± 5.31 a	125.93 ± 1.77 e	8.32 ± 0.03 d
YT	11.90 ± 0.43 a	21.17 ± 4.21 a	8.17 ± 2.03 b	329.20 ± 2.77 b	8.51 ± 0.03 c
CK	1.90 ± 0.11 d	13.41 ± 3.60 a	2.93 ± 0.28 b	82.57 ± 5.62 f	9.35 ± 0.04 a

CK is the control group, SDW is Erect Milkvetch, ZHMX is Alfalfa, PJC is Phyllanthus pinnatifida, NT is Lemongrass, YT is Brassica; different letters in the same column represent significant differences between different dominant plants ($P < 0.05$), the same letters represent no significant differences ($P > 0.05$), the same below

Table 2 Sample sequencing data statistics

	Sample	Sequence Number	Bases Number	Average Length	OTUs
Bacteria	CK	54,107	22,407,319	414	3176
	NT	43,680	18,096,211	414	3551
	PJC	30,938	12,796,306	414	2792
	SDW	42,418	17,550,476	414	2502
	YT	44,438	18,417,887	414	3056
	ZHMX	36,984	15,297,300	414	3457
	Average	42,094	17,427,583	414	3089
	Total	252,565	104,565,499	2484	18,534
Fungi	CK	43,857	10,725,109	245	1089
	NT	42,280	9,943,241	235	1138
	PJC	37,597	9,069,883	242	869
	SDW	41,828	10,034,476	240	659
	YT	45,217	10,829,159	239	847
	ZHMX	45,524	10,762,120	236	1050
	Average	42,717	10,227,331	239	942
	Total	256,303	61,363,988	1437	5652

clustering of effective sequences. Among them, the number of microbial OTUs in the NT rhizosphere soil was the highest, with a total of 3551 bacterial OTUs and 1138 fungal OTUs.

A random sample of all sample sequences was taken to construct dilution curves for bacterial (Fig. 1a) and fungal (Fig. 1b) sequences in terms of the number of sequences sampled versus the number of OTUs they could represent, from which the adequacy of the amount of sequencing for each sample was determined. Figure 1 shows that the dilution curves of each sample gradually flatten as the sequencing amount increases, indicating that the increase in the number of OTUs becomes less pronounced. At this sequencing depth, the sequencing data are sufficiently large to cover the majority of microbial species in the samples, allowing for a comprehensive reflection of the microbial community structure and diversity in the samples.

Different advantages of plant rhizosphere soil microbial alpha diversity

The diversity of microorganisms in the research environment can be reflected by analyzing alpha diversity, which includes a series of statistical analysis indices to estimate the species abundance and diversity of the environmental community. Statistical analysis of the alpha diversity index of rhizosphere soil microbial communities of different dominant plants showed that the overall bacterial microbial community in the soil was higher than the fungal microbial community, indicating that bacteria dominate the soil microbial environment. Among them, the diversity of soil microbial communities in the rhizosphere of PJC was significantly lower than that of other dominant plants ($P < 0.05$); the diversity of soil microorganisms in the rhizosphere of SDW also showed significant differences compared to other dominant plants ($P < 0.05$). In the rhizosphere bacterial community, the

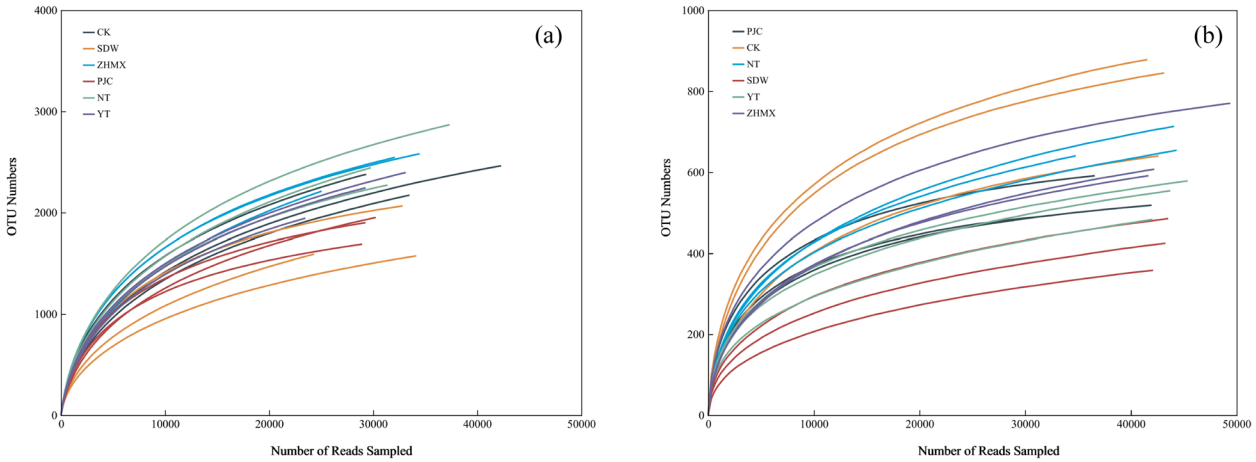

Fig. 1 Rarefaction curves based on the Mothur algorithm. **a** shows the bacterial community rarefaction curve, and (**b**) shows the fungal community rarefaction curve; when the curve tends to flatten, it indicates a reasonable amount of sequencing data. CK, the control group; SDW, Erect Milkvetch; ZHMX, Alfalfa; PJC, Phyllanthus Pinnatifida; NT, Lemongrass; YT, Brassica

Ace index of ZHMX was the highest, significantly higher than that of PJC and SDW ($P<0.05$); the Chao1 index and Shannon index of NT were the highest, significantly higher than those of PJC and SDW ($P<0.05$); there was no significant difference in the microbial coverage of different dominant plant species in the bacterial community ($P>0.05$), all reaching over 97%. Among the fungal communities, the microbial community diversity of ZHMX was significantly better than that of the other dominant plants ($P<0.05$); the microbial coverage reached more than 99%. The overall microbial community diversity of legume inter-rhizosphere soil was better than that of the grass inter-rhizosphere soil microbial community, among which the ZHMX and NT microbial communities were more significant (Table 3).

Analysis of soil microbial community composition between the roots of different dominant plants

Based on the abundance table of soil rhizosphere microorganisms and the species annotation table, the specific and shared microbial OTU numbers of each dominant plant were obtained, and their Venn diagram was drawn. Among them, there were 1258 shared OTUs among different dominant plants in the bacterial community, with the highest number in NT and the lowest in PJC, which were 236 and 147, respectively (Fig. 2a); there were 239 shared OTUs among different dominant plants in the fungal community, with the highest number in CK and the lowest in SDW, which were 188 and 49, respectively (Fig. 2b).

Table 3 Diversity Index of Rhizosphere Soil Microbial Communities with Different Advantages of Plants

	Sample	Ace	Chao1	Coverage	Shannon	Simpson
Bacteria	CK	3187.81±84.73c	3214.81±93.05b	0.9770±0.0026a	6.07±0.11b	0.0071±0.0008a
	NT	3371.29±238.96c	3356.25±258.64b	0.9748±0.0022a	6.10±0.09b	0.0124±0.0017a
	PJC	2339.95±196.15a	2340.85±178.52a	0.9822±0.0024a	5.26±0.30a	0.0711±0.0304b
	SDW	2530.74±210.50ab	2325.79±91.77a	0.9807±0.0036a	5.36±0.30a	0.0328±0.0086ab
	YT	3020.55±180.50bc	2995.21±186.31b	0.9733±0.0012a	5.81±0.08ab	0.0206±0.0023a
	ZHMX	3506.34±195.66c	3292.97±18.71b	0.9727±0.0040a	5.88±0.26ab	0.0348±0.0154ab
Fungi	CK	834.89±83.27bc	841.84±86.06cd	0.9957±0.0004ab	3.83±0.29b	0.0853±0.0237ab
	NT	875.69±23.63c	881.87±15.96cd	0.9952±0.0004a	3.59±0.09b	0.0916±0.0077ab
	PJC	596.25±31.34a	592.62±35.14a	0.9975±0.0002d	3.60±0.14b	0.0949±0.0144ab
	SDW	647.10±34.12a	592.30±38.76ab	0.9968±0.0001cd	2.98±0.18a	0.1313±0.0164b
	YT	762.79±24.09ab	728.16±17.64bc	0.9963±0.0001bc	3.88±0.10b	0.0482±0.0074a
	ZHMX	911.73±42.56c	902.39±35.04d	0.9962±0.0003bc	3.76±0.22b	0.0653±0.0145a

Note: CK is the control group, SDW is Erect Milkvetch, ZHMX is Alfalfa, PJC is Phyllanthus pinnatifida, NT is Lemongrass, YT is Brassica; different letters in the same column represent significant differences between different dominant plants ($P < 0.05$), the same letters represent no significant differences ($P > 0.05$)

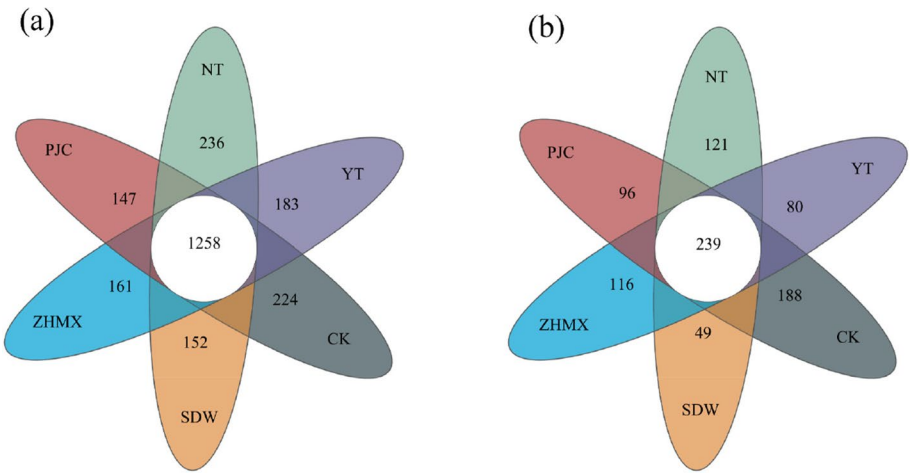

Fig. 2 Venn diagram of different dominant plants. **a** shows the Venn diagram of bacterial communities in the inter-rhizosphere soil of different dominant plants, and (**b**) shows the Venn diagram of fungal communities in the inter-rhizosphere soil of different dominant plants. CK, the control group, SDW, Erect Milkvetch, ZHMX, Alfalfa, PJC, Phyllanthus pinnatifida, NT, Lemongrass, YT, Brassica

Different dominant plants harbored varieties of microbial community compositions with different relative abundances (Fig. 3). Microbial community analysis showed that at the phylum level, Ascomycota was dominant in the fungal community, accounting for more than 70% of the inter-rhizosphere soil communities of different dominant plants (Fig. 3a). Among the bacterial communities, Firmicutes was dominant in the CK group, accounting for 26.62% of the bacterial community. The abundance of Actinobacteriota was relatively high among

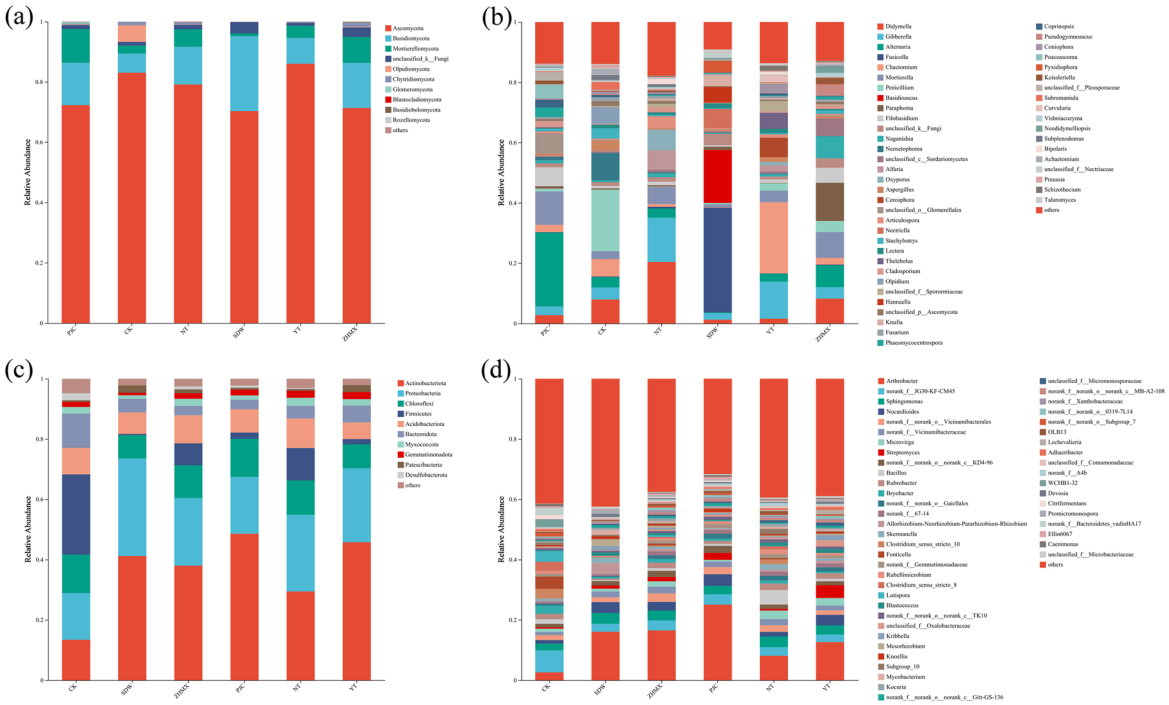

Fig. 3 Composition of soil microbial communities in the inter-rhizosphere of different dominant plants. **a**, **b** statistical comparison of fungal communities at the phylum level and at the genus level, respectively; **c**, **d** statistical comparison of bacterial communities at the phylum level and at the genus level, respectively. Different colored columns represent different species, and the length of the column represents the size of the proportion of that species. CK, the control group, SDW, Erect Milkvetch, ZHMX, Alfalfa, PJC, Phyllanthus pinnatifida, NT, Lemongrass, YT, Brassica

the other dominant plants, accounting for 41.47% in the SDW group, 37.96% in the ZHMX group, 48.56% in the PJC group, 29.42% in the NT group and 45.73% in the YT group. However, it rarely appeared in the CK group, accounting for only 13.40% (Fig. 3c).

At the genus level, there are differences in microbial communities among different dominant plants. In the fungal community, the PJC group had the highest abundance of *Alternaria*, accounting for 24.54% of the total. The CK group had the highest abundance of *Penicillium*, accounting for 24.40% of the total. The NT group had the highest abundance of *Didymella*, accounting for 20.40% of the total. The SDW group had the highest abundance of *Fusicolla*, accounting for 34.75% of the total. The YT group had the highest abundance of *Chaetomium*, accounting for 23.59% of the total. The ZHMX group had the highest abundance of *Paraphoma*, accounting for 12.62% of the total (Fig. 3b). In the bacterial community, the highest abundance of *JG30-KF-CM45* was observed in the CK group. *JG30-KF-CM45* belongs to heterotrophic bacteria, and studies have shown that *JG30-KF-CM45* is related to nitrogen, phosphorus, and COD concentrations [9]. Among other dominant plant bacterial communities, the abundance of *Arthrobacter* was relatively high, with an average abundance of more than 15%. In CK processing, the abundance of *Arthroacter* only accounted for 2.6% (Fig. 3d).

The analysis of the comparison between different dominant plant rhizosphere soil microbial groups showed that at the phylum level (Fig. 4), Ascomycota, Mortierellomycota, Chytridiomycota and Chytridiomycota abundances were significantly different between different groups of fungal communities ($P<0.05$) (Fig. 4a). The abundance of Actinobacteriota was higher among the different groups of the bacterial community, except for the CK group. The abundance of Actinobacteriota in the CK group was significantly lower than that in the other groups ($P<0.05$), while the abundance of Firmicutes and Bacteroidetes was significantly higher than that in the other groups ($P<0.05$); the abundance of Proteobacteria in the SDW group was significantly higher ($P<0.05$), while the abundance of Firmicutes was significantly lower than that in the other groups ($P<0.05$) (Fig. 4c).

At the genus level, between different groups of fungal communities, the abundances of *Didymella*, *Alfaria* and *Oxyporus* were significantly higher in the NT group than in the other groups ($P<0.05$); the abundances of *Alternaria* and *unclassified_o__Glomerellales* were significantly higher in the PJC group than in the other groups ($P<0.05$); the abundances of *Fusicolla* and *Basidioascus* were significantly higher in the SDW group than in the other groups ($P<0.05$), while the abundances of *Chaetomium* and *Mortierella* were significantly lower than in the other groups ($P<0.05$); the abundance of *Chaetomium* in the YT group was significantly higher than that in the other groups ($P<0.05$); the abundances of *Penicillium* and *Neosetophoma* in the CK group were significantly higher than those in the other groups ($P<0.05$); and the abundances of *Gibberella*, *Alfaria* and *Oxyporus* were all higher in the NT and YT groups than in the other groups ($P<0.05$) (Fig. 4b). Among the different groups of bacterial communities, the abundance of *Arthrobacter* was significantly higher in the PJC group than in the other groups ($P<0.05$); the abundance of *Allorhizobium*, *Neorhizobium*, *Pararhizobium*, *Rhizobium* was significantly higher in the SDW group than in the other groups ($P<0.05$); the abundance of *Bacillus* in the NT group was significantly higher than in the other groups ($P<0.05$); the abundance of *Fonticella*, groups ($P<0.05$) (Fig. 4d).

Environmental factors determining the structure of rhizosphere soil microbial communities of different dominant plants

Using Spearman correlation heatmaps and distance-based redundancy analysis (db-RDA) to analyze the potential relationship between different dominant plant microbial communities and soil physicochemical properties, the analysis results show the following:

At the phylum level, in different dominant plant rhizosphere soil fungal communities (Fig. 5a), the abundance of Mortierellomycota was significantly positively correlated with SOM and AN ($P<0.05$) and significantly negatively correlated with pH ($P<0.05$); AK was significantly positively correlated with Basidiobolomycota ($P<0.05$). In the bacterial community (Fig. 5c), pH was significantly positively correlated with Bacteroidota ($P<0.05$) and highly significantly negatively correlated with Methylomirabilota ($P<0.01$); AK was highly significantly positively correlated with Actinobacteriota ($P<0.01$), significantly negatively correlated with Cyanobacteria and Bacteroidota ($P<0.05$), and highly significantly negatively correlated with Deinococcota ($P<0.01$); SOM was significantly positively correlated with Gemmatimonadota and Methylomirabilota ($P<0.05$) and significantly negatively correlated with Halanaerobiaeota and Armatimonadota ($P<0.05$); and AN was significantly negatively correlated with Armatimonadota ($P<0.05$).

At the genus level, among the different dominant plant rhizosphere soil fungal communities (Fig. 5b), pH was significantly positively correlated with Aspergillus ($P<0.05$) and significantly negatively correlated with *Mortierella*, *Alternaria*, and *Filobasidium* ($P<0.05$); SOM was significantly positively correlated with *Oxyporus* and *Articulospora* ($P<0.05$) and significantly negatively correlated with *Penicillium* and *Aspergillus* ($P<0.05$); AP was significantly positively correlated with *Oxyporus* and

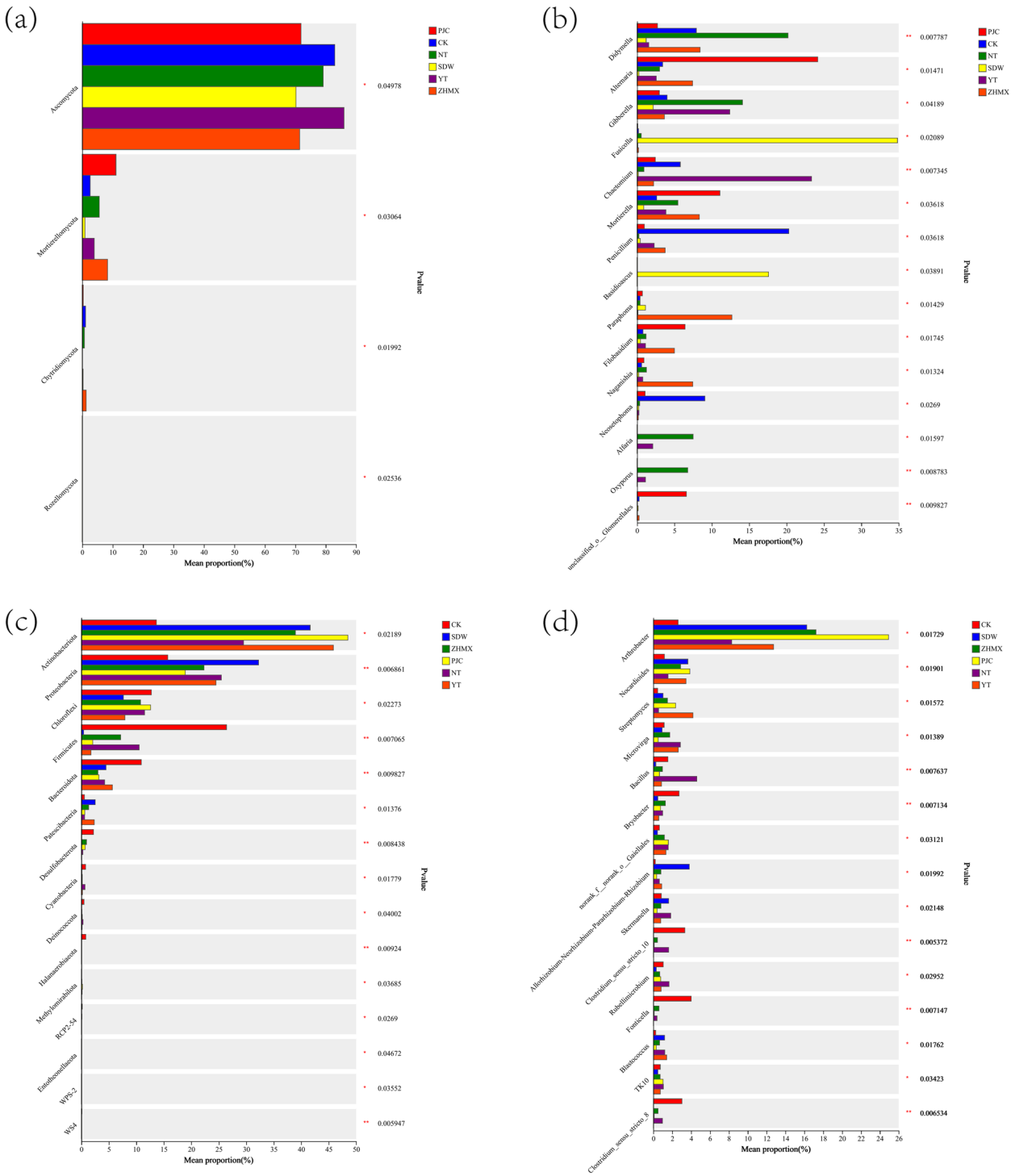

Fig. 4 Statistical comparison of relative abundance among groups of soil microorganisms in the inter-rhizosphere of different dominant plants based on the Kruskal-Wallis rank sum test. **a**, **b** statistical comparison of fungal communities at the phylum level and at the genus level, respectively; **c**, **d** statistical comparison of bacterial communities at the phylum level and at the genus level, respectively. Different colored bars indicate different groupings; the rightmost column shows *P* values, * represents $P \leq 0.05$ and ** represents $P \leq 0.01$. CK, the control group, SDW, Erect Milkvetch, ZHMX, Alfalfa, PJC, Phyllanthus pinnatifida, NT, Lemongrass, YT, Brassica

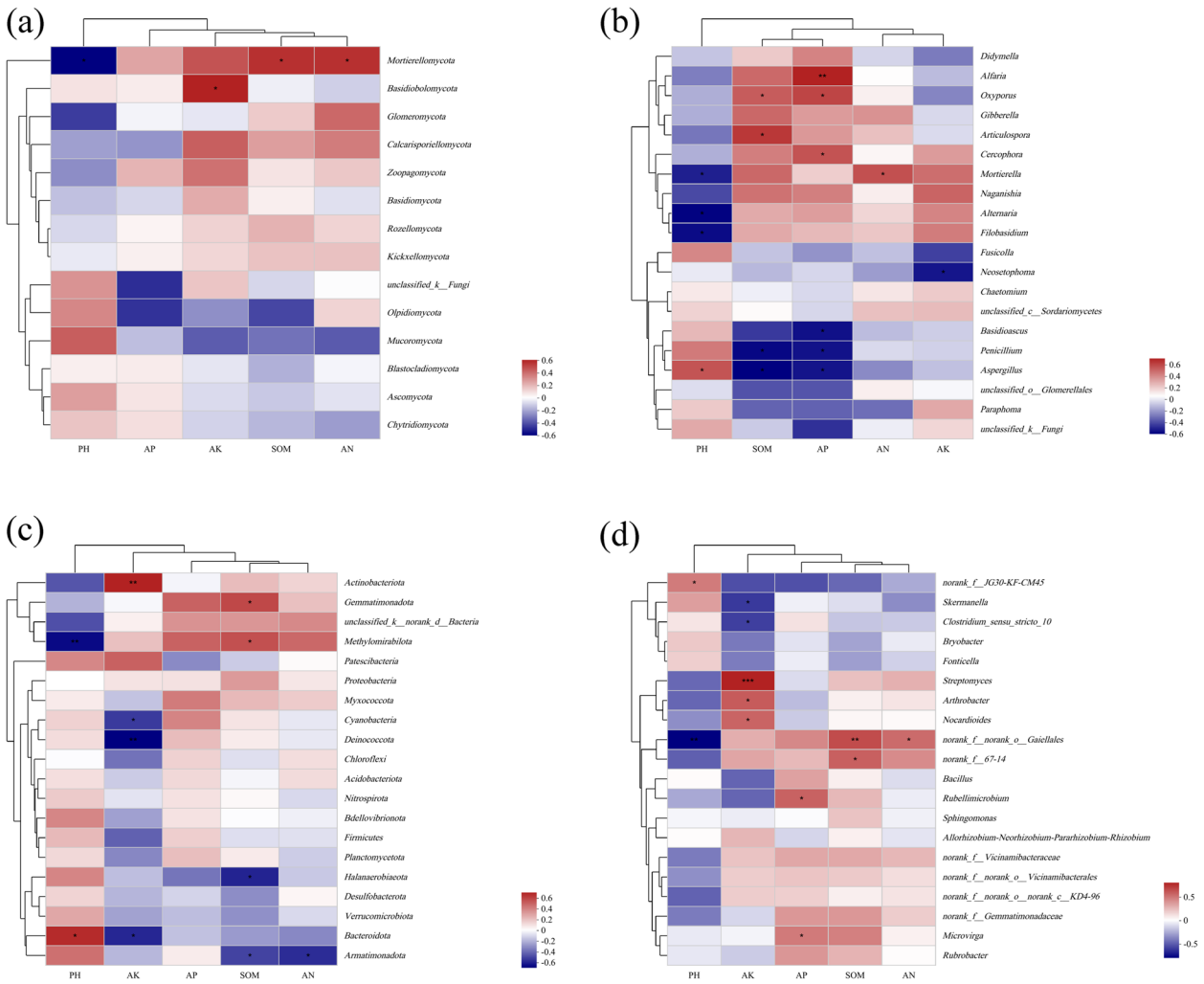

Fig. 5 Spearman correlation heatmaps of the top 20 abundance-ranked microbial communities in the rhizosphere soil. **a** for spearman correlation heatmap at the phylum level in the fungal community; **b** for spearman correlation heatmap at the genus level in the fungal community; **c** for spearman correlation heatmap at the phylum level in the bacterial community; **d** for spearman correlation heatmap at the genus level in the bacterial community; X-axis and Y-axis represent environmental factors and species, respectively; * represents $P < 0.05$, ** represents $P < 0.01$, *** represents $P < 0.001$. CK, the control group, SDW, Erect Milkvetch, ZHMX, Alfalfa, PJC, Phyllanthus pinnatifida, NT, Lemongrass, YT, Brassica

Cercophora ($P < 0.05$), highly significantly positively correlated with *Alfaria* ($P < 0.01$), and significantly negatively correlated with *Basidioascus*, *Penicillium*, and *Aspergillus* ($P < 0.05$); AN was significantly positively correlated with *Mortierella* ($P < 0.05$); and AK was significantly negatively correlated with *Neosetophoma* ($P < 0.05$). In the bacterial community (Fig. 5d), pH was significantly positively correlated with *JG30-KF-CM45* ($P < 0.05$) and highly significantly negatively correlated with *Gaiellales* ($P < 0.01$); AK was significantly positively correlated with *Arthrobacter* and *Nocardioides* ($P < 0.05$), highly significantly positively correlated with *Streptomyces* ($P < 0.001$), and significantly negatively correlated with *Skermanella* and *Clostridium_sensu_stricto_10* ($P < 0.05$); AP was significantly positively correlated with *Rubellimicrobium* and *Microvirga* ($P < 0.05$); SOM was significantly positively correlated with *67 – 14* ($P < 0.05$) and highly significantly positively correlated with *Gaiellales* ($P < 0.01$); and AN was significantly positively correlated with *Gaiellales* ($P < 0.05$).

The db-RDA redundancy analysis was used to further identify the main environmental factors affecting the soil microbial community structure (Fig. 6). The results of db-RDA redundancy analysis based on the Bray–Curtis distance algorithm at the genus level showed that the total explained degrees of fungal and bacterial communities were 22.53% and 25.62%, respectively. The influence of pH and SOM on soil microbial communities was highly

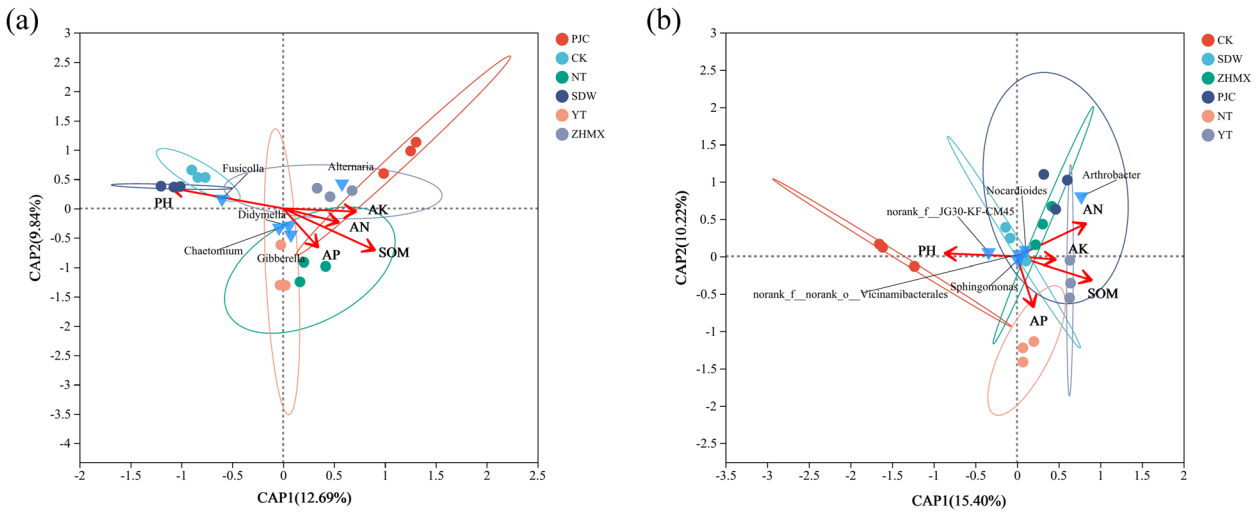

Fig. 6 The plots of db-RDA redundancy analysis plots based on Bray–Curtis distance algorithm. **a** for fungal community, **b** for bacterial community. Different colors or shapes of points in the plot represent different sample groups of rhizosphere soil; red arrows represent environmental factors, and the length of the environmental factor arrows can represent the degree of influence of the environmental factors on species data. CK, the control group, SDW, Erect Milkvetch, ZHMX, Alfalfa, PJC, Phyllanthus pinnatifida, NT, Lemongrass, YT, Brassica

significant ($P<0.01$). Among the fungal communities, the confidence ellipse distance between the CK and SDW groups was closer, indicating that the fungal community composition was more similar between the CK and SDW groups; *Fusicolla* genus showed a positive correlation with pH and a negative correlation with SOM, whereas *Alternaria* exhibited negative correlations with both pH and SOM. PH was the strongest environmental factor affecting the rhizosphere fungal community ($R^2=0.9125$, $P=0.001$), followed by SOM ($R^2=0.9024$, $P=0.001$), AP ($R^2=0.3481$, $P=0.02$), AK ($R^2=0.3397$, $P=0.056$), and AN ($R^2=0.2302$, $P=0.15$). In the bacterial communities, the *JG30-KF-CM45* genus showed a positive correlation with pH, while the *Arthrobacter* genus showed a positive correlation with AN and a negative correlation with SOM. There were some differences in the bacterial community composition between the CK group and the other groups in terms of community composition. And the influence of SOM on the bacterial community in rhizosphere soil was extremely significant ($P<0.01$), and SOM was the environmental factor with the strongest effect on the soil microbial community ($R^2=0.8079$, $P=0.001$), followed by AK ($R^2=0.7481$, $P=0.001$), PH ($R^2=0.6502$, $P=0.001$), AP ($R^2=0.4363$, $P=0.015$), and AN ($R^2=0.1733$, $P=0.232$).

Predictive analysis of microbial functions in different rhizosphere soils

Functional prediction analysis of PICRUSt2 in bacterial communities

According to PICRUSt2, bacterial community functional prediction was conducted by aligning sequencing data with the KEGG database. A bar chart of COG functional abundance and a heatmap based on the KEGG database were generated. Through the composition and differential analysis of KEGG metabolic pathways, the differences and changes in functional genes of microbial communities between different groups of samples can be observed. This is an effective method to study the metabolic functional changes of community samples in response to environmental changes. KEGG metabolic pathways divide biological metabolic pathways into three levels: Level 1, Level 2, and Level 3. The results of Level 1 and Level 2 are shown in Figure (Fig. 7).

According to the function bar chart, unknown function had the highest abundance among different groups, ranging from 18.6 to 19.1%. In addition, amino acid transport and metabolism was the largest proportion in all groups, being the most important function in different groups. The proportion of *amino acid transport and metabolism* in the CK group was lower than that in the dominant plant rhizosphere soil in the other groups (Fig. 7a). According to the heatmap of Level 1 (Fig. 7b), genes in different sample groups are associated with 6 metabolic pathways, namely, *metabolism*, *genetic information processing*, *environmental information processing*, *cellular processes*, *human diseases*, *and organismal systems*. Among them, the functional gene abundance of metabolism was significantly higher than that of the other 5 functional genes, indicating that metabolism was the main functional gene in the samples. Further analysis was conducted on the predicted gene secondary functional layer. At the Level 2 level (Fig. 7c), it was found to be associated with 46 metabolic pathways, including *Global and Over View Maps*

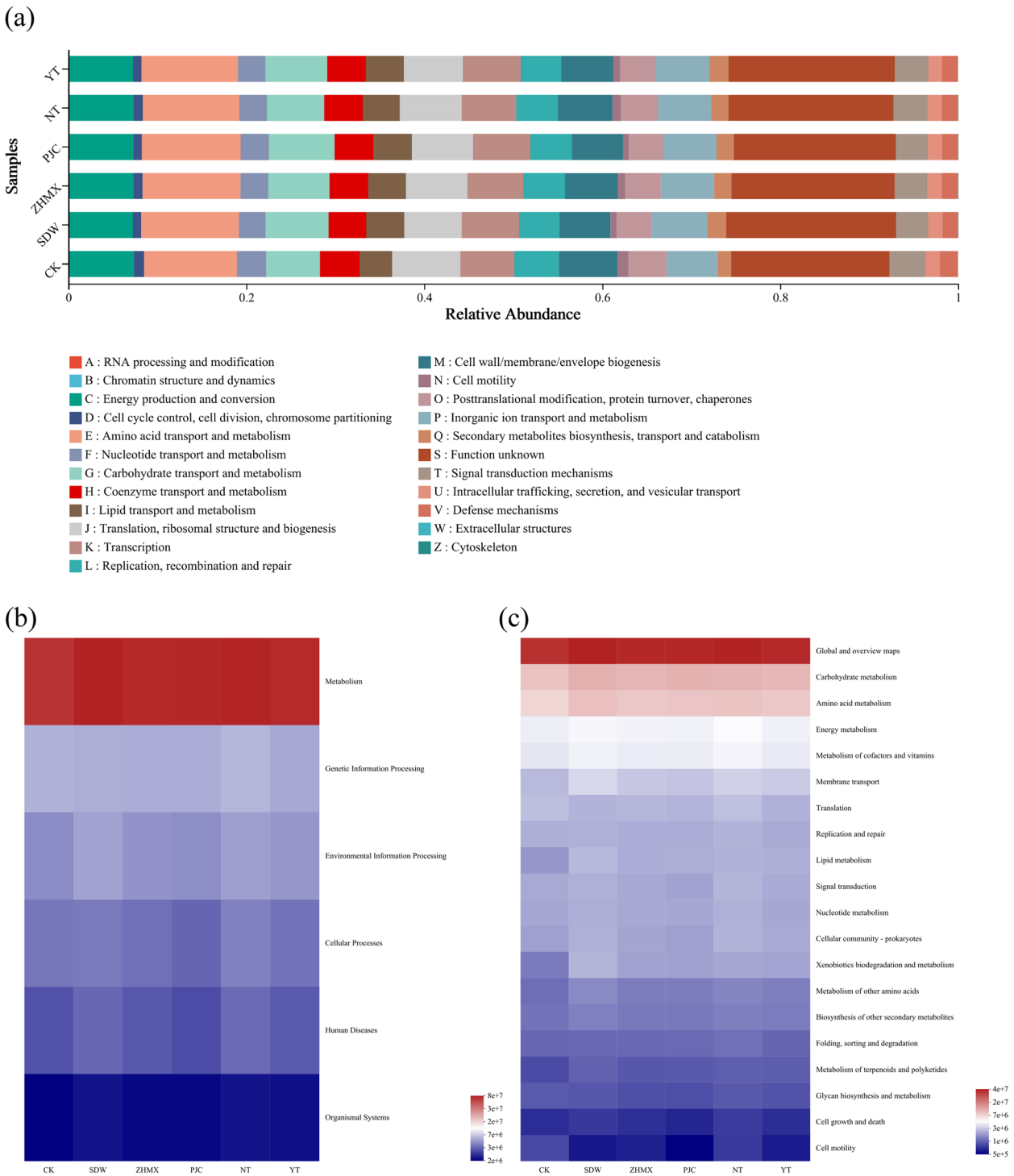

Fig. 7 For the PICRUSt2 functional prediction analysis of bacterial communities. **a** is the bar chart of COG functional classification statistics, (**b**) and (c) are the Heatmap graphs based on the KEGG database, (**b**) is at Level 1, and (**c**) is at Level 2. CK, the control group, SDW, Erect Milkvetch, ZHMX, Alfalfa, PJC, Phyllanthus pinnatifida, NT, Lemongrass, YT, Brassica

and *Carbohydrate Metabolism*. In terms of functional abundance, *Global and Overview Maps* had significantly higher abundance than other functional genes in the top 20 functional genes, while *Carbohydrate Metabolism* and *Amino Acid Metabolism* had relatively higher abundance.

Functional prediction of FUNGuild analysis in the fungal community

Based on fungal species classification, FUNGuild can obtain the ecological functions of corresponding fungi. Predictive analysis of different beneficial plant rhizosphere fungal communities using FunGuild. The analysis results (Fig. 8) show that the main functional groups of fungal communities are *pathotrophs* and *saprotrophs*. In the PJC group, *Animal Pathogens* and *Plant Pathogens* were dominant, accounting for 25.54% of the total, and their function was mainly *Pathotrophic*. In the CK, NT, and SDW groups, *undefined saprotrophs* were dominant, with the SDW group reaching 70.95%, indicating a main function of *saprotrophy*. In the YT group, *Animal Pathogen-Dung Saprotroph-Endophyte-Epiphyte-Plant Saprotroph-Wood Saprotroph* were dominant, accounting for 23.64% of the total, indicating a main function of *saprotrophy*. In the ZHMX group, *unknown* fungal communities and *undefined saprotrophs* were dominant, accounting for 20.53% and 18.56%, respectively.

Discussion

In this study, the soil microbial community in the drainage site of the Shengli coalfield was analyzed in depth using high-throughput sequencing technology. The results showed that the soil microbial community showed

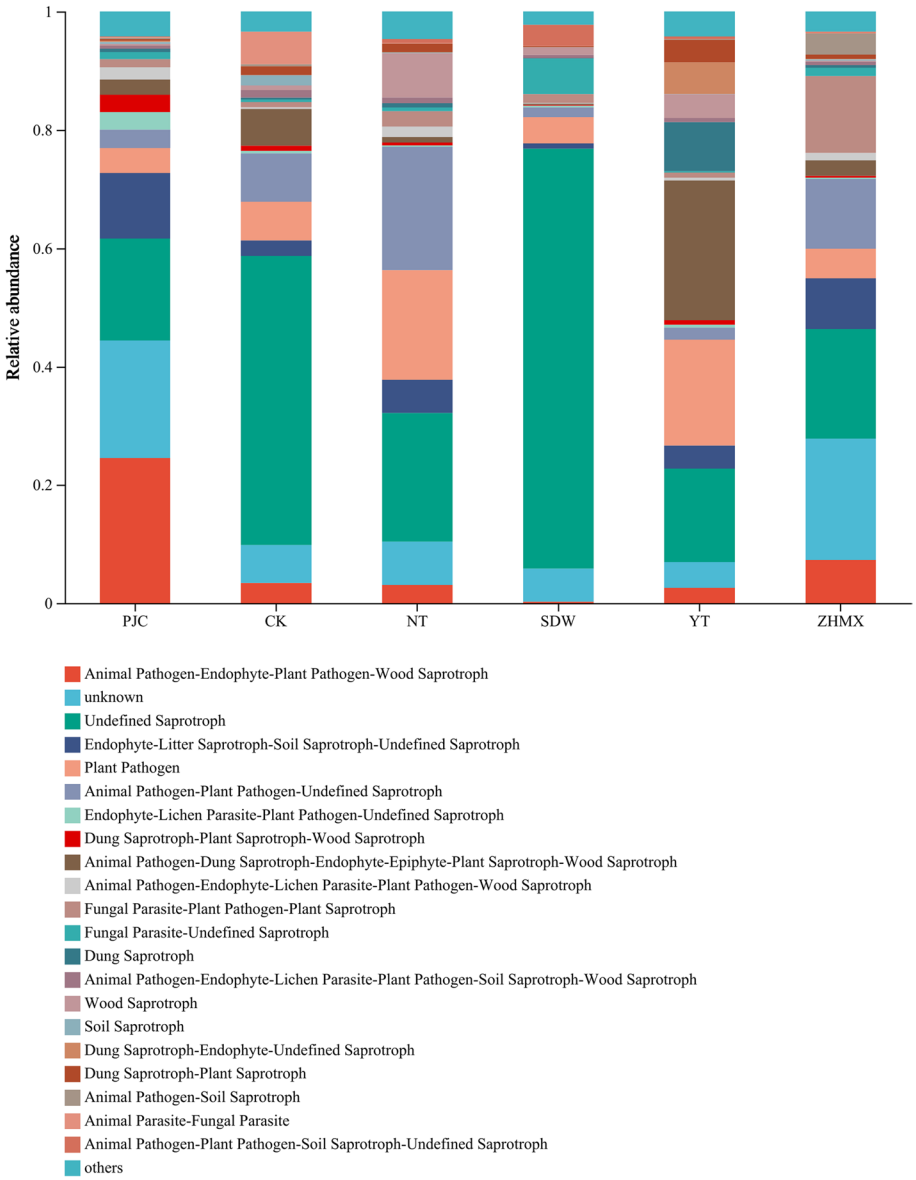

Fig. 8 Bar chart of predicted relative abundance of fungal nutritional types based on FUNGuild functional prediction analysis. CK, the control group, SDW, Erect Milkvetch, ZHMX, Alfalfa, PJC, Phyllanthus pinnatifida, NT, Lemongrass, YT, Brassica

rich diversity in the study area. By analyzing the relationship between individual samples and soil physicochemical properties, we found that the soil environment on the slope of the drainage site was significantly improved after 15 years of restoration, which is consistent with Courtney et al. [10], among which the PJC group had the best effect on the improvement of soil environmental physicochemical properties. The AP and AK contents of rhizosphere soil in different dominant plant groups were significantly elevated compared to those in the CK group. Bronick et al. [11] found that land reclamation contributed to an increase in the proportion of soil aggregates, thus reducing rainfall- and irrigation-induced soil nutrient loss, which may be one of the reasons for the elevated AP and AK contents of rhizosphere soils in the different dominant plant groups relative to those in the CK group soils. However, the alkaline nitrogen content of the rhizosphere soil of different dominant plants in the drainage field was low. Huang et al. [12] obtained the same conclusion in a study of soil physicochemical properties in the No. 1 mine of the Shengli coalfield, which may be related to the insufficient restoration years of the mine itself. Li [13] and Wang et al. [14] concluded that both organic matter content and nitrogen content are lost to varying degrees during mining and require at least several decades to recover to near natural levels. It has been shown that there is a correlation between vegetation type and soil physicochemical properties [15, 16], different dominant plant species may impact soil physicochemical properties, thus resulting in differences in soil microorganisms and communities. Xue et al. [17] also came to the same conclusion.

To further understand the driving factors of soil microbial community changes in the Shengli Coalfield drainage site, we also explored the relationship between soil environmental factors and microbial community structure through db-RDA redundancy analysis. The results of this study showed that in the fungal community, the genus *Fusicolla* was positively correlated with pH and negatively correlated with SOM, while the genus *Alternaria* was negatively correlated with both pH and SOM, and in the bacterial community, the genus *JG30-KF-CM45* was positively correlated with pH, and the genus *Arthrobacter* was positively correlated with AN and negatively correlated with SOM which indicated that pH and SOM significantly affected the composition of soil microbial community. Zeng et al. [18] also obtained the same conclusion in a study of microbial communities in different vegetation gradients on the Loess Plateau. Many studies have shown that soil pH is a key factor in soil microbial diversity [19, 20]. Lauber et al. [21] found that the diversity of soil bacterial communities in different regions was related to soil pH. Therefore, the hypothesis is proposed that different soil environments can determine the composition of microbial communities. Shi et al. [22], in a study of soil bacterial communities in a wind-deposited sand region of western China, noted that soil microbial communities play an important role in the regulation of soil ecosystems while suggesting that soil properties can influence the composition of bacterial communities. In addition, Zhao et al. [23], in a study of karst mountain ecosystems on soil microbial community dynamics, showed that vegetation succession could significantly enhance soil nutrients in the area and then proposed that vegetation succession significantly determined the changes in soil microbial communities. Zakavi et al. [24] conducted a study on the variations in bacterial community diversity and their impact on crop growth along an altitudinal gradient in arid and semi-arid regions. They discovered that elevation leads to an increase in microbial community diversity and a decrease in bacterial biomass. Additionally, they observed that bacteria at higher altitudes have the ability to enhance plant growth. Furthermore, Zakavi et al. [25] examined the influence of various soil textures on bacterial diversity and plant growth. Their research revealed that bacteria obtained from different soil textures exerted distinct effects on plant growth. The above previous studies demonstrated a close relationship between soil physicochemical properties and the soil microbial community and verified the hypothesis proposed previously.

Different dominant plants possess unique physiological properties and metabolic pathways that enable them to selectively influence the soil microbial community between roots [26, 27].Qiao et al. [28] in their study on legume rhizomes promoting nitrogen fixation in soil microbial communities mentioned that legumes have the ability to fix nitrogen, and their root secretions may be rich in nitrogenous compounds, which would attract microbial taxa capable of utilizing these compounds, thus altering the composition of the soil microbial community at the inter-root level. Concurrently, the symbiotic association between legume roots and rhizobacteria not only supplies nitrogen to the plant, but also impacts the chemical milieu of the inter-root soil, indirectly influencing other microorganisms [29]. *Graminaceae* may release specific organic substances, like sugars and organic acids, from their root systems to provide carbon and energy sources for soil microbes [30], fostering the growth and proliferation of certain microorganisms while suppressing others, thus guiding the evolution of the inter-root microbial community towards a more favorable growth and adaptation to the environment. Dominant plants can also impact microbial communities by interacting with soil microbes [31]. Plants release signaling molecules like phytohormones and volatile organic compounds, which

soil microorganisms can detect and respond to, influencing microbial activity and community structure [32, 33]. For instance, some plants release signaling molecules that attract beneficial microorganisms to their root systems, forming inter-root facultative microbial communities [34]. These microorganisms enhance plant growth by producing phytohormones, solubilizing phosphorus and potassium, among other activities. In return, plants provide a conducive environment and nutrients, establishing a mutually beneficial symbiotic relationship [35].

By analyzing alpha diversity indicators in each sample, including species richness, evenness and diversity index, we found no significant increase in the microbial community diversity index between different dominant plants and CK groups. Previous studies have shown that soil properties contribute the most to the distribution of microorganisms, while other environmental factors, such as temperature and altitude, have a smaller impact [36, 37]. Zhou et al. [38] also demonstrated this in their study of a rare earth mining area. Markowicz et al. [39] pointed out in their study of dominant plants in uncultivated coal mine dumps in the Silesian Highlands in Poland that the lack of environmental factors such as insufficient water, lack of available nutrients, high temperatures, and high salinity levels may have a significant impact on microbial functional diversity. Therefore, the lack of a significant increase in the diversity index between different dominant plants and CK groups in this study may be due to the poorer nutrient environment of the mine drainage site soil and the deficiency of nitrogen content in the soil environment leading to this phenomenon. The rhizosphere soil microbial diversity of legumes in the study was significantly better than that of grasses, and we conjecture that legumes can accelerate the ecological recovery of degraded soils. Li et al. [40] verified this conjecture in a study of abandoned farmland on the Loess Plateau in China. Gao et al. [41] found that legumes increase soil resistance to ecosystem disturbance by comparing soil resistance to an ecosystem disturbance, the removal of understory vegetation, with and without legumes in a mixed forest plantation in southern China. Li et al. [42] studied the effects of legume-grape plant species on plant productivity and soil nitrogen during secondary succession in subalpine meadows of abandoned cropland on the eastern Tibetan Plateau, and found that an increase in the abundance of leguminous plants promotes the productivity of the community. Therefore, we believe that planting leguminous plants can effectively improve the fertility of the soil, and accelerate the restoration of degraded soils.

Microbial community structure plays an important role in the restoration of soil ecology [43, 44]. In this study, we also investigated the effect of the drainage field of the Shengli coalfield on the soil microbial community structure. By comparing the microbial community composition of soil microorganisms between the rhizosphere of different dominant plants and the CK group, we found significant changes in the composition of the microbial community between different groups. Bacteria were found to be the major component of the rhizosphere soil microorganisms in the experiment [45, 46], and the bacterial community of different dominant plant groups was dominated by the phyla Actinobacteriota, Proteobacteria, Chloroflexi and Firmicutes. Shu et al. [44], in a study of bacterial communities in rare earth mine watersheds, found that the phyla Actinobacteriota, Proteobacteria, and Chloroflexi were more prevalent in highly polluted areas, while these bacterial microorganisms emitted different biological mechanisms to resist extreme environments. It has been noted that bacteria of the phyla Actinobacteriota and Proteobacteria are the most active bacteria in contaminated soils [47, 48], indicating that bacteria of the phyla Actinobacteriota and Proteobacteria are more tolerant to extreme environments. The increased abundance of these two bacterial phyla is mainly due to physiological adaptations of bacteria, possibly leading to the evolution of more sensitive species [49]. Chao et al. [50] also pointed out in their study on rare earth mines that the soil in the mining area contains abundant Actinobacteriota, Proteobacteria, and Firmicutes, which can coexist in extreme environments. Therefore, we believe that these bacterial phyla have the potential for the remediation of contaminated soil in mining areas [51]. The fungal community was dominated by the Ascomycota and Basidiomycota phyla. The Basidiomycota phylum was the main ectomycorrhizal fungus, with the abundance of the Basidiomycota phylum in the CK group significantly lower than that in the dominant plant group. Zhang et al. [52], in a study on the Tibetan Plateau targeting microbial communities in permafrost, concluded that the ratios of Ascomycota and Basidiomycota phyla were related to microbial community characteristics. They mentioned that the decrease in the ratio of Ascomycota to Basidiomycota may be associated with an increase in ectomycorrhizal fungi and an increase in vegetation coverage. The Basidiomycota phylum, as saprophytic fungi, plays a crucial role in the decomposition of lignin and cellulose [53, 54], which explains the significantly higher SOM content in different plant groups than in the CK group. The phylum Ascomycota is generally considered to be the largest phylum in the kingdom of Fungi [55]. Research has shown that the phylum Ascomycota and the phylum Basidiomycota can produce high levels of chelators, which can effectively protect cells from damage caused by heavy metal ions [56]. In summary, in different dominant plant groups, the microbial community composition is mainly composed of species

with strong resistance to extreme environments. The soil properties and decomposition ability in the soil are significantly improved compared to the CK group, indicating that after years of restoration, the microbial environment in the rhizosphere soil has been somewhat improved, but it has not yet reached the standard of the natural state. Although the microbial diversity in the group is relatively low, there are still a large number of environmentally specific species, which is consistent with the concept of the " are ecosphere " mentioned by Shu et al. [44].

The results of this study indicate that different dominant plants have a significant impact on the structure of soil microbial communities. These changes may have potential impacts on soil ecological functions; therefore, we conducted functional prediction analysis on microbial communities of different plant groups and studied their functions. PICRUSt2 can clearly demonstrate bacterial functions by comparison with the KEGG database, and bacterial functions to some extent reflect the size of soil fertility. Using PICRUSt2 to predict the functional diversity of bacterial communities in the rhizosphere of different dominant plant groups, a total of 6 metabolic pathways mainly related to *metabolism* function were identified in the first functional level, and a total of 46 metabolic pathways mainly related to *global and overview map* functions were identified in the second functional level. The functional diversity is abundant. The abundance of metabolic functions in bacterial communities was significantly higher than that of other functions, indicating that different soil environments may be conducive to the metabolism, growth, and proliferation of target microorganisms, which is similar to the findings of Thiour-Mauprivez et al. [57]. Wang et al. [58], in a study of bacterial wilt affecting the rhizosphere soil bacterial community of sesame, noted that changes in the structure of the rhizosphere soil bacterial community cause a corresponding adjustment in the function of rhizosphere soil bacteria. However, the PICRUSt2 analysis has certain limitations. Its predictions are restricted by short read lengths and limited information, potentially resulting in less precise and comprehensive predictions of microbial functions. Due to the unavailability of full-length sequences of microbial genes, there is a possibility of misdiagnosed or omitted gene functions, thus impacting the thorough understanding of microbial community functions. Therefore, it is recommended to perform full-length sequencing in combination with other omics technologies, such as transcriptomics, proteomics, and metabolomics, to understand specific microbial functions [59]. FUNGuild provides a solid foundation for studying fungal ecological functions [60]. The predicted results show that the main functional types of soil fungi are saprotrophic and pathotrophic, which is consistent with the composition of fungal communities in different groups. The Basidiomycota phylum is abundant in the community as saprophytic fungi, which may be related to the greater adaptability of saprophytes to the external environment [61]. Although FUNGuild partially resolves fungal function, there are limitations to the method. FUNGuild predicts fungal functions mainly based on literature and data, which may be inaccurate or impossible to predict for some newly discovered or less studied fungal species. Moreover, this prediction method, based on existing knowledge, is difficult to reveal potential and undiscovered functions of fungi in complex ecosystems, limiting the comprehensive understanding of fungal community functions [62, 63].

Conclusion

In this study, high-throughput sequencing technology was utilized to analyze the microbial community of soil that had been restored for 15 years on the slope of the Shengli Coalfield drainage field. The aim was to investigate the characteristics of the restored microbial community and its potential ecological functions. The study's results indicated that the soil environment had been significantly enhanced after years of restoration, despite varying degrees of nitrogen depletion in each experimental group. Specifically, the microbial community structure and soil physicochemical properties of the inter-root soils of different dominant plants exhibited varying degrees of optimization. Among them, *Phyllostachys* edulis was particularly effective in improving the soil environment. Furthermore, strains adapted to specific environments emerged in the soil of all experimental groups, and these strains demonstrated some protective efficacy for plant growth and reproduction.

Through in-depth analysis, it was discovered that pH and the content of organic matter (SOM) were the dominant factors controlling the composition of the microbial community, which had a significant impact on the soil microbial community. The function of the soil microbial community is closely linked to the diverse developmental strategies adopted by the microbial community to adapt to the mining environment, and these strategies contribute to maintaining the stability of the community. Considering the high cost of microbial remediation technology in large-scale applications in mining areas, integrating microbial remediation technology with other related technologies shows great potential for improving the mining environment.

Materials and methods

Overview of the study area

The test area is located in the dumping ground of the West No. 2 open-pit coal mine in Xilinhot City, Xilingol

League, Inner Mongolia Autonomous Region, with geographical coordinates of 43°57'~44°01' north latitude and 116°00'~116°06' east longitude. It belongs to a temperate semiarid continental climate, with short and hot summers and long and cold winters. The annual precipitation is relatively low, showing dry characteristics. The precipitation is mainly concentrated in the summer, with an average annual precipitation of 286.9 mm and an annual evaporation of 1760 mm. The average annual temperature in the mining area is 1.7 ℃. The hottest month is July, with an average monthly temperature of 20.8 ℃. The coldest month is January, with an average monthly temperature of 19.8 ℃. There is a large temperature difference between day and night, mainly in spring.

Test area selection

The experimental area selected for the study is a slope that has undergone natural recovery for 15 years. The slope underwent artificial intervention in 2008, and the slope restoration measures adopted were biofence restoration measures: biofences are woven into a grid-like fence with branches and stems of plants such as willows, seabuckthorns, and tamarisks as the biological material. Each biofence has a size of 5 m×5 m and is laid flat on the soil dumping slope and fixed with stakes. The slope has a gradient of approximately 30 ° and a length of 23 m.

Test material

The main dominant plants in the open-pit coal mine spoil heap were selected as the research objects. The dominant plants were selected as artificially planted plants with a high growth advantage, including Erect Milkvetch (*Astragalus adsurgens*, SDW), Lemongrass (*Caragana korshinskii*, NT), Alfalfa (*Medicago sativa*. ZHMX), Phyllanthus pinnatifida (*Elymus dahuricus*, PJC), and Brassica Rapa (*Brassica campestris*, YT). The dominant plants selected were chosen from uniform slopes. Bare soil was used as the control group (CK). Five samples of each dominant plant were collected in August 2022, and three replicates were set for each sample group, for a total of 18 sample groups. Take the complete plant and use shaking method to remove non-rhizosphere soil. Take 2–3 g of rhizosphere soil and quickly place it in liquid nitrogen for preservation. After returning to the laboratory, store it at −80 ℃ for freezing.

Determination of soil physicochemical properties

Soil samples were collected in late August, with samples taken at a distance of 0.5 m from the planting of dominant plants. The sampling method used was multipoint sampling, and soil from the 0–10 cm layer was collected for soil nutrient determination. The measurement indices included the following: Soil pH: Using an acidity meter (PHS-3D type pH meter) equipped with a 5:1 soil to water ratio soil solution, the pH of the clear solution was determined. Soil organic matter: potassium dichromate volumetric-external heating method. Soil alkaline decomposition of nitrogen: alkaline diffusion method. Soil fast-acting phosphorus: 0.5 mol/L $NaHCO_3$ leaching - molybdenum antimony anticolorimetric method. Soil fast-acting potassium: NH_4OAc leaching - flame photometric method.

Extraction and PCR amplification of soil microbial DNA groups

Total microbial genomic DNA was extracted from rhizosphere soil samples using the E.Z.N.A.® soil DNA Kit (Omega Bio-tek, Norcross, GA, U.S.) according to manufacturer's instructions. The quality and concentration of DNA were determined by 1.0% agarose gel electrophoresis and a NanoDrop2000 spectrophotometer (Thermo Scientific, United States) and kept at −80 ℃ prior to further use. Specific primers with barcodes were synthesized according to the designated sequencing region. PCR amplification of soil bacterial 16 S rRNA was performed using specific primers 338 F (5′-ACTCCTACGGGA GGCAGCAG-3′) and 806R (5′-GGACTACHVGGG TWTCTAAT-3′); fungal amplification was selected from ITS1F (5′-CCTGGTCATTTAGAGGAAGTAA-3 ′) and ITS2R (5′-GCTGCGTTCTTCATCGATGC-3′).

PCR amplification was performed using Trans Gen AP221-02 (Trans Start Fastpfu DNA Polymerase). Each sample was run in triplicate, and the PCR products from the same sample were mixed and analyzed by 2% agarose gel electrophoresis. Gel extraction of the PCR products was performed using the AxyPrep DNA Gel Recovery Kit (AXYGEN), followed by elution with Tris-HCl. Subsequently, electrophoresis was conducted using a 2% agarose gel. According to the preliminary quantitative results of electrophoresis, the PCR products were quantified using the Quanti Fluor™-ST Blue Fluorescence Quantification System (Promega) and then mixed in the corresponding proportions according to the sequencing requirements of each sample. Illumina libraries were constructed using the Tru Seq™ DNA Sample Prep Kit, and the library was sequenced on the Illumina platform. High-throughput sequencing was performed by Shanghai Meiji Biomedical Technology Co., Ltd.

Illumina PE300 sequencing

Purified amplicons were pooled in equimolar amounts and paired-end sequenced on an Illumina PE300 platform (Illumina, San Diego, USA) according to the standard protocols by Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China). The raw sequencing reads were deposited into the NCBI Sequence Read Archive (SRA) database (Accession Number: SRP455032).

Biological information analysis

Raw FASTQ files were de-multiplexed using an in-house perl script, and then quality-filtered by fastp version 0.19.6 [64] and merged by FLASH version 1.2.7 [65] with the following criteria: (1) the reads were truncated at any site receiving an average quality score of < 20 over a 50 bp sliding window, and the truncated reads shorter than 50 bp were discarded, reads containing ambiguous characters were also discarded; (2) only overlapping sequences longer than 10 bp were assembled according to their overlapped sequence. The maximum mismatch ratio of overlap region is 0.2. Reads that could not be assembled were discarded; (3) Samples were distinguished according to the barcode and primers, and the sequence direction was adjusted, exact barcode matching, 2 nucleotide mismatch in primer matching. Then the optimized sequences were clustered into operational taxonomic units (OTUs) using UPARSE 11 [66] with a 97% sequence similarity level. The taxonomy of each OTU representative sequence was analyzed by RDP Classifier version 2.2 [67] against the 16 S rRNA gene database (Silva v138) and the ITS fungus database using a confidence threshold of 0.7.

Statistical analysis

Excel 2021 was used for data organization, SPSS 26.0 was utilized for one-way variance analysis (ANOVA, $P \leq 0.05$) and Duncan's test to analyze the relationship between soil physicochemical properties and community diversity, and multiple group tests were performed on microbial communities using the Kruskal–Wallis H test. Based on the Bray–Curtis distance algorithm, principal coordinates analysis (PCoA) was plotted using R language tools to investigate the similarities and differences in microbial community composition among different groups. Spearman correlation analysis was used to evaluate the correlation between soil traits and microbial communities, and the relationship between microbial community structure and soil physicochemical properties was divided by the distance-based redundancy analysis (db-RDA) method. Functional prediction of bacterial communities was performed using the PICRUSt software package for PICRUSt2 prediction analysis, while functional prediction of fungal communities was performed using FUNGuild (Version 1.0) software.

Acknowledgements

We appreciate the support of the fund, which has made our experiment run smoothly.

Authors' contributions

W.Z was the lead author of the manuscript, responsible for designing the experimental methods, conducting the investigation and research, analyzing the experimental data, visualizing the experimental results, and drafting the initial manuscript. R.H. was a secondary author on the paper and was primarily responsible for data analysis and sample collection for the paper.M.L. and X.D. participated in reviewing and revising the manuscript.H.S. also participated in the investigation and research process. M.W. is the main corresponding author of the manuscript, responsible for generating the research concept, acquiring research funding, collecting research resources, verifying and validating the experimental design, supervising and guiding the research topic, and reviewing and revising the manuscript.J.Y. is the co-corresponding author, responsible for revising the paper and offering guidance on experimental design.

Funding

This research is supported by Science and Technology Major Project of Inner Mongolia(2020ZD0020) and Natural Science Foundation of Inner Mongolia Autonomous Region (2023MS03012).

Data availability

All data generated or analyzed during this study are included in this article. The raw reads of sequencing data is available at NCBI BioProject SRA database under the accession number PRJNA1005421.

Declarations

Ethics approval and consent to participate

This article does not contain any studies with human or animal subjects.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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Received: 15 August 2023 Accepted: 10 January 2025
Published online: 12 March 2025

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