

MOLECULAR ECOLOGICAL NETWORK CHARACTERISTICS OF MICROBIAL COMMUNITIES IN THE RHIZOSPHERE OF THE ENDANGERED PLANT *CATHAYA ARGYROPHYLLA*

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Abstract. The endangered plant *Cathaya argyrophylla* has a narrow habitat range, limited distribution area, and sparse population, thus facing severe survival threats. This study investigated its rhizosphere microbial communities and molecular ecological networks (MENs) across different sites in Huaping using metagenomic sequencing. Results showed that rhizosphere microbiota were predominantly bacterial, including 16 bacterial phyla such as Pseudomonadota, Actinomycetota, Acidobacteriota, and three archaeal phyla such as Euryarchaeota and Nitrososphaerota, as well as one fungal phylum such as Ascomycota, accounting for more than 85% of the total microbial abundance in the samples; dominant genera were all bacterial genera, including *Bradyrhizobium*, *Streptomyces*, and *Pseudomonas*. Alpha diversity analysis showed significant differences in species richness (observed_species) and diversity indices (Shannon, Simpson) among different sites. MENs analysis indicated that network complexity followed the order: Yezhutang < Hongtan < Xietangwan, where Xietangwan had the highest network density (0.496). Positive interaction analysis revealed that intradomain interactions were mainly between bacteria-bacteria and fungi-fungi, while interdomain interactions were primarily dominated by bacteria-fungi, bacteria-archaea, and bacteria-virus interactions. Key network nodes significantly correlated with soil physicochemical properties. These findings demonstrate that unique microbial communities assemble in the rhizosphere of *C. argyrophylla*, which is crucial for its environmental adaptation.

Keywords: Huaping, soil microorganisms, molecular ecological network, rare and endangered plants, *Cathaya argyrophylla*

Introduction

Cathaya argyrophylla, a unique ancient species of the pine family endemic to China, is listed in the IUCN Red List and is known as the ‘giant panda of the plant world,’ holding extremely high ecological value and scientific research significance (Tan et al., 2022). Its distribution is discontinuous, mainly limited to subtropical mountainous areas in Guangxi, Hunan, Sichuan, and Guizhou provinces of China (Tan et al., 2022). However, due to small population size, habitat fragmentation, narrow distribution range, low germination rate, and poor environmental adaptability, the population of *C. argyrophylla* has sharply declined, approaching extinction, and its future survival status is of great concern (Fan et al., 2020; Hu et al., 2014). In recent years, many scholars have conducted in-depth studies on the mechanisms leading to its endangerment, focusing on aspects such as community structure types, living environment, reproductive patterns, and biological characteristics (Wang et al., 2010, 2025, 2006; Huang et al., 2022; Xiao et al., 2022; Qian et al., 2016). Currently, researchers have conducted more studies on *C.*

argyrophylla populations in Hunan and Guizhou provinces (Xie et al., 2023; Wei et al., 2024). For example, Xie et al. (2023) studied the soil communities of *C. argyrophylla* at four natural spatial distribution points in Hunan Province and found that soil properties are the main factors causing changes in rhizosphere soil bacterial and fungal communities, with nitrogen being the primary driving force for changes in soil microbial communities. The Huaping Nature Reserve, as one of the important distribution areas of *C. argyrophylla*, provides an ideal site for studying the diversity and interaction mechanisms of its rhizosphere microbial communities due to its unique ecological environment.

The rhizosphere is an ecosystem with complex microbial communities and interactions, considered as a secondary genomic reservoir due to its importance in plant growth (Brunel et al., 2020). Rhizosphere microorganisms not only participate in nutrient cycling and stress resistance regulation but may also play a crucial role in the survival and reproduction of endangered plants (Liu et al., 2023). For example, certain microorganisms can promote nutrient uptake by plants, enhance disease resistance, while others may form symbiotic relationships with plants, jointly resisting external environmental pressures (Singh et al., 2025). The survival and reproduction of the *C. argyrophylla* are closely related to the surrounding rhizosphere microbial community. In studies of the Huaping *C. argyrophylla*, differences in the structure and function of its rhizosphere microbial community have been revealed, but research on their interaction mechanisms is relatively limited (Wang et al., 2025). Molecular Ecological Network Analysis (MENA) is an emerging research method that can deeply analyze the complexity of microbial communities and their interaction mechanisms, revealing the potential roles of microbial communities in maintaining plant health and ecosystem stability (Chen et al., 2017).

This study takes the microbial community at the rhizosphere of the Huaping *C. argyrophylla* as the research object. By using metagenome sequencing technology and molecular ecological network analysis methods, a molecular ecological network of the rhizosphere microbial community of the Huaping *C. argyrophylla* is constructed. The topological structure characteristics of the network are analyzed. Specifically: (1) Revealing the composition and diversity of the rhizosphere microbial community of the Huaping *C. argyrophylla*; (2) Elucidating the interaction mechanisms of the rhizosphere microbial community of the *C. argyrophylla*, providing a theoretical basis for formulating scientific and effective conservation and restoration strategies. It also offers new perspectives for the study of interaction mechanisms between endangered plants and microorganisms.

Materials and methods

Study area overview and soil sample collection

Huapi Nature Reserve (109°48'54"-109°58'20"E, 25°31'10"-25°39'36"N) is located in the mid-subtropical monsoon climate zone, with distinct dry (September to the following February) and wet (March to August) seasons. The annual average temperature is 12-14°C; the annual average precipitation is 2000-2200 mm; relative humidity is 85%-90%; the altitude of the reserve ranges from 1000 to 1500 m, with mountain red soil, mountain yellow soil, and mountain yellow-brown soil from bottom to top. The region has a rich variety of plant species, including over 1000 higher plants, among which the most precious is the *C. argyrophylla* (Hu et al., 2014).

In March 2023, three populations of *C. argyrophylla* were selected as research subjects in the region, namely Hongtan, Xietangwan, and Yezhutang. The site conditions and forest characteristics of the three sampling points are shown in *Table 1*. In each of the three sample plots, nine healthy *C. argyrophylla* trees were randomly selected from areas with relatively uniform slopes. The litter and weeds covering the target trees were removed, and approximately 500 g of soil was collected from a depth of 0–20 cm using a soil auger (inner diameter 5.0 cm) and a shovel, and placed into sterile self-sealing bags. The loosely attached soil on the surface of the *C. argyrophylla* fine Rhizospheres (diameter ≤ 2 mm) was gently shaken off, and the rhizosphere soil adhering to the rhizospheres was collected using a soft brush. Three soil samples were taken from each tree at intervals of 1 m in a triangular pattern, and mixed to form one soil sample, resulting in a total of 27 samples (9 soil samples per plot). Sampling information was recorded, and the samples were stored and transported back to the laboratory using an insulated portable box with built-in biological ice packs. In the laboratory, fresh soil samples were sieved through a 2 mm steel sieve and immediately stored at -80°C for soil metagenome sequencing.

Table 1. Site conditions and stand characteristics

Indexes	H	X	Y
Latitude (N)	25°36'23"	25°36'3"	25°36'14"
Longitude (E)	109°57'15"	109°55'6"	109°54'54"
Altitude (m)	920–980	1290–1320	1350–1420
Slope (°)	45	45~70	45~75
Diameter at breast height (cm)	20.01	22.37	25.78
Height of tree (m)	6.52	9.77	12.72
The age of a tree (a)	>50	>100	>100

H: Hongtan; X: Xietangwan; Y: Yezhutang. The same below

Determination of soil physicochemical properties

The determination of soil physicochemical properties refers to the methods in the ‘National Environmental Protection Standard of the People’s Republic of China’ and the ‘Forestry Industry Standard of the People’s Republic of China’. Among them, the soil moisture content (SWC) was measured using the gravimetric method (YH-C30002 electronic balance, Sartorius Scientific Instruments, Beijing, China). The pH value was measured using the potentiometric method, with a water - to - soil ratio of 2.5:1, using an ST2100 pH meter (OHAUS Instruments, Shanghai, China). The soil organic carbon (SOC) content was measured using the potassium dichromate oxidation with external heating method. The total nitrogen (TN) content was measured using sulfuric acid digestion followed by the Kjeldahl nitrogen determination method. The content of available nitrogen (AN) in soil was determined by alkaline hydrolysis diffusion method. The total phosphorus (TP) content in soil was determined using the sodium hydroxide alkali melting molybdenum antimony colorimetric method (TU-1901 UV visible spectrophotometer, Beijing Purkinje General Instrument Co., Ltd.). The content of available phosphorus (AP) was determined using the sodium bicarbonate/sodium fluoride hydrochloric acid extraction molybdenum antimony colorimetric method (TU-1901 UV visible spectrophotometer, Beijing Purkinje General Instrument Co., Ltd.). The total potassium (TK) content in the soil was measured using NaOH alkali fusion and flame

photometry with a TAS-990F flame atomic absorption spectrophotometer from Beijing Purkinje General Instrument Co., Ltd. The available potassium (AK) content in soil was measured using ammonium acetate solution extraction flame spectrophotometry with a TAS-990F flame atomic absorption spectrophotometer from Beijing Purkinje General Instrument Co., Ltd. Soil microbial biomass carbon (MBC) and nitrogen (MBN) were extracted using chloroform fumigation and measured by a carbon nitrogen analyzer (Sartorius Scientific Instruments).

DNA extraction and metagenomic sequencing

Extract sample DNA according to the HiPure Soil DNA Kit manual, and preliminarily determine the integrity of the bands using 1% agarose gel electrophoresis. Then, use the Qubit 4.0 fluorometric quantitation system to measure the concentration, ensuring that each sample has a concentration of $\geq 5 \text{ ng } \mu\text{L}^{-1}$ and a total amount of $\geq 50 \text{ ng}$. The purity assessment is performed by the NanoDrop One microspectrophotometer, and samples with $\text{OD}_{260/280} < 1.8$ or $\text{OD}_{260/230} < 1.5$ are excluded to meet subsequent library construction requirements. Qualified DNA is submitted to Nanjing Jishi Huayuan Biotechnology Co., Ltd. for quality inspection. After passing the inspection, it is ultrasonically fragmented into approximately 300 bp fragments for library construction. Qualified libraries are sequenced using the Illumina Novaseq-PE 150 platform for metagenomic sequencing. The raw image data obtained from sequencing is converted into Raw Data (Raw Reads) through base calling and stored in FASTQ (fq) file format, containing sequencing sequences and quality information. The statistical results of the sample sequencing data are shown in *Table 2*.

Bioinformatics analysis

Base calling was performed using Illumina Casava 1.8 software. Clean sequences were assembled using Megahit (v1.2.9), and the optimal results were selected. Gene prediction was conducted on contigs ($\geq 500 \text{ bp}$) using MetaGeneMark (3.38), with sequences shorter than 100 nt filtered out. The assembled gene sequences (non-redundant gene sequences) were classified into species using Kraken (2.1.2) software with default parameters, compared against bacterial (Bacteria), fungal (Fungi), archaeal (Archaea), and viral (Viruses) database sequences, and separately compared against each individual database to obtain abundance information at different taxonomic levels (domain, phylum, class, order, family, genus, species) for each sample.

Based on metagenomic data, using the MENA platform to optimize the processing of abundance data for the top fifty dominant phyla, calculate the Pearson correlation between each phylum, then construct a microbial molecular ecological network based on random matrix theory (RMT), and calculate its topological structure parameters, including the number of nodes, number of connections, centrality (CD), density (D), average connectivity (avgK), average clustering coefficient (avgCC), and average path distance (GD). According to the intra-module connectivity (Z_i) and inter-module connectivity (P_i) of nodes, all nodes in the network are divided into four categories: (1) module hubs ($Z_i \geq 2.5$ and $P_i < 0.62$); (2) connectors ($Z_i < 2.5$ and $P_i \geq 0.62$); (3) network hubs ($Z_i \geq 2.5$ and $P_i \geq 0.62$); (4) peripheral nodes ($Z_i < 2.5$ and $P_i < 0.62$). Among them, module hubs, connectors, and network hubs are considered key nodes in the microbial molecular ecological network (Deng et al., 2012; Qin et al., 2023). Finally, the network structure visualization is achieved using Gephi-0.9.2 software.

Table 2. Statistical evaluation table of sample sequencing data

Sample ID	Read number	Base number	Q30(%)	Q20(%)
H1	41266916	12380074800	91.79	96.96
H2	41748691	12524607300	91.82	96.94
H3	35268992	10580697600	91.07	96.59
H4	52677191	15803157300	90.89	96.52
H5	49425714	14827714200	91.08	96.64
H6	41930445	12579133500	91.62	96.83
H7	49815082	14944524600	91.3	96.71
H8	48020541	14406162300	91.97	97.01
H9	46489189	13946756700	90.82	96.47
X1	43037056	12911116800	91.63	96.78
X2	45359440	13607832000	91.43	96.7
X3	40670619	12201185700	90.3	96.21
X4	40500820	12150246000	91.33	96.67
X5	42742532	12822759600	91.55	96.86
X6	41583439	12475031700	90.48	96.31
X7	40859138	12257741400	91.2	96.68
X8	45658958	13697687400	89.03	95.7
X9	41835144	12550543200	88.75	95.39
Y1	35042487	10512746100	89.3	95.9
Y2	39913326	11973997800	89.28	95.83
Y3	44595908	13378772400	88.47	95.32
Y4	46050192	13815057600	89.98	96.16
Y5	45363891	13609167300	89.67	96.03
Y6	35590907	10677272100	89.44	95.92
Y7	44930196	13479058800	87.28	94.75
Y8	49858849	14957654700	89.89	96.16
Y9	57584150	17275245000	93.02	97.4

Sample ID: Sample Name; Read Number: Total number of paired-end reads in Clean Data; BaseNumber: Total number of bases in Clean Data; Q30(%): Percentage of bases with quality value greater than or equal to 30 in Clean Data; Q20(%): Percentage of bases with quality value greater than or equal to 20 in Clean Data

Data statistical analysis

Using one-way ANOVA to analyze the differences in the physicochemical properties of the soil at the Rhizosphere zone of the *C. argyrophylla* and the species indices (observed_species diversity index), Shannon diversity index, and Simpson diversity index of the microbial communities at different sampling points at tche phylum and genus levels. Tukey's HSD and Duncan's multiple comparison tests were used to examine intergroup differences, calculations performed using IBM SPSS Statistics 26.0 (IBM SPSS Inc., Chicago, IL, USA). Pearson correlation coefficients were used to analyze the relationship between the physicochemical properties of the soil at the Rhizosphere zone of the *C. argyrophylla* and the key nodes of the molecular ecological network structure, calculations performed through the MENA platform. Data were initially processed and analyzed using Excel 2019; graphs were created using GraphPad Prism 8.3 software and the Genesky Bio-cloud platform.

Results

Soil physicochemical properties at the Rhizosphere zone of the Cathaya argyrophylla

The moisture content did not significantly differ between H and Y ($P > 0.05$) but significantly differed from X ($P < 0.05$) (Table 3); organic carbon, total nitrogen, and total potassium content did not significantly differ between X and Y ($P > 0.05$) but significantly differed from H ($P < 0.05$); total phosphorus, available phosphorus, and microbial biomass carbon and nitrogen did not significantly differ among the three sampling points ($P > 0.05$); pH and available nitrogen content significantly.

Table 3. Soil physicochemical properties (mean $\pm$ SD, $n = 9$)

Physicochemical properties	H	X	Y
SWC (%)	26.25 $\pm$ 2.49a	18.06 $\pm$ 5.58b	28.46 $\pm$ 3.80a
pH	4.45 $\pm$ 0.17a	4.13 $\pm$ 0.22b	4.28 $\pm$ 0.15ab
SOC (g/kg)	15.76 $\pm$ 4.45a	74.69 $\pm$ 45.92b	72.34 $\pm$ 26.06b
TN (g/kg)	2.72 $\pm$ 0.40a	4.55 $\pm$ 2.06b	3.99 $\pm$ 1.07b
TP (g/kg)	0.46 $\pm$ 0.03a	0.42 $\pm$ 0.09a	0.35 $\pm$ 0.03a
TK (g/kg)	12.49 $\pm$ 0.22a	7.40 $\pm$ 0.51b	6.44 $\pm$ 0.64b
AN (mg/kg)	206.30 $\pm$ 63.48a	362.94 $\pm$ 168.34b	329.04 $\pm$ 83.90ab
AP (mg/kg)	2.54 $\pm$ 0.79a	4.39 $\pm$ 1.11a	2.02 $\pm$ 0.30a
AK (mg/kg)	32.57 $\pm$ 2.25a	32.31 $\pm$ 3.00a	21.53 $\pm$ 2.74b
MBC (mg/kg)	1012.83 $\pm$ 281.34a	1015.29 $\pm$ 137.00a	1173.55 $\pm$ 179.30a
MBN (mg/kg)	53.66 $\pm$ 17.92a	50.74 $\pm$ 28.45a	53.48 $\pm$ 21.71a

Site names were the Hongtan (H), Xietangwan (X) and Yezhutang (Y); SWC, soil water content; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, available nitrogen; AP, available phosphorus; AK, available potassium; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen. Different lowercase letters indicated significant differences in different populations of *C. argyrophylla* ($P < 0.05$)

The structural characteristics of microbial communities in the rhizosphere of the Cathaya argyrophylla

In the microbial community at the Rhizosphere of *C. argyrophylla*, the top 20 most abundant phyla were selected as dominant phyla (Fig. 1A). The study found that these phyla include bacterial phyla such as Pseudomonadota, Actinomycetota, Acidobacteriota, Myxococcota, Bacillota, Planctomycetota, Bacteroidota, Thermodesulfobacteriota, Cyanobacteriota, Gemmatimonadota, Deinococcota, Chloroflexota, Verrucomicrobiota, Nitrospirota, Campylobacterota, and Spirochaetota; as well as archaeal phyla such as Euryarchaeota, Nitrososphaerota, and Thermomicrobiota. Additionally, it includes fungal phylum such as Ascomycota. These phyla account for more than 85% of the total microbial relative abundance in each sample (16 bacterial phyla, 1 fungal phylum, and 3 archaeal phyla), indicating their significant ecological functions in the *C. argyrophylla* Rhizosphere ecosystem.

Among the microbial communities at the Rhizosphere of the *C. argyrophylla*, the top 20 in relative abundance were selected as dominant genera (Fig. 1B). The study found that the genera *Bradyrhizobium*, *Streptomyces*, *Pseudomonas*, *Burkholderia*, *Mycobacterium*, *Paraburkholderia*, *Mesorhizobium*, *Mycolicibacterium*,

Sphingomonas, *Rhizobium*, *Cupriavidus*, *Nocardioides*, *Amycolatopsis*, *Lysobacter*, *Methylobacterium*, *Granulicella*, *Microbacterium*, *Variovorax*, *Micromonospora*, and *Rhodococcus* are all bacterial genera. No fungal, archaeal, or viral genera were identified. The dominant genera in the *C. argyrophylla* Rhizosphere microbial community are all bacterial genera, and no fungal, archaeal, or viral genera were found in the list of dominant genera. This may be related to the choice of research methods (such as DNA extraction and sequencing bias) or specific environmental conditions of the *C. argyrophylla* Rhizosphere.

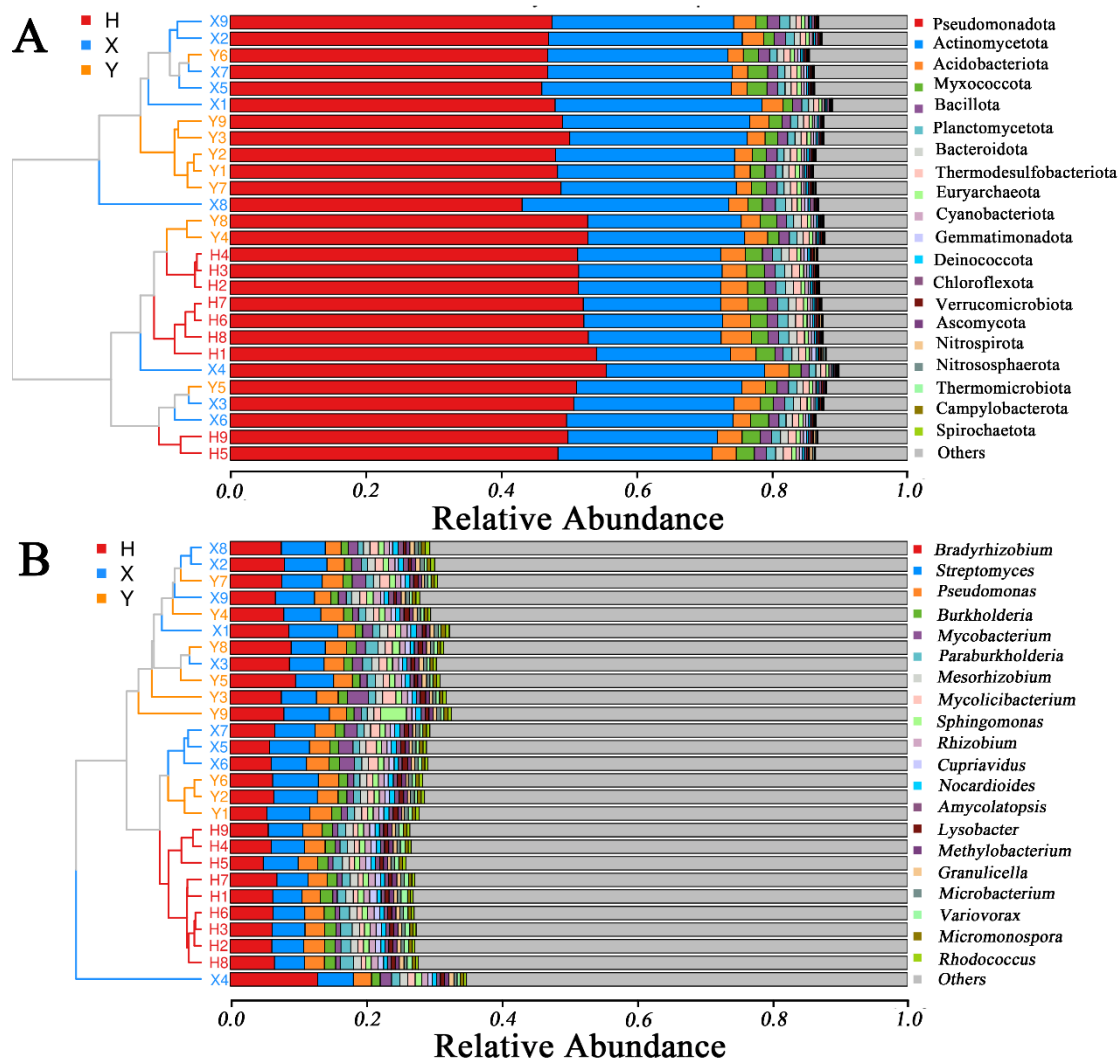


Figure 1. Species composition of microbial communities at the phylum (A) and genus (B) levels in the rhizosphere of *C. argyrophylla*

The alpha diversity characteristics of microbial communities at the Rhizosphere of *C. argyrophylla*

One-way ANOVA analysis indicates that at the phylum level (Fig. 2A), the Observed species diversity index in the Hongtong differed extremely significantly from that in the Yezhutang ($P < 0.001$), indicating a high degree of dissimilarity in species richness between these two locations. The Xietangwan and the Yezhutang also showed significant

differences ($P < 0.05$), further reflecting the influence of geographical distance and environmental conditions on microbial community composition. The Shannon diversity index of the Hongtan differed significantly from that of Xietangwan ($P < 0.05$), while no significant differences were observed in the remaining comparisons ($P > 0.05$). The Simpson diversity index between pairwise comparisons of the Hongtan, Xietangwan, and the Yezhutang showed no significant differences ($P > 0.05$), suggesting that despite differences in species richness and diversity, the distribution of dominant species may be relatively consistent.

Additionally, at the genus level (Fig. 2B), the Observed_ species diversity index in Xietangwan differed significantly from that in the Yezhutang ($P < 0.05$), with no significant differences in the remaining comparisons ($P > 0.05$). The Shannon diversity index of the Hongtan differed extremely significantly from that of Xietangwan ($P < 0.01$), with no significant differences in the remaining comparisons ($P > 0.05$). The Simpson diversity index of the Hongtan also differed extremely significantly from that of Xietangwan ($P < 0.01$), with no significant differences in the remaining comparisons ($P > 0.05$). These results further support the significant impact of geographical distance and environmental factors on microbial community structure.

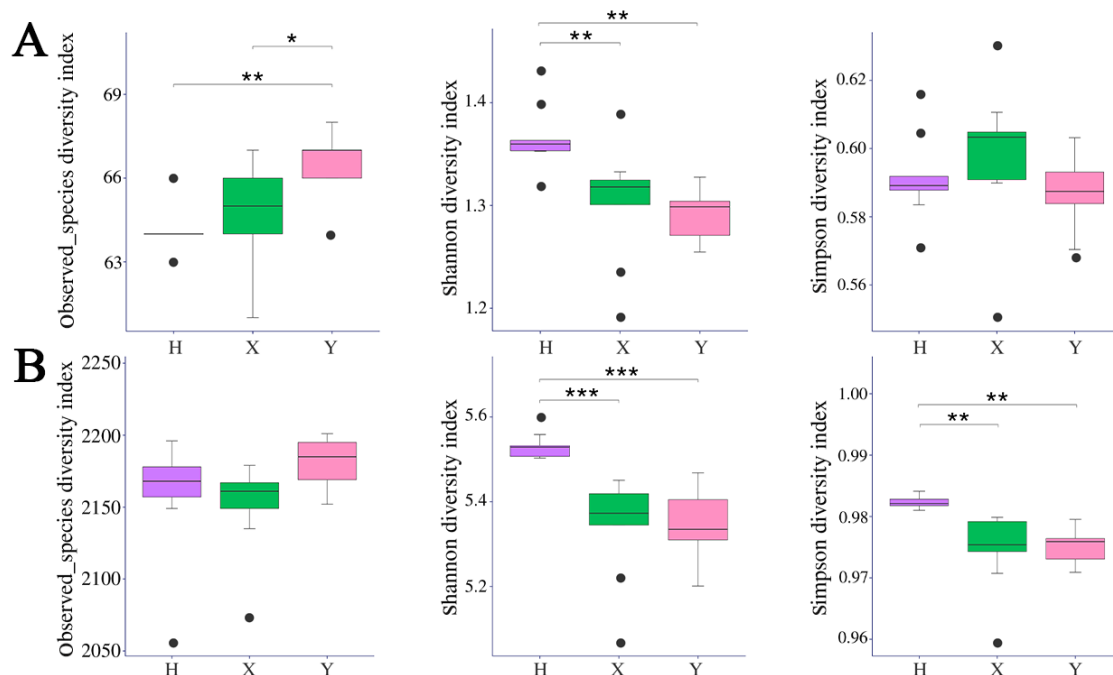


Figure 2. Analysis of alpha diversity at the phylum (A) and genus (B) levels of microbial communities associated with the rhizosphere of *C. argyrophylla*. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Molecular ecological network structure characteristics of microbial communities at the Rhizosphere of *C. argyrophylla*

In the constructed MENs (Table 4), the average clustering coefficient (avgCC), average connectivity (avgK), density (D), and total links are all represented as: $Y < H < X$. The centrality (CD), average path distance (GD), efficiency, and maximum eigenvector centrality are represented as: $X < H < Y$. The maximum degree is represented

as: $Y < H = X$, the maximum betweenness is represented as: $H < X < Y$, while the maximum stress centrality and transitivity (Trans) are represented as: $Y < H < X$. This result indicates that the complexity of network interactions among the Rhizosphere microbiota of the *C. argyrophylla* is $Y < H < X$.

The microbial molecular ecological network of the Yezhutang is the most loosely connected, with a network density is Yezhutang (0.385) < Hongtan (0.493) < Xietangwan (0.496) (Table 4); compared to the Hongtan and Xietangwan, the Yezhutang has the fewest edges (472); the nodes with the highest degree, highest betweenness, highest stress centrality, and highest eigenvector centrality in the Hongtan are all from the phylum Archaea; in Xietangwan, the nodes with the highest degree, highest betweenness, and highest stress centrality are all from the phylum Cyanobacteria, but the node with the highest eigenvector centrality is from the phylum Acidobacteria; in the Yezhutang, the nodes with the highest degree, highest stress centrality, and highest eigenvector centrality are all from the phylum Microsporidia, but the node with the highest betweenness is Candidatus_Omnitrophica..

Table 4. Topological properties of rhizosphere microbial interactions network relative to sample plot

Network indexes	H	X	Y
Total nodes	50	50	50
Total links	604	608	472
Average degree (avgK)	24.160	24.320	18.880
Average clustering coefficient (avgCC)	0.568	0.599	0.447
Average path distance (GD)	1.507	1.505	1.616
Maximal degree	34	34	29
Nodes with max degree	Nitrososphaerota	Cyanobacteriota	Microsporidia
Centrality (CD)	0.209	0.206	0.215
Maximal betweenness	25.977	32.765	39.194
Nodes with max betweenness	Nitrososphaerota	Cyanobacteriota	Candidatus_Omnitrophica
Maximal stress centrality	255	278	236
Nodes with max stress centrality	Nitrososphaerota	Cyanobacteriota	Microsporidia
Maximal eigenvector centrality	0.199	0.188	0.214
Nodes with max eigenvector centrality	Nitrososphaerota	Acidobacteriota	Microsporidia
Density (D)	0.493	0.496	0.385
Transitivity (Trans)	0.570	0.597	0.456
Efficiency	0.517	0.514	0.627

The molecular ecological network diagram (Fig. 3A) and chord diagram (Fig. 3B) indicate that intra-domain interactions within the bacterial community are primarily between Acidobacteria and Chloroflexi, while intra-domain interactions within the fungal community are mainly between Ascomycota and Basidiomycota.

Further statistical analysis revealed (Fig. 4) that the nodes of the molecular ecological networks of the Rhizosphere microbiomes of the three sampling points were all peripheral nodes, without module hubs, connectors, or network hubs. This may be related to the selection of dominant microbial communities; that is, key microbial communities were not included in the statistical calculations. On the other hand, dominant microbial communities are not necessarily key microbial communities.

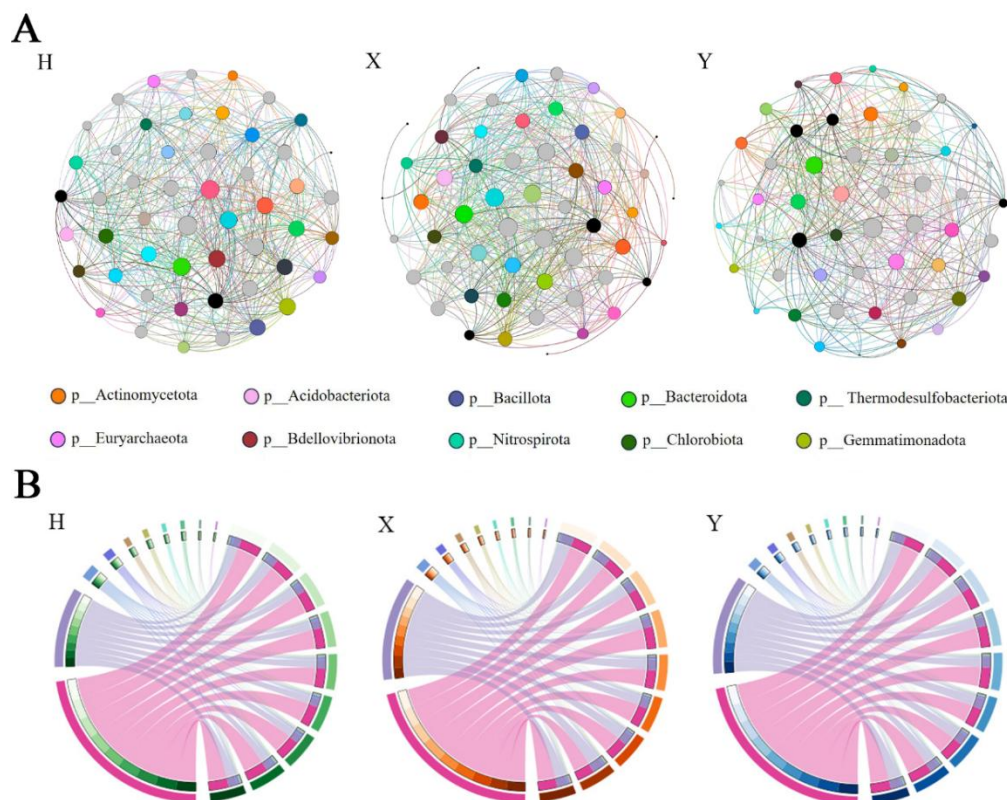


Figure 3. Molecular ecological network of *C. argyrophylla* rhizosphere microbiota (A) and its interaction string diagram at the phylum level (B). Each node in A represents a microorganism, and the color of the node represents the phylum level of microorganisms; A line represents the interaction between nodes, and the line color is consistent with the node color. In B, Green represents H1-H9 from light to deep, orange represents X1-X9 from light to deep, and blue represents Y1-HY from light to deep

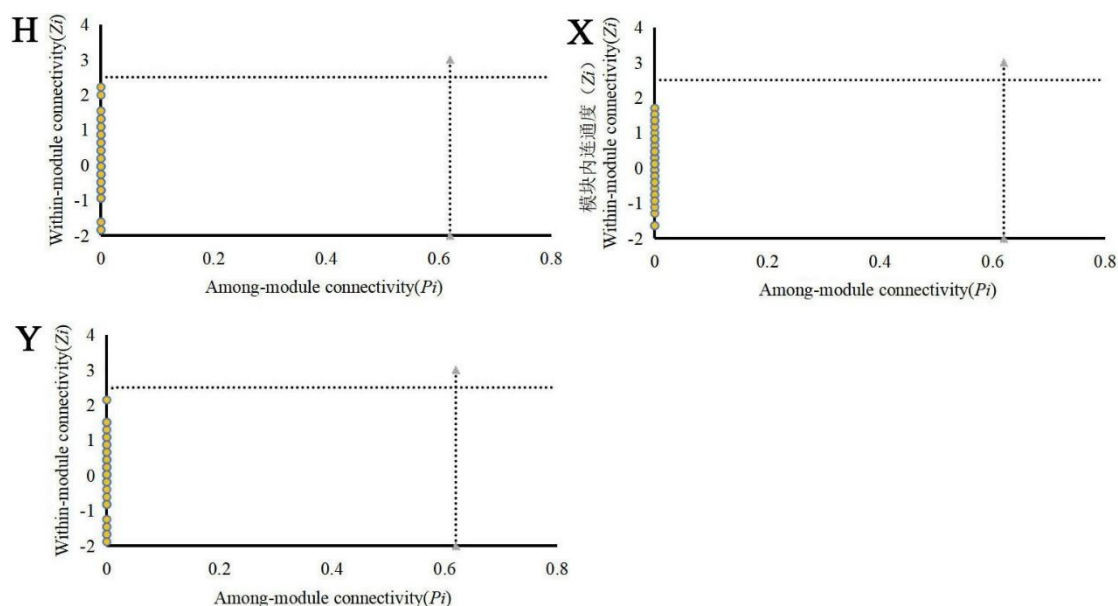


Figure 4. Distribution map of topological roles of nodes in the molecular ecological network of microbial communities at the rhizosphere of *C. argyrophylla*

In Hongtan (Fig. 5H), the positive interactions between bacteria-bacteria, fungi-fungi, archaea-archaea, virus-virus, bacteria-fungi, bacteria-archaea, bacteria-virus, fungi-archaea, fungi-virus, and archaea-virus were 45.70%, 0.00%, 0.17%, 0.17%, 5.63%, 2.65%, 9.27%, 0.17%, 0.99%, 0.00%, 16.89%, 0.00%, 0.00%, 0.17%, 5.30%, 7.28%, 3.97%, 0.50%, 0.33%, and 0.83%, respectively. In Xietangwan (Fig. 5X), these positive interactions were 44.08%, 0.16%, 0.16%, 0.16%, 6.58%, 3.95%, 3.95%, 0.16%, 0.00%, 0.99%, 24.34%, 0.00%, 0.00%, 0.00%, 2.14%, 6.09%, 6.25%, 0.16%, 0.66%, and 0.16%, respectively. In Yezhutang (Fig. 5Y), the corresponding positive interactions were 35.59%, 0.42%, 0.00%, 0.21%, 2.75%, 4.03%, 5.51%, 0.21%, 0.64%, 0.21%, 28.81%, 0.00%, 0.00%, 0.00%, 7.20%, 6.57%, 7.20%, 0.00%, 0.00%, and 0.64%, respectively.

By comparing intra-domain and inter-domain interactions, it was found that the three populations' distribution areas all exhibited stronger intra-domain interactions among bacteria, while stronger inter-domain interactions were observed between bacteria and fungi, bacteria and archaea, and bacteria and viruses (Fig. 5), indicating that intra-domain interactions among bacteria dominate in all three locations.

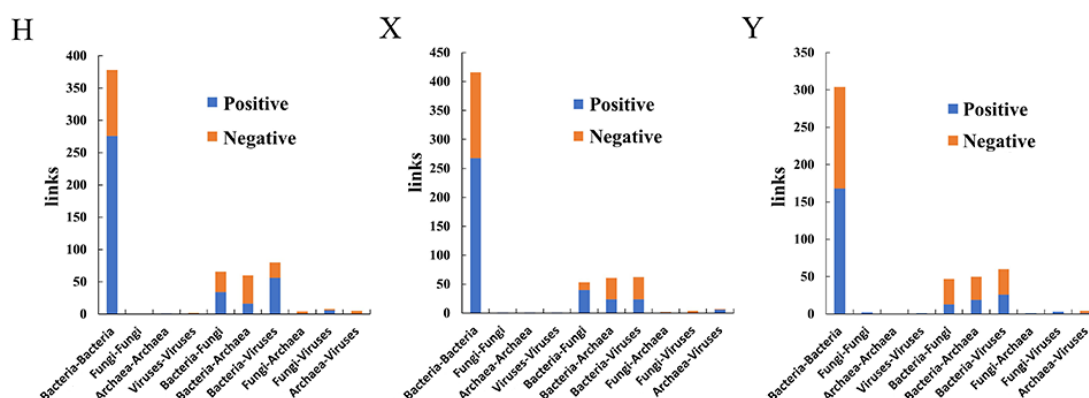


Figure 5. Interaction relationships in the molecular ecological network of microbial communities at the rhizosphere of *C. argyrophylla*

Pearson correlation analysis reveals (Table 5) that the phylum Crenarchaeota in Hongtan is significantly correlated with AK and MBN ($P < 0.05$); in Xietangwan, the phylum Cyanobacteria is significantly correlated with AN, TK, AK, and MBC ($P < 0.05$), and the phylum Acidobacteria is significantly correlated with TP, AP, TK, and MBC ($P < 0.05$); in Yezhutang, the phylum Microsporidia is significantly correlated with pH, SOC, TN, AN, TP, AP, AK, and MBC ($P < 0.05$), and Candidatus_Omnitrophica is significantly correlated with pH, TN, and AN ($P < 0.05$).

Discussion

The impact of the rhizosphere on the microbial community of the C. argyrophylla

Rhizosphere-associated microorganisms have a significant impact on plant growth and development, not only participating in soil nutrient cycling and organic matter decomposition but also enhancing plants' resistance to biotic and abiotic stresses (Li et al., 2022). This study found that the microbial community in the Rhizosphere zone of the *C. argyrophylla* is mainly composed of bacterial phyla, including *Pseudomonas* and

Actinobacteria, with the fungal phylum Ascomycota also occupying a relatively dominant position. Among them, the *Pseudomonas* and Actinobacteria phyla may play key roles in soil nutrient cycling, organic matter degradation, and promoting plant growth (Li et al., 2022; Ellen et al., 2015; Yadav et al., 2018), while the Ascomycota phylum, as the main fungal phylum, may be crucial in lignin degradation and symbiotic relationships (Wang et al., 2017). Xie et al. (2023) investigated the soil microbial communities at four distribution sites of *C. argyrophylla* in Hunan, China, and also found that the dominant phyla included Actinobacteria, Acidobacteria, and the fungal phylum Ascomycota, consistent with the results of this study. This phenomenon indicates that despite significant differences in environmental conditions across different regions, certain microbial communities, due to their unique adaptability and competitiveness, can dominate various environments. This stability may be closely related to the ecological niches, metabolic functions, and interactions of these dominant microbial communities with other organisms.

Table 5. The Pearson correlation between key nodes of the microbial interaction network at the rhizosphere of *C. argyrophylla* and soil physicochemical properties

Indexes	H	X		Y	
	Nitrososphaerota	Cyanobacteriota	Acidobacteriota	Microsporidia	Candidatus_Omnitrophica
SWC	0.144	0.191	0.12	0.051	0.251
pH	0.275	0.238	0.39	0.003	0.013
SOC	0.054	0.083	0.296	0.024	0.056
TN	0.5	0.053	0.253	0.007	0.006
AN	0.105	0.031	0.247	0.004	0.004
TP	0.36	0.117	0.043	0.003	0.066
AP	0.67	0.059	0.02	0.01	0
TK	0.195	0.004	0.001	0.109	0.096
AK	0.038	0.015	0.056	0.029	0.212
MBC	0.053	0.019	0.008	0.002	0.123
MBN	0.007	0.097	0.34	0.06	0.111

The key network nodes of different *C. argyrophylla* populations are all positively correlated with soil physicochemical properties; the numbers in the table indicate significance (*P*)

Additionally, the dominant genera of microbial communities in the rhizosphere of the *C. argyrophylla* are all bacterial genera, including genera such as *Bradyrhizobium*, *Streptomyces*, and *Pseudomonas*. These genera play significant roles in soil nitrogen fixation, antibiotic production, organic matter degradation, and inhibition of phytopathogenic bacteria (Li et al., 2022; Zhong et al., 2024; Zhang et al., 2025). However, Xie et al. (2023) found that the genus *Russula* was dominant, which is inconsistent with this study. This discrepancy may be due to the stronger competitive abilities of genera such as *Bradyrhizobium* and *Streptomyces* in Huaping, making them dominant. They form more effective symbiotic relationships with the *C. argyrophylla*, efficiently fixing nitrogen, and thus occupying a dominant position in the rhizosphere environment. The diversity of rhizosphere microbial communities also plays a crucial role in plant growth and adaptation to environmental changes (Ren et al., 2025). In this study, there were significant differences in alpha diversity of microbial communities among different sampling sites (Hongtan, Xietangwan, and Yezhutang). Xiong et al. (2020) studied Rhizosphere-rhizosphere soil samples from three different potato cultivation areas and found significant differences in alpha diversity of bacterial communities in the

rhizosphere of potatoes among different regions, consistent with the results of this study. This may reflect differences in environmental conditions, plant factors, human activities, microbial interactions, and random factors among different sampling sites, which have important impacts on plant growth, health, and adaptability.

Previous studies (Wang et al., 2025) have shown that soil pH and TK content are the dominant factors causing differences in the structure and function of Rhizosphere-associated soil microbial communities at three sampling points of the *C. argyrophylla*. This study reveals the composition and diversity characteristics of *C. argyrophylla* Rhizosphere-associated soil microbial communities and emphasizes the dominant role of bacterial phyla and genera in ecosystem functions, but does not further explore the association between environmental factors and diversity. Future research can investigate the specific functions of these dominant microbial groups and their interactions with environmental factors such as soil pH, nutrient content, and plant health status to more comprehensively understand the ecological functions of *C. argyrophylla* Rhizosphere-associated soil microbial communities and their roles in forest ecosystems.

The impact of the rhizosphere on the molecular ecological network of the C. argyrophylla microbiome.

Molecular ecological networks can effectively reflect the complexity and stability of microbial ecological networks. By constructing and analyzing molecular ecological networks, one can deeply understand the structure, function, and dynamic changes of microbial communities, providing new perspectives and methods for microbial ecology research (Deng et al., 2012). In molecular ecological networks, a higher average clustering coefficient indicates tighter connections between communities; a higher average connectivity suggests a more complex network structure; the number of nodes and connections reflects the size of the network; and a smaller average path distance indicates closer connections between species (Deng et al., 2012). This study found that the average clustering coefficient (avgCC), average connectivity (avgK), density (D), and total links of the network were $Y < H < X$, while centrality (CD) and average path distance (GD) were $X < H < Y$. These results indicate that the complexity of the microbial network in the Rhizosphere zone soil of the *C. argyrophylla* follows $Y < H < X$, with the network at location X having higher connection density and shorter path distances, which may reflect stronger functional redundancy and stability of the microbial community at this site (Zhou et al., 2010). In terms of network density, the microbial network at Yezhutang is the loosest (density of 0.385), with significantly fewer total links (472) compared to Hongtan (0.493) and Xietangwan (0.496). This difference may be related to different environmental conditions at various sites (such as soil nutrients, moisture, and vegetation cover), further affecting the composition and interaction patterns of microbial communities (Zhou et al., 2010). The higher network density in Hongtan and Xietangwan suggests that microbial communities at these two sites may have stronger functional synergy and ecological stability. The node with the highest degree, the node with the highest betweenness, the node with the highest stress centrality, and the node with the highest eigenvector centrality in Hongtan are all from the phylum Nitrososphaerota, a key phylum in archaea driving the ammonia oxidation process, with efficient energy capture and carbon fixation strategies, allowing them to dominate oligotrophic environments (Lehtovirta-Morley et al., 2024). The node with the highest degree in Xietangwan is from the phylum Cyanobacteriota, a core phylum in bacteria with oxygenic photosynthetic capabilities, which symbiotically associates with lichens, mosses, etc., providing carbon

and nitrogen nutrition (Almeida et al., 2023). The node with the highest betweenness in Yezhutang is from the *Candidatus_Omnitrophica*, a strictly anaerobic bacterium with the potential to degrade complex organic matter, playing important roles in the carbon and sulfur cycles but lacking complete pathways for synthesizing essential amino acids and coenzymes, depending on symbiosis or parasitism with other microorganisms (Kizina et al., 2022). Additionally, the nodes with the highest degree, highest stress centrality, and highest eigenvector centrality in Yezhutang are from the phylum Microsporidia, a highly specialized group of obligate intracellular parasites in fungi, which can cause microsporidiosis when parasitizing hosts (Ran et al., 2024).

The interactions among rhizosphere microorganisms play a crucial role in plant competition, maintaining biodiversity, and the Earth's ecosystem (Zhu et al., 2022). In this study, the interactions within the bacterial community mainly involved the Acidobacteriota and Chloroflexota phyla, while within the fungal community, the interactions were primarily concentrated on the Ascomycota and Basidiomycota phyla. Research by Huang et al. (2021) also indicated that the main interactions within the bacterial community were between the Acidobacteriota and Chloroflexota phyla, and within the fungal community, the interactions were mainly between the Ascomycota and Basidiomycota phyla. These results suggest that the Acidobacteriota and Chloroflexota phyla may play significant roles in soil organic matter degradation and nutrient cycling (Gonalves et al., 2024; Duan et al., 2024), while the Ascomycota and Basidiomycota phyla may dominate in lignin degradation and symbiotic relationships (Wang et al., 2017; Kohler et al., 2015). Additionally, inter-domain interaction analysis showed that the interactions between bacteria and fungi, bacteria and archaea, and bacteria and viruses were relatively strong, indicating that bacteria may act as core groups in microbial communities, forming complex interaction networks with other microbial groups such as fungi, archaea, and viruses. Shi et al. (2022) also found that the cross-domain interactions between bacteria and fungi were more frequent, and these cross-domain interactions may be of significant importance in the material cycling and energy flow of soil ecosystems. The interactions between bacteria and bacteria accounted for 45.70%, 44.08%, and 35.59% in Hongtan, Xietangwan, and Yezhutang, respectively, indicating that intra-domain interactions within the bacterial community were dominant at all three sites. In contrast, the proportions of interactions between bacteria and fungi, bacteria and archaea, and bacteria and viruses were relatively low but showed significant differences across different sites. For example, the proportion of interactions between bacteria and fungi in Hongtan (5.63%) was higher than that in Yezhutang (2.75%), while the proportion of interactions between bacteria and viruses in Yezhutang (5.51%) was significantly higher than in Hongtan (9.27%) and Xietangwan (3.95%). These differences may reflect functional differentiation and environmental adaptation of microbial communities at different sites.

Huang et al. (2017) studied the nutrient content and microbial quantity of *Camellia oleifera* rhizosphere and non-rhizosphere soil across different seasons, finding that the nutrient content and microbial quantity of rhizosphere and non-rhizosphere soils showed a consistent seasonal trend, generally as follows: summer > autumn > spring > winter. During summer and autumn, the nutrient content and microbial quantity of *Camellia oleifera* rhizosphere soil exhibited a significant 'rhizosphere enrichment'. Yu et al. (2025) et al., found that the rhizosphere soil microbial community is also significantly influenced by interannual dynamics, indicating that the temporal dynamic changes in microbial activity have a significant impact on plant growth, soil nutrient cycling, and the plant's

ability to acquire nutrients. Therefore, whether the winter variation characteristics of the three *Taxus* populations are consistent with those in summer, and whether the bulk soil microbial community variation characteristics are consistent with those of the rhizosphere soil, still require further research. Additionally, although this study revealed the complex interaction patterns and network topological features of the *Taxus* rhizosphere soil microbial community through microbial ecological network analysis, it was limited to the phylum classification level. Future research can further combine the classification levels of genus or species and functional gene analysis, as well as environmental factor data, to explore the specific ecological functions of these microbial interaction networks and their impact on soil ecosystem stability. Moreover, research on key nodes can provide theoretical basis for the regulation and ecological restoration of soil microbial communities.

Conclusion

The rhizosphere microbiome of the endangered plant *C. argyrophylla* is primarily composed of bacteria, with 16 bacterial phyla, 3 archaeal phyla, and 1 fungal phylum being dominant. At the genus level, bacteria are entirely dominant, highlighting their crucial role in rhizosphere ecological functions. The alpha diversity indices (observed species, Shannon, Simpson) of Hongtan, Xietangwan, and Yezhutang show significant differences, indicating that geographical microenvironments have a significant impact on microbial community structure. Xietangwan has the highest network complexity (with more edges and higher density), while Yezhutang has the loosest network, suggesting that high-complexity networks may enhance ecological functional stability. Interactions within the bacterial domain are significantly stronger than those between other groups, while cross-domain interactions mainly involve associations between bacteria and fungi, archaea, and viruses, indicating that bacteria play a pivotal role in rhizosphere material cycling and signal transmission. This study provides a theoretical basis for elucidating the rhizosphere microecological mechanisms of the endangered plant *C. argyrophylla* and the conservation of soil microbial resources.

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