

DIVERSITY AND COMMUNITY ASSEMBLY OF ABUNDANT AND RARE BACTERIAL TAXA IN MINING AREAS

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(Received 22nd Sep 2025; accepted 15th Dec 2025)

Abstract. Rhizosphere microorganisms are closely related to plant growth. Due to a lack of systematic understanding of the diversity characteristics and assembly processes of soil microbial communities under human disturbance. This study investigated these parameters along with influencing factors of the rhizosphere soil in a mining area. We found that there was no significant difference in soil bacterial communities among different plants in this area. Soil organic matter (SOM) was the main parameter affecting α -diversity of rhizosphere soil bacterial communities, while total phosphorus (TP) and pH dominated variation of community structure. SOM and salinity were significantly positively correlated with α -diversity of abundant taxa, while soil environmental parameters were not significantly related to α -diversity of rare taxa. The β -diversity of rare taxa was significantly higher than that of abundant taxa, whereas abundant taxa had a wider niche. The assembly processes of both rare and abundant taxa were mainly stochastic. Dispersal limitation contributed the most to abundant taxa. Rare taxa were mainly determined by both dispersal limitation and undominated processes. These results broaden our understanding of the structure and ecological assembly mechanisms of rhizosphere bacterial communities in mining areas.

Keywords: *bacterial community, rhizosphere soil, mining area disturbance, vegetation restoration, microbial-plant symbiosis*

Introduction

The rapid development of the mining industry has promoted the progress of human society and civilization. China produces about 3.6 billion tons of coal every year, accounting for 55% of the global production (Luo et al., 2019). High-intensity coal mining has caused a series of ecological and environmental problems. Mining activities destroy surface ecosystems, therefore, more attention should be paid to environmental problems and sustainable socio-economic development in mining areas. Under the triple pressures of soil compaction, water shortage, and intensive underground coal mining, cracks of different depths and widths are more likely to form (Liu et al., 2019). Some studies have focused on the impact of coal mining cracks on soil physicochemical properties, and found that soil moisture, temperature, and bulk density decreased (Wu et al., 2019; Zhang et al., 2015). In addition, coal mining also leads to the loss of nutritional elements, such as nitrogen, phosphorus, and potassium (Luo et al., 2019), leading to the destruction of the rhizosphere environment, the withering and death of surface vegetation (Bi et al., 2019). As the most widely distributed and active component in terrestrial ecosystems, microorganisms are of great significance for driving ecosystem material cycling and nutrient transformation, and act as regulators of subsurface ecological processes (Wang et al., 2023; Yang et al., 2023). Soil bacterial communities are closely related to soil physicochemical properties, enzyme activities, and vegetation cover types, helping to restore ecosystem functions and playing an important role in mine restoration (Wang et al., 2023). Rhizosphere microbial communities have been proven to promote plant community recovery by influencing ecosystem functions such as element cycling

and primary production (Wang et al., 2023). If only engineering measures such as vegetation reconstruction, landform modification, and soil improvement are implemented without microbial participation, the potential for ecological restoration will be limited, and the effect of restoration will be reduced. Therefore, mine ecological restoration must pay attention to soil microbial succession, ecological processes, and restoration potential.

Microbial communities are highly diverse, with a large number of rare taxa coexisting with a small number of abundant taxa (Jiao and Lu, 2020). However, dominant species (i.e., high-abundance species) are few, and most are rare species with relative abundances below 0.1% or even 0.01% (Dai et al., 2022). Abundant and rare taxa have different characteristics and functional features in various ecosystems (Xu et al., 2021). Abundant taxa play a crucial role in nutrient cycling and show stronger environmental adaptability (Wan et al., 2021). Compared with abundant taxa, rare taxa are also important in maintaining ecosystem functions, such as sulfate reduction, organic matter degradation, and resistance to disturbance (Chen et al., 2019; Sauret et al., 2014). Abundant and rare taxa interact with each other and jointly regulate changes in soil nutrients. Diverse rare taxa play an important role in maintaining community diversity and multifunctionality. However, the diversity patterns of abundant and rare taxa in mining areas are still poorly understood. Determining the composition of soil microbial communities is the basis for understanding the distribution patterns of soil biodiversity, and provides theoretical knowledge for understanding how biotic or abiotic factors and microbial interactions influence microbial community structure.

Deterministic and stochastic processes are generally considered to influence microbial community assembly (Jiao and Lu, 2020). Deterministic processes can be explained by niche theory, which assumes that biotic and abiotic factors, such as interspecific interactions and environmental selection, affect community structure (Yang et al., 2022). The contributions of these two processes to the assembly of rare and abundant taxa remain controversial. Studies in coastal wetlands and the Qinghai–Tibet Plateau have shown that rare taxa are more limited by dispersal than abundant taxa (Jiao et al., 2017; Yang et al., 2022), while in farmlands and Cd-contaminated soils, abundant taxa are more strongly affected by dispersal limitation (Nyirabuhoro et al., 2021). Environmental parameters can influence the balance between deterministic and stochastic processes (Jiao and Lu, 2020). Studies (Ma et al., 2024; Yang et al., 2023) have shown that vegetation restoration types significantly affect the assembly processes of soil microbial communities. However, it is still unclear whether abundant and rare taxa in mining soils exhibit consistent assembly processes. Studying the assembly patterns of rhizosphere microorganisms in mining areas can provide theoretical evidence for subsequent grassland restoration.

Materials and methods

Study area

The Shendong mining area is located in the ecotone between the northern Loess Plateau and the Mu Us Sandy Land. The regional ecological environment is fragile, with severe soil desertification, water scarcity, and serious soil erosion. With the continuous expansion of mining activities, the ecological environment of the Shenfu–Dongsheng mining area has been deteriorating. The Shangwan Mine of the Shenfu–Dongsheng mining area is located in Yijinhualuo Banner, Ordos City, Inner Mongolia Autonomous Region (E109°30'–110°30', N38°50'–39°50', *Fig. 1*). The area is characterized by a temperate continental climate, with a mean annual temperature of 7.3°C and an average

annual precipitation of 358.2 mm. Rainfall is generally concentrated between July and September. Large-scale surface subsidence and fissures are present across the mining area. The natural vegetation type is a transition from typical steppe to desert steppe, mainly consisting of perennial, xerophytic, tufted grasses, xerophytic shrubs, and semi-shrubs. Dominant species include *Caragana intermedia* (*C. intermedia*), *Thymus mongolicus* (*T. mongolicus*), *Setaria viridis* (*S. viridis*), *Cleistogenes squarrosa* (*C. squarrosa*), *Lespedeza bicolor* Turcz. (*L. bicolor*), and *Caragana korshinskii* Kom (*C. korshinskii*).

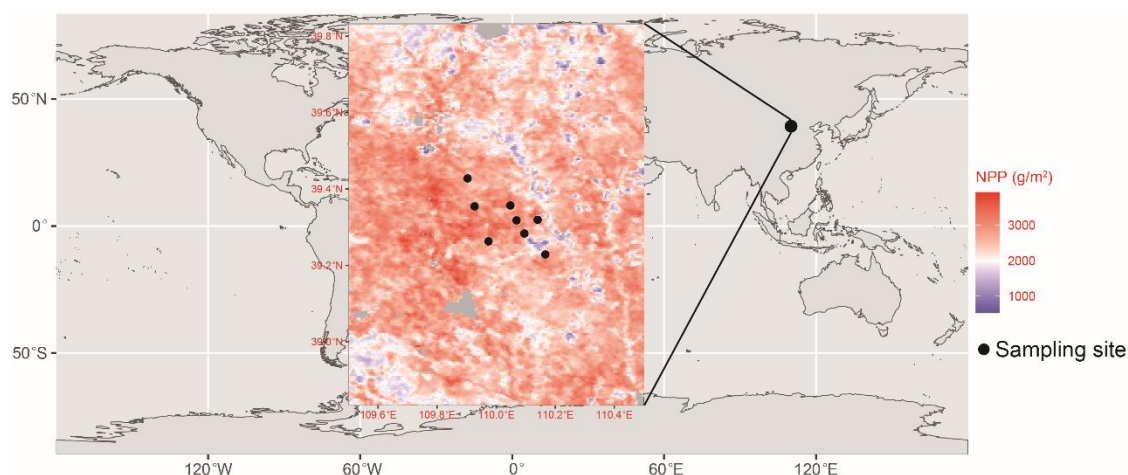


Figure 1. Study area and sampling site. NPP is net primary productivity from moderate resolution imaging spectroradiometer (MOD17A3HGF). Multiple samples were collected from a single sampling site

Sampling

Rhizosphere soils were collected along the direction of underground mining tunnels. Soils located 1-2 cm from plant roots were considered rhizosphere soils. The sampled plant species included *L. bicolor*, *C. korshinskii*, *Artemisia ordosica* (*A. ordosica*), *Hippophae rhamnoides* (*H. rhamnoides*), and *S. viridis*. Among them, 8 rhizosphere soil samples were collected from *L. bicolor*, 5 from *C. korshinskii*, 13 from *A. ordosica*, 1 from *H. rhamnoides*, and 9 from *S. viridis*, resulting in a total of 36 samples. After removing litter and gravel, each rhizosphere soil sample was divided into two subsamples: one air-dried and sieved for soil physicochemical property analysis, and the other stored at -80°C for 16S rRNA sequencing.

Microbial sequencing

Microbial sequencing was performed by Majorbio Bio-Pharm Technology Co., Ltd. Genomic DNA was extracted using a commercial DNA extraction kit according to the manufacturer's instructions. The integrity and purity of the DNA were assessed by 1% agarose gel electrophoresis, while DNA concentration and purity were determined using a NanoDrop One spectrophotometer. PCR amplification and electrophoretic detection of the products were conducted with genomic DNA as the template. Depending on the selected sequencing region, barcoded primers and Premix Taq were used for PCR amplification. The concentrations of PCR products were compared using GeneTools

Analysis Software (Version 4.03.05.0, SynGene), and the required volume of each sample was calculated based on equal mass. PCR products from all samples were then pooled. Mixed PCR products were purified using the E.Z.N.A.® Gel Extraction Kit, and target DNA fragments were eluted with TE buffer.

Subsequent library preparation was carried out following the standard protocol of the NEBNext® Ultra™ DNA Library Prep Kit for Illumina®. Sequencing was performed on the Illumina MiSeq high-throughput sequencing platform. The raw sequencing data of all samples were merged and filtered, and sequences with 97% similarity were clustered into operational taxonomic units (OTUs), with chimeric sequences removed simultaneously. Representative sequences of each OTU were compared against reference databases to obtain taxonomic annotations. The resulting species annotation table and OTU table were used for downstream analyses.

Soil parameter determination

Soil pH and salinity were determined using the potentiometric method with a pH/salinity meter (soil-to-water ratio 1:5, w/v). Soil organic matter (SOM) content was measured by the potassium dichromate oxidation method with external heating. Total nitrogen (TN) concentration was analyzed using an elemental analyzer (Vario EL, Elementar, Germany). Total phosphorus (TP) was determined by the sulfuric acid-perchloric acid digestion method followed by colorimetric analysis using a spectrophotometer. Total potassium (TK) was measured by flame photometry after sample digestion. These physicochemical parameters were selected as they are key indicators of soil fertility and microbial habitat quality, directly influencing microbial diversity and community structure.

Data processing

OTUs with relative abundance greater than 0.1% were classified as abundant taxa, those with relative abundance less than 0.01% were classified as rare taxa, and OTUs with relative abundance between 0.01% and 0.1% were considered intermediate taxa (Jiao et al., 2017). α -diversity of soil bacterial communities, including Shannon index, Simpson index, richness index, and Chao1 index, were calculated using the vegan package (Oksanen et al., 2022) in R (version 4.2.1, www.r-project.org). Principal Coordinates Analysis (PCoA) and Redundancy Analysis (RDA) were also performed using the vegan package (Oksanen et al., 2022). Correlation analyses between bacterial communities and soil parameters were conducted with the corrplot package (Wei and Simko, 2024). Niche width of bacterial communities was calculated using the spaa package (Zhang, 2025). Statistical differences were first assessed by one-way ANOVA. If a significant effect was found, multiple comparisons were performed using the least-significant difference test.

Community assembly processes of bacterial communities were assessed using null model analysis (Stegen et al., 2013). The null model quantifies the deviation of observed community phylogenetic distance from random expectation; greater deviation indicates stronger influence of deterministic processes, while smaller deviation indicates dominance of stochastic processes. The picante package was used to calculate the β -nearest taxon index (β NTI) and Raup-Crick matrix (RCbray). When $|\beta$ NTI| > 2, community assembly is considered deterministic, with β NTI > 2 indicating heterogeneous selection and β NTI < -2 indicating homogeneous selection. When

$|\text{BNTI}| < 2$, stochastic processes dominate; among these, $\text{RCbray} > +0.95$, $\text{RCbray} < -0.95$, and $|\text{RCbray}| < 0.95$ indicate dispersal limitation, homogenizing dispersal, and undominated processes, respectively.

Results

Soil environmental parameter

No significant differences were observed among the rhizosphere soils of the five plant species (Table 1). The rhizosphere soils of *S. viridis* exhibited the highest TN and TP contents, at $3.45 \text{ g} \cdot \text{kg}^{-1}$ and $471 \text{ mg} \cdot \text{kg}^{-1}$, respectively. *A. ordosica* showed the highest TK and salt contents, at 3.04% and $4.57 \text{ g} \cdot \text{kg}^{-1}$, respectively. The rhizosphere soils of *C. korshinskii* had the highest SOM content, reaching $1.86 \text{ g} \cdot \text{kg}^{-1}$.

Table 1. Soil environmental parameters

	TN (g/kg)	TP (mg/kg)	TK (%)	Salt (g/kg)	SOM (g/kg)	pH
Whole	2.72 ± 1.8	358.11 ± 160	2.72 ± 0.61	3.88 ± 2.68	1.67 ± 0.56	8.54 ± 0.16
<i>A. ordosica</i>	2.95 ± 2.03	$284 \pm 99.2\text{b}$	3.04 ± 0.67	4.57 ± 3.50	1.72 ± 0.58	8.52 ± 0.20
<i>L. bicolor</i>	2.25 ± 0.96	$398 \pm 158\text{ab}$	2.43 ± 0.21	3.36 ± 2.10	1.52 ± 0.52	8.58 ± 0.11
<i>C. korshinskii</i>	1.62 ± 0.29	$324 \pm 149\text{ab}$	2.46 ± 0.87	2.89 ± 0.62	1.86 ± 0.32	8.41 ± 0.21
<i>S. viridis</i>	3.45 ± 2.37	$471 \pm 183\text{a}$	2.65 ± 0.48	3.93 ± 2.71	1.64 ± 0.72	8.61 ± 0.11
<i>H. rhamnoides</i>	2.47	156	2.97	3.83	1.6	8.6
	ns	*	Ns	ns	ns	ns

The bottom row presents the p-values from ANOVA. * and ns indicate the $p < 0.05$ and $p > 0.05$, respectively. Different letters indicate the difference is significant

Bacterial community β -diversity, structure, and influencing parameters

The α -diversity of rhizosphere soil bacterial communities was significantly positively correlated with SOM content (Fig. 2A, $p < 0.05$). Soil pH was significantly negatively correlated with the relative abundance of Proteobacteria and significantly positively correlated with Rokubacteria (Fig. 2B, $p < 0.01$). Both SOM and salinity were significantly positively correlated with the relative abundances of Actinobacteria and Chloroflexi ($p < 0.05$), while salinity was also significantly positively correlated with the relative abundance of Acidobacteria ($p < 0.05$). No distinct clustering of rhizosphere bacterial community structure was observed among different plant species (Fig. 2C), and permutation tests confirmed that plant species did not have a significant effect on bacterial community structure ($p < 0.05$).

Redundancy analysis (RDA) indicated that six environmental factors together explained 15.67% of the variation in bacterial community structure at the OTU level (Fig. 2D). Among these factors, TP and pH contributed most significantly to the variation, with contributions of 0.47 and 0.18, respectively ($p < 0.05$).

The α -diversity of abundant taxa was significantly positively correlated with SOM (Fig. 3A), whereas rare taxa showed no significant correlations with soil factors (Fig. 3B). Actinobacteria, Proteobacteria, Acidobacteria, and Chloroflexi were the four most abundant phyla in both abundant and rare taxa, accounting for 91.6% and 76.5% of the total abundance, respectively. Abundant taxa were distributed across nine phyla, while rare taxa were distributed across fifteen phyla. Within abundant taxa, soil salinity was

significantly positively correlated with the relative abundances of Acidobacteria, Chloroflexi, Gemmatimonadetes, and Nitrospirae (Fig. 3C, $p < 0.05$). SOM was significantly positively correlated with Chloroflexi and Nitrospirae ($p < 0.05$), and pH was significantly positively correlated with Proteobacteria and Bacteroidetes ($p < 0.05$). Among rare taxa, TP and TK were significantly negatively and positively correlated with Chloroflexi, respectively (Fig. 3D, $p < 0.05$). pH was significantly positively correlated with Chloroflexi ($p < 0.05$), and salinity was significantly positively correlated with Gemmatimonadetes ($p < 0.05$).

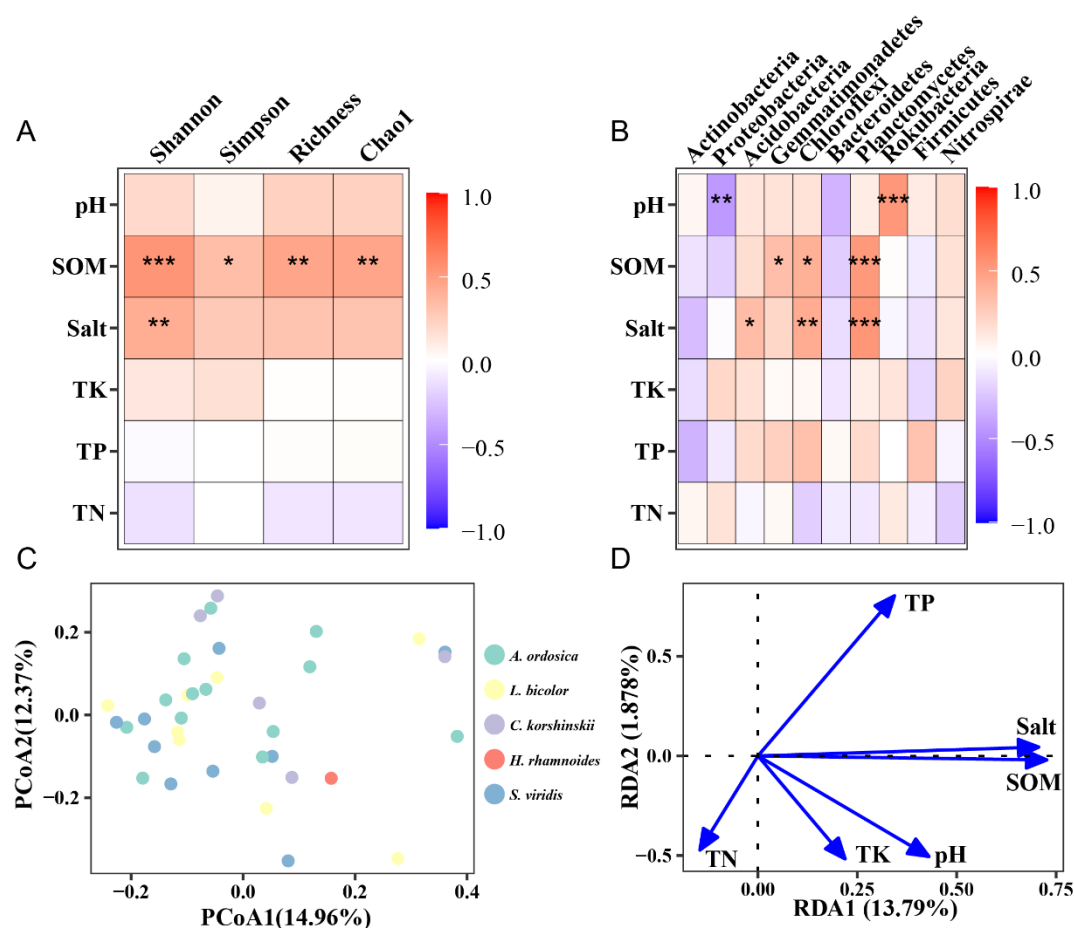


Figure 2. The diversity of whole bacterial communities and their relationships with soil factors. (A) the correlation analysis between bacterial α -diversity and soil factors. (B) the correlation analysis between bacterial phyla and soil factors. (C) The PCoA of bacterial community. (D) The RDA of bacterial community. Statistical significance is indicated by asterisks: * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$

Plant species had no significant effect on the community structures of either abundant or rare taxa (Fig. 4A, Fig. 4B). TP and SOM significantly influenced the community structure of abundant taxa, explaining 16.4% and 33.7% of the variation, respectively (Fig. 4C, $p < 0.05$). Rare taxa were more strongly influenced by soil environmental factors, with TN, TP, salinity, SOM, and pH all having significant effects (Fig. 4D, $p < 0.05$). Among these factors, soil salinity contributed most to the variation in rare taxa, accounting for 43.7%.

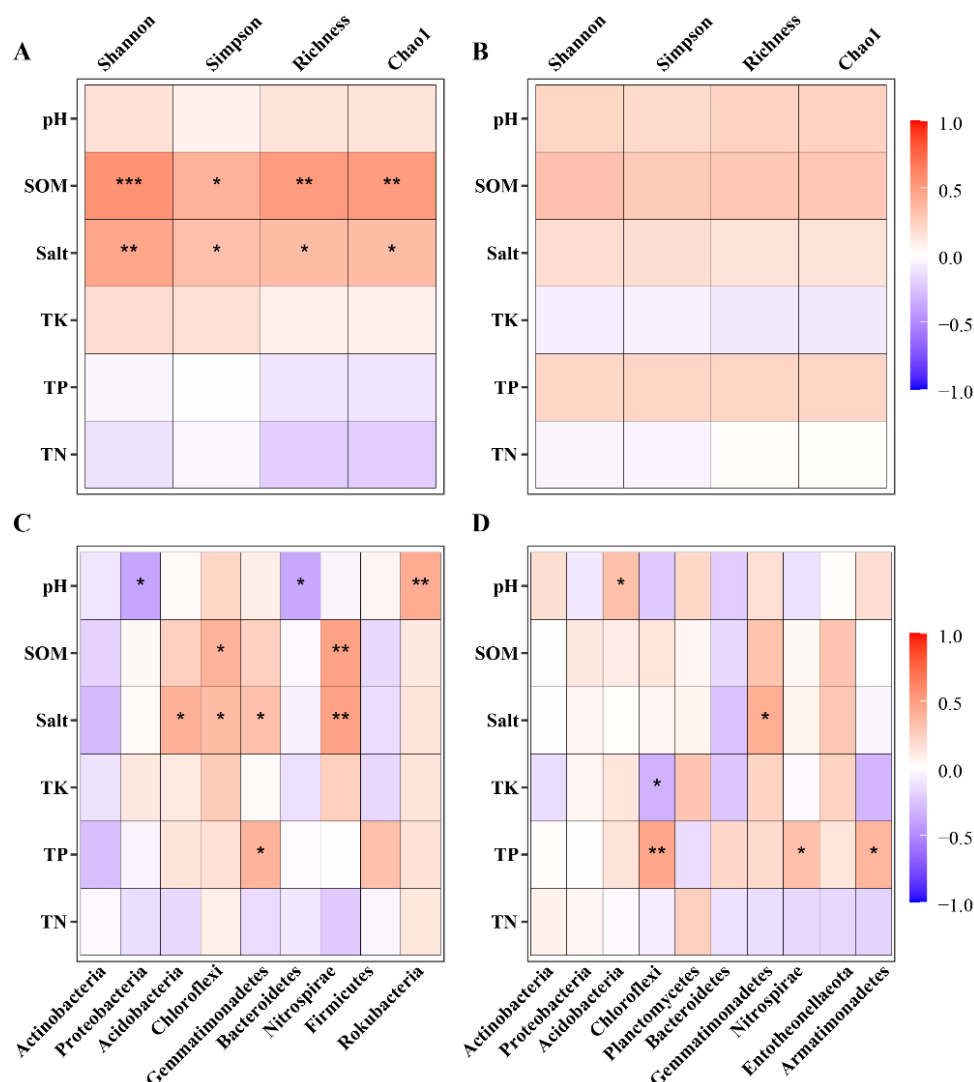


Figure 3. The α -diversity of abundant and rare taxa and correlations between bacterial community composition and soil factors. (A) the correlation analysis between abundant bacterial α -diversity and soil factors. (B) the correlation analysis between rare bacterial α -diversity and soil factors. (C) the correlation analysis between abundant bacterial phyla and soil factors. (D) the correlation analysis between rare bacterial phyla and soil factors. Statistical significance is indicated by asterisks: * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$

Diversity and structural characteristics of abundant and rare taxa

When bacterial communities were partitioned based on relative abundance, the Shannon index followed the pattern: total community > intermediate taxa > abundant taxa > rare taxa (Fig. 5A, $p < 0.05$). The Chao1 index showed a similar trend ($p < 0.05$). Rare taxa exhibited significantly higher β -diversity than both intermediate and abundant taxa ($p < 0.05$).

At the class level, abundant and rare taxa were mainly distributed among Thermoleophila, Alphaproteobacteria, Actinobacteria, Gammaproteobacteria, and Subgroup_6. The relative abundance of Actinobacteria was significantly higher in abundant taxa than in rare taxa ($p < 0.05$).

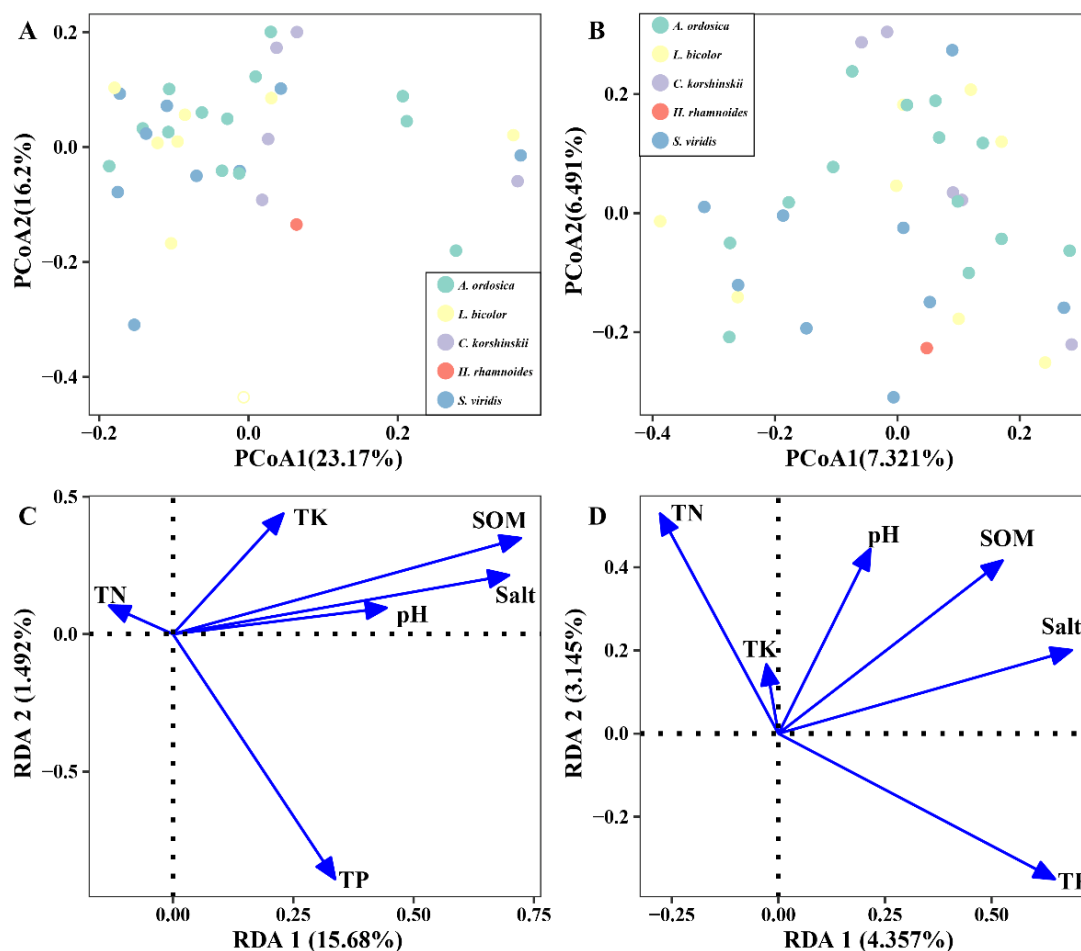


Figure 4. Community structure of abundant and rare bacterial taxa and their influencing factors. (A) and (B) the PCoA of abundant and rare bacterial community, respectively. (C) and (D) the RDA of abundant and rare bacterial community, respectively

Abundant taxa exhibited significantly greater niche width than rare taxa (Fig. 6A, $p < 0.05$), indicating less niche overlap. Both abundant and rare taxa had 4.3% of $|\beta NTI|$ values greater than 2 (Fig. 6B), representing deterministic processes in community assembly. The stochastic processes of bacterial communities were further classified based on RCbray. For abundant taxa, 78.7% of the assembly was attributed to dispersal limitation, 0.16% to homogenizing dispersal, and 16.8% to undominated processes, while 3.97% and 0.32% were due to heterogeneous selection and homogeneous selection, respectively (Fig. 6C). In rare taxa, 46.8% of the assembly was due to dispersal limitation, 1.26% to homogenizing dispersal, and 47.6% to undominated processes, with 2.69% and 1.58% attributed to heterogeneous selection and homogeneous selection, respectively. These results indicate that abundant taxa were primarily governed by dispersal limitation, whereas rare taxa were mainly controlled by undominated processes.

The community assembly processes of rhizosphere bacterial communities were generally similar across different plant species, although the abundant taxa of *C. korshinskii* and *S. viridis* were not influenced by deterministic processes (Fig. 6D, E).

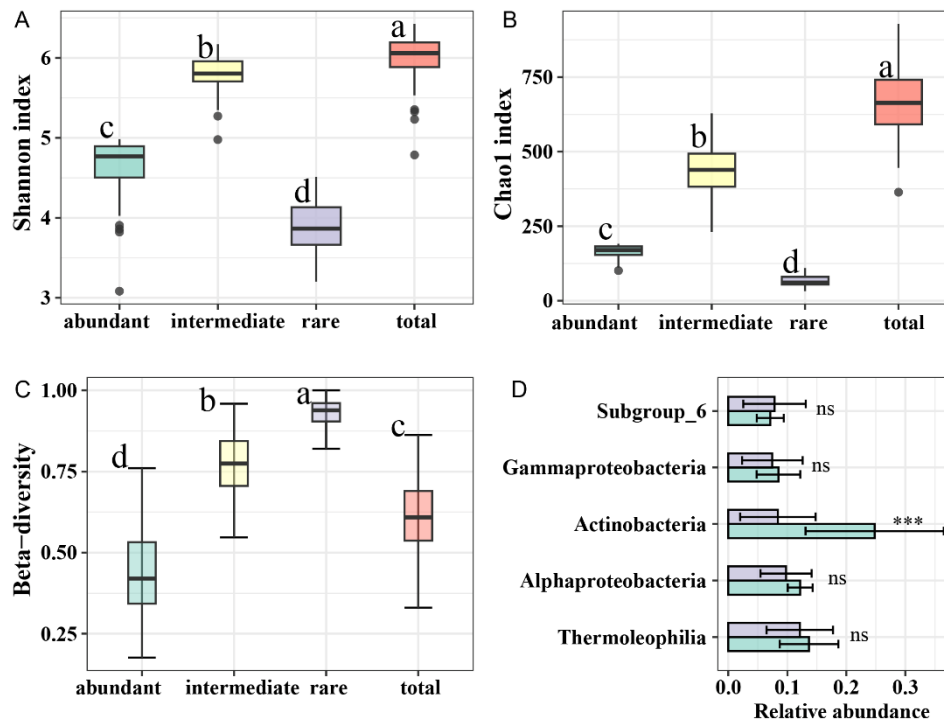


Figure 5. The α -diversity and β -diversity of abundant and rare group. Abundant is abundant group. Intermediate is intermediate group. Rare is rare group. Total is the whole community. ns denotes no significant difference, and *** denotes the difference is significant at 0.001 level. Different letters indicate the difference is significant. Community assembly patterns of abundant and rare taxa

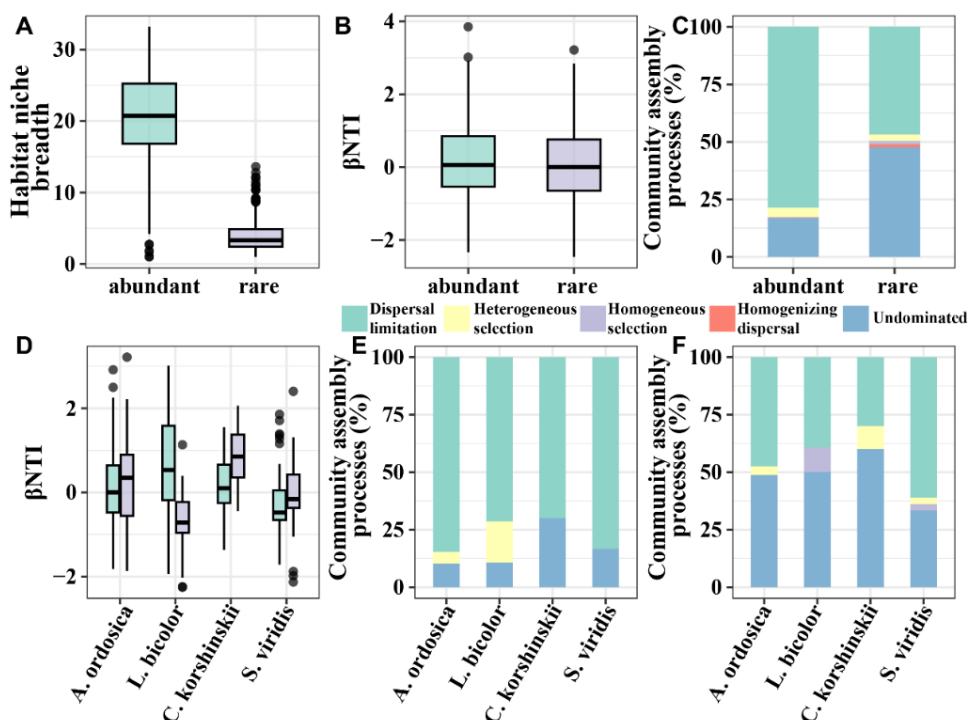


Figure 6. Niche width and community assembly processes of abundant and rare taxa

Discussion

Soil microorganisms are highly sensitive to external environmental changes and can serve as bioindicators of land degradation and ecological restoration (Ma et al., 2023; Zhang et al., 2023). Mining activities alter soil properties, thereby affecting soil microbial communities in terrestrial ecosystems (Ma et al., 2023). In this study, we found that the factors influencing α - and β -diversity of bacterial communities differed. SOM and salinity were significantly positively correlated with the α -diversity of rhizosphere soil bacterial communities. In agricultural ecosystems, higher SOM content typically enhances bacterial α -diversity (Liang et al., 2020; Tang et al., 2023). In the mining area, SOM and salinity were significantly positively correlated with the α -diversity of abundant taxa, whereas rare taxa α -diversity showed no significant correlations with soil environmental factors, indicating that SOM and salinity primarily affect abundant taxa. Bacteria and fungi are considered key drivers of SOM decomposition. Higher SOM content provides a richer carbon source, supporting diverse metabolic pathways, thereby promoting the growth and reproduction of abundant taxa and increasing their diversity (Zhang et al., 2024). Although abundant taxa are fewer in number, their broader ecological niches allow them to reach higher abundance, making them more sensitive to changes in SOM. Salinity also participates in physiological processes such as osmotic regulation, and moderate salinity may facilitate normal physiological functions of many bacteria within abundant taxa. In this study, soil salinity was 3.05‰, which does not reach a stressful level. Additionally, salinity measured as soluble salts includes trace elements essential for life, which may differ from the negative effects of salinity in saline-alkali soils. Rare taxa, due to their low abundance, respond more slowly to environmental changes, so the influence of environmental factors on their α -diversity was not detectable at the observational scale of this study. This finding is important for understanding soil ecosystems in mining areas. In ecological restoration, regulating SOM and salinity may be an effective strategy to increase the diversity of abundant bacterial taxa, thereby enhancing soil ecological functions such as nutrient cycling and soil fertility.

Rare taxa exhibited higher β -diversity, consistent with previous studies (Qin et al., 2022; Yang et al., 2022). Differences in β -diversity are primarily driven by species turnover, with rare taxa being more dispersed than abundant taxa (Qin et al., 2022). No significant differences in rhizosphere soil bacterial β -diversity were observed among different plant species, suggesting that the background soil conditions in the mining area are the main drivers of β -diversity. Abundant and rare taxa showed distinct responses to environmental factors in soil ecosystems. Rare taxa were more strongly influenced by multiple soil factors, including TN, TP, salinity, SOM, and pH. Therefore, microbial communities should be analyzed by partitioning into subgroups to better understand their responses. Future studies could further explore the effects of different environmental factors on the ecological functions of abundant and rare taxa, as well as their interactions, to provide a more comprehensive understanding of soil ecosystem function and stability. Actinobacteria, Proteobacteria, Chloroflexi, and Acidobacteria were the dominant abundant phyla in the mining area, consistent with previous studies (Li et al., 2014; Wu et al., 2022; Ma et al., 2024). These phyla exhibit strong environmental adaptability and occupy broad ecological niches. Overall, the composition of abundant taxa was more strongly influenced by environmental factors than that of rare taxa.

Understanding the processes driving community assembly is crucial for ecosystem management. Determining the assembly mechanisms of abundant and rare microbial taxa helps elucidate the generation and maintenance of biodiversity in ecosystems. Our results

indicate that stochastic processes dominate the assembly of rhizosphere soil bacterial communities in mining areas, but the specific stochastic processes differ between abundant and rare taxa. The assembly of abundant taxa was primarily governed by dispersal limitation, whereas rare taxa were mainly influenced by undominated processes. In wetland ecosystems, the assembly of abundant taxa is also largely driven by stochastic processes (Yang et al., 2022). In montane forest ecosystems, dispersal limitation has a greater influence on the aggregation of abundant taxa (Jiao and Lu, 2020). However, some studies (Jiao et al., 2017; Mo et al., 2018) have reported that dispersal limitation predominantly governs rare taxa, which may be attributable to habitat and geographic factors (Jiao and Lu, 2020; Shi et al., 2018; Wang et al., 2017). The higher dispersal limitation observed in abundant taxa is likely due to their competitive advantage in the mining environment, occupying major ecological niches, with distribution limited by dispersal rather than environmental selection.

Conclusion

This study investigated the diversity and assembly processes of abundant and rare bacterial taxa in the rhizosphere of plants in the Shangwan mining area, as well as the environmental factors influencing them. The results indicated that plant species had no significant effect on soil bacterial community diversity. The relationships between α -diversity of abundant and rare taxa and soil environmental factors differed: rare taxa α -diversity showed no significant correlation with soil properties, whereas abundant taxa α -diversity was significantly positively correlated with SOM and soil salinity. These findings suggest that SOM and salinity primarily influence overall community α -diversity by affecting abundant taxa. Rare taxa exhibited significantly higher β -diversity than abundant taxa and were more strongly influenced by environmental factors. Both abundant and rare taxa were predominantly assembled through stochastic processes, highlighting their important roles in maintaining community structure under environmental fluctuations.

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