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RECEIVED 24 November 2023

ACCEPTED 21 February 2024

PUBLISHED 06 March 2024

CITATION

Xu H, Li N, Li W, Wang H, Shao Y, Liu J,
Zhang J, Wang J and Shang S (2024)
Composition and diversity of rhizosphere
microorganisms of *Suaeda salsa* in the
Yellow River Delta.
Front. Ecol. Evol. 12:1343672.
doi: 10.3389/fevo.2024.1343672

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Composition and diversity of rhizosphere microorganisms of *Suaeda salsa* in the Yellow River Delta

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Introduction: *Suaeda salsa* is a typical wetland plant species in coastal areas that plays an important role in protecting the marine eco-environment. The rhizosphere microorganisms of *S. salsa* are responsible for its growth and development.

Method: Eighteen samples were collected from three areas, including the natural *S. salsa*-growing area (YDJ), artificial *S. salsa* restoration area (YDB), and nonrestoration area (BKS), and high-throughput sequencing technology was employed to explore the characteristics of the rhizosphere microorganisms of *S. salsa* in the Yellow River Delta.

Results: The results illustrated that the abundance and diversity of soil bacteria were highest in the YDJ group, fungal abundance was highest in the YDJ group, and fungal diversity was greatest in the YDB group. In total, 26,663 operational taxonomy units (OTUs) were found in soil bacteria, among which 9,095, 8,023, and 11,001 were detected in the BKS, YDB, and YDJ groups, respectively. 11,619 OTUs were found in soil fungi, among which 4,278, 4,552, and 5,100 were detected in the BKS, YDB, and YDJ groups, respectively. The YDJ group had the highest number of OTUs for bacteria and fungi among the three groups.

Discussion: *S. salsa* in natural wetland conditions tended to be similar to artificially restored *S. salsa*. The composition of fungi in the *S. salsa* rhizosphere had greater similarities than that of the bacteria. Proteobacteria had the highest abundance among bacterial communities, and Ascomycota, Basidiomycota, and Olpidiomycota were dominant in the fungal communities of the three groups. The correlation results found that power of hydrogen (pH) was significantly and negatively correlated with the abundance of Acidobacteriota and Proteobacteria. Meanwhile, electrical conductivity (EC) was significantly and positively correlated

with the abundance of Firmicutes and negatively correlated with that of Proteobacteria. Regarding fungi, pH and EC were significantly and negatively correlated with the abundance of Chytridiomycota. Our findings provided some theoretical data for *S. salsa* conservation and wetland restoration.

KEYWORDS

rhizosphere microorganisms, restoration, high-throughput sequencing, root, *Suaeda salsa*

1 Introduction

For better growth, plants must obtain sufficient nutrients and water from the soil, and microorganisms actively participate in these substance and energy flow processes (Bailey et al., 2011). Microorganisms are the most active biological members in the soil, and they play an important role in substance circulation and energy transform between plants and soil (Liao et al., 2023). They are associated with organic matter decomposition and nutrient acquisition (Jansson & Hofmockel, 2020). In soil, the diversity of microorganisms is high, and the interaction between plants and microbes is intensive. The root exudates of plants can attract more plant growth-promoting bacteria, thus affecting the rhizospheric microbial community (Ahkami et al., 2017). Conversely, rhizosphere microorganisms represent an important indicator of the soil ecosystem. Plant species and their growth can affect the soil environment and change the microbial community structure and diversity. In the vigorous growth period of the plant, associated microbial metabolic groups and the functional diversity of the community tend to increase (Meena et al., 2017).

Suaeda salsa is an annual salt-tolerant herb (Cheng et al., 2014) that grows in deserts, lakesides, saline-alkali land, and coastal wetlands (Li et al., 2021). It can absorb and accumulate salt in the body and release certain secretions to change the physical and chemical properties of the soil (Sun et al., 2013). It is a typical plant species in coastal wetlands with many ecological functions, such as decelerating waves and tidal currents, providing a habitat and food source for marine organisms, filtering nutrients in estuarine and coastal waters, stabilizing pollutants, and purifying water (Sun et al., 2013). Because of the overexploitation of coastal regions and global climate change in recent years, most estuarine wetlands have encountered great ecosystem degradation problems, causing severe damage to biodiversity (Martens et al., 2018) and landscape diversity (Carugati et al., 2018). Therefore, restoring damaged wetlands has become an important eco-environmental protection measure. In particular, *S. salsa* has been used as an appropriate species in wetland restoration in the Yellow River Delta of China because it is a native species with great salt resistance and landscaping value. Previous studies found that the root exudates of *S. salsa* may be the main driving force of soil bacteria under

environmental changes (Liu et al., 2020), and the *S. salsa* root-associated microorganisms could improve other plants growth and resistance under salt stress (Wang et al., 2022). A study also found that the Biochar had the potential to improve the restoration of *S. salsa* in coastal wetlands (Cai et al., 2021). However, little information is available regarding the interaction or correlation between *S. salsa* and its rhizospheric microorganisms, especially in the restoration process. In our study, samples were collected in areas with natural *S. salsa* growth, artificial *S. salsa* restoration, and nonrestoration, and high-throughput sequencing technology was used to better understand the composition of soil microorganisms in *S. salsa* vegetation and demonstrate the effects of *S. salsa* restoration on soil microorganisms. We aim to provide some basic data for the restoration of coastal ecosystems.

2 Materials and methods

2.1 Study area and sampling collection

The Yellow River Delta in northern China is the most prominent newborn wetland (Wang et al., 2012). In this area, riverine sediment deposition in the intertidal zone of the Bohai Sea promotes the rise and desalination of the low tide flats. The middle and high tidal beaches are successively covered by alkali, *Tamarix* and reed vegetation from low to high tidal flats. There are large areas of *Phragmites australis* and *S. salsa* swamps in the Yellow River Delta. And the pH of the soil in Yellow River Deltas is between 7.8 and 8.5, and the electrical conductivity (EC) of soil Yellow River Deltas is 0.24 dS/m~ 4.83 dS/m (Li et al., 2023).

2.2 Detection of soil physical and chemical indicators

In the present study, 18 soil samples were collected from the natural *S. salsa*-growing area (YDJ), artificial *S. salsa* restoration area (YDB), and nonrestoration area (BKS). Each sample was collected in a quadrat using the five-point sampling method. At each sampling station, the whole plant of *S. salsa* was excavated and

associated plants were removed. Then, a brush was used to move the soil adhered to the surface of the roots of *S. salsa* into a sterile sampling bag. Bulk soils were also collected and then thoroughly mixed to obtain one bulk soil sample. In each sample, a 20 g soil sample was weighed in a 250 ml shaker flask with 100 ml water and placed on a reciprocating degree constant temperature oscillator for 30 min. After standing for 30 min, the extracts were filtered or centrifuged and collected in a 100 ml beaker until measured. Then, the EC of soil samples was measured using an electrical conductivity instrument. The pH of the samples was measured using a pH meter.

2.3 Soil DNA extraction, PCR amplification, and sequencing

For bacterial community analysis, the V3–V4 regions of the 16S rRNA gene were amplified using the PCR primers 341F (5'-CCTACGGGNGGCWGCAG-3') and 805R (5'-GACTACHVGGGTATCTAATCC-3') (Cai et al., 2017). The primers ITS1F (5'-CTTGGTCATTTAGAGGAAGTAA-3') and ITS2R (5'-GCTGCGTTCTTCATCGATGC-3') were used to amplify the transcribed spacer region ITS1 for fungal community analysis (Saravanakumar et al., 2017). The library was constructed using Illumina MixSeq for sequencing. The sequencing data are available at NCBI (<https://www.ncbi.nlm.nih.gov/>, accession numbers PRJNA949580 and PRJNA949571).

2.4 Data analysis

To explore the similarity of different samples in terms of species diversity, QIIME software (Version 1.9.1) was used to calculate alpha and beta diversity (Bolyen et al., 2019). The graph was drawn using R (Version 3.4.4) (McMurdie & Holmes, 2013). The Chao1 and ACE indices measure species abundance as the number of species. The Shannon and Simpson indices are used estimate species diversity. The variance of soil properties between two groups was determined using one-way analysis of variance (ANOVA) (Kim et al., 2009). Based on the random matrix theory, the OTU data were used to construct molecular ecological network models of soil microorganisms in three different groups. And the interactions among soil microorganisms were analyzed (Xiao et al., 2022).

3 Results

3.1 Alpha diversity analysis

In the present study, indices, including ACE, Chao1, Simpson, and Shannon, were used to assess the alpha diversity of bacteria (Table 1) and fungi (Table 2). Our results revealed that the ACE, Chao1, Simpson, and Shannon indices were highest in the YDJ group and significantly different from those in the YDB group ($P < 0.05$), suggesting the great abundance and diversity of soil bacteria

in the natural *S. salsa*-growing area. No significant differences were observed for the four parameters between the YDB and BKS groups ($P > 0.05$).

For fungi, the ACE (1077.1960) and Chao1 (1077.1667) indices were higher in the YDJ group than in the YDB and BKS groups, suggesting the great abundance of fungi in the natural *S. salsa*-growing area. However, the differences in the Simpson and Shannon indices were not significant among the three groups, indicating that *S. salsa* does not strongly affect fungal diversity.

In this study, 26,663 OTUs were found in three groups of soil bacteria. The OTU numbers of YDJ group were higher than in the BKS and YDB groups (Figure 1). In total, 981, 242, and 363 OTUs were shared by the BKS and YDB, YDB and YDJ, and BKS and YDJ groups, respectively. Additionally, 11,619 OTUs were found in three groups of soil fungi. The OTU numbers of YDJ group were higher than in the BKS and YDB. Of these, 976, 994, and 952 OTUs were shared by the BKS and YDB, YDB and YDJ, and BKS and YDJ groups, respectively. The YDJ group had the greatest number of OTUs for both bacteria and fungi.

3.2 Soil microbial community structure analysis

The microbial community structure at the phylum level in the three groups is presented in Figure 2. Proteobacteria, Bacteroidota, and Gemmatimonadota were the dominant bacterial groups (accounting for 53.0% of all species) in the BKS group. Proteobacteria, Bacteroidota, and Acidobacteriota dominated in the YDB group (62.9%), and Proteobacteria, Desulfobacterota, and Chloroflexi were the major contributors in the YDJ group (57.5%). It was obvious that Proteobacteria had the greatest abundance in all three groups (30.9%, 42.9%, and 40.3% in the BKS, YDB, and YDJ groups, respectively). Regarding fungi, Ascomycota, Basidiomycota, and Olpidiomycota were dominant in all three groups (accounting for 90.4%, 85.9%, and 85.7% of fungi in the BKS, YDB, and YDJ groups, respectively). It could also be observed that Olpidiomycota had great abundance (13.5%) in the BKS group but low abundance in the YDB and YDJ groups (2.7% and 2.8%, respectively).

At the genus level, the top 30 microbial groups are presented in Figure 3 for bacteria. Except for the unclassified species, the *Woeseia* (3.1%) and *Pelagibius* (1.3%) were the dominant bacterial genera in YDJ group; the *Limibaculum* (2.8%), *Halomonas* (1.7%), and *Lactobacillus* (1.3%) were the dominant bacterial genus in YDB groups; the *Lactobacillus* (2.6%), *Ardenticatena* (1.8%), *Sphingomonas* (1.2%) and *Rehaibacterium* (1.1%) were the dominant bacterial genera in BKS groups.

For fungi, the top 10 microbial groups are presented in Figure 3. The *Olpidium*, *Thermoascus*, and *Fusarium* dominated in the BKS group (28.3%); *Thermoascus*, *Cladosporium*, and *Fusarium* dominated in the YDB group (18.4%); and *Xeromyces*, *Fusarium*, and *Thermoascus* dominated in the YDJ group (28.9%). *Xeromyces* was the most abundant genera in the YDJ (15.2%), and the *Olpidium* was the most abundant genera in BKS groups (13.5%).

TABLE 1 Alpha diversity indices of bacteria in the three groups.

Sample	ACE	Chao1	Simpson	Shannon
BKS	1891.2100±162.7968ab	1890.5242±162.7418ab	0.9955±0.0005a	9.2820±0.1371b
YDB	1780.5715±94.6253b	1778.7887±94.6017b	0.9962±0.0004ab	9.4143±0.7876b
YDJ	2275.2172±131.0164a	2274.1957±131.0433a	0.9975±0.0004a	10.0217±0.0514a

BKS: bare mudflat; YDB: artificial *S. salsa*-restoration area; YDJ: naturally *S. salsa*-growing area. Lower-case letters represent level of significance.

3.3 Principal component analysis (PCA)

PCA enables the classification of multiple samples, further demonstrating the differences in species diversity among the samples. Bacterial PCA plots revealed a contribution of 25.55% for PC1 and 16.12% for PC2. In comparison, fungal PCA plots revealed a contribution of 57.69% for PC1 and 14.56% for PC2 (Figure 4). For bacteria, the YDB samples were more distant and dispersed from those in the other two groups on the axes in the two coordinate plots, indicating that the YDB group had low similarity with the other two groups in terms of bacteria composition. For fungi, the YDJ group was more distant and dispersed from the other two groups on the axes in the two coordinate plots, indicating that the YDJ group had low similarity with the other two groups in terms of fungal composition.

3.4 Rhizosphere microbial network analysis

At the bacterial level, the molecular ecological network of the bacterial community and the leading network characteristic parameters were calculated to describe the structure of the bacterial molecular network. The R^2 of the exponential distribution relationship of the three groups (BKS, YDB and YDJ) were 0.754, 0.821, and 0.697, respectively. The similarity thresholds were 0.920, 0.940, and 0.920, which aligned with the power law (Table 3). At the fungi level, the molecular ecological network of the fungal community and the leading network characteristic parameters were calculated to describe the structure of the fungal molecular network. The R^2 of the exponential distribution relationship of the three groups (BKS, YDB and YDJ) were 0.743, 0.557, and 0.603, respectively. The similarity thresholds were 0.910, 0.880, and 0.910 in three groups (BKS, YDB and YDJ), which aligned with the power law (Table 4). Our result indicates that the node relationship in the constructed bacterial and fungal molecular

network model is reasonable and practical and can be further analyzed.

The total number of nodes and connections in a microbial molecular network can reflect the size of the network and the complexity of the relationships among species. This study's BKS, YDB, and YDJ bacterial networks comprised 294, 347,319 nodes and 1420, 1265, and 1232 edges, respectively. This study's BKS, YDB, and YDJ fungal networks contained 166, 200, and 235 nodes and 492, 539, and 688 edges, respectively. The results showed that the number of bacterial connections and total nodes and modules in BKS soil was the highest, the connectivity degree was the highest, and the interaction between species was the strongest (Figure 5). The groups of YDJ soil had the highest number of fungal connections, total number of nodes and modules, the highest connectivity degree, the most vital interaction among species, and the most complex relationship among species (Figure 6).

3.5 Permutation multivariate analysis of variance (PERMANOVA)

R^2 calculated via PERMANOVA indicates the degree of explanation of sample differences by subgroup. A larger R^2 indicates a higher degree of explanation of differences by subgroup, indicating a more significant difference in subgroups. The R^2 values of 0.197 ($P = 0.001$) in PERMANOVA for bacteria and 0.126 ($P = 0.001$) in PERMANOVA for fungi indicate a high and significant degree of difference among the groups (Figure 7).

In the present study, two soil physicochemical properties (EC and pH) of 18 samples were investigated to analyze the relationships among the groups (Figure 8). Our results found that for bacteria, pH was significantly and negatively correlated with the abundance of Acidobacteriota and Proteobacteria, whereas EC was significantly and positively correlated with the abundance of Firmicutes and negatively correlated with the abundance of Proteobacteria. For

TABLE 2 Alpha diversity indices of fungi in the three groups.

Sample	ACE	Chao1	Simpson	Shannon
BKS	906.6932±126.8089	906.6667±126.8071	0.9573±0.0184	7.1820±0.5554
YDB	979.7116±36.2185	979.6904±36.2098	0.9777±0.0012	7.4286±0.3352
YDJ	1077.1960±88.6264	1077.1667±88.6158	0.9633±0.0109	7.2485±0.2778

BKS: bare mudflat; YDB: artificial *S. salsa*-restoration area; YDJ: naturally *S. salsa*-growing area.

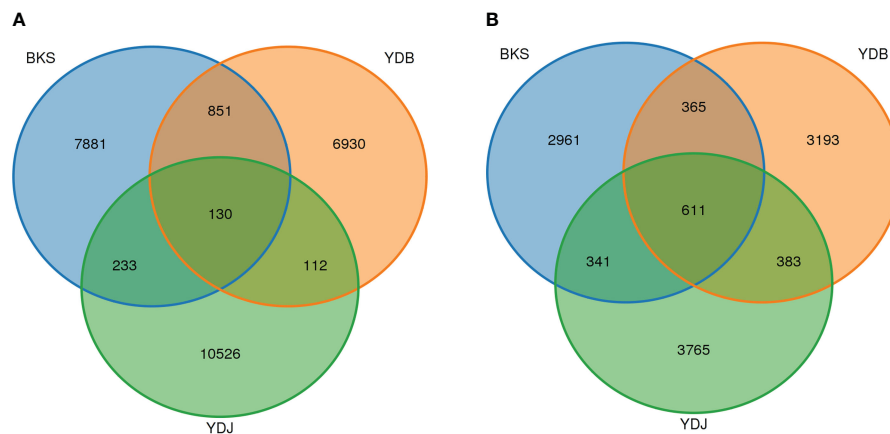


FIGURE 1 Venn diagram presenting the number of shared and unique OTUs among the different groups. (A) Soil bacteria; (B) soil fungi. BKS: bare mudflat; YDB: artificial *S. salsa* restoration area; YDJ: natural *S. salsa*-growing area.

fungi, pH and EC were significantly and negatively correlated with the abundance of Chytridiomycota (Figure 9).

4 Discussion

Soil microorganisms are involved in several processes occurring in soil (e.g., soil energy transfer, nutrient cycling, and improvement of soil physicochemical properties). They are massive driving forces of nutrient sources and sinks in the soil ecosystem (Liang et al., 2017). They can affect humus formation, increase soil fertility, and provide nutrients to plants by decomposing organic matter (Ayangbenro et al., 2022). The formation of the rhizosphere’s microbial community is associated with plants and soil. As the primary source of rhizosphere microorganisms, plants play an important role in the stable development of rhizosphere communities (Delgado-González et al., 2022). Our results showed

that most indices of microbial communities differed among the three study groups, suggesting that the existence and growth of *S. salsa* change microbial communities.

Regarding bacteria, the alpha diversity analysis illustrated that the abundance and diversity of soil bacteria were highest in the YDJ group. We speculated that the rhizosphere microorganisms of *S. salsa* in the naturally growing area had a more complex bacterial community structure. Meanwhile, fungal abundance was higher in the YDJ group than in the YDB and BSK groups, whereas fungal diversity was lower in the YDJ group than in the YDB group. The rhizosphere bacteria and fungi of *S. salsa* exhibited differences in complexity in the different groups. There are interactions between plants and rhizosphere bacteria. The structure of the rhizospheric microbial community is not static because it is influenced by microorganisms, host plants, and the soil environment. Therefore, the microbial community adhering to plant roots is constantly changing, thereby forming a complicated rhizospheric microbial

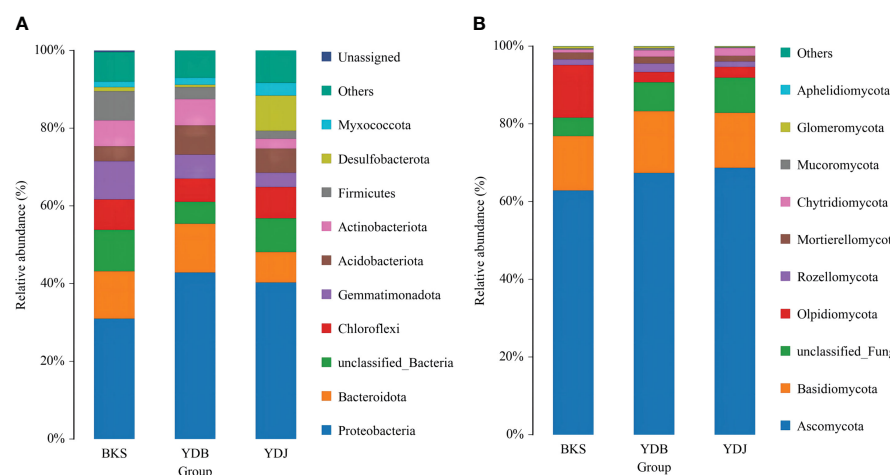
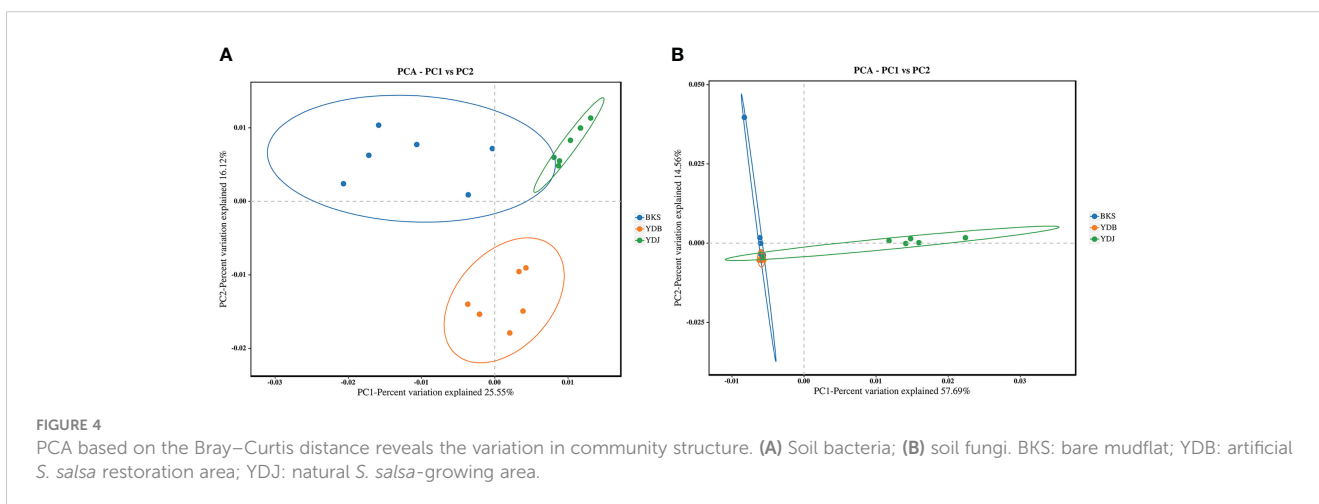
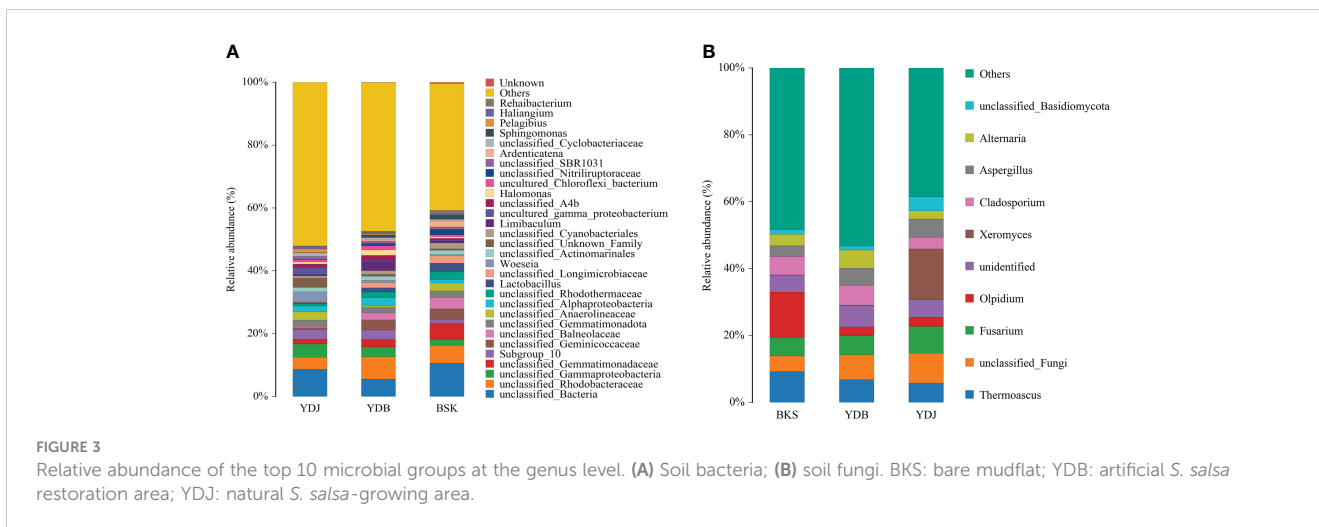


FIGURE 2 Relative abundance of the top 10 microbial groups at the phylum level. (A) Soil bacteria; (B) soil fungi. BKS: bare mudflat; YDB: artificial *S. salsa* restoration area; YDJ: natural *S. salsa*-growing area.



network. The OTU results illustrated that the YDJ group had the greatest numbers of bacteria and fungi. The fungal community composition in the *S. salsa* rhizosphere tended to have strong similarity among the three groups, differing from the results for bacteria. The PCA results demonstrated that the YDB group had low similarity with the other two groups regarding bacterial composition. The YDJ group had low similarity with the other two groups regarding fungal composition. Some root exudates produced by plants attract fungi, bacteria, and other

microorganisms in the soil to accumulate in its roots (Weidenhamer et al., 2023). These attracted microorganisms in turn promote the growth and development of the plants. Hence, the diversity of microbial communities in plant rhizosphere soil is much higher than that in nonplant rhizosphere soil.

Concerning the dominant microbial groups in the three sampling groups, Proteobacteria was the main bacterial phylum in rhizosphere soil, coinciding with the findings of previous research (Zuo et al., 2021). It can effectively promote the

TABLE 3 Characteristic parameters of the molecular ecological network of soil bacteria in three groups.

Characteristic parameters of network	Treatment		
	BKS	YDB	YDJ
Total nodes	294	347	319
Total links	1420	1265	1232
Similarity threshold	0.920	0.940	0.920
R square of power-law	0.754	0.821	0.697
Average path distance	4.258	4.631	5.353

TABLE 4 Characteristic parameters of the molecular ecological network of soil fungi in three groups.

Characteristic parameters of network	Treatment		
	BKS	YDB	YDJ
Total nodes	166	200	235
Total links	492	539	688
Similarity threshold	0.910	0.880	0.910
R square of power-law	0.743	0.557	0.603
Average path distance	4.186	4.925	5.273

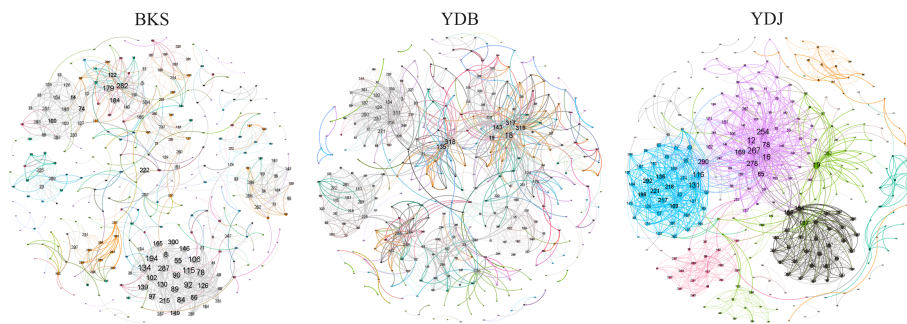


FIGURE 5
Molecular ecological network model of soil bacteria in different groups. Each node in the figure represents an OTU, and the lines between nodes indicate that there is a significant correlation ($p < 0.05$), the red lines represent positive interactions, and the green lines represent negative interactions. BKS: bare mudflat; YDB: artificial *S. salsa* restoration area; YDJ: natural *S. salsa*-growing area.

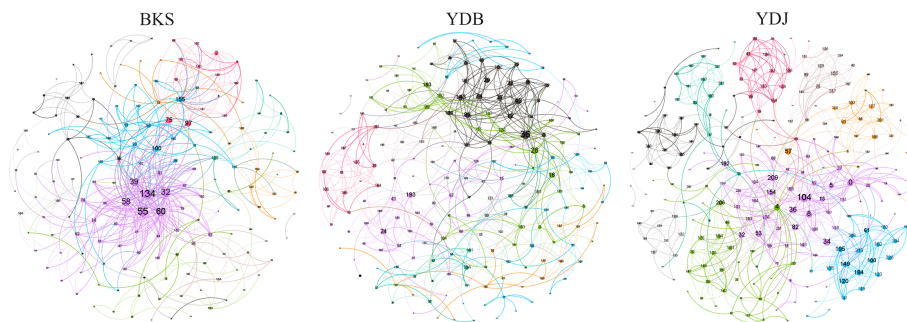


FIGURE 6
Molecular ecological network model of soil fungi in different groups. Each node in the figure represents an OTU, and the lines between nodes indicate that there is a significant correlation ($p < 0.05$), the red lines represent positive interactions, and the green lines represent negative interactions. BKS: bare mudflat; YDB: artificial *S. salsa* restoration area; YDJ: natural *S. salsa*-growing area.

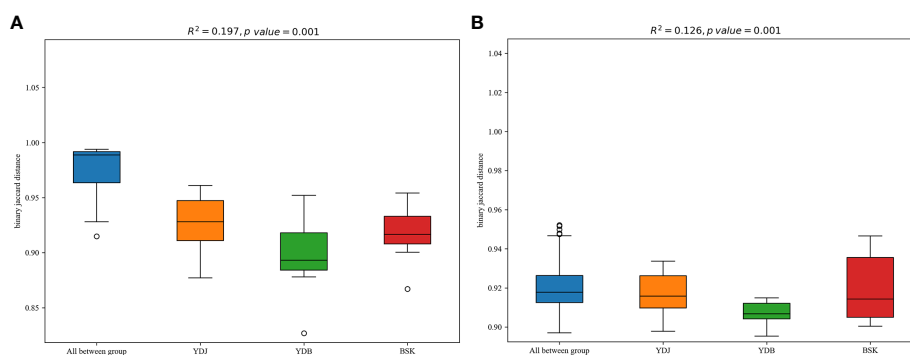


FIGURE 7
PERMANOVA among the different groups. **(A)** Soil bacteria; **(B)** soil fungi. BKS: bare mudflat; YDB: artificial *S. salsa* restoration area; YDJ: natural *S. salsa*-growing area.

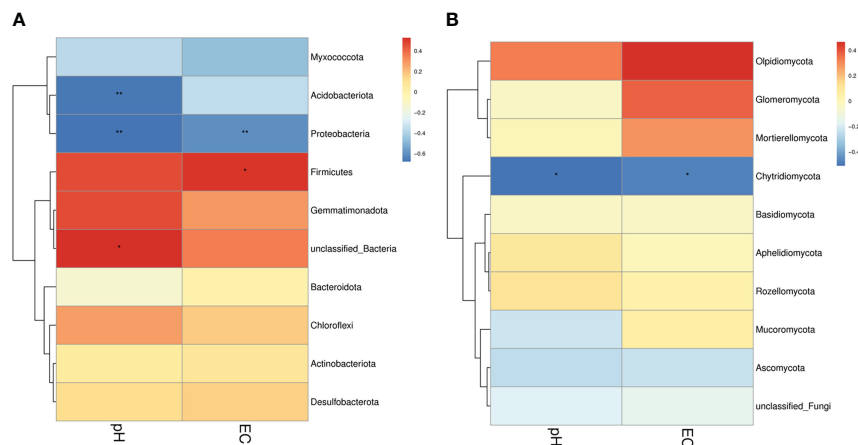


FIGURE 8 Correlation between soil microorganisms and soil physicochemical properties. **(A)** Relationship between the bacterial phylum and soil physicochemical properties. **(B)** Relationship between the fungal phylum and soil physicochemical properties. Different colors indicate different levels of correlation. * and ** denote statistical significance at $P \leq 0.05$ and $P \leq 0.01$, respectively.

absorption of trace elements in soil by plants, thus enhancing the resistance of plants. Proteobacteria were also reported to play an important role in low-molecular-weight substrates in different environments (Goldfarb et al., 2011). In terms of fungi, a previous study found that Ascomycota was the predominant microflora in marine environments (Panno et al., 2013). *S. salsa* is mainly distributed in coastal areas, and it is deeply affected by the marine environment, which might explain the great abundance of Ascomycetes in the rhizosphere of *S. salsa*. The present study found that the *Xeromyces* were the most abundant genera in the YDJ, and the *Olpidium* was the most abundant genera in BKS groups. The *Xeromyces* can survive arid conditions and is considered one of the most adaptable species in the biological world. Previous studies found that the *Olpidium* species are recognized as a common fungal parasite for the roots of diverse plant species (Lay et al., 2018), while we found that the *Olpidium* was the most abundant genera in BKS groups. We speculated that the abundant genera of *Olpidium* dominant might be variations in the succession stages, and the *S. salsa* did not survive after the restoration (Li et al., 2023). Ecological network analysis showed that

the YDJ group had the highest number of fungal connections and the most complex relationship among species. Previous studies found that higher nodes and connections indicated complex interspecies relationships and high network stability (Feng et al., 2022). The higher the soil microbial community diversity, the more stable the soil ecosystem (Feng et al., 2022). Thus, we speculated that the YDJ group had high functionality and ability to withstand external stress (Coban et al., 2022).

Our results revealed significant differences among the groups (Figure 10). A previous study found that the abundance value of biological metabolic pathways in the rhizosphere of *S. salsa* was higher than that in bare soil. In terms of metabolic pathway, glutathione metabolism, proteins involved in photocoooperation, photosynthesis, chlorocyclohexane and chlorobenzene degradation of bacteria in rhizosphere soil were prominent, indicating that the bacterial community metabolic pathway was improved by the coverage of *S. salsa* (Sun et al., 2020). Regarding the top five gene families, including general function prediction, amino acid transport and metabolism, and carbohydrate transport and metabolism, genetic diversity was higher in the YDB group

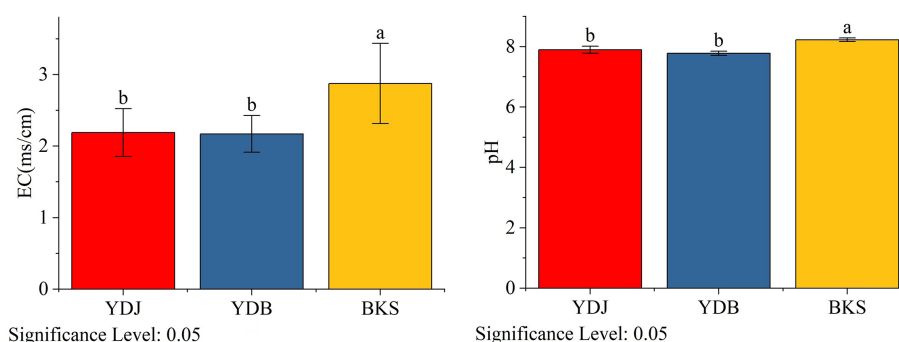


FIGURE 9 Analysis of soil physical and chemical properties in different groups. BKS: bare mudflat; YDB: artificial *S. salsa* restoration area; YDJ: natural *S. salsa*-growing area.

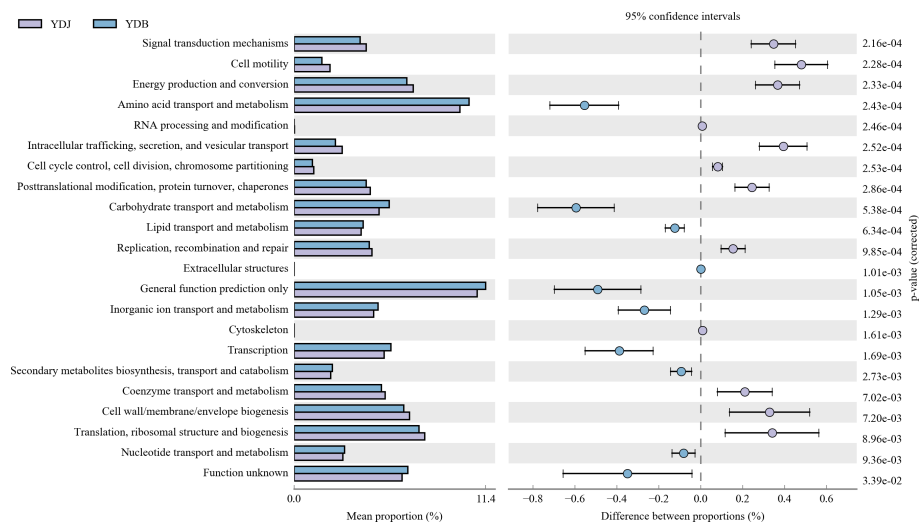


FIGURE 10 High relative abundance in COG functional annotation. Different colors denote different groups. Different functional parts are presented in the figure. YDB: artificial *S. salsa* restoration area; YDJ: natural *S. salsa*-growing area.

than in the YDJ group. Regarding translation, ribosomal structure and biogenesis, and cell wall/membrane/envelope biosynthesis, genetic diversity was higher in the YDJ group than in the YDB group.

5 Conclusions

In conclusion, the *S. salsa* wetland in natural conditions tended to be similar to the artificial *S. salsa*-restoration. The composition of fungi in the *S. salsa* rhizosphere had greater similarities rather than that of the bacteria. Proteobacteria was observed with the highest abundance in bacterial communities, and Ascomycota, Basidiomycota, and Olpidiomyota were dominant in the fungi communities of the three groups.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repositories and accession numbers can be found in the article.

Author contributions

HX: Writing – original draft. NL: Writing – original draft. WL: Software, Writing – original draft. HW: Writing – original draft. YS: Writing – original draft. JL: Writing – original draft. JZ: Writing – review & editing. JW: Writing – review & editing. SS: Writing – review & editing.

Funding

The author(s) declare that financial support was received for the research, authorship, and/or publication of this article. This work was supported by the Natural Science Foundation of Shandong Province (ZR2021QD082). Taishan Industrial Experts Program; Science and Technology Support Plan for Youth Innovation of Colleges and Universities in Shandong Province (2022KJ088).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2024.1343672/full#supplementary-material>

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