The diversity pattern of soil bacteria in the rhizosphere of different plants in mountain ecosystems

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Abstract

Research on the composition and diversity of rhizosphere microbial communities of different plant species can help to identify important microbial functional groups or functional potentials, which is of great significance for vegetation restoration and ecological reconstruction. To provide scientific basis for the management of mountain ecosystem, the diversity pattern of rhizosphere bacterial community was investigated using 16S rRNA high-throughput sequencing method among different host plants (*Cirsium japonicum*, *Artemisia annua*, *Descurainia sophia*, *Lepidium apetalum*, *Phlomis umbrosa*, and *Carum carvi*) in Tomur Peak National Nature Reserve, China. The results showed that the richness and diversity of rhizosphere bacteria were highest in *Descurainia sophia*, and lowest in *Lepidium apetalum*. Proteobacteria, Acidobacteriota, and Actinobacteria were the common dominant phyla, and *Sphingomonas* was the predominant genera. Furthermore, there were some specific genera in different plants. The relative abundance of non-dominant genera varied among the plant species. Canonical correspondence analysis indicated that available (AK), total phosphorus (TP), total potassium (TK), and soil organic matter (SOM) were the main drivers of bacterial community structure. Based on PICRUSt functional prediction, the bacterial communities in all samples encompass six primary metabolic pathways and 47 secondary metabolic pathways. The major secondary metabolic pathways (with a relative abundance of functional gene sequences > 3%) include 15 categories. Co-occurrence network analysis revealed differences in bacterial composition and interactions among different modules, with rhizosphere microorganisms of different plants exhibiting distinct functional advantages. This study elucidates the distribution patterns of rhizosphere microbial community diversity in mountain ecosystems, which provides theoretical guidance for the ecological protection of mountain soil based on the microbiome.

Introduction

Rhizosphere microorganisms refer to the microbial communities existing in the plant rhizosphere, which includes bacteria, fungi, and many other microorganisms. As research into microbial diversity and function deepens, increasing evidence indicates that rhizosphere microorganisms have a significant impact on plant growth and development (Chang et al. 2024; Liu et al. 2023; Song et al. 2020), such as promoting plant growth and preventing pathogen infection (Berg et al. 2006). Rhizosphere microorganisms can improve the nutritional status of the host plant by establishing symbiotic relationships with plants, and enhancing the absorption efficiency of nutrients such as phosphorus and potassium (Lundberg et al. 2012). Additionally, rhizosphere microorganisms can secrete vitamins, amino acids, and other regulatory substances to promote plant growth (Philippot et al. 2013). Furthermore, certain rhizosphere microorganisms can secrete antimicrobial substances, which is beneficial for crops to avoid infection by indigenous pathogens (Burke et al. 2011; Pii et al. 2015).

Rhizosphere microorganisms play a key role in supporting the nutrition and health of host plants (Berg & Smalla 2009). In turn, rhizosphere microorganisms are generally influenced by soil type (Rasche et al. 2006), environmental conditions (Raaijmakers et al. 2008), plant genotype (Gilbert et al. 2011), and plant growth stages (Rajput et al. 2021). Root exudates and decaying litter mediate the diversity and community composition of soil bacteria by affecting the types and concentrations of soil nutrients (Rudrappa et al. 2008). Studies have shown that root exudates can significantly affect the diversity of soil bacterial communities. For example, the diversity of acidophilic soil bacterial communities increases with the rise of organic acid secretions (Powell et al. 2015). Soil pH increased with the elevation, and soil nutrient elements also changed, which affected the community structure and diversity of rhizosphere bacteria (Qiu et al. 2022). Overall, the rhizosphere is an environment where a large number of microorganisms interact extensively. The interaction between plants and rhizosphere microorganisms can generate a strong selective pressure that influences the rates and patterns of microbial evolution and the composition of the rhizosphere microbiome (Chaparro et al. 2014). These complex plant-associated rhizosphere microbial communities are also considered to be the second genome of plants, which are crucial for the health of agricultural plants (Turner et al. 2013).

Mountain ecosystems cover approximately 25% of the world's land surface and are mostly distributed in high-altitude areas (Adamczyk et al. 2019). Their unique geographical and environmental features provide diverse habitat conditions for the growth of different plant species. In mountainous ecosystems, due to gradient changes in environmental factors such as altitude, climate, and soil, the distribution of plant species also exhibits corresponding patterns (Barry 2008; Huss 2011; Khan et al. 2024). Plant genotypes under different vegetation types are adapted to specific mountainous environments, and correspondingly, the rhizosphere microbial community structure also undergoes diverse changes due to the differences in plant genotypes. According to reports, the structure of rhizosphere microbial communities varies significantly among different plant species (Körner 2021), and even among different genotypes of individual species (Floc'h et al. 2020). The changes in rhizosphere microbial communities of different plants further affect ecological processes, such as material cycling and energy flow, which are closely related to the overall structure and function of mountainous ecosystems (Bendix et al. 2021; Carboni et al. 2017; Hotaling et al. 2017; Štursová et al. 2016; Zhao et al. 2019). It is clear that in mountain ecosystems, an in-depth study of plant rhizosphere microbial communities can help us clarify the operating mechanisms of the ecosystem and understand how plants and microorganisms coexist with each other. However, there are still some shortcomings at present. Firstly, the research area is limited, that is, mostly concentrated in some typical mountainous areas, with less involvement in some remote or special terrain mountainous areas (Berendsen et al. 2012). Furthermore, there is a lack of research on the differences in rhizosphere microorganisms among different plants, which limits our in-depth understanding of the fine structure and function of mountain ecosystems. Then we will not be able to conduct targeted intervention and regulation according to the characteristics of different plant rhizosphere microorganisms.

The Tomur Peak National Nature Reserve is a super large comprehensive nature reserve in China, featuring a forest ecosystem type, with the most complete natural vertical belt at the southern foot of the Tianshan Mountains. The region boasts abundant flora and fauna resources, possesses significant ecological service value, and holds an important position among the world's natural heritage sites. In recent years, the government has strengthened the management of the Tomur Peak, reduced various human disturbances, and its vegetation richness and coverage have been significantly improved. However, the ecosystem still exhibits a certain degree of degradation. This study employed high-throughput sequencing technology to analyze the bacterial communities and diversity in the rhizosphere of various plants located at Tomur Peak. Additionally, the correlation between soil physicochemical factors and bacterial communities was investigated, and the bacterial function was predicted. By elucidating the differences in the structure and diversity of rhizosphere bacterial

communities among different vegetation types in Mount Tomur, it can provide scientific basis for promoting vegetation restoration and ecological protection of mountain ecosystem.

Materials and methods

Experimental sites and soil sampling

The Tomur Peak National Nature Reserve (79°50'- 80°53'E, 41°40'- 42° 21'N) is located in Xinjiang Uygur Autonomous Region, China. It features a temperate continental climate, characterized by an average annual precipitation of less than 700mm and an average annual temperature of 7.9℃. The geology and terrain here are complex, with a varied and unpredictable climate. In high-altitude regions, there was abundant rainfall and moist air, while low-altitude areas experienced scarce precipitation and distinct desert features. The vegetation types within the protected area exhibit a diverse range and distinct vertical distribution characteristics. The sampling area for this study were located in the subalpine forest-steppe zone, with an altitude ranging from 2600 to 2900 meters. The dominant herbaceous plants are *Stipa capillata*, *Phlomis umbrosa*, *Festuca ovina*, *Cirsium japonicum*, *Taraxacum mongolicum*, *Helictotrichon macrostachyum*, and *Carum carvi*. The main soil types are mountain brown desert soil, mountain brown calcareous soil, and mountain chestnut calcareous soil.

In July 2023, six dominant plants species were collected, including Asteraceae (*C. japonicum* and *Artemisia. annua*), Brassicaceae (*Descurainia. sophia* and *Lepidium. apetalum*), Labiatae (*P. umbrosa*), and Apiaceae (*C. carvi*). The sampling method was multi-point mixed sampling, involving the random placement of 12 points along an "S"-shaped route within the sample area, ensuring a distance of no less than 20 meters between each point. For each plant at each sampling point, select 1–2 healthy individuals that are growing vigorously and have a consistent crown size. Carefully dig up the entire plant, gently shake off any loosely attached soil from the root system, and use a sterile brush to collect the tightly adhering soil within a few millimeters of the root system's surface. The samples from each of the three adjacent sample sets were mixed into one replicate, resulting in 4 replicates per plant. The samples were packaged in sterile containers and transported to the laboratory at low temperature in a vehicle-mounted refrigerator. A portion of the sample was used for soil genomic DNA extraction, while the remaining portion was naturally air-dried and sieved through a mesh for soil property determination.

Soil physicochemical analyses

The soil physicochemical analyses were conducted according to the methods of (Xie et al. 2011; Bao. 2000). Briefly, the soil pH was determined by a pH meter in soil-water suspensions (1:2.5 w/v ratio). The electrical conductivity (EC, soil: H_2O ratio of 1:5) was measured with a conductivity meter. Potassium dichromate bulk density and the potassium dichromate sulfuric acid boiling method were used to measure soil organic matter (SOM) and total nitrogen (TN), respectively. Sulfuric acid and perchloric acid boiling with the molybdenum antimony resistance colorimetric method was used to measure total phosphorus (TP). Available nitrogen (AN), phosphorus (AP), and potassium (AK) contents were measured using alkaline hydrolysis diffusion, molybdenum blue, and fame photometry methods, respectively.

DNA extraction and amplicon sequencing of the bacterial 16S

The total genomic DNA was extracted using the OMEGA Soil DNA Kit, and the DNA integrity was detected through agarose gel electrophoresis. Universal primers 515F (5'-GTGCCAGCMGCCGCGGTAA-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') were used to amplify the V3-V4 region of the 16S rRNA gene (Liu et al. 2024), with each DNA template repeated three times.

All PCR mixtures contained 15 μL of Phusion High-Fidelity PCR Master Mix (New England Biolabs), 0.2 μM primers, and 10 ng of genomic DNA template. Pre-denature at 95℃ for 3 minutes, then denature at 95℃ for 30 seconds and extend at 72℃ for 30 seconds, repeating this cycle 30 times in total, and finally extend at 72℃ for 5 minutes. The qualified PCR products were purified and quantified, and the same amount of mixed samples were taken according to their concentration. The PCR products were then detected using 2% agarose gel electrophoresis and the target bands were recovered. The sequencing library was generated using the NEBNext®Ultrarm DNA Library Preparation Kit (Illumina, USA). The quality of the library was assessed using a Qubit@ 2.0 fluorometer and the library was sequenced using the Illumina NovaSeg 6000 platform.

Statistical analysis

Based on the PCR amplification primers and Barcode sequences, the raw data from the Illumina Novaseq instrument were preliminarily demultiplexed to obtain the original data for each sample. After Barcode sequence and low quality base were removed, the original sequences of each sample were assembled using the Flash (V1.2.7) software to obtain clean tags. Subsequently, chimeric sequences were filtered out to obtain the final valid data (Effective Tags). After the non-repetitive sequences were extracted by Usearch, the operational taxonomic unit (OTU) clustering was performed for the non-repetitive sequences with a similarity of 0.97, and the sequence with the highest frequency was identified as the representative sequence. The MUSCLE (Version 3.8.31) software was used for multi-sequence alignment to obtain the classification status of all OTU represented sequences. Species annotation was performed using the Blast method in Qiime software (Version 1.9.1) and the Unit (V7.2) database, and the community composition of each sample was statistically analyzed at various classification levels.

The α-diversity and β-diversity of bacterial communities were calculated based on QIIME (v1.8.0) and R software. The ecological functional categories of rhizosphere soil bacteria were analyzed using the FUNGuild software. The linear regression model of R language was used to analyze the changing trends of environmental parameters, species abundance and functional categories (Bokulich et al. 2018; Callahan et al. 2016). The Redundancy analysis (RDA) was

used to study the correlation between bacterial communities and soil properties. Data were analyzed using One Way ANOVA and Duncan's multiple comparison based on SPSS 25.0. The sequencing data had been submitted to the BioProject database at NCBI (accession number: PRJNA1190513).

Results

Soil physicochemical properties

The results of soil physicochemical propertiess were described by Gong et al (2024). The soil overall exhibited a weakly alkalinity, with the pH in the rhizosphere soil of *C. carvi and P.umbrosa* were higher than those of other plants. The TN, AN, TP, AP, AK, and SOM values of *D. sophia* were significantly higher than those of other plants. The TN, AN, TP, and SOM values of *C. carvi* were the lowest, but the pH value was the highest. The results indicated that compared to *C. carvi*, *D. sophia* was higher demand and utilization efficiency for soil nutrients.

Analysis of abundance and diversity of bacterial communities

The effective data lengths for each sample ranged from 415 to 421 bp, with an average length of 419 bp (Table 1). Through Miseq sequencing analysis, 2,349,580 raw sequences were obtained, and after the quality control of the sequencing data, a total of 515,191 valid sequences were obtained. The Coverage index for the samples was closed to 1, indicating that nearly all sequences has detected, and the sequencing results can fully reflect the bacterial diversity in the samples. Significant differences were found in the ACE and Chao1 indices among samples. The richness of bacterial communities was ranked in the order of *D. sophia* > *C. japonicum* > *A. annua* > *C. carvi* > *P. umbrosa* > *L. apetalum*, indicating that the growth of *D. sophia* may increase the diversity of rhizosphere bacteria. Among all samples, the Shannon index of *C. japonicum* was the highest.

Table 1
Statistic of 16S amplitor sequence data of rhizosphere bacteria and α-diversity analysis

Sample name	Seq amount	OTUs amount	ACE index	Chao1 index	Simpson index	Shannon index	Good' Coverage
RDS	88923	3456	2699.75 ± 201.45a	2711.88 ± 201.75a	0.9985 ± 0.0006ab	10.42 ± 0.12ab	0.999
RLA	84452	3430	2287.75 ± 192.69b	2295.55 ± 195.25b	0.9978 ± 0.0005bc	10.11 ± 0.12c	0.9993
RPU	87247	2432	2290.00 ± 87.48b	2303.00 ± 89.45b	0.9973 ± 0.0015c	10.11 ± 0.12c	0.9990
RCC	82199	3348	2450.25 ± 426.57ab	2475.87 ± 441.21ab	0.9980 ± 0.0000abc	10.25 ± 0.23bc	0.9993
RCJ	85265	2771	2624.00 ± 148.00a	2613.24 ± 170.08ab	0.9990 ± 0.0006a	10.49 ± 0.05a	0.999
RAA	87105	2767	2489.50 ± 43.45ab	2502.25 ± 46.57ab	0.9980 ± 0.0000abc	10.30 ± 0.04abc	0.999

Different letters in the same column indicated a significant difference ($P < 0.05$). RDS, RLA, RPU, RCC, RCJ, and RAA represented the rhizosphere soil of *D. sophia*, *L. apetalum*, *P. umbrosa*, C. carvi, *C. japonicum*, and *A. anmua*, respectively.

According to the OTUs cluster analysis, the common number of OTUs for all rhizospheres was 208 (Fig. 1). The unique OTUs of *D. sophia*, *L. apetalum*, *P. umbrosa*, *C. carvi*, *C. japonicum*, and *A. annua* accounted for 3248, 3222, 3140, 2568, 2559 and 2224 respectively. Based on the clustering analysis, it was evident that the number of OTUs in the *D. sophia* was the highest, whereas that in the *P. umbrosa* was the lowest. The results indicated that *D. sophia* has a stronger adaptability to mountain ecosystems compared to *P. umbrosa*, which providing a suitable growth environment for rhizosphere bacteria.

PCoA analysis showed that the contribution rates of the first and the second principal component were 54.2% and 18.03%, respectively, totalling 72.23% (Fig. 2), which could well distinguish the bacterial community structure. The bacterial communities of *P. umbrosa*, *C. japonicum*, and *C. carvi* clustered together, indicating that indicating that their bacterial community structures were similar. However, the bacterial community of *L. apetalum* was completely separated from that of other plants, indicating that its bacteria community structure was significantly different from of other plants. The distinct microbial community distribution pattern of *L. apetalum* implied that it may had unique biological functions.

Analysis of bacterial community composition

A total of 43 phyla, 113 classes, 265 orders, 381 families, and 788 genera were affiliated in all samples. Proteobacteria, Acidobacteriota, and Actinobacteria were the common dominant phyla (Fig. 3A). In particular, the relative abundances of Proteobacteria and Actinobacteria in *D. sophia* were the highest than that in other plants, indicating that there were differences in the composition and abundance of bacterial communities among host plants. In addition, a large number of taxa remain unclassified at the phylum level, suggesting that there were many novel groups at Tomur Peak that were worthy of further study.

In the rhizosphere soil of *D. sophia, L. apetalum, P. umbrosa, C. carvi, C. japonicum*, and *A. annua*, the bacterial genera identified were 531, 398, 418, 467, 468, and 408, respectively (Fig. 3B). Among them, the dominant genus was *Sphingomonas*. Specially, the relative abundance of unidentified genera approached 80%, which means that there were still a large number of unknown microbial resources in this area, and they may contain unique genes and functions. In addition, there were endemic species among different plant species, as well as some groups with lower abundances. Overall, all samples specifically enriched certain bacterial genera, and this difference may be related to the characteristics of the host plants themselves. Although the six plant species grow in the same habitat, their rhizosphere soil physicochemical properties differed, and the rhizosphere microenvironments varied, resulting in diverse bacterial

community structures. This reflected the host specificity of the rhizosphere bacterial community structure, that was, plant species were actively selective on the structure of rhizosphere microbial community.

Correlation analysis between bacterial community structure and soil properties

The Spearman correlation between species abundance and environmental factors at the genus level was analyzed (Fig. 4). *Aeromonas* was significantly negatively correlated with TK but positively correlated with AP ($P < 0.05$). *RB41* was significantly negatively correlated with AP but positively correlated with TK. *Pseudomonas* was negatively correlated with TN ($P < 0.05$).

Redundancy analysis (RDA) reflected the relationship between bacterial community structure and environmental factors among different vegetation. The first and second axes can reflect the influence of key factors on bacterial community structure, with a cumulative explanatory variation of 60.57% (Fig. 5). The replacement test showed that the environmental factors that driving the bacterial communities structure of different vegetation were AK ($R^2 = 0.712$, $P = 0.0005$), TP ($R^2 = 0.596$, $P = 0.0005$), TK ($R^2 = 0.571$, $P = 0.0005$) and SOM ($R^2 = 0.543$, $P = 0.0005$).

Functional prediction of bacterial communities

The annotation information and abundance for the OTUs in the KEGG primary functional metabolic pathways were shown in Table 2. The function of rhizosphere bacteria includes 6 primary metabolic pathways, and the relative abundance ranked in the order of metabolism < genetic information processing < environmental information processing < cellular processes < human diseases < organismal systems. Among them, environmental information processing, cellular processes, and human diseases in the rhizosphere soil of *P. umbrosa* were significantly higher than those other plants ($P < 0.05$).

Table 2
Variations in composition of bacterial functional communities in rhizosphere soil of different plants

Sample name	Metabolism	Genetic_Information_Processing	Environmental_ Information_Processing	Cellular_Processes	Human_Diseases	Organismal_Systems
RDS	0.4833 ± 0.0004b	0.2154 ± 0.0014a	0.1289 ± 0.0008bc	0.0759 ± 0.0005c	0.0271 ± 0.0002c	0.0187 ± 0.0000ab
RLA	0.4871 ± 0.0009a	0.2165 ± 0.0011a	0.1253 ± 0.0011d	0.0761 ± 0.0008c	0.0262 ± 0.0002d	0.0181 ± 0.0001d
RPU	0.4778 ± 0.0015c	0.2044 ± 0.0008c	0.1346 ± 0.0013a	0.0792 ± 0.0001a	0.0297 ± 0.0003a	0.0185 ± 0.0000bc
RCC	0.4830 ± 0.0027b	0.2177 ± 0.0027a	0.1269 ± 0.0011cd	0.0762 ± 0.0004c	0.0268 ± 0.0001c	0.0187 ± 0.0002a
RCJ	0.4836 ± 0.0007b	0.2099 ± 0.0010b	0.1296 ± 0.0011b	0.0783 ± 0.0002ab	0.0277 ± 0.0003b	0.0181 ± 0.0001a
RAA	0.4847 ± 0.0015ab	0.2097 ± 0.0005b	0.1280 ± 0.0011bc	0.0782 ± 0.0002b	0.0279 ± 0.0002b	0.0184 ± 0.0000c

Different lowercase letters indicated significant differences among different vegetation types ($P < 0.05$). The data were presented as mean ± standard deviation (n = 4). RDS, RLA, RPU, RCC, RCJ, and RAA represented the rhizosphere soil of *D. sophia*, *L. apetalum*, *P. umbrosa*, C. carvi, *C. japonicum*, and *A. anmua*, respectively.

All the samples included 47 secondary metabolic pathways, among which the main metabolic pathways (with a relative abundance of functional gene sequences > 3%) comprised 15 categories (Table 3). The abundances of translation, carbohydrate metabolism, lipid metabolism, and folding, sorting, and degradation functions for the rhizosphere bacteria in *C. carvi* were significantly higher than those in *P. umbrosa* ($P < 0.05$). The abundances of prokaryotic cellular groups, carbohydrate metabolism, lipid metabolism, and folding, sorting, and degradation functions for the rhizosphere bacteria in *D. sophia* were significantly higher than those in *A. anmua* ($P < 0.05$). The abundances of transcription, cell growth and death, and signaling transduction for the rhizosphere bacteria in *A. annua* were significantly higher than those in other vegetation types ($P < 0.05$). The abundances of metabolism, membrane transport, cell growth and death, and signaling transduction for the rhizosphere bacteria in *P. umbrosa* were significantly higher than those in other vegetation types ($P < 0.05$). The abundances of amino acid metabolism, energy metabolism, lipid metabolism, coenzyme factors, and vitamin metabolism, and sorting, and degradation for the rhizosphere bacteria in L. apetalum were significantly greater than those in other plants ($P < 0.05$). The abundances of cell growth and death, signaling transduction, and nucleotide metabolism for the rhizosphere bacteria in *C. japonicum* were significantly greater than those in other vegetation types ($P < 0.05$).

Table 3
Relative abundance information of secondary function of rhizosphere bacterial community in different plants

Secondary functional categories	RDS	RLA	RPU	RCC	RCJ	RAA
Translation	0.0922 ± 0.0016a	0.0922 ± 0.0007a	0.0828 ± 0.0002c	0.0943 ± 0.0028a	0.0865 ± 0.0007b	0.0869 ± 0.0002bc
Cellular community prokaryotes	0.0222 ± 0.0001a	0.0212 ± 0.0001bc	0.0204 ± 0.0001cd	0.0220 ± 0.0009ab	0.0205 ± 0.0002cd	0.0201 ± 0.0001d
Transcription	0.0181 ± 0.0001b	0.0181 ± 0.0001b	0.0182 ± 0.0002b	0.0182 ± 0.0001b	0.0182 ± 0.001b	0.0186 ± 0.0001a
Carbohydrate metabolism	0.1081 ± 0.0005a	0.1063 ± 0.0007ab	0.1036 ± 0.0013c	0.1078 ± 0.0003a	0.1052 ± 0.0006bc	0.1067 ± 0.0015ab
Metabolism	0.0168 ± 0.0000ab	0.0166 ± 0.0000b	0.0171 ± 0.0002a	0.0167 ± 0.0000b	0.0166 ± 0.0001b	0.0167 ± 0.0002b
Amino acid metabolism	0.1012 ± 0.0007b	0.1034 ± 0.0004a	0.0994 ± 0.0002c	0.1011 ± 0.0003b	0.1010 ± 0.0002b	0.1005 ± 0.0003b
Membrane transport	0.0923 ± 0.0007ab	0.0879 ± 0.0005c	0.0939 ± 0.0012a	0.0901 ± 0.0018bc	0.0903 ± 0.0011bc	0.0883 ± 0.0011c
Replication and repair	0.0745 ± 0.0007b	0.0761 ± 0.0002ab	0.0780 ± 0.0003a	0.0741 ± 0.0019b	0.0781 ± 0.0003a	0.0781 ± 0.0001a
Cell growth and death	0.0085 ± 0.0001b	0.0083 ± 0.0001c	0.0090 ± 0.0001a	0.0085 ± 0.0001bc	0.0089 ± 0.0000a	0.0089 ± 0.0001a
Energy metabolism	0.0471 ± 0.0002b	0.0478 ± 0.0002a	0.0469 ± 0.0001b	0.0462 ± 0.0004c	0.0471 ± 0.0000b	0.0467 ± 0.0002bc
Signal transduction	0.0354 ± 0.0003c	0.0366 ± 0.0009b	0.0390 ± 0.0002a	0.0359 ± 0.0005bc	0.0383 ± 0.0003a	0.0384 ± 0.0002a
Lipid metabolism	0.0377 ± 0.0007a	0.0373 ± 0.0002a	0.0347 ± 0.0000c	0.0383 ± 0.0006a	0.0358 ± 0.0002b	0.0356 ± 0.0001bc
Metabolism of cofactors and vitamins	0.0343 ± 0.0000b	0.0347 ± 0.0002a	0.0344 ± 0.0000b	0.0339 ± 0.0002c	0.0344 ± 0.0001b	0.0340 ± 0.0000bc
Folding, sorting and degradation	0.0306 ± 0.0010a	0.02296 ± 0.0003a	0.0256 ± 0.0001b	0.0317 ± 0.0017a	0.0270 ± 0.0003b	0.0268 ± 0.0001b
Nucleotide metabolism	0.0319 ± 0.0003bc	0.0329 ± 0.0003a	0.0329 ± 0.0001a	0.0314 ± 0.0007c	0.0330 ± 0.0001a	0.0327 ± 0.0000ab

Different lowercase letters indicated significant differences between different vegetation types ($P < 0.05$). The data were presented as mean ± standard deviation (n = 4). RDS, RLA, RPU, RCC, RCJ, and RAA represented the rhizosphere soil of *D. sophia*, *L. apetalum*, *P. umbrosa*, *C. carvi*, *C. japonicum*, and *A. anmua*, respectively.

Analysis of symbiotic network patterns of rhizosphere bacteria among different plants

Bacterial community co-occurrence network revealed the potential interactions within the rhizosphere bacterial communities in different plants (Fig. 6). The thicker the line, the stronger the correlation between microorganisms. The green and red lines indicated positive and negative correlations. The co-occurrence patterns of rhizosphere bacterial communities differ among plant types, with the majority of interspecies associations being positive correlations. The bacterial network nodes of the six plants primarily belonged to the phyla Acidobacteriota and Actinobacteria. A total of 264 edges in all samples were significantly correlated with OTUs with high abundance ($P < 0.05$, $|rho| > 0.65$), of which 177 (67.04%) were positively correlation and 87 (32.96%) were negatively correlation, with an average clustering coefficient of 0.048. When combining OTUs, a total of 1314 nodes was detected, especially the module number, negative and positive cohesion of *P. umbrosa* were greater than other plants. Additionally, among all the samples, *D. sophia* and *P. umbrosa* showed higher modularity, indicating that their rhizosphere bacterial ecological networks had strong internal interactions.

Discussion

As a key role in soil material circulation and energy flow, rhizosphere microorganisms can decompose and transform complex organic materials, and then release nutrients that can be absorbed and utilized by plants to nourish mountain soil. It can also improve soil structure and enhance soil water and fertilizer retention ability through their own metabolic activities, which creates a good environment for the growth of mountain vegetation and is conducive to maintaining the stability of mountain ecosystems (Cui et al. 2024). Comparing the diversity of rhizosphere microbial communities associated with different plants in mountainous habitats can aid in identifying specific associations between plants and microbial communities. This information is beneficial for selecting more suitable plant species for ecological restoration and establishing a reasonable vegetation layout (Körner. 2021; Xu et al. 2019). Moreover, it can further clarify how soil properties affect the composition of microbial communities and how plants shape the rhizosphere microbial environment, there by providing more evidence for a comprehensive interpretation of the relationship among soil, plant, and microorganism.

Vegetation types and rhizosphere bacterial community diversity have long been considered to be closely related (Deng et al. 2018). In our study, the principal coordinate analysis revealed similarities in the rhizosphere bacterial community structure between *P. umbrosa* and *C. carvi*, suggesting that variations in vegetation types can influence bacterial community diversity, which was consistent with previous studies (Hernández-Cáceres et al. 2022). Plants shape soil bacterial communities by selecting the microbial community in the soil and using litter and other factors to affect the diversity of soil bacterial communities. Plant residues are the main source of nutrition for rhizosphere soil bacteria but there are significant differences in the quantity and types of litter between different plants, which may be the main reason for the significant differences in rhizosphere bacteria among different vegetation types in mountainous areas (Urbanová et al. 2015).

In our study, the dominant bacterial groups of different plants were similar but there were significant differences in their relative abundance. This result is consistent with previous reports that plant species influence the composition of soil microbial communities in ecosystems (Gil-Martínez et al. 2021; Wei et al. 2018). Proteobacteria, Actinobacteria, and Acidobacteriota were the dominant bacterial phyla, which is essentially the same as in other mountainous soil (Meng et al. 2019; Qiu et al. 2022; Zhang et al. 2022). The results indicates that, despite the influence of different soil and vegetation types on soil bacterial diversity and community structure, the dominant bacterial phyla remain largely similar. Studies have shown that (Bromke. 2013) changes in vegetation types can significantly reduce the relative abundance of *Microbacterium*, *Scomarilla*, *Sphingomonas*, and *Bryobacter* genus in the phylum Acidobacteriota. This indicates that a small number of genera in the same phyla have different adapted characteristics, and certain genera are sensitive to changes in environmental factors. In our study, the abundance of the Chlofroflexota phylum exhibited significant changes when vegetation types shifted, particularly in plants of the Brassicaceae family such as *D. sophia* and *L. apetalum*. This suggests a certain dependency of the Chlofroflexota phylum on cruciferous Brassicaceae. These observations imply that certain bacterial genera in the environment serve as indicators and can characterize changes in habitat quality (Choi et al. 2024). In our study, the bacterial composition in the rhizosphere soil of different vegetation types showed similarities at the phylum and genus classification levels but their relative abundance varied. This may be related to the different root exudates of plants, which in turn changes the bacterial community structure (Wu et al. 2024).

In our study, rhizosphere bacteria were involved in six primary metabolic pathways and 47 secondary metabolic pathways. Among them, the major secondary metabolic pathways include 15 categories, which fully demonstrate their functional richness. In the primary functional layer, the metabolic function system accounts for the largest proportion, indicating it is important for the growth of rhizosphere bacteria. Studies have shown that the main role of metabolic function is to ensure bacterial growth by taking up nutrients, such as amino acids, carbohydrates, and vitamins (Shi et al. 2019). In the secondary functional layer, amino acid metabolism, cofactor and vitamin metabolism, and carbohydrate metabolism account for a higher proportion. Amino acid metabolism can help bacteria absorb amino acids, which is beneficial for accelerating the mineralization of organic matter and promoting the absorption in plants (Rivett & Bell. 2018). The cofactors and vitamins metabolism is related to bacterial nitrogen fixation and photosynthesis (Bromke. 2013), while carbohydrate metabolism is closely related to nitrogen fixation and phosphorus solubilization (Polónia et al. 2014). We hypothesize that these functional genes can promote plant growth, which plays an important role in improving plant resistance to the environment.

The complex interconnections among microorganisms influence their community structure and function. Co-occurrence network analysis can be used to reveal the co-occurrence patterns among microbial members and the complex associations within the community, which provide a new perspective for the analysis of soil microbial community structure (Faust & Raes. 2012; Jiao et al. 2017). In our study, the main nodes of microbial co-occurrence patterns correspond with the dominant phyla, further indicating that Proteobacteria, Actinobacteria, and Acidobacteriota are the dominant bacterial phyla. In the network, positive correlations may be attributed to cooperation, while negative correlations may be due to competition (Ku et al. 2023). The co-occurrence patterns of rhizosphere bacteria in Tomur Peak exhibit a relatively high positive correlation, suggesting that bacteria adapt to similar ecological niches through synergistic cooperation (Yang et al. 2020). Multiple network-level topological features indicate that bacterial networks comprise more of nodes and exhibit more complex and stable edges, regardless of plant species. This model is better able to better adapt to environmental changes. This finding aligns with previous research results (Jiao et al. 2019).

High-throughput sequencing analysis revealed that the dominant bacterial groups among different plants on Tomur Peak exhibit similarity, albeit with notable differences in relative abundance. The functional annotation imply that certain bacteria may have played a crucial role in the growth and environmental adaptation of plants on Tomur Peak. However, our study only conducted a preliminary exploration of bacterial functions in different plant species based on PICRUSt and FUNGuild. The exact functions of various groups are not yet clear. In the future, we will use metagenomic technology to further explore the rhizosphere bacterial community structure and functions in Tomur Peak. In addition, on the basis of this study, we will enrich as many culturable strains as possible by improving the type of medium and simulating the natural ecological conditions of Tomur Peak. We hope to isolate beneficial strains with anti-stress and growth-promoting effects, which can provide reference for promoting the development of plants in Tomur Peak.

Conclusion

The study of rhizosphere bacterial community diversity and function can deepen the understanding of the relationship between plants and soil microorganisms, which has theoretical guidance for the use of biological materials to restore degraded ecosystems. In our study, the rhizosphere bacterial communities of different plants in Tomur Peak showed significant differences. The rhizosphere bacteria composition of different vegetation types was similar but the relative abundances were different at the phylum and genus level. Furthermore, there are unique genera between different plant species, and whether these unique genera are related to the ability of plants to improve soil nutrition in mountainous areas requires further research. The bacterial network has more positive connections than negative connections, indicating that there is a strong synergistic effect between rhizosphere bacteria of different plants. Overall, this study contributes to understanding the adaptive mechanisms of mountain plants to their environment, which provides a scientific evidence for habitat conservation.

Declarations

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author Contributions Maryamgul Yasen performed the experiments, analyzed the data. Mingyuan Li analyzed the data, authored or reviewed drafts of the paper. Jilian Wang conceived and designed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft. All authors read and approved the final manuscript.

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Data Availability All data sets and materials generated or analyzed in this study are available from the appropriate authors upon reasonable request. No datasets were generated or analysed during the current study.

Ethical Approval Not applicable.

Consent All authors agreed with the content of the manuscript and given consent to take part and consent publish the manuscript.

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Figures

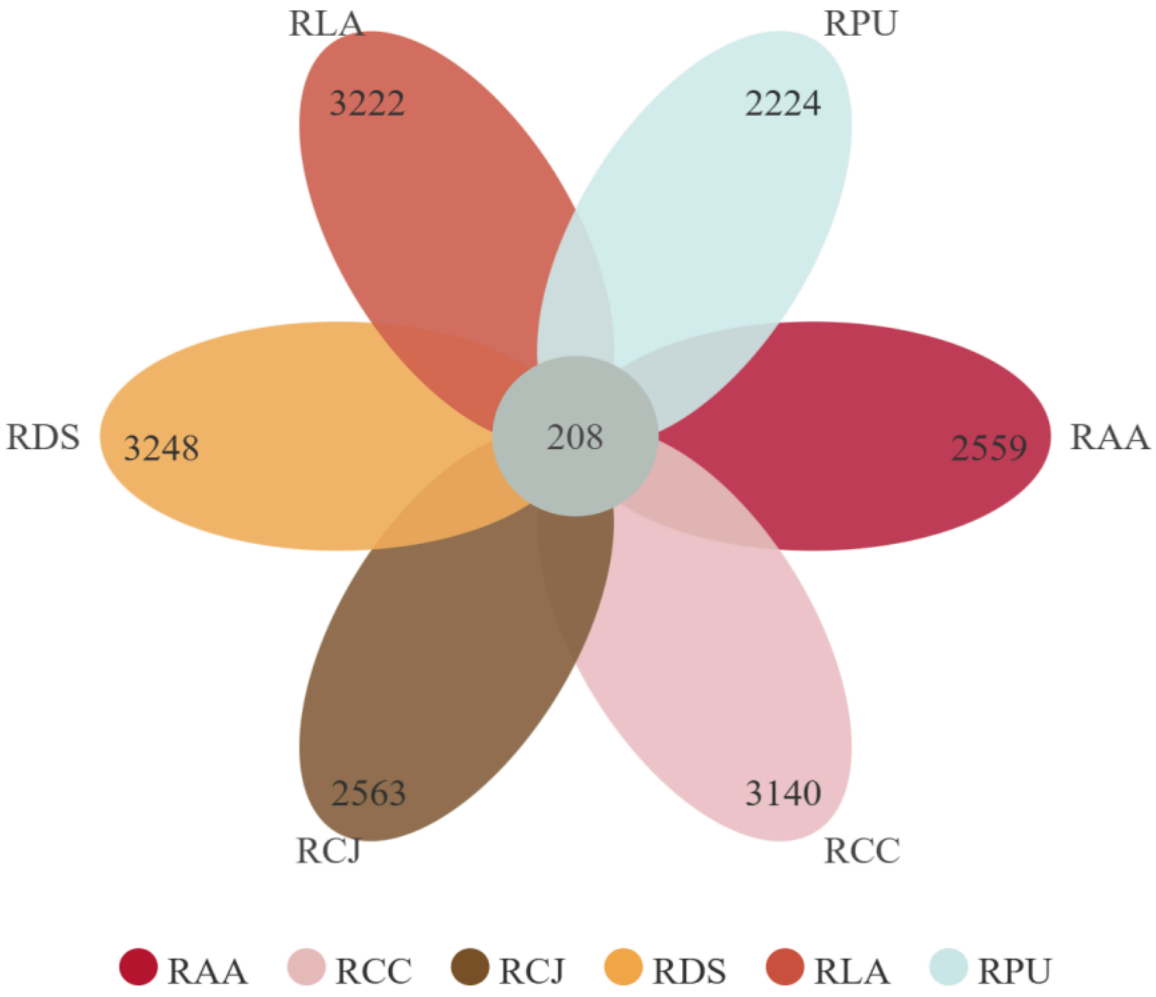

Figure 1

Analysis of common and unique OTUs of rhizosphere bacteria from different plant species. RDS, RLA, RPU, RCC, RCJ, and RAA represented the rhizosphere soil of *D. sophia*, *L. apetalum*, *P. umbrosa* , *C. carvi*, *C. japonicum*, and *A. anmua*, respectively.

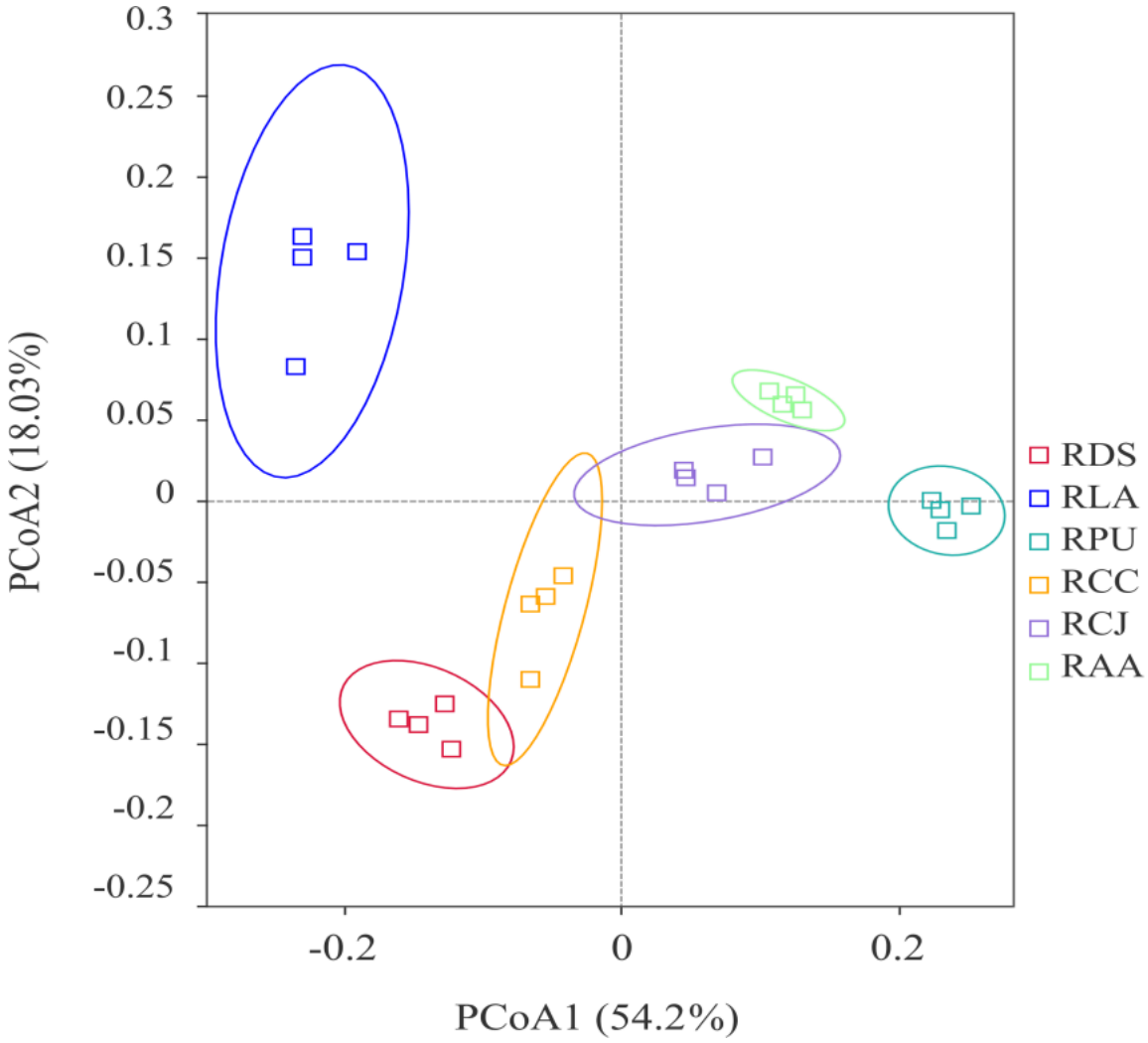

Figure 2

PCoA plots of different samples based on weighted UniFrac distance. RDS, RLA, RPU, RCC, RCJ, and RAA represented the rhizosphere soil of *D. sophia*, *L. apetalum*, *P. umbrosa* , *C. carvi*, *C. japonicum*, and *A. anmua*, respectively.

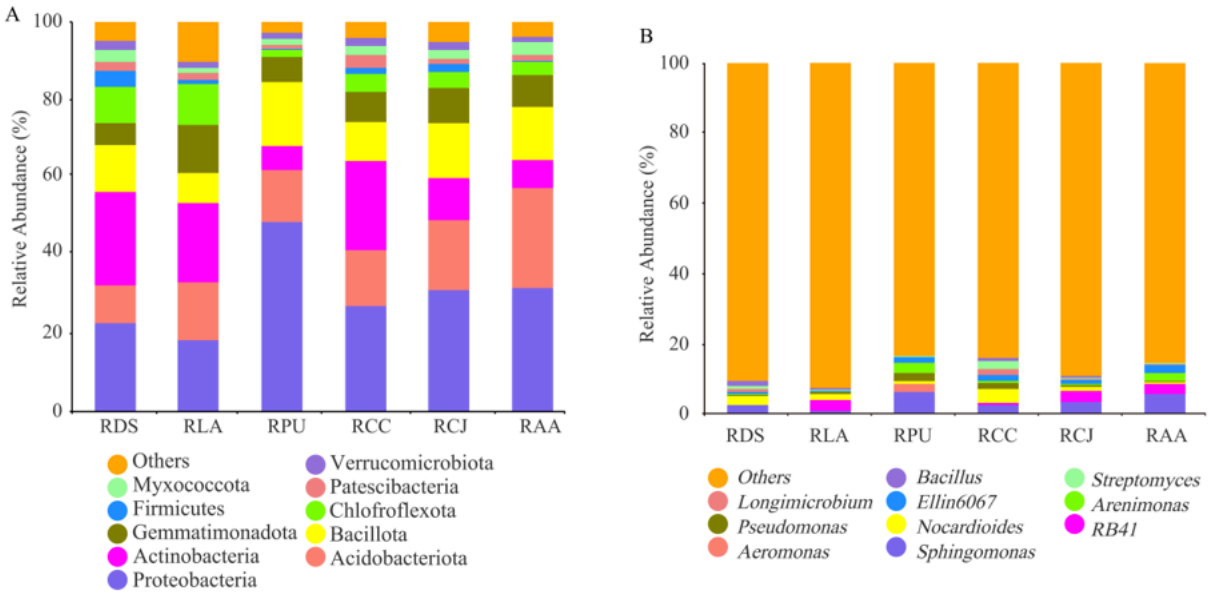

Figure 3

The relative abundances of bacteria at the phylum level (A) and the genus level (B). RDS, RLA, RPU, RCC, RCJ, and RAA represented the rhizosphere soil of *D. sophia*, *L. apetalum*, *P. umbrosa* , *C. carvi*, *C. japonicum*, and *A. anmua*, respectively.

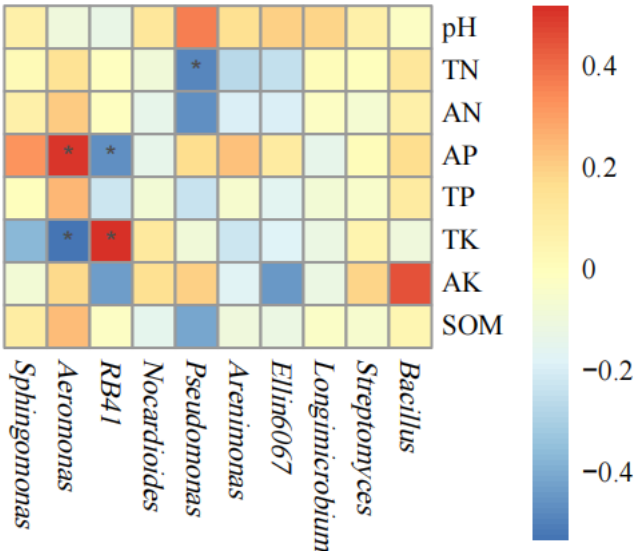

Figure 4

Analysis of Spearman correlation between the bacterial genera and environmental factors.

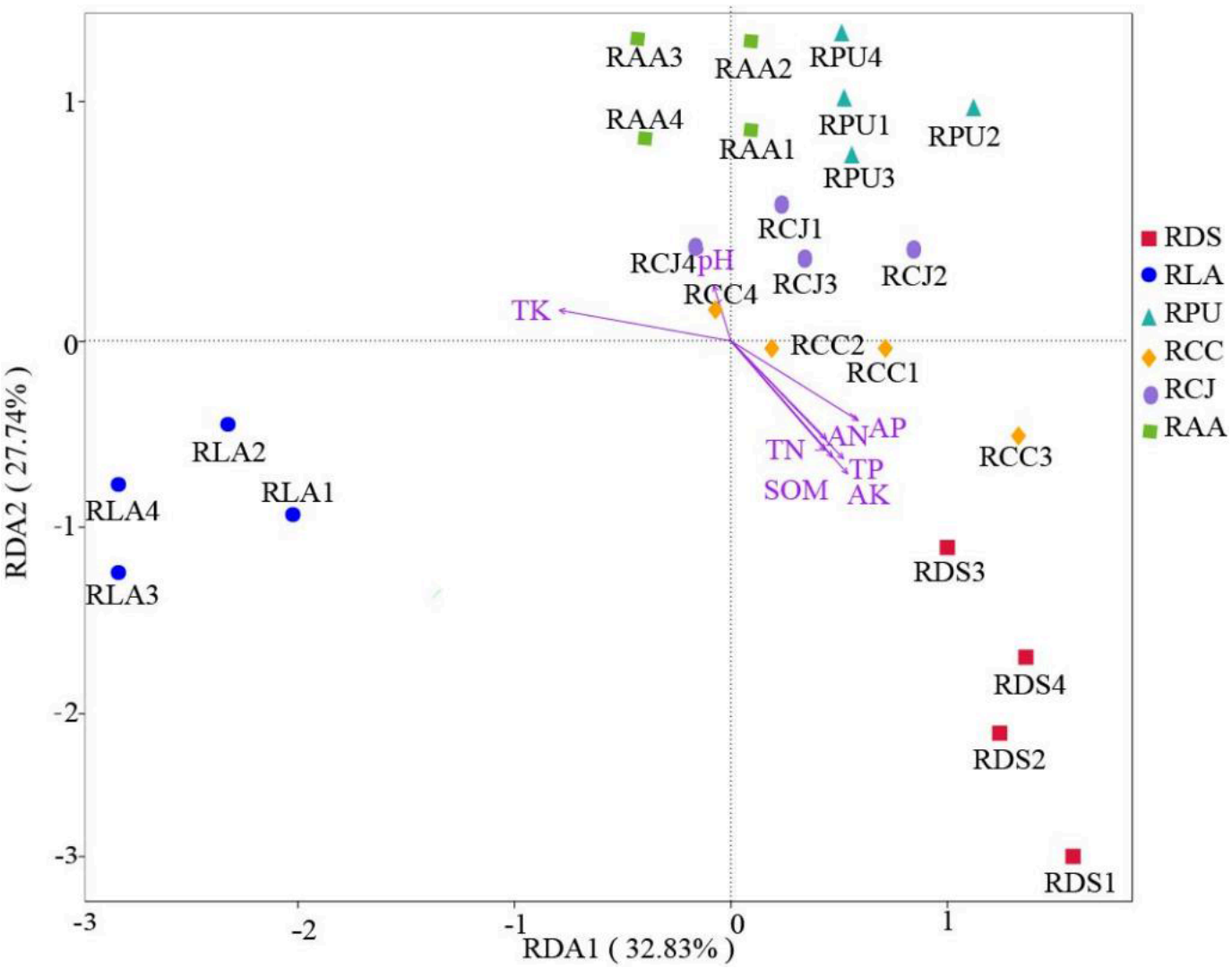

Figure 5

RDA analysis of rhizosphere bacterial community and environment factors. RDS, RLA, RPU, RCC, RCJ, and RAA represented the rhizosphere soil of *D. sophia*, *L. apetalum*, *P. umbrosa* , *C. carvi*, *C. japonicum*, and *A. anmua*, respectively.

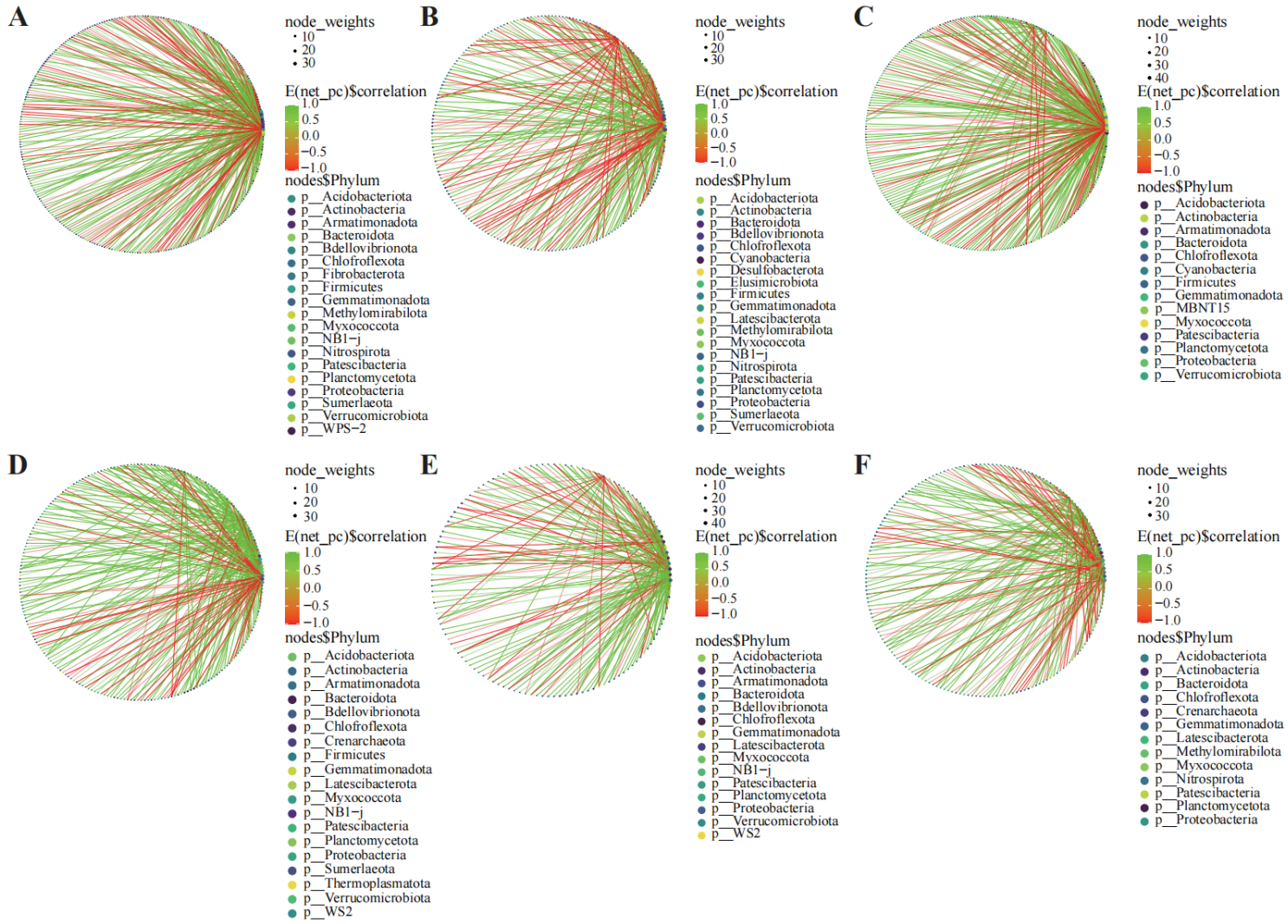

Figure 6

Symbiotic network diagram of bacterial community. Different node-colors were used to distinguish different phyla, and node sizes were used to indicate the relative abundance of OTUs. Edges represented statistical interactions between OTUs, and the green edges represented positive correlations, the rede dges represent negative correlations. The width of each edge reflectsed the Spearman correlation coefficient between nodes. Figures A, B, C, D, E, and F represented *D. sophia*, *L. apetalum*, *P. umbrosa*, *C. carvi*, *C. japonicum*and *A. anmua*, respectively.