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Original Research

Structural Composition and Diversity of Bacterial Communities in High- and Low-Yielding Moso Bamboo Forests

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Abstract

Background: Bacterial communities play an important role in helping plants absorb nutrients, promoting plant development, and preventing diseases. Moso bamboo (*Phyllostachys edulis* [Carriere] J. Houzeau) has a long history of cultivation and important economic value. **Methods**: In this study, high-throughput sequencing technology was utilized to analyze the differences in the diversity of endophytic and root zone soil bacterial communities between high-yielding (HY) and low-yielding (LY) *P. edulis* forests in subtropical China. **Results**: Notably, the soil conditions and bacterial communities in Yong'an (YA) and Jiangle (JL) differed, but the bacterial community structures in the root zone soil of both regions were similar with the dominant bacterial phyla composed of Proteobacteria, Acidobacteriota, and Actinobacteriota. The Chao1 and Shannon indices of the root zone soil and endophytic bacterial communities in the LY were higher than those in the HY. Moreover, the bacterial community structures of HY and LY were significantly different. Notably, the relative abundances of Actinobacteriota, Myxococcota, and Cyanobacteria were higher in the HY soil samples. The bacterial community differences between the tissues and root zone soil of HY and LY indicated that healthy HY *P. edulis* plants were enriched with specific bacterial communities, suggesting associations between yield and both endophytic and root zone soil bacterial communities. **Conclusions**: The findings of this study provide a basis to regulate artificial bacterial communities to benefit the future cultivation of HY *P. edulis*.

Keywords: endophytes; root zone soil; high-throughput sequencing; plant growth; symbiosis

1. Introduction

Moso bamboo (*Phyllostachys edulis* [Carriere] J. Houzeau) is an important non-timber forest species that is widely distributed in tropical and subtropical regions of the world, including the Asia-Pacific region, the Americas, and Africa [1]. *P. edulis* has a long history of cultivation [2]. In China, *P. edulis* covers approximately 6 million ha, accounting for 70% of the total area of bamboo in China [3]. *P. edulis* has important economic, cultural, and ecological value; it provides edible bamboo shoots, bamboo wood, ornamental, and value as a sustainable and renewable resource [4,5].

Plant growth is affected by various factors, including environmental conditions [6,7] and microorganisms [8,9]. An increase in plant yield is often attributed to increased nutrient uptake from the soil during growth. Soil microorganisms participate in various biochemical processes and are the primary decomposers of organic matter, which enables the nutrients to be easily absorbed by plants, thus, enhancing plant growth. Soil microbes adjust the soil pH and create favorable conditions for the functional microbes to fully play their roles and promote plant growth [10]. *Sphingomonas* sp. Cra20 enhances water uptake and water use efficiency by improving root development, thereby promoting plant growth under drought conditions [11].

In long-term production, we found that the high-yielding (HY) *P. edulis* forest has fewer diseases and insect pests, high economic benefits, and good quality bamboo and can be used for both deep processing and enhancing the benefits to farmers. In the past, farmers have always thought that the difference between HY and low-yielding (LY) sites could be the result of different levels of nutrients in the soil, but the constant application of chemical fertilizers to the soil did not improve the soil nutrient status but instead caused adverse consequences, such as soil compaction. In a previous study, we noticed that the soil of a *P. edulis* forest with a stable yield had well-balanced and not very abundant microbial communities [8], and a previous study postulated that the spatial and temporal variation in the soil microbial communities affects the availability of soil nitrogen, thereby affecting plant growth and reproduction [12,13]. Thus, the yield of *P. edulis* can be affected by changes in the soil microbial communities. However, the physiological, genetic, and environmental mechanisms that affect the yield of *P. edulis* remain unclear. In this study, we collected plant tissue and soil samples from HY and LY *P. edulis* forests and analyzed the composition and

Table 1. Indicators of high-yielding (HY) and low-yielding (LY) forests of *Phyllostachys edulis*.

	Yield Indicators		Structural Factor Indicator		
	Wood (t/hm^2)	Shoots (t/hm^2)	Standing density (plant/hm^2)	Operating density (plant/hm^2)	Mean diameter at breast height (cm)
HY forest	12	3.5	≥3000	≥2250	≥9
LY forest	4.5	1	≤1800	≤1650	≤8

Table 2. Sample categories and codes.

Sampling point	Category	Sample	Code	Sampling point	Category	Sample	Code
Yong'an	high-yield forests	rhizomes	YAF-A	Jiangle	high-yield forests	rhizomes	JLF-A
		root	YAF-B			root	JLF-B
		stem	YAF-C			stem	JLF-C
		leaves	YAF-D			leaves	JLF-D
		root zone soil	YAF-E			root zone soil	JLF-E
		bulk soil	YAF-F			bulk soil	JLF-F
	low-yield forests	rhizomes	YAD-A		low-yield forests	rhizomes	JLD-A
		root	YAD-B			root	JLD-B
		stem	YAD-C			stem	JLD-C
		leaves	YAD-D			leaves	JLD-D
		root zone soil	YAD-E			root zone soil	JLD-E
		bulk soil	YAD-F			bulk soil	JLD-F

diversity of their microbial community structure using high-throughput sequencing technology. This study aimed to elucidate the relationship between soil microbes and endophytic microbes and the yield of *P. edulis* and provide empirical guidance to alleviate the problems associated with the production of *P. edulis* in LY.

2. Materials and Methods

2.1 Location of the Sampling Sites

Two sampling sites located in Sanming City, Fujian Province, China, were selected for sample collection. One was located in the bamboo forest base of Sanshe Village, Xiyang Town, Yong'an (YA) City (25.94°N, 117.36°E), and the other was located in the bamboo forest base of Wu Village, Jiangle (JL) County (26.73°N, 117.47°E). Table 1 outlines the indicators of the HY and LY *P. edulis* forests.

2.2 P. edulis Tissue and Soil Sample Collection

The bamboo rhizome, rhizome root, stem, leaf, root zone soil, and bulk soil of *P. edulis* were randomly collected from the HY and LY forest plots in April 2021 with a similar slope (5–10%) and orientation (south or southeast slope). Random sampling was conducted at intervals of 100 m in the high- and LY bamboo forests that covered approximately 5 ha. The bamboo rhizome was selected from the belowground part that contained the buds and was located 50 cm from the root of *P. edulis* plants. The materials from the rhizome roots that were sampled were the roots on the rhizome. The leaves were randomly collected, while the stem was collected from the stem section at approximately 130–150 cm from the ground. Soil samples from within 1 cm and approximately 30 cm from the root system were selected as the root zone soil and bulk soil samples, respectively. Each group of samples was replicated three times. The samples were placed in sterile sample bags within 24 h after collection and stored at –20 ℃.

2.3 Total DNA Extraction

A total of 24 samples were collected, and there were three random replicates of each sample (Table 2). Total DNA was extracted from the plant and soil samples using DP305 and DP336 Kit (TianGen, Beijing, China) following the manufacturer's instructions [12]. DNA quality and quantity checks were conducted by 1% agarose gel electrophoresis [14]. DNA samples that passed the quality testing were stored at –20 ℃.

2.4 16S rDNA High-Throughput Sequencing

The 16S rDNA (V5–V7 region) from 72 samples of bamboo tissue and soil from the HY and LY forests in JL and YA was subjected to high-throughput sequencing. Primers were designed according to the conserved regions and were followed by the addition of sequencing adapters to the ends of the primers [12,15]. Polymerase chain reaction (PCR) amplification was performed, and the products were purified, quantified, and homogenized to construct a sequence library. The library was first checked for quality [12,15]. Libraries that passed the quality control were sequenced using the Illumina NovaSeq 6000 platform (Illumina, San Diego, CA, USA). Libraries of small fragments were constructed using the paired-end sequencing mode (Beijing Novogene Co., Ltd., Beijing, China) [12]. Amplicon sequence variants (ASVs) were clustered by splicing and filtering reads.

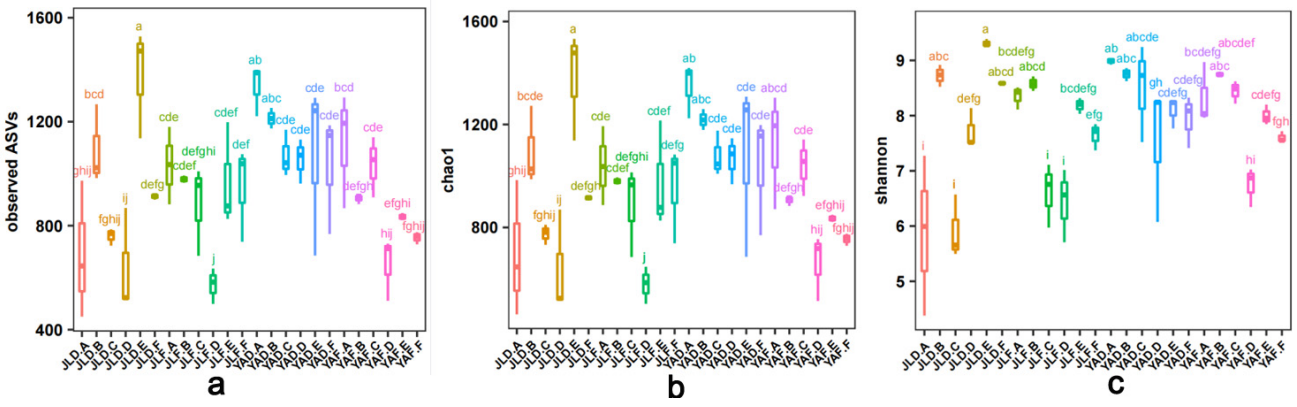

Fig. 1. α-diversity estimates of the bacterial communities. (a) Number of observed amplicon sequence variants (ASVs). (b) Chao1 indices. (c) Shannon diversity indices. The α-diversity estimates are based on three biological replicates for the bamboo rhizome, rhizome root, stems, leaves, root zone soil, and bulk soil of high-yielding (HY) and low-yielding (LY) bamboo forests in Yong'an (YA) and Jiangle (JL), which were calculated in mothur with 10,000 iterations.

2.5 Sequence Processing and Analysis

Raw sequences were assembled and analyzed using FLASH software (v 1.2.7, Beijing Institute of Genomics, Beijing, China). The data were subsequently filtered using FASTP (v 0.19.6, Beijing Institute of Genomics, Beijing, China) and USEARCH tools (v 10.0, Edgar,R.C., USA) to obtain high-quality sequences [16]. QIIME2 software (v 2022.2, Gregory Caporaso, Northern Arizona University, Flagstaff, AZ, USA) was then utilized to denoise the high-quality sequences and filter out sequences with an abundance <5 to obtain the final ASVs and feature table using the DADA2 (v 1.8, GitHub Inc., Stanford University, Stanford, CA, USA) or deblur module. The classify-sklearn module in QIIME2 was used to compare the ASVs obtained against the database to extract the species information for each ASV. A pre-trained Naive Bayes classifier was utilized to annotate the species for each ASV. The QIIME2 plugin was then used to visualize the composition of species. The α-diversity was then calculated; dilution curves were drawn, and the UniFrac distance was estimated using QIIME2. The UniFrac distance was used to study the β-diversity of the bacterial community structure. An ADONIS analysis was performed using the built-in adonis function in QIIME2. A principal coordinate analysis graph was drawn using the R statistical computing environment (v 3.3.1, R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria) to visualize the bacterial community structure in more detail. *t*-tests were performed in R to analyze the significant differences between the species at each taxonomic level and to identify species with significant differences in the composition of the bacterial communities between different tissues and soils of *P. edulis* at the phylum level.

3. Results

3.1. Analysis of the α-Diversity of Sample Sequencing Results

A total of 5,723,699 high-quality sequences were obtained, with an average of 61,586–90,452 valid sequences among all the samples. The sample coverage rate of each group was >98%, indicating that the sequencing accuracy was reliable. Notably, the diversity of root zone soil bacterial communities and root endophytic bacterial communities of *P. edulis* in the LY samples was greater than that in the HY samples ($p < 0.05$). The peak values of the root zone bacterial communities of LY samples ranged from 1100 to 1500 ASVs, while those of the HY samples reached a maximum of 820 ASVs. There were 950–1250 ASVs in the peak range of endophytic bacterial communities in the roots of LY, while those of the HY samples reached as high as 900 ASVs. A statistical analysis of the α-diversity did not indicate any difference in the richness of ASVs (Fig. 1a). The Chao1 and Shannon indices revealed significant differences between the LY and HY communities (Fig. 1b,c).

3.2 Principal Coordinate Analysis (PCA) of the Sequencing Results

A principal coordinate analysis (PCA) was performed on the sequencing results of the 72 samples based on the weighted and unweighted UniFrac distances. The community structures of root zone soil bacteria and endophytes of the HY and LY samples were also compared to determine the primary influencing factors. The bacterial communities of different samples (soil, rhizomes, roots, stems, and leaves) showed significant clustering and the community compositions of the samples were significantly different. The PCA results based on weighted UniFrac distances showed that the root zone soil, bulk soil, and rhizome root samples of the HY and LY forests in the two regions clus-

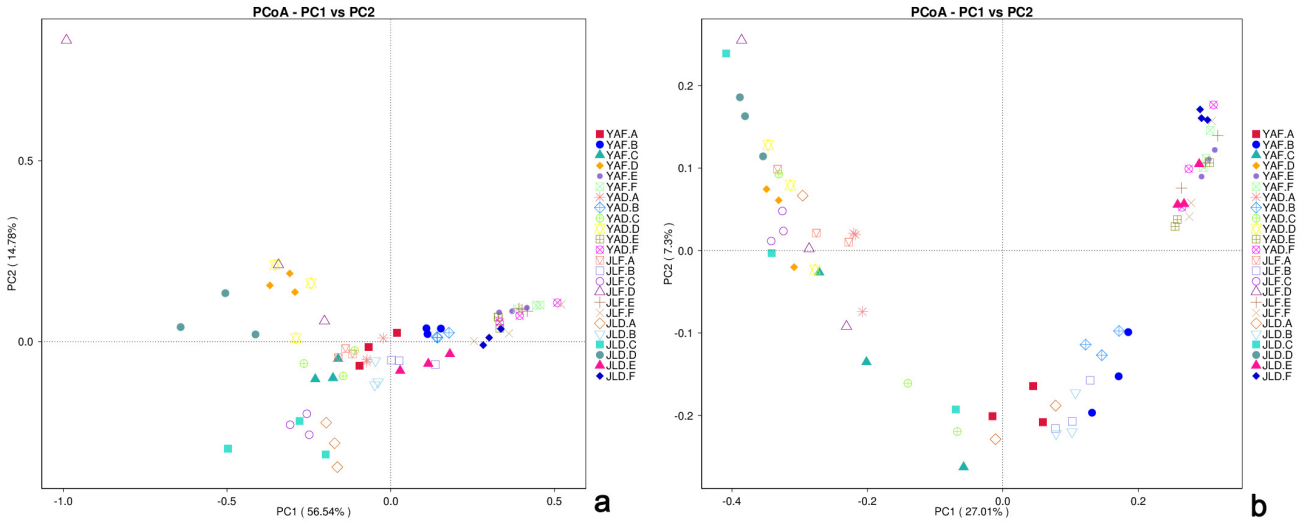

Fig. 2. Principal coordinate analysis based on weighted and unweighted UniFrac distances. (a) β-diversity based on the weighted UniFrac distance difference visualized by a principal coordinate analysis (PCA). (b) β-diversity based on the unweighted UniFrac distance difference visualized by a PCA.

tered together but were separate from the stem, rhizome, and leaf samples (Fig. 2a). The results of an Adonis analysis indicated that there were significant differences between the two groups ($R^2 = 0.824, p < 0.001$). The principal components principal component I (PC1) and principal component II (PC2) in the PCA based on the unweighted UniFrac distances represented 27.01% and 7.3% overlap, respectively (Fig. 2b). The bamboo root zone soil samples and the bulk soil samples in the HY forests in the two study sites had a close distance. The distances between the HY forest whip root samples and the bamboo whip samples in the two places were similar. A similar trend was also observed in the bamboo whip roots and bamboo whip samples from the LY forests in both study sites. These findings indicated that there were similar compositions in the bacterial community between the HY forest samples and the LY forest samples in both study sites. The stem and leaf samples from the HY and LY forests in JL and YA were relatively discrete from those of the root zone and bulk soil samples. Similarly, the Adonis analysis showed significant differences between these samples ($R^2 = 0.597, p < 0.001$).

3.3 Analysis of the Relative Abundance of Bacterial Taxa

3.3.1 The Relative Abundance of Bacterial Taxa at the Phylum Level

The relative abundance of bacterial taxa at the phylum level was compared to investigate the specific variation in the bacterial taxa among the endophytic and root zone soil between the HY and LY forests in more detail. Annotation of the species revealed that Proteobacteria, Acidobacteriota, and Actinobacteriota were the dominant phyla (Fig. 3).

In YA, the relative abundance of Proteobacteria in the HY forest was higher than that of the LY forest, while the relative abundance of Firmicutes was lower. Moreover, the relative abundances of Proteobacteria, Bacteroidota, Actinobacteriota, Cyanobacteria, Bdellovibrionota, and Myxococcota were higher, while the relative abundance of Verrucomicrobiota was lower. Similarly, a comparison of the bacterial taxa of bamboo stems in LY revealed higher relative abundances of Proteobacteria, Actinobacteriota, Verrucomicrobiota, and Bdellovibrionota in the HY forest and lower relative abundances of Acidobacteriota and Firmicutes. The relative abundances of Verrucomicrobiota, Cyanobacteria, Bdellovibrionota, and Myxococcota in the HY forest were higher than those in the LY forest. However, the relative abundance of Firmicutes was lower in the bamboo leaf samples. The relative abundances of Actinobacteriota, Verrucomicrobiota, and Myxococcota in the HY forest were higher than those in the LY forest. In contrast, the relative abundances of Bacteroidota and Cyanobacteria were lower in the root zone soil samples. The relative abundances of Proteobacteria, Bacteroidota, and Myxococcota were higher in the HY forest than in the LY forest. However, the relative abundances of Firmicutes and Cyanobacteria were lower in the bulk soil samples. Moreover, the relative abundances of Chloroflexi and Firmicutes in the HY forest were lower than those in the LY forest in the bamboo tissue and soil samples. Within YA, the relative abundance of Bacteroidota in the rhizome roots samples and the root zone soil samples in the HY forest was significantly lower than that in the LY forest.

The relative abundance of Chloroflexi in the YH forest was significantly higher than that in the LY forest in JL, while the relative abundance of Proteobacteria was lower than that in the LY root zone soil. The Acidobacteriota were more abundant in the HY forest, while Bacteroidota and Cyanobacteria had a lower relative abundance in the rhizome roots. Similarly, Acidobacteriota was

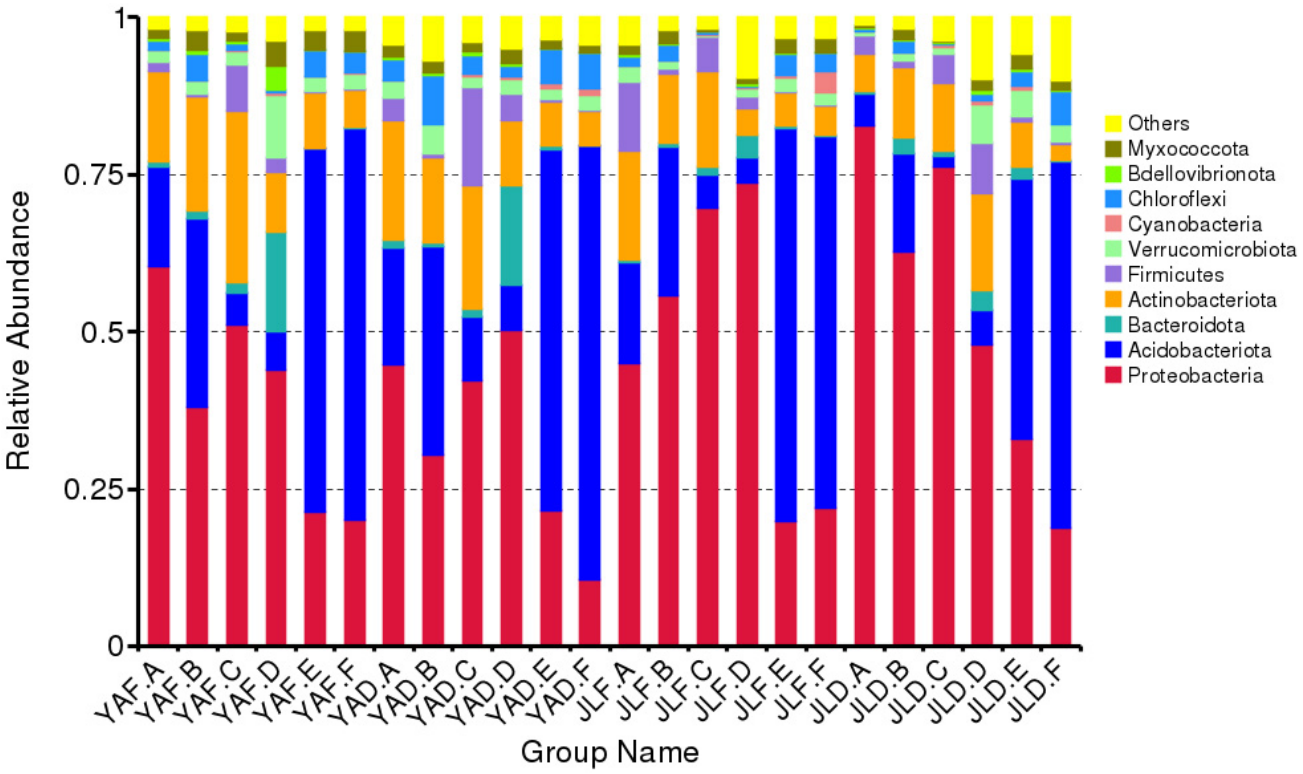

Fig. 3. Dominant bacterial phyla detected in the bamboo rhizome, rhizome root, stems, leaves, root zone soil, and bulk soil samples.

the most abundant bacterial phylum, while Verrucomicrobiota and Cyanobacteria were the least abundant in bamboo stems in the HY forest compared with the LY forest in JL. The Proteobacteria in the HY-JL forest were more abundant, while Actinobacteriota, Firmicutes, Verrucomicrobiota, and Chloroflexi were significantly less abundant than those in the LY bamboo leaves. The relative abundances of Bacteroidota and Bdellovibrionota in the root zone in the HY forest were lower than those in the LY forest. In the bulk soil samples, the relative abundances of Actinobacteriota and Myxococcota were higher than those in the HY-JL forest. Acidobacteriota in the various tissues and soil samples was more abundant in the HY-JL forest than in the LY-JL forest, while the Cyanobacteria were less abundant in tissue samples from the HY-JL forest.

3.3.2 A Phylogenetic Analysis of the Bacterial Taxa

Representative sequences of the top 100 genera obtained were used to determine the phylogenetic relationships of taxa at the genus level. The sequences were first subjected to multiple sequence alignment, and the trees were reconstructed to visualize their evolutionary relationships.

Fig. 4 shows the results of the phylogenetic analysis of changes in the bacterial taxa in the JL samples. *Candidatus* Uzinura, *Ralstonia*, *Cupriavidus*, *Arthrobacter*, and *Chujaibacter* were relatively more abundant, while *Streptococcus*, *Weissella*, and *Xanthomonas* were less abundant in the rhizomes of the HY forest than in the LY forest. Similarly, *Methylocella*, *Bryocella*, and *Chujaibacter* were significantly relatively more abundant, while *Weissella* and *Candidatus* Udaeobacter were less abundant in the rhizome roots of HY forest than in the LY forest. *Candidatus* Uzinura, *Arthrobacter*, *Pseudarthrobacter*, and *Chujaibacter* were relatively more abundant in the stems of the HY forest, while *Candidatus* Xiphinematobacter was much less abundant. *Weissella*, *Nitrospira*, and *Leuconostoc* were relatively less abundant in bamboo leaves in the HY forest. *Pseudomonas*, *Methylobacterium-Methylorubrum*, and chloroplasts were relatively less abundant in the root zone and bulk soil samples in HY.

Notably, *Chujaibacter* was relatively more abundant in all the JL samples except for bamboo leaves. *Pseudomonas* was relatively more abundant in the plant tissue samples and less abundant in the soil samples. Subgroup_2 was less abundant in the plant tissue samples, which differed slightly from the soil samples. In addition, *Ralstonia* was relatively more abundant in the bamboo rhizome, root, and root zone soil of *P. edulis* in the HY forest, while *Streptococcus* and *Methylobacterium-Methylorubrum* were relatively abundant in all the samples.

Fig. 4 shows the bacterial taxa analysis of the YA samples. *Gryllotalpicola*, *Xanthomonas*, and *Weissella* were relatively highly abundant in the bamboo rhizome in HY. *Methylocella* and *Bryocella* were relatively more abundant in the HY samples, while mle1-7 was less abundant in the

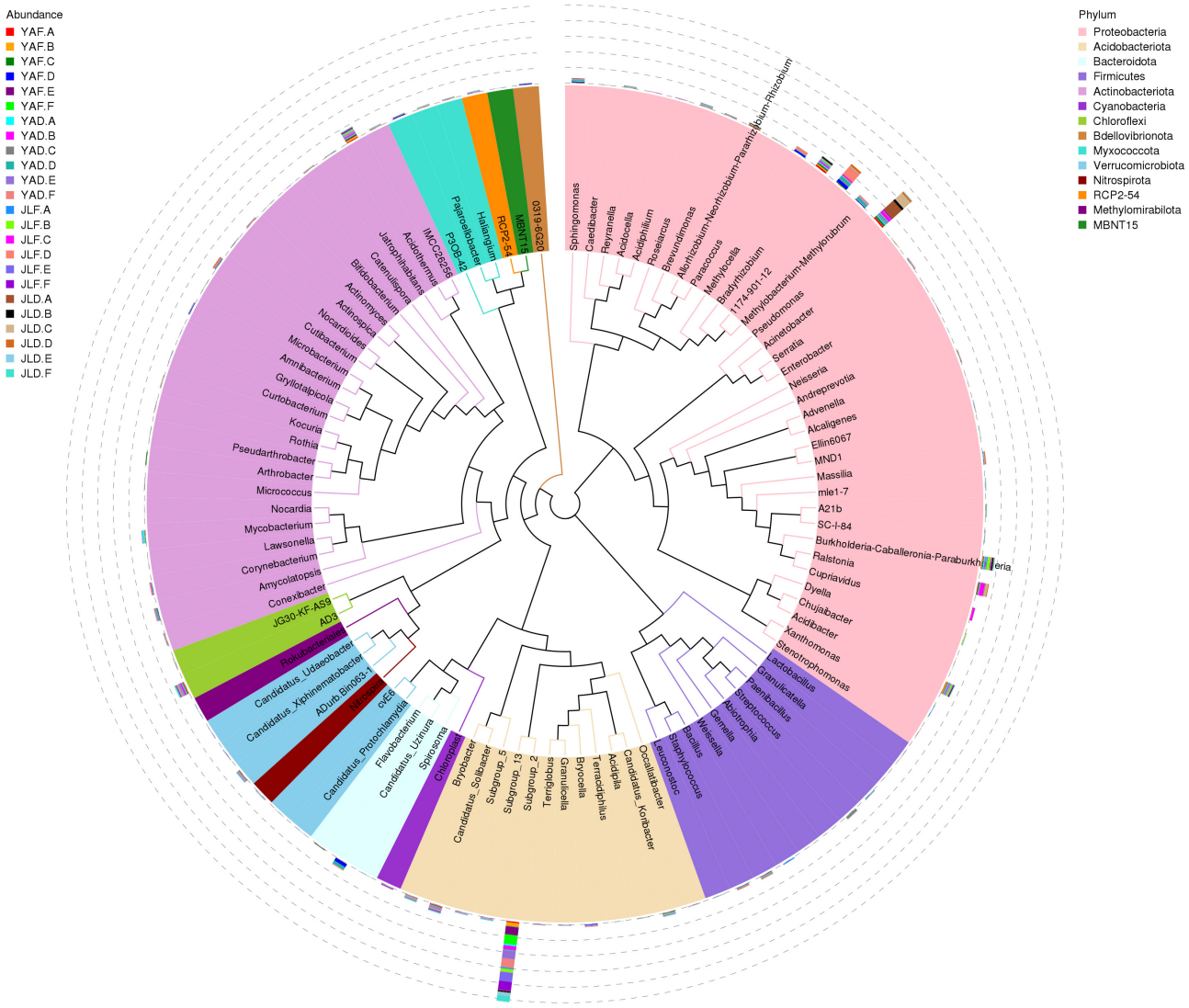

Fig. 4. Phylum-level clustering diagram of the relative abundance of the top 100 genera. Taxonomic dendrogram showing the core bacterial microbiome of each plant tissue. The color ranges identify genera within the tree.

rhizome root. *Candidatus* Uzinura and *Cupriavidus* were significantly relatively more abundant in the bamboo stem in the HY forest than in the bamboo stem in the LY forest. *Weissella* and *Candidatus* Xiphinematobacter were significantly more abundant in bamboo leaves in the HY forest than in the LY forest, while Subgroup_13 and *Actinomyces* were significantly less abundant than those in the LY forest. In the root zone bacterial communities, *Streptococcus* in the HY forest was relatively more abundant, while *Pseudomonas* was less abundant than that in the LY forest. In the bulk soil samples, *Pseudomonas* in the HY forest was significantly more abundant than in the LY forest. Notably, *Pseudomonas* was relatively less abundant in the HY forest in all the samples except the bulk soil samples, while *Methylocella* and *Burkholderia-Caballeronia-Paraburkholderia* were relatively more abundant in the plant tissues of the HY forest.

A comparison of the bacterial taxa in JL and YA revealed that *Pseudomonas* was relatively more abundant in the HY-YA forest, which contrasted with the situation in JL. *Candidatus* Uzinura was significantly more abundant in the HY-YA forest than in the LY-YA forest, but it only occurred in plant tissues. *Streptococcus* and *Burkholderia-Caballeronia-Paraburkholderia* were relatively less abundant in the HY-YA forest. However, JL exhibited the opposite pattern.

3.4 β-Diversity Analysis

The abundance of Actinobacteriota increased ($p < 0.05$) in the root zone soil of HY forest compared with the corresponding abundances in the bulk soil of YA, while it decreased in NB1-j ($p < 0.05$) (Fig. 5a). The abundances of Proteobacteria, Bacteroidota, and Bdellovibrionota increased, while that of Nitrospiota decreased ($p < 0.05$) (Fig. 5b). Notably, the abundances of Patescilbacte-

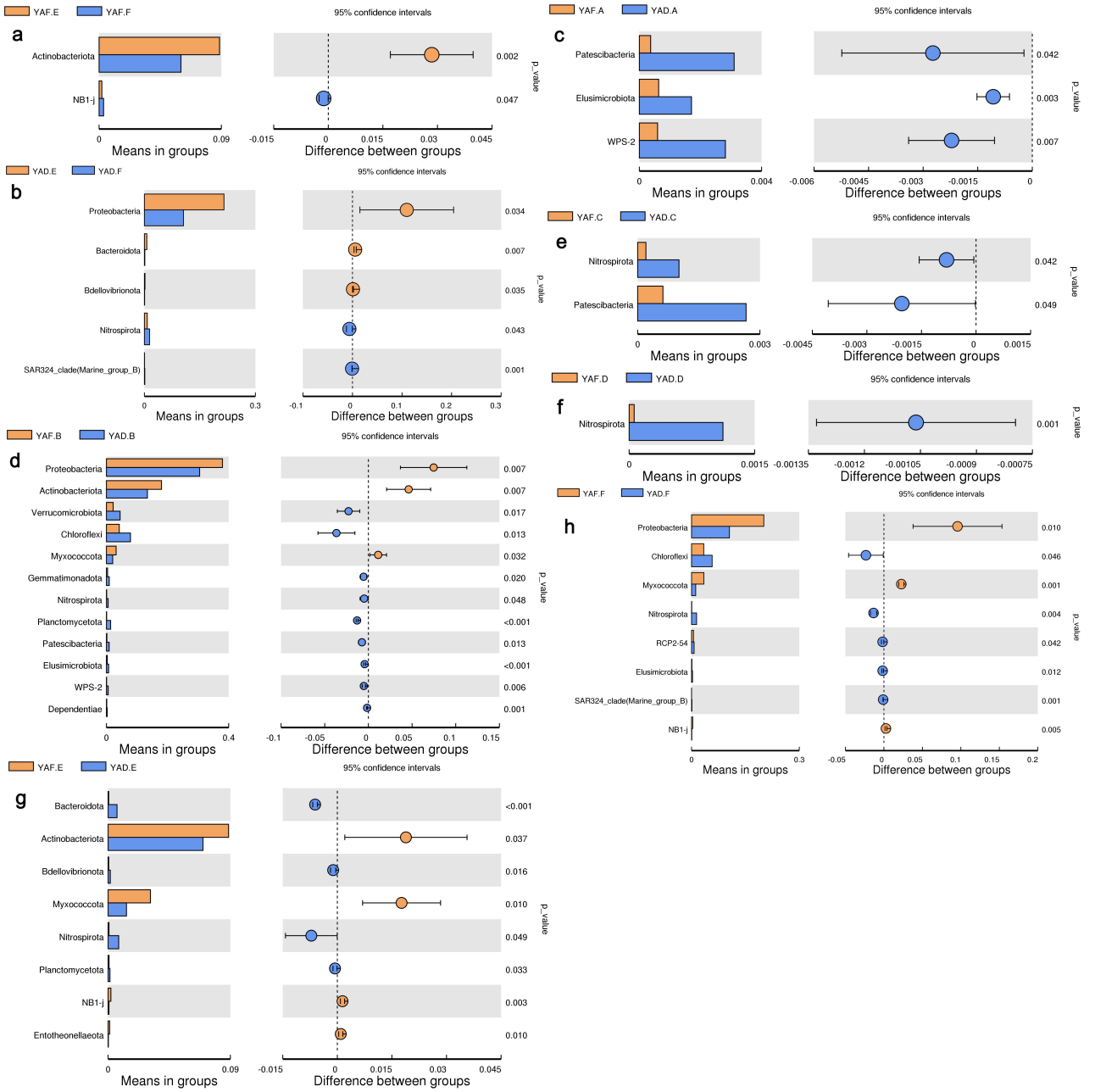

Fig. 5. Comparison of the abundances between Yong'an (YA) bamboo forest sample groups. The left side of each figure shows the differences in species abundance between groups. Each bar graph represents the mean value of species with significant differences in abundance between and within groups. The right side displays the confidence of the difference between groups. The left end of each circle in the figure represents the lower limit of the 95% confidence interval of the mean difference, while the right end represents the upper limit of the 95% confidence interval of the mean difference. The center of the circle represents the mean difference, and the color of the circle represents the *p*-value of the significant differences between the groups that correspond to the different species. (a–h) Samples from YA, including the root zone soil and bulk soil of the high-yielding YA (HY-YA) forest, root zone soil and bulk soil of the low-yielding YA (LY-YA) forest, bamboo rhizome of the HY-YA and LY-YA forests, roots of the HY-YA and LY-YA forests, bamboo stem of the HY-YA and LY-YA forests, bamboo leaves of the HY-YA and LY-YA forests, root zone soil of the HY-YA and LY-YA forests, and soil of the HY-YA and LY-YA forests.

ria, Elusimicrobiota, WPS-2, Nitrospirota, Patescilbacteria, and Chloroflexi were lower in the HY forest than those in the LY forest among different samples of *P. edulis* ($p < 0.05$) (Fig. 5c–h). The abundances of Proteobacteria, Actinobacteriota, and Myxococcota in the LY forest were higher than those in the HY forest ($p < 0.05$) (Fig. 5c–h).

In JL, there was a decrease in the abundance of Planctomycetota in the root zone soil of *P. edulis* ($p < 0.05$)

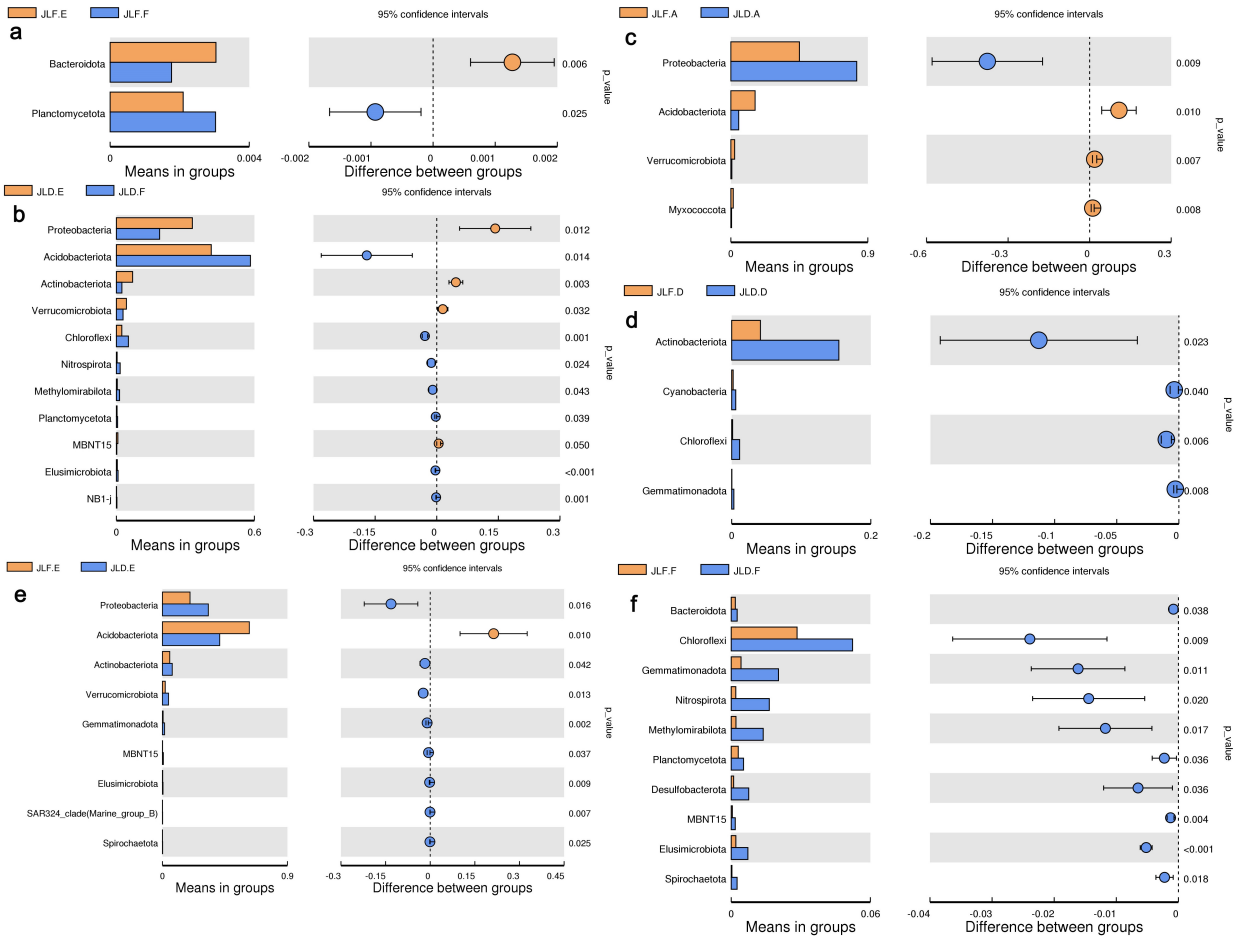

Fig. 6. Comparison of abundances between the Jiangle (JL) bamboo forest sample groups. The left side of each figure shows the differences in species abundance between groups. Each bar graph represents the mean value of species with significant differences in abundance between and within groups. The right side displays the confidence of difference between groups. The left end of each circle in the figure represents the lower limit of the 95% confidence interval of the mean difference, while the right end represents the upper limit of the 95% confidence interval of the mean difference. The center of the circle represents the mean difference, and the color of the circle represents the *p*-value of the significant differences between the groups that correspond to the different species. (a–f) Samples from JL, including the root zone soil and bulk soil of the high-yielding JL (HY-JL) forest, root zone soil and bulk soil of the low-yielding JL (LY-JL) forest, bamboo rhizome of the HY-JL and LY-JL forests, bamboo leaves of the HY-JL and LY-JL forests, root zone soil of the HY-JL and LY-JL forests, and soil of the HY-JL and LY-JL forests.

compared with the corresponding abundances in the bulk soil (Fig. 6a,b). Notably, there were no differences in the root endophytic and stem bacterial communities between the HY-JL and LY-JL forests at the phylum level. However, there were significant differences in the endophytic bacterial communities between the HY and LY forests in the rhizomes, leaves, and root zone soil ($p < 0.05$) (Fig. 6c–e). The bacterial community abundance in the soil samples of *P. edulis* in the LY forest was generally higher than that in the HY forest (Fig. 6f).

4. Discussion

The LY forests of Moso bamboo impose economic losses and damage the ecological environment. Microorganisms directly or indirectly impact plant physiology through mechanisms such as symbiosis, co-habitation, mutualism, and pathogenicity [17]. In this study, the HY and LY *P. edulis* forests in YA and JL (Sanming, Fujian, China) were selected to evaluate the regularity and abundance of the endophytic and root zone soil bacterial community structures between the HY and LY forests.

4.1 Common Characteristics of the Bacterial Communities of the P. edulis Forests in Both Study Sites

The bacterial community structures, particularly the root zone soil bacterial community structures of the HY bamboo, were highly similar at both study sites based on various measures. (1) There were no differences in the root zone soil samples between the HY and LY forests based on the Shannon indices. (2) The PCA indicated that the

root zone soil samples of the HY forests at both study sites shared more similarities than the other samples. (3) The dominant bacteria in the root zone soil of *P. edulis* in the HY forests in the two regions were very similar. The three dominant bacterial phyla were Proteobacteria, Acidobacteriota, and Actinobacteriota, and they accounted for 89.3% of the total bacterial community. (4) The relative abundance of Subgroup_2 in the root zone soil of the HY forests was high at both study sites and shared similar proportions. (5) The relative abundances of Actinobacteriota and Chloroflexi in the root zone and bulk soil samples of the HY forest were higher than those of the tissue samples, while those of Proteobacteria, Firmicutes, Actinobacteriota, and Bacteroidota were lower at both study sites.

The bacterial community structures of the LY forests at both sites also exhibited unique characteristics. (1) The root zone soil and root endophytic bacterial communities of the LY forests were higher than those in the HY forests (Fig. 1). (2) The principal coordinate analysis revealed that the soil samples in the root zone soil of *P. edulis* in the HY and LY forests were highly variable and irregular. (3) In YA, the proportions of Chloroflexi and Firmicutes in the tissue samples of the LY forest were significantly higher than those in the HY forest, but no such characteristics were observed in JL. The proportions of Acidobacteriota in the tissue samples from the LY-JL forest were significantly lower than those of the HY-JL forest. All the highlighted characteristics suggest that there were significant differences in the endophytic bacterial communities between the LY and HY forests.

4.2 Effects of the Bacterial Communities on Soil and P. edulis Plants

This study found that the diversity of the root zone soil bacterial community was higher than that of the bulk soil (Fig. 1). The abundance of rhizobacteria of *P. edulis* is primarily mediated by plant exudates [17–19]. The benefits of the diversity of bacterial communities in the root zone are as follows: the root zone soil bacterial community promotes plant growth and resists adverse environmental conditions by participating in various physiological processes, such as soil nutrient cycling and organic decomposition [20]. Thus, the interaction between plant roots and rhizosphere microorganisms can potentially affect ecosystem functions through material cycling [21]. The interaction of various microbes contributes to the flow of nutrients to the companion species [22]. However, the continuous increase in bacterial abundance in the soil environment depletes the performance of plants that would enable survival [22,23]. For example, the Chao1 and Shannon indices of the soil samples of *P. edulis* in the LY forest were higher, indicating a high diversity of soil microbial species, which may not contribute to high yields. The root exudates of HY might mediate the interaction between microorganisms, producing positive feedback and causing similar root zone soil bacterial community structures of the HY forests at both study sites. Such positive feedback can explain the reduction in bacterial species diversity in the root zone soil of the HY forests compared with that of the LY forests [24].

The endophytic bacterial community structure has more variation than the rhizosphere bacterial community. This phenomenon can be attributed to the microenvironment or niche (roots, stems, and leaves) within the plant that provides relevant biotic and abiotic gradients. For example, the availability of soluble organic compounds can lead to niche differentiation, which causes the bacterial communities of the stems and leaves to be significantly different from those of the roots and soil [25]. In this study, a PCA revealed that the endophytic bacterial community was relatively scattered and varied significantly. The key factors that shaped this variation were the nature of endogenous colonization and competence, including bacterial motility and the ability to produce cell wall degrading enzymes, among other factors [26,27]. The variation may also be caused by the interaction with the innate immune system of the host plants [28] and fluctuations in abiotic conditions, such as temperature, humidity, and access to nutrients, which are all distinct from fluctuations in the rhizospheric buffer [29]. The differences in the endophytic bacterial communities in different tissues of *P. edulis* were caused by the plant responses to biotic stress, abiotic stress, different nutrient conditions, and plant immune responses. Therefore, the interaction of the bacterial communities causes variation in the yield of *P. edulis*.

4.3 The Relationship between Bacterial Community Abundance, Variation, and Functions

4.3.1 The Relationship between the Bacterial Communities with an Increased Relative Abundance and Their Functions in HY Forest

The relative abundances of Actinobacteriota, Myxococcota, and Cyanobacteria were higher in the soil samples of HY forest. Actinobacteriota increases the contents of soil nutrients and organic matter, enhances the efficiency of nitrogen use in soil and plant tissues, and improves plant yield by promoting photosynthesis [30]. Myxococcota is an aerobic bacterium that inhabits the soil surface layer and may have important ecological and evolutionary effects on many soil prokaryotic species [31]. Cyanobacteria can fix nitrogen, which significantly increases crop yield, micronutrient contents, and levels of leaf chlorophyll [32]. Herein, there was a relatively high abundance of Cyanobacteria in the soils of HY forest, indicating that the HY *P. edulis* plants are more effective at harboring soil microbes that can fix nitrogen. Subgroup_2 are members of Acidobacteriota and mediate nutrient cycling in the soil [33]. Notably, there was a high abundance of Subgroup_2 in the root bacterial community and soil bacterial community in HY-YA, indicating the HY-YA forests have a high ability for nutrients to cycle between the roots and soil.

In this study, Proteobacteria, Acidobacteriota, and Actinobacteriota were the dominant phyla of the root zone soil and among endophytic (rhizomes and roots) bacteria of *P. edulis*. This finding was consistent with that obtained from *Arabidopsis thaliana* [34], indicating that the *Phyllostachys* microbial community follows some general principles of microbial community establishment. These bacteria can symbiotically produce positive effects on Moso bamboo, promote its growth, and improve its physiological status [35]. Proteobacteria and Acidobacteriota are indicators of the soil nutrient status; Proteobacteria is associated with nutrient-rich soils, while Acidobacteriota is associated with nutrient-poor soils [36]. Acidobacteriota maintains the ecological status and can improve the low rate of nutrient utilization of plants by interacting with other microorganisms [37]. In this study, the relative abundances of Acidobacteriota, Actinobacteriota, Bdellovibrionota, and Myxococcota increased in the endophytic bacterial community of HY forests. Notably, some members of Acidobacteriota can degrade complex biopolymers, such as xylan, pectin, and chitin, thus, playing an important role in the utilization of limited soil nutrients [38]. The relative abundance of Firmicutes in the bamboo rhizome in the HY forest increased. Firmicutes are often involved in the decomposition of organic matter and nitrogen fixation, which are affected by soil pH [39]. In this study, the relative abundances of Actinobacteriota and Bacteroidota in the bamboo stem increased in the HY forest. Similarly, Bacteroidota plays an important role in degrading complex organic matter [40].

4.3.2 The Relationship between the Bacterial Communities with a Reduced Relative Abundance and Their Functions in the HY Forest

Compared with the LY forest, not all the bacterial communities in the HY forest can increase the abundance of bacterial communities, which benefits plant growth. For example, *Methylobacterium-Methylorubrum*, which assists in the production of plant hormones and the fixation of atmospheric nitrogen, showed a very low relative abundance in the root zone soil and root endophytic bacterial communities of Moso bamboo. The relative abundances of Bacteroidota, Verrucomicrobiota, and Firmicutes in the rhizome root also decreased in the endophytic bacterial community of the HY forest. Bacteroidota is the primary member of the bacterial community that degrades a series of high molecular weight organic compounds, including proteins and carbohydrates [12,41]. In this study, the relative abundance of Cyanobacteria decreased in the bamboo rhizome. Similarly, the relative abundances of Acidobacteriota, Cyanobacteria, and Myxococcota in the bamboo stems also decreased. The ability of Cyanobacteria to express plant cytochrome P450 enzymes has an important function in the biosynthesis of many secondary metabolites in plants [41,42]. The abundances of Chloroflexi and Firmicutes in the tissue samples of the HY-YA forest were significantly lower than those in the LY-YA forest. The relative abundances of Acidobacteriota, Actinobacteriota, Firmicutes, and Chloroflexi in the bamboo leaf samples from the HY forest were lower in the two regions. Actinobacteriota increases the photosynthetic response of plants, thereby increasing their yield [43]. Similarly, Chloroflexi uses light energy to convert organic matter into energy [44].

4.3.3 Variation in the Representative Bacterial Populations

Plant growth-promoting rhizosphere (PGPR) bacteria are beneficial microorganisms that inhabit the rhizosphere of plants [45]. Previous studies have postulated that *Pseudomonas*, which is a genus of PGPR Proteobacteria, can dissolve phosphate and produce siderophores, ammonia, and indole-3-acetic acid (IAA), thus, promoting seed germination and plant growth [46–48]. Herein, the relative abundance of *Pseudomonas* in the root zone soil bacterial community of the HY forest was significantly low. Notably, the relative abundance of *Pseudomonas* in the root zone soil bacterial community of the LY-YA forest was nine times higher than that in the HY-YA forest. This observation suggests that the phosphates in the root zone soil of HY forest had been dissolved by *Pseudomonas* and transformed into substances that could be absorbed by plants [49]. Similarly, the relative abundance of *Streptococcus* in the root endophytic and root zone soil bacterial communities of the HY-YA forest was nine times higher than that in the LY-YA forest, but its role in soil and plant growth is unclear.

The bacterial communities in the root zone soil and various tissues of the HY and LY forests were significantly different, indicating that healthy HY *P. edulis* cultivation requires a well-balanced microbial community. It is hypothesized that the HY root zone soil exudates and mucus-derived nutrients first attract organisms to the *in vivo* environment of *P. edulis*, followed by fine-tuning between HY *P. edulis* and bacteria. The associated bacteria must be highly competitive to successfully colonize the roots because of the different nutritional conditions and positive responses of the plant immune systems. Thus, *P. edulis* plants in the HY forests should be enriched with special functional bacteria so that the composition and abundance of bacteria and the growth of Moso bamboo are coordinated with each other. The findings of this study provide a foundation for the future development of HY *P. edulis* under regulation using artificial bacteria.

Owing to the regional nature of this study, the sampling sites were concentrated in southeast China, which can only represent the characteristics of bacterial colonies in the HY and LY *P. edulis* forests in southeast China. The selection of 16S rDNA (V5–V7 region) has largely avoided the interference of plant mitochondria and chloroplast genomes, but the isolation of cultivatable bacteria has been planned during the next phase of research, and it is necessary to mutually verify the results of this study. In ad-

dition, future research plans to use the beneficial bacteria in the cultivatable bacteria to regulate the bacterial population in the LY *P. edulis* forests.

5. Conclusions

This study systematically describes the bacterial community diversity and composition of different tissues and soil in the HY and LY *P. edulis* forests. The samples were collected from the HY and LY forests in two different areas for comparative analysis. Research conducted in multiple areas instead of collecting samples in only one place should result in more reliable research conclusions. The results showed that the bacterial communities, particularly the root zone soil samples, of the HY *P. edulis* forests in YA and JL were very similar. The principal coordinate distance between the root zone soil samples of the high-yielding forest was closer than that of the other samples, and the dominant microflora of the root zone soil of HY *P. edulis* forest was also very similar. The diversity indices of the root zone soil and root endophytic bacterial community in LY *P. edulis* forests were higher than those in the HY *P. edulis* forest, and the principal coordinate distances between the root zone soil samples in the LY *P. edulis* forests were long and irregular. In short, the bacterial community structure of Moso bamboo in the HY *P. edulis* forest has some degree of commonality, but there are substantial differences between the endophytic bacterial communities in HY and LY *P. edulis* forests.

Availability of Data and Materials

The original sequences obtained by sequencing have been uploaded to the NCBI SRA database under accession number PRJNA 888850 (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA888850).

Author Contributions

ZY and HP designed the research study. FL performed the research. YY analyzed the data. ZY, FL and HP wrote the manuscript. All authors contributed to editorial changes in the manuscript. All authors read and approved the final manuscript. All authors have participated sufficiently in the work to take public responsibility for appropriate portions of the content and agreed to be accountable for all aspects of the work in ensuring that questions related to its accuracy or integrity.

Ethics Approval and Consent to Participate

Not applicable.

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Conflict of Interest

The authors declare no conflict of interest.

References

[1] Xu Q, Jiang P, Xu Z. Soil microbial functional diversity under intensively managed bamboo plantations in southern China. Journal of Soils and Sediments. 2008; 8: 177–183.

[2] Ge W, Zhang Y, Cheng Z, Hou D, Li X, Gao J. Main regulatory pathways, key genes and microRNAs involved in flower formation and development of moso bamboo (*Phyllostachys edulis*). Plant Biotechnology Journal. 2017; 15: 82–96.

[3] Jiang ZH. Bamboo and Rattan in the World. Chinese Forestry Publishing House: Beijing. 2007.

[4] Li P, Zhou G, Du H, Lu D, Mo L, Xu X, *et al*. Current and potential carbon stocks in Moso bamboo forests in China. Journal of Environmental Management. 2015; 156: 89–96.

[5] Wang B, Wei WJ, Liu CJ, You WZ, Niu X, Man RZ. Biomass and carbon stock in Moso bamboo forests in subtropical China: characteristics and implications. Journal of Tropical Forest Science. 2013; 25: 137–148.

[6] Arduini I, Baldanzi M, Pampana S. Reduced Growth and Nitrogen Uptake During Waterlogging at Tillering Permanently Affect Yield Components in Late Sown Oats. Frontiers in Plant Science. 2019; 10: 1087.

[7] Dubey A, Kumar A, Malla MA, Chowdhary K, Singh G, Ravikanth G, *et al*. Approaches for the amelioration of adverse effects of drought stress on crop plants. Frontiers in Bioscience-Landmark. 2021; 26: 928–947.

[8] Chen J, Wu Q, Li S, Ge J, Liang C, Qin H, *et al*. Diversity and function of soil bacterial communities in response to long-term intensive management in a subtropical bamboo forest. Geoderma. 2019; 354: 113894.

[9] Araujo R. Advances in Soil Engineering: Sustainable Strategies for Rhizosphere and Bulk Soil Microbiome Enrichment. Frontiers in Bioscience-Landmark. 2022; 27: 195.

[10] Chaparro JM, Sheflin AM, Manter DK, Vivanco JM. Manipulating the soil microbiome to increase soil health and plant fertility. Biology and Fertility of Soils. 2012; 48: 489–499.

[11] Luo Y, Wang F, Huang Y, Zhou M, Gao J, Yan T, *et al*.*Sphingomonas* sp. Cra20 Increases Plant Growth Rate and Alters Rhizosphere Microbial Community Structure of Arabidopsis thaliana Under Drought Stress. Frontiers in Microbiology. 2019; 10: 1221.

[12] Yuan ZS, Liu F, He SB, Zhou LL, Pan H. Community structure and diversity characteristics of rhizosphere and root endophytic bacterial community in different *Acacia species*. PLoS ONE. 2022; 17: e0262909.

[13] Lu T, Ke M, Lavoie M, Jin Y, Fan X, Zhang Z, *et al*. Rhizosphere microorganisms can influence the timing of plant flowering. Microbiome. 2018; 6: 231.

[14] Smalla K, Wieland G, Buchner A, Zock A, Parzy J, Kaiser S, *et al*. Bulk and Rhizosphere Soil Bacterial Communities Studied by Denaturing Gradient Gel Electrophoresis: Plant-Dependent Enrichment and Seasonal Shifts Revealed. Applied and Environmental Microbiology. 2001; 67: 4742–4751.

[15] Xu N, Tan G, Wang H, Gai X. Effect of biochar additions to soil on nitrogen leaching, microbial biomass and bacterial community structure. European Journal of Soil Biology. 2016; 74: 1–8.

[16] Magoč T, Salzberg SL. FLASH: fast length adjustment of short reads to improve genome assemblies. Bioinformatics. 2011; 27: 2957–2963.
[17] Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM. The role of root exudates in rhizosphere interactions with plants and other organisms. Annual Review of Plant Biology. 2006; 57: 233–266.
[18] Baudoin E, Benizri E, Guckert A. Impact of artificial root exudates on the bacterial community structure in bulk soil and maize rhizosphere. Soil Biology and Biochemistry. 2003; 35: 1183–1192.
[19] Ma X, Zarebanadkouki M, Kuzyakov Y, Blagodatskaya E, Pausch J, Razavi BS. Spatial patterns of enzyme activities in the rhizosphere: Effects of root hairs and root radius. Soil Biology and Biochemistry. 2018; 118: 69–78.
[20] Evelin H, Kapoor R, Giri B. Arbuscular mycorrhizal fungi in alleviation of salt stress: a review. Annals of Botany. 2009; 104: 1263–1280.
[21] Singh BK, Millard P, Whiteley AS, Murrell JC. Unravelling rhizosphere–microbial interactions: opportunities and limitations. Trends in Microbiology. 2004; 12: 386–393.
[22] Bever JD, Platt TG, Morton ER. Microbial Population and Community Dynamics on Plant Roots and their Feedbacks on Plant Communities. Annual Review of Microbiology. 2012; 66: 265–283.
[23] Bever JD, Mangan SA, Alexander HM. Maintenance of Plant Species Diversity by Pathogens. Annual Review of Ecology, Evolution, and Systematics. 2015; 46: 305–325.
[24] Vogelsang KM, Bever JD. Mycorrhizal densities decline in association with nonnative plants and contribute to plant invasion. Ecology. 2009; 90: 399–407.
[25] Beckers B, Op De Beeck M, Weyens N, Boerjan W, Vangronsveld J. Structural variability and niche differentiation in the rhizosphere and endosphere bacterial microbiome of field-grown poplar trees. Microbiome. 2017; 5: 25.
[26] Hardoim PR, van Overbeek LS, Elsas JDV. Properties of bacterial endophytes and their proposed role in plant growth. Trends in Microbiology. 2008; 16: 463–471.
[27] Compant S, Clément C, Sessitsch A. Plant growth-promoting bacteria in the rhizo- and endosphere of plants: their role, colonization, mechanisms involved and prospects for utilization. Soil Biology and Biochemistry. 2010; 42: 669–678.
[28] Jones JDG, Dangl JL. The plant immune system. Nature. 2006; 444: 323–329.
[29] Bulgarelli D, Schlaeppi K, Spaepen S, van Themaat EVL, Schulze-Lefert P. Structure and Functions of the Bacterial Microbiota of Plants. Annual Review of Plant Biology. 2013; 64: 807–838.
[30] AbdElgawad H, Abuelsoud W, Madany MMY, Selim S, Zinta G, Mousa ASM, *et al*.Actinomycetes Enrich Soil Rhizosphere and Improve Seed Quality as well as Productivity of Legumes by Boosting Nitrogen Availability and Metabolism. Biomolecules. 2020; 10: 1675.
[31] Murphy CL, Yang R, Decker T, Cavalliere C, Andreev V, Bircher N, *et al*.Genomes of Novel *Myxococcota* Reveal Severely Curtailed Machineries for Predation and Cellular Differentiation. Applied and Environmental Microbiology. 2021; 87: e0170621.
[32] Renuka N, Prasanna R, Sood A, Bansal R, Bidyarani N, Singh R, *et al*. Wastewater grown microalgal biomass as inoculants for improving micronutrient availability in wheat. Rhizosphere. 2017; 3: 150–159.
[33] Berkelmann D, Schneider D, Hennings N, Meryandini A, Daniel R. Soil bacterial community structures in relation to different oil palm management practices. Scientific Data. 2020; 7: 421.
[34] Schlaeppi K, Dombrowski N, Oter RG, Ver Loren van Themaat E, Schulze-Lefert P. Quantitative divergence of the bacterial root microbiota in Arabidopsis thaliana relatives. Proceedings of the National Academy of Sciences of the United States of America. 2014; 111: 585–592.
[35] Bruto M, Prigent-Combaret C, Muller D, Moënne-Loccoz Y. Analysis of genes contributing to plant-beneficial functions in Plant Growth-Promoting Rhizobacteria and related Proteobacteria. Scientific Reports. 2014; 4: 6261.
[36] Gottel NR, Castro HF, Kerley M, Yang Z, Pelletier DA, Podar M, *et al*. Distinct Microbial Communities within the Endosphere and Rhizosphere of Populus deltoides Roots across Contrasting Soil Types. Applied and Environmental Microbiology. 2011; 77: 5934–5944.
[37] Castro HF, Classen AT, Austin EE, Norby RJ, Schadt CW. Soil Microbial Community Responses to Multiple Experimental Climate Change Drivers. Applied and Environmental Microbiology. 2010; 76: 999–1007.
[38] Church MJ. Resource control of bacterial dynamics in the sea. In Kirchman DL. (ed.) Microbial Ecology of the Oceans (pp. 335–382). John Wiley & Sons: Chichester. 2008.
[39] Berendsen RL, Pieterse CMJ, Bakker PAHM. The rhizosphere microbiome and plant health. Trends in Plant Science. 2012; 17: 478–486.
[40] Dedysh SN, Sinninghe Damsté JS. Acidobacteria eLS. John Wiley & Sons, Ltd: Chichester. 2018.
[41] O'Brien FJM, Dumont MG, Webb JS, Poppy GM. Rhizosphere bacterial communities differ according to fertilizer regimes and cabbage (*Brassica oleracea* var. capitata L.) harvest time, but not aphid herbivory. Frontiers in Microbiology. 2018; 9: 1620.
[42] Xue Y, He Q. Cyanobacteria as cell factories to produce plant secondary metabolites. Frontiers in Bioengineering and Biotechnology. 2015; 3: 57.
[43] Wang J, Li L, Xie J, Xie L, Effah Z, Luo Z, *et al*. Effects of nitrogen fertilization on soil CO_2 emission and bacterial communities in maize field on the semiarid Loess Plateau. Plant Soil. 2023; 1–17.
[44] Krzmarzick MJ, Crary BB, Harding JJ, Oyerinde OO, Leri AC, Myneni SCB, *et al*. Natural Niche for Organohalide-Respiring Chloroflexi. Applied and Environmental Microbiology. 2012; 78: 393–401.
[45] Shabaan M, Asghar HN, Zahir ZA, Zhang X, Sardar MF, Li H. Salt-Tolerant PGPR Confer Salt Tolerance to Maize Through Enhanced Soil Biological Health, Enzymatic Activities, Nutrient Uptake and Antioxidant Defense. Frontiers in Microbiology. 2022; 13: 901865.
[46] Costa-Gutierrez SB, Lami MJ, Santo MCC, Zenoff AM, Vincent PA, Molina-Henares MA, *et al*. Plant growth promotion by Pseudomonas putida KT2440 under saline stress: role of eptA. Applied Microbiology and Biotechnology. 2020; 104: 4577–4592.
[47] Qessaoui R, Bouharroud R, Furze JN, El Aalaoui M, Akroud H, Amarraque A, *et al*.Applications of New Rhizobacteria Pseudomonas Isolates in Agroecology via Fundamental Processes Complementing Plant Growth. Scientific Reports. 2019; 9: 12832.
[48] Rieusset L, Rey M, Muller D, Vacheron J, Gerin F, Dubost A, *et al*.Secondary metabolites from plant-associated Pseudomonas are overproduced in biofilm. Microbial Biotechnology. 2020; 13: 1562–1580.
[49] Brígido C, Glick BR, Oliveira S. Survey of Plant Growth-Promoting Mechanisms in Native Portuguese Chickpea Mesorhizobium Isolates. Microbial Ecology. 2017; 73: 900–915.