Engineering and Technology Journal e-ISSN: 2456-3358

Volume 11 Issue 01 January-2026, Page No.-8440-8450

DOI: 10.47191/etj/v11i01.04, I.F. – 8.482

Characteristics and Functional Analysis of Rhizosphere Bacterial Communities of the Endangered Plant Taihangia Rupestris

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ABSTRACT: Rhizosphere microbial communities play a crucial role in plant health and growth, with each plant species harboring a unique assemblage of rhizosphere microorganisms. *Taihangia rupestris* (Yu and Li), an endangered species, holds significant research value. In this study, 16S rRNA high-throughput sequencing technology combined with bioinformatics methods was employed to analyze the characteristics and functions of rhizosphere bacterial communities of the endangered plant *T. rupestris*. The results showed that the core dominant bacterial phyla in the rhizosphere of *T. rupestris* were Proteobacteria, Acidobacteriota, and Actinobacteriota. There were significant differences in the complexity of bacterial co-occurrence networks among *T. rupestris* populations from different habitats. Functional prediction indicated that chemoheterotrophy, aerobic chemoheterotrophy, nitrate reduction, and phototrophy were the main metabolic functions of the rhizosphere bacterial community. These functions can improve soil fertility by promoting the decomposition of soil organic matter and nutrient cycling. Further analysis confirmed that the core position of bacterial communities in the rhizosphere of *T. rupestris* provides essential nutrient supply for the plant's growth in impoverished cliff habitats and significantly enhances its environmental adaptability. This study clarifies the key bacterial taxa and their ecological functions in the rhizosphere of *T. rupestris*, reveals the intrinsic link between rhizosphere microorganisms and the habitat adaptability of *T. rupestris*, and provides important theoretical basis and scientific support for the subsequent development of conservation strategies for this endangered species.

KEYWORDS: Rhizosphere microbial; Endangered plants; *Taihangia rupestris*; High-throughput sequencing

INTRODUCTION

Rhizosphere soil bacteria serve as the core hub for material cycling and energy flow in the plant-soil system, and are key biological components maintaining the stability of terrestrial ecosystems [1]. The rhizosphere microenvironment, a specialized zone where plant roots interact with soil, has its bacterial community structure jointly regulated by root exudates, soil physicochemical properties, and external environmental stresses. These bacteria profoundly influence plant growth and development, stress resistance, and community assembly through nutrient activation, disease antagonism, growth hormone synthesis, and alleviation of environmental stresses [2, 3]. In recent years, with the continuous innovation of high-throughput sequencing technology and microbial ecology research methods, the functional diversity of rhizosphere soil bacteria and their interaction mechanisms with plants have become research hotspots in the field of ecology [4]. Numerous studies have confirmed that a healthy rhizosphere bacterial community can significantly improve the efficiency of plant nutrient absorption and enhance plant resistance to adverse conditions such as drought, salinity, and heavy metal pollution. Conversely, imbalances in the rhizosphere bacterial community structure may restrict plant growth and even trigger the outbreak of soil-borne diseases [5, 6]. However, research on the unique adaptability of rhizosphere soil bacteria in special habitats and their supporting roles for host plants remains

insufficient.

Cliff ecosystems are typical extreme habitats characterized by steep terrain, shallow soil layers, poor water and fertilizer retention capacity, and drastic temperature fluctuations [7]. Compared with conventional habitats such as plains and forests, cliff habitats have relatively low biodiversity but a high proportion of endemic species. These species have evolved a series of unique morphological, structural, physiological, and ecological strategies to adapt to extreme living environments through long-term natural selection [4, 8]. Meanwhile, the closed and isolated nature of cliff habitats effectively avoids threats to species survival from human disturbance and habitat destruction, making them the primary survival habitat for the endangered plant *T. rupestris* [5]. Nevertheless, cliff ecosystems are highly vulnerable—once disturbed, they are prone to degradation and difficult to restore [9, 10]. Additionally, the scarcity and heterogeneity of soil resources in cliff habitats further intensify the competitive pressure among plants and profoundly shape the structure and functional characteristics of rhizosphere soil bacterial communities, forming a unique plant-bacteria interaction system [7]. Therefore, systematic analysis of the physicochemical characteristics of cliff ecosystems and their regulatory mechanisms on plants and rhizosphere soil bacteria is an important prerequisite for conducting conservation research on the endangered plant *T. rupestris*.

As an important component of biodiversity, the endangered plant *T. rupestris* carries unique genetic resources that are irreplaceable for maintaining ecosystem stability, providing ecological services and promoting innovation and development in agriculture, medicine, and other fields [11, 12]. In recent years, affected by multiple factors such as global climate change, habitat destruction, overexploitation, and biological invasion, the population size of *T. rupestris* has continued to decline, and the risk of species extinction has increased, posing a serious threat to regional ecological security and biodiversity conservation [13]. Currently, conservation research on *T. rupestris* mainly focuses on resource investigation, ex situ conservation, artificial propagation, and habitat restoration. However, most studies have not fully considered its interaction with rhizosphere soil bacteria, resulting in insufficient pertinence and effectiveness of conservation measures. Furthermore, due to the particularity of cliff habitats and the difficulty of research, basic biological information on *T. rupestris* remains scarce, and its endangered mechanism is unclear, which greatly limits the progress of conservation work. Therefore, in-depth research on the conservation of *T. rupestris* in special habitats, revealing its endangered mechanism, and formulating scientific and effective conservation strategies have become an urgent need in the field of biodiversity conservation.

Based on the above research background, this study takes the endangered plant *T. rupestris* in cliff habitats as the research object, focusing on rhizosphere soil bacteria to carry out systematic research, which has important theoretical significance and practical value. At the theoretical level, by clarifying the regulatory mechanisms of cliff habitats on the structure and function of rhizosphere soil bacterial communities of *T. rupestris*, and revealing the role of rhizosphere soil bacteria in the process of *T. rupestris* adapting to extreme habitats, this study can enrich the research content of plant ecology and microbial ecology in extreme habitats, improve the theoretical system of plant-bacteria interactions, and provide a new perspective for analyzing the adaptation and endangered mechanisms of *T. rupestris*.

1 MATERIALS AND METHODS

1.1 Sample Collection

Soil samples of *T. rupestris* used in this study were collected from the Southern Taihang Mountains, Henan Province (113°19′—113°30′E, 35°27′—36°33′N) (Table 1). Within the sampling area of *T. rupestris*, a mixed sampling method of 3 points per quadrat was adopted, and a total of 9 mixed samples were collected. First, the coverings on the soil surface, including plants, visible roots, gravel, moss, and litter, were removed with a shovel. Then, a sterile spoon was used to collect the rhizosphere soil of *T. rupestris* at a depth of 10–20 cm below the ground. After exposing the rhizosphere, large soil aggregates were slowly removed, and the soil adhering to the

rhizosphere of *T. rupestris* was brushed off with a sterile brush. Rhizosphere soil samples were collected one by one from *T. rupestris* within the selected area, quickly sieved through a 2 mm sterile sieve to remove fine plant debris, and the sieved soil samples were placed in sterile EP tubes, immediately frozen in liquid nitrogen, and stored at –80 °C for later use.

Table 1 Sampling localities of 3populations of *T. rupestris*

Sampling sites	Locations	Longitude(E)	Latitude(N)	Altitude(m)
XZG	Xiaozhaigou, Henan	113°19′02″ E	35°28′01″ N	640
ZYF	Zhuyufeng, Henan	113°22′16″ E	35°27′06″ N	960
GS	Guanshan, Henan	113°30′49″ E	35°33′48″ N	940

1.2 DNA Extraction and PCR Amplification

Total soil DNA was extracted using the E.Z.N.A™ MagBind Soil DNA Kit (Omega Bio-tek, USA, Cat. No. M5635-02) according to the manufacturer's instructions. After accurate quantification of genomic DNA using the Qubit®4.0 DNA Detection Kit, PCR amplification was performed. The target region for PCR amplification was the V3-V4 variable region of the bacterial 16S rRNA gene, with the following primers: 338F (5'-ACTCCTACGGGAGGCAGCAG-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3'). Quantitative determination, normalization, library construction, and sequencing of PCR amplicons were completed by Sangon BioTech (Shanghai) Co., Ltd. Paired-end sequencing was performed on the Illumina MiSeq platform. Raw data were merged using PEAR software (version 0.9.8) with default parameters, and the output files were converted to FASTA/QUAL format. Further, OTUs (Operational Taxonomic Units) were clustered at 97% sequence similarity using Usearch software (version 11.0.667), and chimeras and singleton OTUs were removed [14, 15]. Representative OTU sequences were selected based on abundance and taxonomically annotated using the RDP database[16].

1.3 Data Processing

A multi-dimensional analysis approach was adopted to systematically analyze the structural and functional characteristics of the rhizosphere microbial community of T. rupestris. First, based on OTU richness indices, Mothur software (version 3.8.31) was used to calculate α-diversity indices of the rhizosphere soil microbial community, including species richness indices (ACE index, Chao index) and diversity indices (Shannon index, Simpson index) [17, 18]. To compare bacterial community differences among different habitats, non-metric multidimensional scaling (NMDS) and principal component analysis (PCA) based on the Bray-Curtis distance matrix were performed using the vegan package in R software (version 4.5.0) to visualize differences in bacterial community structure among different sampling sites. PERMANOVA test was used to analyze the significance of inter-group differences in community structure[19, 20]. Co-occurrence networks of microorganisms at the phylum level were constructed using the "igraph" and "Hmisc" packages after multiple test correction (Benjamini-Hochberg method, $r > 0.75$, adjusted $p < 0.01$), and visualized with Gephi software [21, 22]. For functional prediction, FAPROTAX software was used to predict the functions of the top 20 most abundant species in the rhizosphere microbial community [23]. Statistical analysis was performed using SPSS 23.0 software, and one-way analysis of variance (One-way ANOVA) combined with Duncan's test (α=0.05) was used to compare differences in rhizosphere soil bacterial community composition and diversity indices among different habitats.

2 RESULTS AND DISCUSSION

2.1 Characteristics of Rhizosphere Soil Bacterial Community Composition of *T. rupestris*

Bacterial sequencing of 9 rhizosphere soil samples from 3 populations yielded a total of 1020883 valid sequences, with an average of 113431 sequences per sample. The number of

sequences per population ranged from 76236 to 127901. At 97% sequence similarity, a total of 6656 OTUs were obtained, belonging to 47 phyla, 144 classes, 379 orders, 663 families, and 1653 genera. The OTU distribution of rhizosphere soil within the same population showed partial overlap and partial uniqueness (Fig. 1). The GS population had the highest number of unique OTUs (4116), followed by the ZYF population (4003), while the XZG population had the fewest (2270). The number of core OTUs shared by all three populations was 5986, which served as the basis for the dominant flora common to all groups. The number of shared OTUs between GS and XZG was 959, between GS and ZYF was 2467, and between XZG and ZYF was 1546. This distribution characteristic indicates that the rhizosphere bacterial communities of the three populations share a broad core group, while also forming unique bacterial taxa due to population differences. The GS and ZYF populations have more unique OTUs, which may be more closely associated with the specificity of their habitats or host metabolic characteristics.

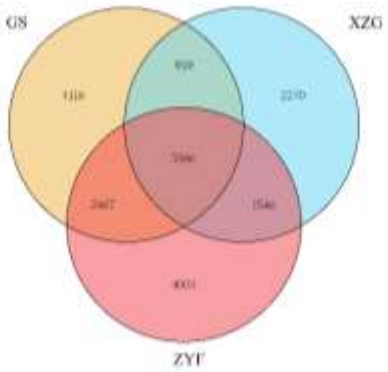

Fig 1 Venn diagram of rhizosphere soil bacterial communities of *T. rupestris*

Taxonomic annotation analysis at the phylum level showed that a total of 11 bacterial phyla were annotated in the rhizosphere of *T. rupestris*. The dominant phyla were Proteobacteria (average relative abundance: 34.5%), Acidobacteriota (21.4%), Actinobacteriota (12.5%) and Chloroflexi (12.4%), accounting for 97.30% of the total relative abundance of all species (Fig. 2A). At the genus level, taxonomic annotation revealed that the average relative abundance of unclassified species in the rhizosphere microorganisms of *T. rupestris* was 30.25%. The top 10 genera in terms of bacterial relative abundance were *RB41* (7.91%), *Crossiella* (4.97%), *Ellin6055* (4.19%), *Sphingomonas* (3.56%), *Stenotrophobacter* (2.11%), *Blastocatella* (2.08%), *Solirubrobacter* (2.03%), *Rubrobacter* (1.38%), *Bryobacter* (1.31%) and *Blastococcus* (1.16%) (Fig. 2B). One-way ANOVA of bacterial phyla showed that Proteobacteria exhibited significant differences among the three sampling sites ($P<0.05$), with the relative abundance in the order XZG>ZYF>GS. In addition, one-way ANOVA of bacterial genera showed that *RB41* and *Blastocatella* were significantly correlated, with *RB41* showing an extremely significant correlation ($P<0.01$). The relative abundances of both genera followed the order XZG<ZYF<GS.

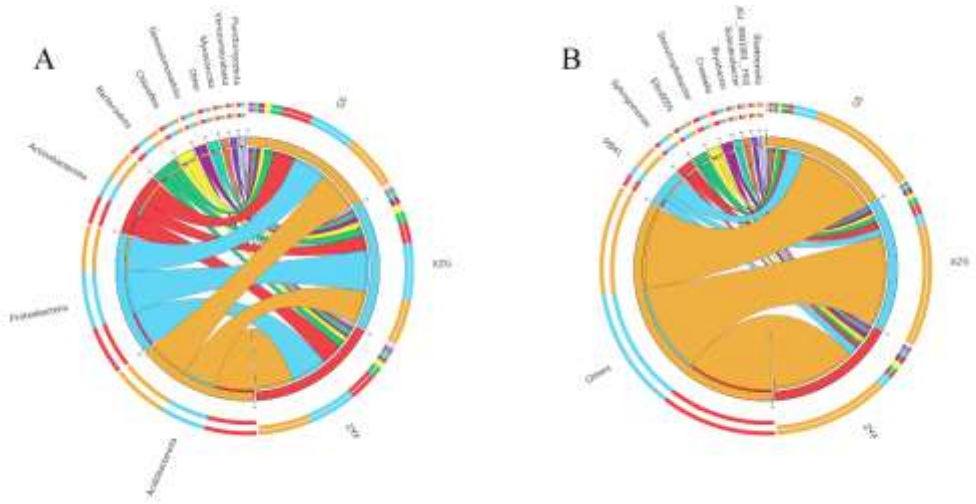

Fig 2 Taxonomic distribution of bacterial. Circos plots show the composition of bacterial at the phylum (A) and genus (B) level in the rhizosphere soil of *T. rupestris*

2.2 Rhizosphere Microbial Diversity of *T. rupestris*

2.2.1 α-diversity Analysis

The ACE and Chao indices reflect community richness, with higher values indicating higher richness. The Shannon and Simpson indices reflect community diversity—higher Shannon index and lower Simpson index indicate higher diversity. The average sequencing coverage of samples was 97.77%, indicating that the sequencing depth met the analysis requirements and the data quality was reliable. The results of α-diversity analysis of the bacterial community showed no significant differences in diversity indices among different sampling sites. Among them, the overall level of the Shannon index was ZYF>GS>XZG, the Chao index was ZYF>GS>XZG, the Ace index was ZYF>GS>XZG, the Simpson index was XZG>ZYF>GS (Table 2).

Table 2 Diversity index of bacterial communities in roots soil of *T. rupestris*

Populations	Shannon	Chao	Ace	Simpson
XZG	6.77 ± 0.19 a	8444.89 ± 1390.18 a	8855.07 ± 1593.45 a	0.01 ± 0.00 a
ZYF	6.93 ± 0.21 a	10002.65 ± 602.66 a	10552.77 ± 727.9 ab	0.01 ± 0.01 a
GS	7.03 ± 0.07 a	9969.22 ± 467.16 a	10645.75 ± 541.68 ab	0.01 ± 0.00 a

Values are presented as mean ± standard deviation. Different lowercase letters in the same column indicate no significant difference among populations (P>0.05).

2.2.2 β-diversity Analysis

The NMDS analysis based on the Bray-Curtis distance showed a stress value of 0.04, indicating that the two-dimensional ordination diagram could well reflect the community similarity among samples. The PERMANOVA test results showed that the inter-group difference was extremely significant (F=3.247, P=0.003) (Fig. 3A). In the NMDS ordination diagram, the XZG, ZYF, and GS groups formed independent clusters with no overlap between groups. The XZG group samples were concentrated in the left region of the ordination diagram, the ZYF group in the middle-right region, and the GS group in the upper-right region, indicating

significant differentiation in the microbial community structure among the three groups of samples. The PCA results showed that PC1 and PC2 explained 18.63% and 16.11% of the community variation, respectively (Fig. 3B). The distribution trend of samples in each group in the ordination diagram was consistent with that of NMDS. The XZG group samples aggregated along the negative axis of PC1 and positive axis of PC2, with small differences in PCA scores within the group. The ZYF group samples were distributed along the negative axis of PC1 and negative axis of PC2, with a slightly higher degree of dispersion than the XZG group. The GS group samples were distributed along the positive axis of PC1 and PC2, showing a certain gradient change on the PC2 axis. The results of the two multivariate statistical analyses mutually confirmed that the microbial community structures of the three groups of sample shad significant inter-group differences and good intra-group repeatability.

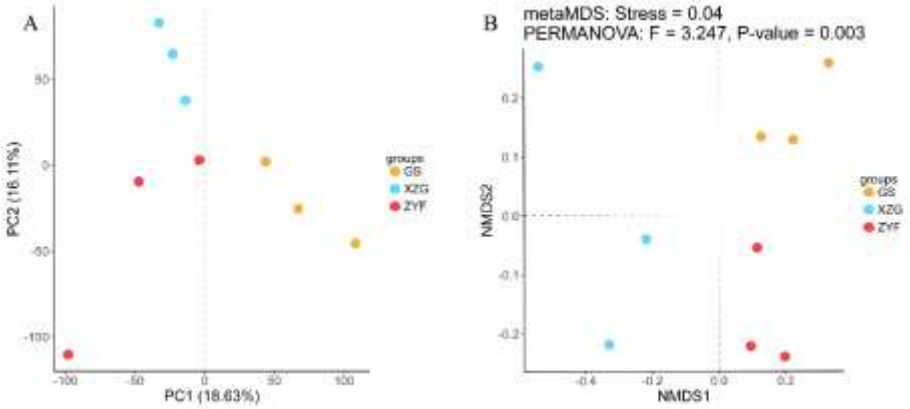

Fig. 3 PCA and NMDS maps of bacteria (A, B) in the roots soil of *T. rupestris*. A: NMDS ordination diagram (Stress=0.04, PERMANOVA: *F*=3.247, *P*=0.003); B: PCA ordination diagram (PC1=18.63%, PC2=16.11%).

2.3 Co-occurrence Network Interactions of Rhizosphere Soil Bacteria of *T. rupestris*

The topological characteristics of bacterial co-occurrence networks in the rhizosphere of *T. rupestris* under three habitats were analyzed (Table 3). The results showed that the total number of nodes in all three networks was 100, indicating that the number of bacterial taxa contained in the networks of each habitat was consistent. However, there were significant differences in the complexity of network connections: the number of edges in the XZG, ZYF, and GS networks was 1681, 1659, and 2041, with corresponding average degrees of 33.62, 33.18, and 40.82, respectively. The difference in average degree directly reflects that the interaction frequency among bacterial taxa in the GS habitat was significantly higher, and the node connection density of its network was significantly higher than that in the XZG and ZYF habitats. Meanwhile, the average path distance and average clustering coefficient of the three networks all reached 1.00, indicating that the rhizosphere bacterial network of *T. rupestris* had extremely short paths for information and material transmission, and the local connections among taxa showed a highly aggregated pattern, suggesting close cooperative or competitive relationships within the rhizosphere microbial community. The modularity coefficient results showed that the modularity coefficients of XZG and ZYF were 0.62 and 0.63, respectively, while that of GS was 0.42, indicating that the bacterial networks in the XZG and ZYF habitats could be divided into more independent functional subgroups, while the network module independence in the GS habitat was relatively weak, and the interaction relationships of its microbial taxa tended to be distributed across modules. Combined with the bacterial co-occurrence networks (Fig. 4A-C), it can be seen that nodes of dominant phyla such as Proteobacteria and Acidobacteriota showed dense connection characteristics in all three networks, further supporting the key position of these taxa as core hubs of the network.

Table 3. Co-occurrence network characteristics of bacteria in rhizosphere soils of *T. rupestris*

	Topological properties	XZG	ZYF	GS
Bacterial	Total nodes	100	100	100
	Total edges	1681	1659	2041
	Average degree	33.62	33.18	40.82
	Average path distance	1.00	1.00	1.00
	Modularity	0.62	0.63	0.42
	Average clustering coefficient	1.00	1.00	1.00

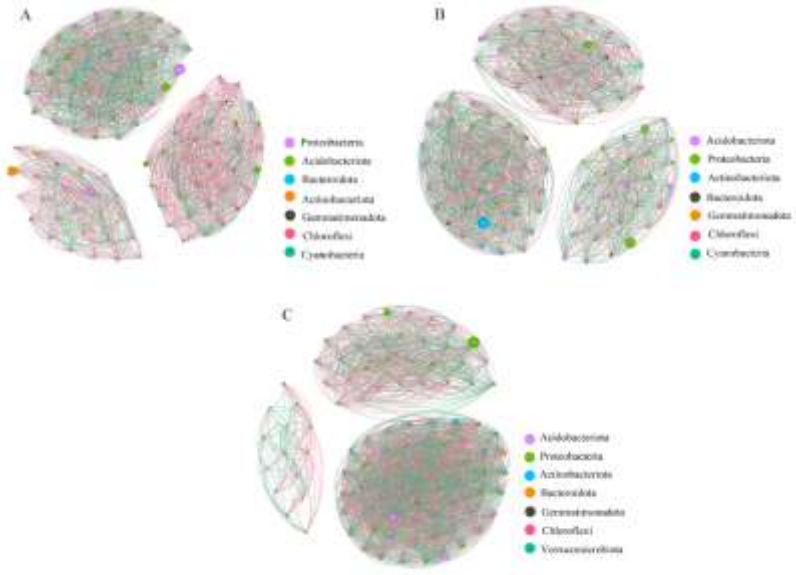

Fig. 4 Network of co-occurring generalists and specialists 90% cutoff OTUs based on correlation analysis. A connection stands for a strong (Spearman's p>0.6) and significant (*p*-value <0.01) correlation. The size of each node is proportional to the number of connections. XZG (A), ZYF (B) and GS (C) bacterial co-occurrence network.

2.4 Functional Prediction of Rhizosphere Soil Bacteria of *T. rupestris*

To better understand the microecological functions of rhizosphere soil microorganisms, FAPROTAX was used to predict the functions of the rhizosphere bacterial community, and a total of 78 functions were identified. Among them, the main functions (abundance >1%) included chemoheterotrophy (20.65%), aerobic chemoheterotrophy (20.20%), and nitrate reduction (1.62%) (Fig. 5). Comparison of functional abundances among the three groups (XZG, ZYF, GS) showed that the proportion of chemoheterotrophy was the highest in XZG (17.76%), followed by ZYF (16.67%) and GS (16.52%), which were slightly lower and relatively close. The distribution trend of aerobic chemoheterotrophy was consistent with that of chemoheterotrophy: XZG (16.89%) > ZYF (16.16%) > GS (16.04%). In contrast, the nitrate reduction function showed an increasing trend: XZG (0.72%) < ZYF (1.39%) < GS (1.43%). In addition, the phototrophy function in GS (1.11%) was significantly higher than that in XZG (0.62%) and ZYF (0.86%), while the chitinolysis function in XZG (0.63%) was higher than that in ZYF (0.58%) and GS (0.77%). Overall, the core functions of the three groups were dominated by

heterotrophic metabolism, but the GS habitat showed more prominent nitrogen cycle-related functions and phototrophy, while the XZG habitat had a relatively higher proportion of heterotrophic metabolism functions, reflecting the differentiated functional characteristics of rhizosphere microorganisms among different samples.

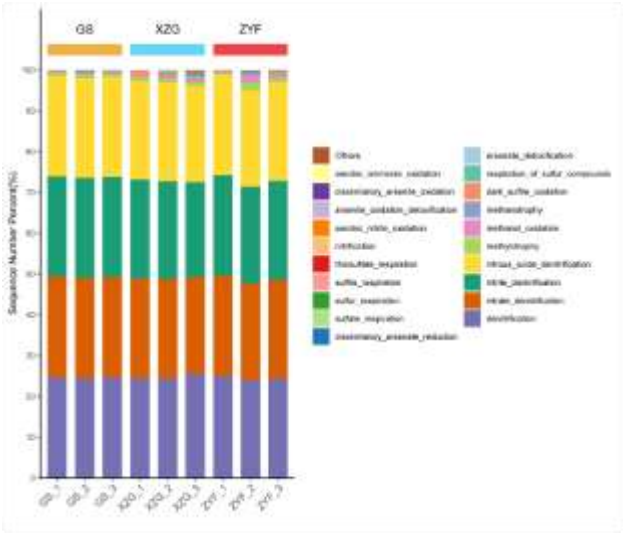

Fig. 5 Guild assignments for the obtained OTUs using the FAPROTAX databases. The mean proportions of bacterial were calculated to estimate their relative abundances in rhizosphere soil of *T. rupestris*.

3 DISCUSSION

The rhizosphere of healthy plants enriches a large number of bacterial, fungal, and other microbial taxa derived from soil, and these microorganisms have evolved independently in diverse ecological environments [24, 25]. The dynamic characteristics of interactions among microorganisms have become a key attribute of plant ecosystems, and such interactions have a significant impact on plant health [26]. Currently, the interaction mechanisms of these microorganisms and their degree of influence on plant health remain to be further clarified. In this study, 16S rRNA high-throughput sequencing technology was used to analyze the community composition and functional characteristics of rhizosphere microorganisms of *T. rupestris*, aiming to reveal the core characteristics of the rhizosphere bacterial community of *T. rupestris* and its regulatory role in the healthy growth of *T. rupestris*.

This study showed that at the phylum level, more than 97% of the rhizosphere bacteria of *T. rupestris* belonged to Proteobacteria, Actinobacteriota, Acidobacteriota, and Chloroflexi. This indicates that the rhizosphere microbial community of *T. rupestris* is rich and diverse, but the main dominant bacteria are still concentrated in Proteobacteria, Acidobacteriota, and Actinobacteriota. The results of collinearity network analysis further confirmed this finding, which is consistent with existing research on rhizosphere soil [27, 28]. In terms of functional characteristics, existing studies have confirmed that Proteobacteria, as a group of Gram-negative bacteria with diverse metabolic types, have the characteristics of efficiently degrading root organic carbon, which gives them a competitive advantage in soil environments with high organic matter content and shows strong environmental adaptability. Acidobacteriota is a core component of the plant-soil microbiome, and can significantly promote crop growth and development and improve productivity by participating in the nitrogen cycle process in ecosystems [29]. Actinobacteriota plays an important role in key ecological processes such as the decomposition of refractory organic matter and mineral weathering by virtue of its unique mycelial structure and spore-forming ability [30, 31]. The enrichment of the above dominant bacterial phyla in the rhizosphere of *T. rupestris* suggests that they play a core role in

the decomposition of organic matter, efficient utilization of nitrogen sources, and the cyclic transformation of key nutrients such as cellulose and lignin in plant residues, thereby effectively improving soil fertility. It is worth noting that *T. rupestris* can still grow normally in impoverished soil enriched with Proteobacteria, and such bacteria can synthesize and provide abundant nutrients through metabolic activities, indicating that the optimal growth state of *T. rupestris* may depend on sufficient nutrient supply. In addition, the ability of these bacteria to form ecological advantages in this habitat may be closely related to their mixotrophic metabolic strategies—that is, they possess both autotrophic and heterotrophic metabolic capabilities, and have diverse energy acquisition methods, which enables them to maintain population survival in extreme environments and significantly enhance the adaptability of *T. rupestris* in impoverished habitats [32, 33]. Based on the results of FAPROTAX functional prediction analysis, chemoheterotrophy, aerobic chemoheterotrophy, nitrate reduction, and phototrophy are the core metabolic functions of the rhizosphere bacterial community of *T. rupestris* (Fig. 4A). A study by Zheng et al. [23] has confirmed that these metabolic functions can provide energy for the growth and reproduction of microorganisms themselves by decomposing a large number of organic substrates. This conclusion further confirms the important regulatory role of rhizosphere bacteria in soil nutrient cycling and efficient utilization in nutrient-poor cliff habitats [34].

4 CONCLUSIONS

In this study, 16S rRNA high-throughput sequencing combined with bioinformatics analysis was used to systematically analyze the structural characteristics and ecological functions of rhizosphere bacterial communities of three populations of the endangered plant *T. rupestris* in the Southern Taihang Mountains. The results clarified that the rhizosphere bacterial community of *T. rupestris* is dominated by core dominant phyla including Proteobacteria, Acidobacteriota, and Actinobacteriota, accounting for 97.30% of the total relative abundance of all species. These dominant phyla effectively improve soil fertility in impoverished cliff habitats by participating in organic matter decomposition, nitrogen cycle, and transformation of refractory organic matter, providing key nutrient support for the growth of *T. rupestris*. There were significant differences in the rhizosphere bacterial community structure of *T. rupestris* among different habitats. β-diversity analysis showed that the three groups of samples formed independent clusters, and the bacterial co-occurrence network in the GS habitat had the highest connection complexity, with more prominent nitrogen cycle and phototrophy functions, while the XZG habitat had a relatively higher proportion of heterotrophic metabolism functions, reflecting the adaptive differentiation of bacterial communities to specific habitats. Functional prediction confirmed that chemoheterotrophy, aerobic chemoheterotrophy, nitrate reduction, and phototrophy are the core metabolic functions, which enhance the environmental adaptability of *T. rupestris* by promoting soil material cycling. This study reveals the intrinsic link between key rhizosphere bacterial taxa and the survival of *T. rupestris* in extreme impoverished habitats, clarifies the important regulatory role of microbial communities in host nutrient supply and stress resistance, provides a new perspective for in-depth understanding of the habitat adaptation mechanism of endangered plants, and offers important theoretical basis and scientific support for formulating conservation strategies for *T. rupestris* populations.

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