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Original Research

Community Structure and Diversity of Rhizosphere Soil and Endophytic Bacteria during the Period of Growth of Moso Bamboo Shoots

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Abstract

Background: The purpose of this study was to elucidate the community structure of rhizosphere soil bacteria and endophytic bacteria during the growth of moso bamboo (*Phyllostachys edulis*) shoots. **Methods**: This study collected the rhizospheric soil samples, tissue samples of rhizome roots, shoot buds, winter bamboo shoots, spring bamboo shoots, and samples of forest soil. Their metagenomic DNA was extracted, and the bacterial community structure and diversity characteristics were compared and analyzed using high-throughput sequencing technology. **Results**: These samples enabled the identification of 32 phyla, 52 classes, 121 orders, 251 families, and 593 genera of bacteria. The phyla primarily included Proteobacteria, Acidobacteria, and Cyanobacteria among others. Proteobacteria was the dominant phylum in the samples of bamboo shoots and rhizome roots, whereas Acidobacteria was dominant in the rhizosphere and forest soil samples. The predominant genera of the rhizome root samples were *Acidothermus*, *Bradyrhizobium* and *Acidobacterium*, and the predominant genera of the soil samples were *Acidothermus* and *Acidobacterium*. **Conclusions**: This study preliminarily revealed the regularity between the growth and development of bamboo shoots and the changes in the community structure of rhizosphere soil and endophytic bacteria, which provides insights into the relationship between growth and the bacterial community structure in different stages of bamboo shoots.

Keywords: community structure; metagenomic DNA; rhizosphere; endophytic bacteria; operational taxonomic unit

1. Introduction

Moso bamboo (*Phyllostachys edulis*) is an important economic species of the Poaceae that is primarily distributed in the Asia-Pacific area, Americas and Africa [1]. There are approximately 4.43 million ha of bamboo forests in China, and they are extremely valuable for forest resources and production [2]. Moso bamboo forests are not only highly valuable economically but also provide ecological benefits [3]. The belowground period of bamboo shoots lasts up to two years from the end of summer to the beginning of autumn, and the plump lateral buds (Fig. 1A) of the half mature bamboo rhizomes begin to develop and differentiate into shoot buds (Fig. 1B). The shoot buds then gradually expand, and the shoot tips bend upwards to form winter bamboo shoots (Fig. 1C) in the early winter. When the temperature increases in the spring, they will continue to grow and emerge from the ground to become spring bamboo shoots (Fig. 1D) [4,5]. The sufficient availability of nutrients is an important prerequisite for the stable and high yields of moso bamboo [6,7].

Many microorganisms are enriched on the surface and interior parts of all terrestrial plants [8]. Studies have shown that the interaction between plants and rhizosphere microorganisms is extremely complex [9] and primarily includes positive interactions, such as promoting the growth of hosts and disease resistance among others, and negative interactions, such as competing with the hosts for nutrients, infecting the host, and causing diseases [10,11]. For example, the primary mechanisms used by beneficial microorganisms in the rhizosphere to promote host resistance to disease include antibiosis, parasitism, competition, and induced systemic resistance [12]. In addition, soil beneficial microorganisms play an important role in soil nutrient cycling [13], and plant beneficial endophytes can improve the ability of plants to transport nutrients and utilize them at an appropriate rate [14]. Currently, managing and manipulating the plant rhizosphere and endophytic microorganisms are still in their infancy [15]. It is necessary to fully understand the components of microbiome to ascertain the driving factors of their process of assembly and interaction with plant hosts to better understand their applications to solve environmental problems in terms of agricultural production and soil health [16,17].

Yuan *et al.* [18] studies have found that growth-promoting endophytic bacteria can increase the chlorophyll content of bamboo leaves and enhance their protective enzyme activities, thereby improving the resistance of bamboo to adverse environmental conditions. The microbiome in the rhizosphere of Moso bamboo varies with space and

time and acts on the availability of soil nitrogen (N), thereby affecting the growth and development of Moso bamboo [19]. Recent studies have found that samples of soil from the root zones of high-yielding forests have lower bacterial richness than those of low-yielding forests. However, the relative abundances of Rhizobiales and Burkholderia in high-yielding Moso bamboo forest samples were higher than those in low-yielding Moso bamboo forest samples. In addition, the bacterial community in the belowground whip root system of the high-yielding Moso bamboo forest is stronger than that of the low-yielding Moso bamboo forest in their ability to utilize nutrients, such as carbon (C), N, and phosphorus (P) [20]. Therefore, this study utilized Illumina NovaSeq (Illumina, San Diego, CA, USA) high-throughput sequencing technology to investigate the structural differences and diversity of rhizosphere soil and endophytic bacterial communities during the growth of bamboo shoots. The purpose was to clarify changes in the bacterial community structure in the tissue and rhizosphere during the growth of bamboo shoots, conduct an in-depth study of the relationship between nutrient absorption and the bacterial community structure of Moso bamboo, and expand the theoretical basis of the current high-yielding cultivation of Moso bamboo.

2. Materials and Methods

2.1 Sample Collection

In this study, the shoot buds, winter bamboo shoots, spring bamboo shoots, and the corresponding rhizome roots, rhizospheric soil and forest soil were collected in Sanshe Village, Xiyang Town, Yongan County, Sanming City, Fujian Province, China (117°46′ E 25°89′ N). Based on the characteristics of the growth of moso bamboo, the shoot buds, rhizome roots, and rhizospheric soil were collected in September 2020 followed by the collection of winter bamboo shoots and their corresponding parts in December 2020. Similarly, spring bamboo shoots with their parts were collected in March 2021. Forest soil from the bamboo forest was sampled as a control in September 2020.

In the sampling area, 30 shoot buds and 24 winter bamboo shoots and spring bamboo shoots were randomly collected [21]. The rhizosphere soil and rhizome root samples were also randomly collected, and the soil attached to the rhizome roots was brushed with a sterile brush to serve as the rhizosphere soil sample (soil particle size $<$1 cm). The rhizome roots were cut into 10 cm long sections with sterile saws and used as the rhizome root samples [21]. All the samples were placed in sterile sample bags immediately after collection, and the same samples were mixed immediately after collection and divided into three parts, which served as three biological replicates. Each part was then placed in a sterile sample bag and stored at –20 °C for further use. Thus, 30 samples were processed. Table 1 and Fig. 1 show the sample code, name and description.

Table 1. The sample codes related to the samples and their corresponding description.

Serial number	Sample code	Sample
1	M1B[1]	Rhizome roots
2	M2B	Rhizome roots
3	M3B	Rhizome roots
4	M1C	Rhizospheric soil
5	M2C	Rhizospheric soil
6	M3C	Rhizospheric soil
7	M1D	Shoot buds (Fig. 1B)
8	M2D	Winter bamboo shoots (Fig. 1C)
9	M3D	Spring bamboo shoots (Fig. 1D)
10	CKC	Forest soil[2]

[1] 1, 2 and 3 in the sample code represent different time points, respectively. 1: September 2020. 2: December 2020. 3: March 2021.

[2] Forest soil was the CK (control), and there was no rhizospheric soil (September 2020).

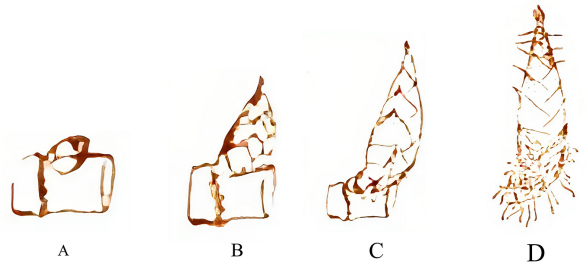

Fig. 1. Process of growth of moso bamboo shoots. (A) Lateral buds. (B) Shoot buds. (C) Winter bamboo shoots. (D) Spring bamboo shoots.

2.2 Genomic DNA Extraction and 16S rRNA High-Throughput Sequencing

This study used pooled samples from each sample bag in which tissue samples were surface-sterilized and certified sterile [22], and the genomic DNA was extracted by a TianGen kit (PD305, Beijing, China) following the manufacturer's instructions [22]. The concentration and purity of genomic DNA were detected by Nanodrop spectrophotometry by Fuguang Precision Instrument (Shanghai) Co., Ltd. (Shanghai, China), and the DNA that met the company's sequencing requirements was stored at –20 °C for later use [23].

Primers were designed based on the conserved regions after the sample genomic DNA had been extracted, and sequencing adapters were added to the ends of primers [24]. PCR amplification was performed, and the sequencing library was formed after the products had been purified, quantified and homogenized. The sequencing library was inspected and quantified before it was sequenced using an Illumina NovaSeq platform with a paired-end sequencing

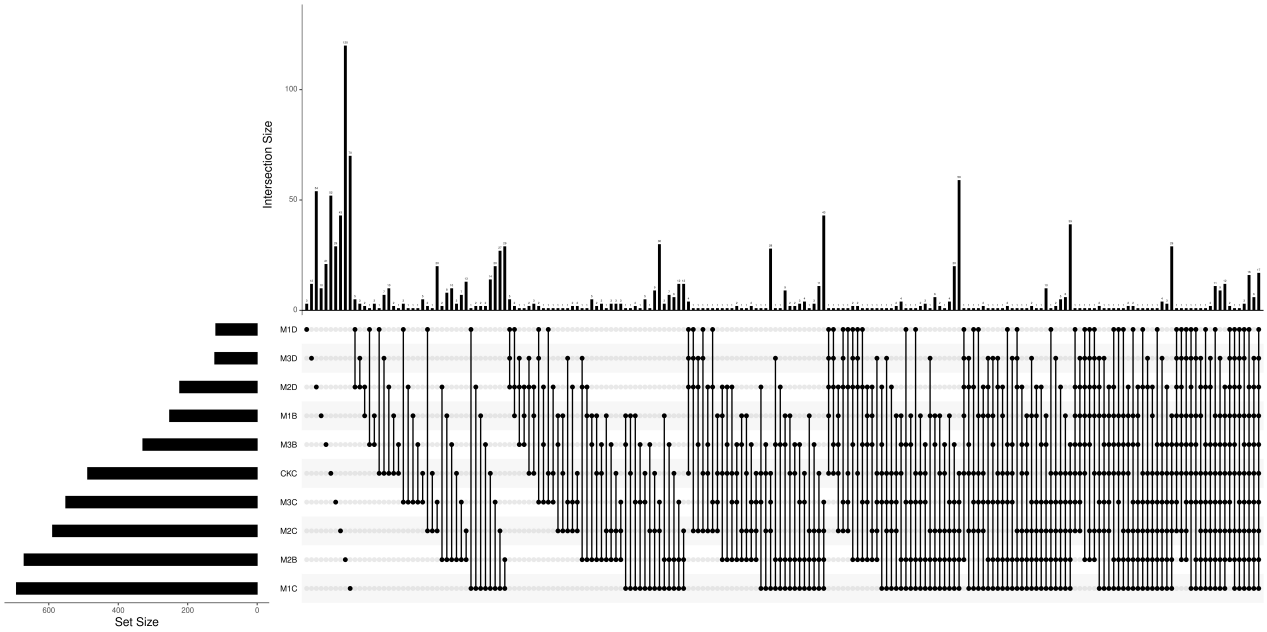

Fig. 2. Comparison of the quantity and distribution of OTUs at different stages of growth of moso bamboo shoots. OTUs, operational taxonomic units.

method to construct a small fragment library for sequencing by Beijing NovaSeq Technology Co., Ltd. (Beijing, China) [24].

2.3 Data Processing and OTU Clustering and Annotation

For the raw reads obtained by sequencing, the unqualified raw reads, including those that contained ambiguous bases, those shorter than 200 bp, and primers were first removed [25]. Raw tags were then generated from the qualified reads, which were assembled by FLASH (V1.2.7, Beijing Institute of Genomics, Beijing, China) [25,26]. Quality filtering of the tags was achieved using QIIME (V1.7.0, Gregory Caporaso, Northern Arizona University, Flagstaff, AZ, USA) [25,27]. Effective tags were obtained after detecting and removing the chimeras with the UCHIME algorithm [28]. Subsequently, all the valid tags were clustered by UPARSE (V7.0.1001, Edgar, Tiburon, CA, USA) [29]. Valid labels were clustered into the same operational taxonomic unit (OTU) when their identity was not lower than 97%. The OTU with the highest frequency was selected as the representative OTU sequence to analyze the species information [30].

2.4 Bioinformatic Analyses

The sample dilution curve was created using R software (Version 3.6.0, R Foundation for Statistical Computing, Vienna, Austria) [31], and the Venn diagrams were drawn after R software was used to analyze the statistics [32]. Indices related to alpha-diversity, such as the Chao 1 and Shannon indices, were calculated using Mothur software (V1.30, The Unversity of Michigan, Ann Arbor, MI, USA). The difference in alpha-diversity index between groups was analyzed using a Wilcoxon rank sum test [33]. A principle coordinates analysis (PCoA) based on the Unweighted UniFrac distance was performed on the sequencing results of 30 samples [34]. A beta-diversity distance matrix was calculated using QIIME, and a hierarchical clustering tree was then plotted using R software. The metabolic function of the microflora was predicted by a PICRUSt analysis based on the OTU trees in the database and the gene information of the OTUs [35].

3. Results

3.1 Analysis of Sequencing Results

A total of 2,666,191 pairs of paired-end reads were obtained by high-throughput sequencing of the bacterial 16S rRNA genes from 30 samples, and 2,437,466 clean tags were obtained after the reads had been spliced and filtered. A total of 64,222 to 93,220 high-quality clean tags were included in each sample, and 4249 bacterial OTUs were obtained by clustering the sequences after quality control based on 97% sequence similarity. The construction of dilution curves showed that the diversity of the soil bacterial communities was much higher than that of the root endophytic bacterial communities. Most root endophytic bacterial communities were saturated at approximately 400 to 900 OTUs, and the soil communities were saturated at approximately 1200 OTUs. The dilution curve of each group gradually flattened, while the amount of sequencing increased, and the number of observed species stabilized. This indicated that the sequencing depth was sufficient to reliably describe the bacterial microbiome associated with these bamboo and soil samples.

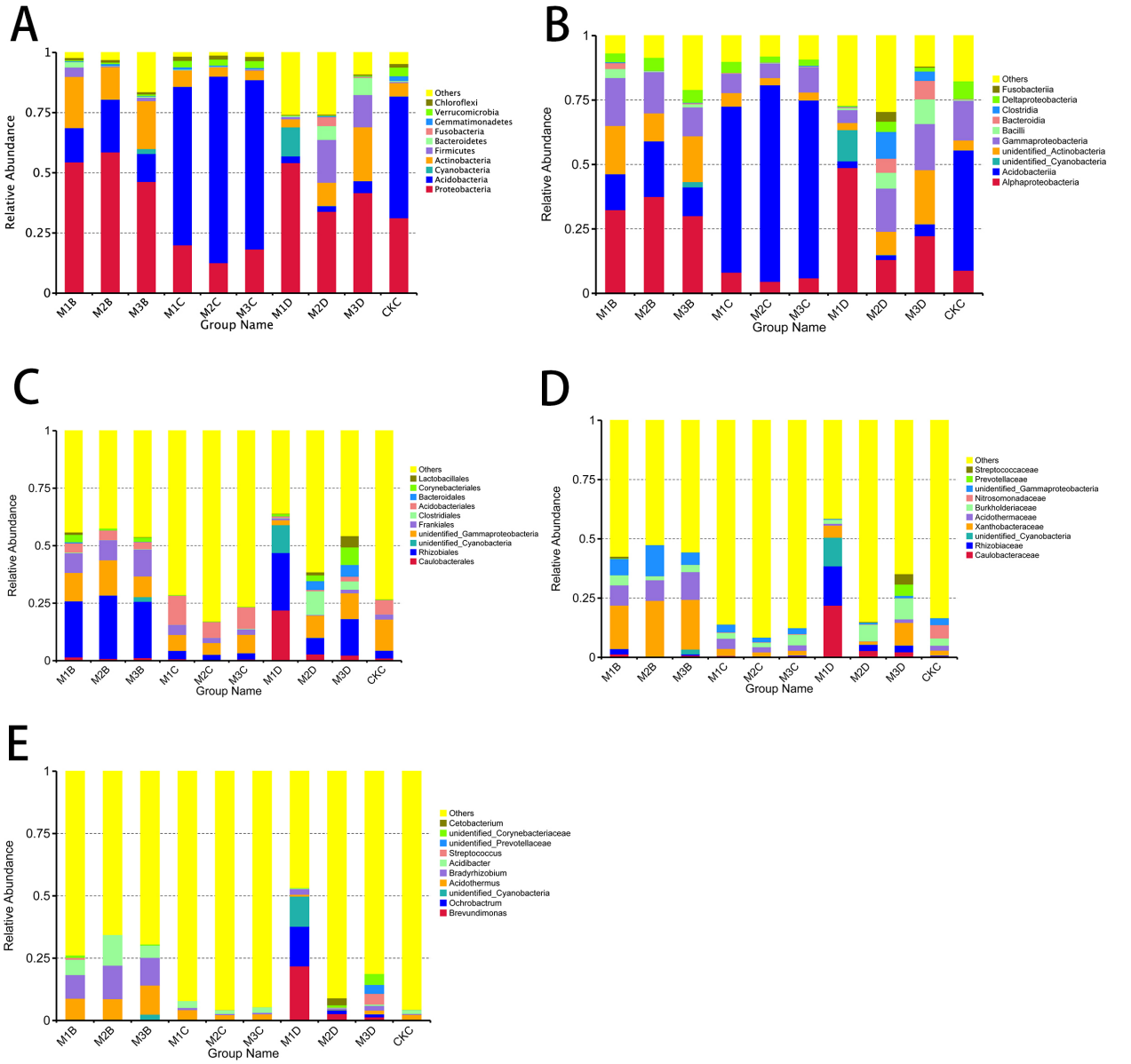

Fig. 3. Relative abundance of the bacterial communities at the phylum level. (A) Phylum level. (B) Class level. (C) Order level. (D) Family level. (E) Genus level.

A total of 32 phyla, 52 classes, 121 orders, 251 families and 593 genera were identified in all the samples. As shown in Fig. 2, there were 704 types of common OTUs in all the rhizome root samples (M1B, M2B, and M3B) and 348404, and 189 specific OTUs, respectively. There were 763 types of common OTUs in all the samples of rhizospheric and control soil (M1C, M2C, M3C and CKC) and 282, 130, 193, and 511 specific OTUs, respectively (Fig. 2). There were 421 common OTUs in the samples of shoot buds, winter bamboo shoots, and spring bamboo shoots samples and 3411780, and 474 specific OTUs, respectively (Fig. 2).

The maximum number of OTUs in the winter bamboo shoots sample (M2D) was 2516, which was one-third more than those in the sample of forest soil CKC (1801) and even nearly twice the number of OTUs (1277) in the rhizospheric soil sample M2C during the period of formation of bamboo shoots in the winter. The shoot buds are new tissues. It was apparent that the M1D sample of shoot buds contained the fewest, which was 1078.

3.2 Analysis of the Composition of Bacterial Community

At the phylum level, Proteobacteria, Acidobacteria, Cyanobacteria, Actinobacteria, Firmicutes, Bacteroidetes, Fusobacteria, Gemmatimonadetes, Verrucomicrobia, and

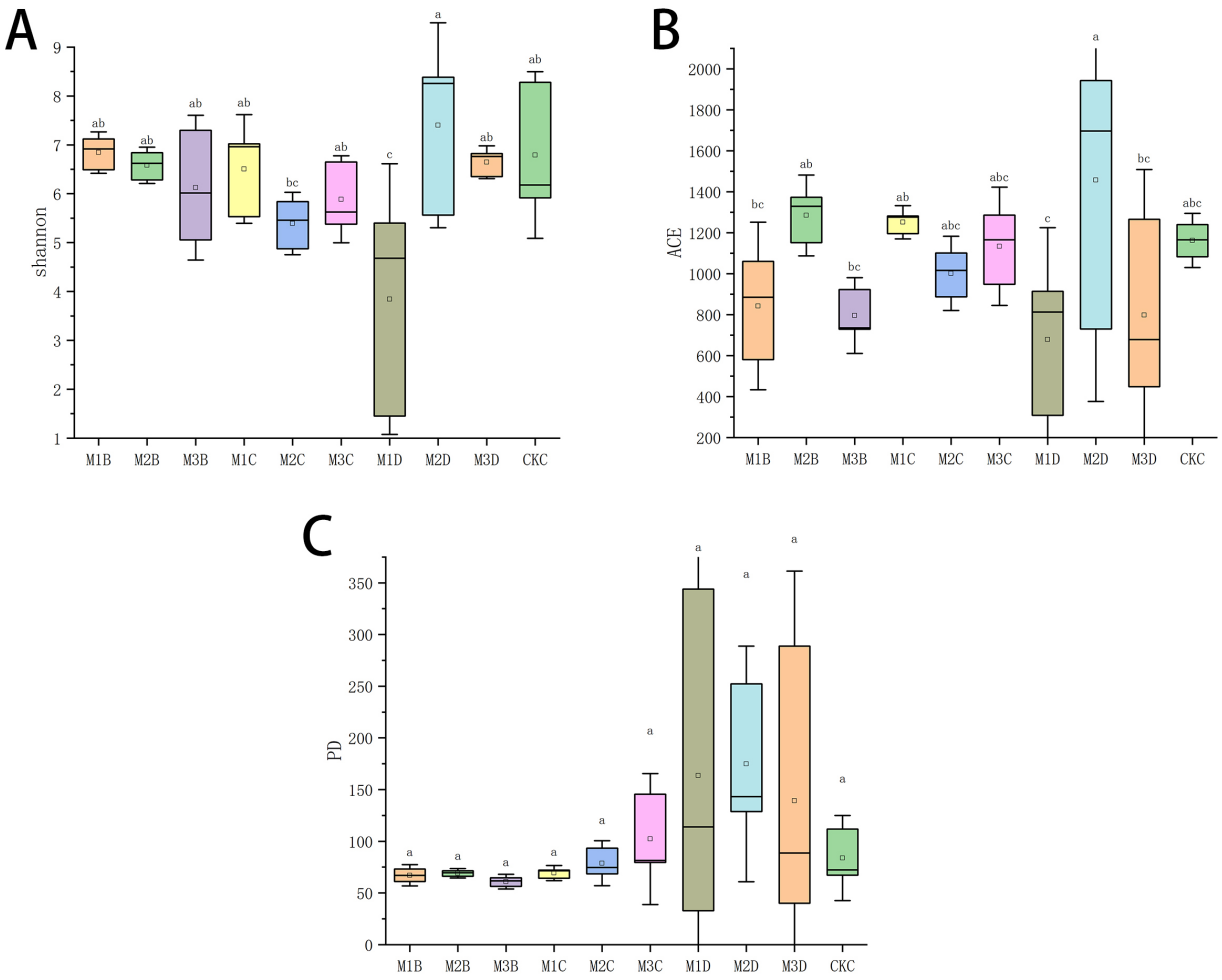

Fig. 4. Box plots show the differences in diversity indices between groups. (A) Shannon index. (B) ACE index. (C) Pedigree diversity index. (The square in the figure notes means average, the horizontal line in the figure notes is the median.)

Chloroflexi were primarily included in all the samples. This analysis showed that Proteobacteria was the dominant phylum in the bacterial community of the rhizome roots and the soil samples (Fig. 3A), and Acidobacteria was the dominant bacterial phylum in all the shoot samples. The bacterial community composition was similar in the rhizome roots and soil samples during the different growth periods, but there were large differences among all the shoot samples. During the process of growing from shoot buds to spring bamboo shoots, Proteobacteria increased and then decreased, while the proportion of Actinobacteria and Bacteroidetes increased. The proportion of Cyanobacteria was 12.07% in the shoot buds (M1D), which was much higher than that of the winter bamboo shoots (0.12%, M2D) and spring bamboo shoots (0.06%, M3D). However, the proportion of Firmicutes at 0.96% in M1D was much lower than those of M2D (17.76%) and M3D (13.37%).

At the class level, it showed that the relative abundance of Gammaproteobacteria kept decreasing in the rhizome root samples, and the relative abundances of Alphaproteobacteria and Acidobacteria increased and then decreased during the growth period of bamboo shoots (Fig. 3B). The relative abundances of Bacilli and Bacteroidia in the rhizome roots (M1B) during the period of germination of the shoot buds were higher than those in the later stages. In all rhizospheric soil samples, the relative abundance of Acidobacteria was lower than that of the CKC, while the relative abundance of Alphaproteobacteria was higher than that of the CKC. The bacterial community composition of bamboo shoot samples varied in different growth stages. The relative abundance of Alphaproteobacteria of the shoot buds (M1D) was 0.48, which was more than twice those of the winter bamboo shoots (M2D, 0.15) and spring bamboo shoots (M3D, 0.22). The proportion of Gammaproteobacteria, Bacilli and Bacteroidetes increased with the growth of bamboo shoots, and M1D had the lowest proportion. The relative abundances of Clostridia, Deltaproteobacteria and Fusobacteria of M2D were higher than those of the other two groups of bamboo shoot samples.

The order level showed that the bacterial community composition did not differ among the rhizome root samples (Fig. 3C). The relative abundances of Frankiales and Acidobacteriales in the rhizospheric soil (M1C) were higher than those in the other soil samples. The relative abundances of Caulobacterales and Rhizobiales in the shoot buds (M1D) were much higher than those in winter bamboo shoots (M2D) and spring bamboo shoots (M3D). Moreover, the proportion of Bacteroidales, Corynebacteriales and Lactobacillales increased in the rhizospheric soil with the growth of bamboo shoots.

The family level showed that there were few differences between the rhizome roots and soil samples in the bacterial community composition, but the relative abundance and composition of Nitrosomonadaceae was much higher in the CKC than that of the rhizospheric soil samples (Fig. 3D). The relative abundances of Caulobacteraceae and Rhizobiaceae were higher in the shoot buds (M1D). Moreover, the relative abundances of Prevotellaceae and Streptococcaceae were higher in the spring bamboo shoots (M3D). In the rhizospheric soil samples, the proportion of Burkholderiaceae increased with the growth of bamboo shoots, and the proportion of Xanthobacteriaceae and Acidophilaceae decreased during the winter shoot period and increased substantially during the period of development of the spring shoots.

The genus level showed that *Acidothermus*, *Bradyrhizobium* and *Acidibacter* were the predominant genera in all the rhizome root samples (Fig. 3E), while *Acidothermus* and *Acidibacter* were the predominant genera in the forest soil samples (CKC). *Brevundimonas* and *Ochrabactrum* were the predominant genera in the shoot buds (M1D), which differed from those in the winter bamboo shoots M2D and spring bamboo shoots (M3D). However, *Cetobacter* (2.78%) of M2D and *Streptococcus* (4.28%) of M3D were higher than than those in M1D and M2D.

3.3 Analysis of the Alpha-diversity of Bacterial Communities

The difference in alpha-diversity index between the groups was analyzed using the Wilcoxon rank sum test. Table 2 and Fig. 4 show the comparison of abundance-based coverage estimator (ACE) index between the rhizome root samples, which indicated that the ACE index of M2B was different from those of M1B and M3B. It was the largest. However, there were no differences from M1B and M3B. In addition, the Shannon and pedigree diversity indices showed no differences. In addition, there were no differences in the Shannon, ACE and pedigree diversity indices among the soil samples. A comparison between the Shannon and ACE indices in the bamboo shoot samples indicated that M1D differed from M2D and M3D, but M2D and M3D did not differ. The pedigree diversity index showed no difference during the comparison.

3.4 Analysis of the Beta-Diversity of Bacterial Community

As shown in Figs. 5,6, the rhizospheric soil samples (M1C, M2C and M3C) were closer in their beta-diversity, while the CKC was farther to some extent. Moreover, the CKC and bamboo rhizospheric soil samples could be distinguished by degrees that were shown by the unwighted pair group method with an arithmetic mean (UPGMA) cluster tree. The rhizome root samples (M1B, M2B and M3B) clustered according to the PCoA analysis, and the UPGMA clustering tree did not reveal any clear differences between the three samples. However, a PCoA analysis showed that the shoot buds (M1D) were far away from the winter bamboo shoots (M2D) and spring bamboo shoots (M3D), and M3D as an independent group differeed from M1D and M2D based on a UPGMA clustering tree analysis.

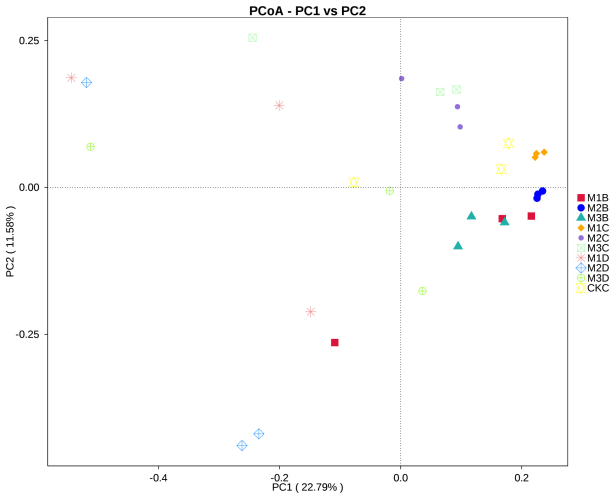

Fig. 5. PCoA analysis based on unweighted UniFrac distances. PCoA, principal coordinates analysis.

3.5 Prediction of Bacterial Functions

As shown in Fig. 7, the rhizosphere soil and endophytic bacteria of moso bamboo clearly differed in their metabolism, cell biological processes and tissue systems. During the growth of moso bamboo, the functions of environmental information processing and human disease were enhanced in the root samples, and the cellular processes and genetic information processing functions decreased. Compared with the CK and rhizospheric soil, the bacteria in rhizospheric soil had stronger functions in environmental information processing, and the shoot buds had much stronger functions in human diseases.

4. Discussion

4.1 Effects of Bamboo Tissue and Rhizospheric soil on the Bacterial Communities

For the rhizospheric soil and the forest soil, the rhizospheric soil sample (M2C) had the fewest numbers and

Table 2. Number of Observed Species and alpha-diversity index of the sample.

Sample Code	Sample	Collection Time	Number of Observed Species	Shannon	ACE[1]	PD[2] whole Tree	Coverage (%)
M1B	Rhizome roots	Sep. 2020	1404	6.84	841.908	67.11	99.4
M2B	Rhizome roots	Dec. 2020	1487	6.58	1284.398	69.08	98.7
M3B	Rhizome roots	Mar. 2021	1182	6.12	795.502	60.89	99.4
M1C	Rhizospheric soil	Sep. 2020	1481	6.51	1251.041	69.26	98.9
M2C	Rhizospheric soil	Dec. 2020	1277	5.39	1001.241	78.77	99.2
M3C	Rhizospheric soil	Mar. 2021	1449	5.89	1133.333	102.16	98.9
M1D	Shoot buds	Sep. 2020	1078	3.84	678.483	163.56	99.3
M2D	Winter bamboo shoots	Dec. 2020	2516	7.40	1456.576	174.76	98.8
M3D	Spring bamboo shoots	Mar. 2021	1210	6.64	797.294	139.11	99.4
CKC	Forest soil	Sep. 2020	1801	6.79	1162.370	83.81	99.2

[1]abundance-based coverage estimator.

[2]phylogenetic diversity.

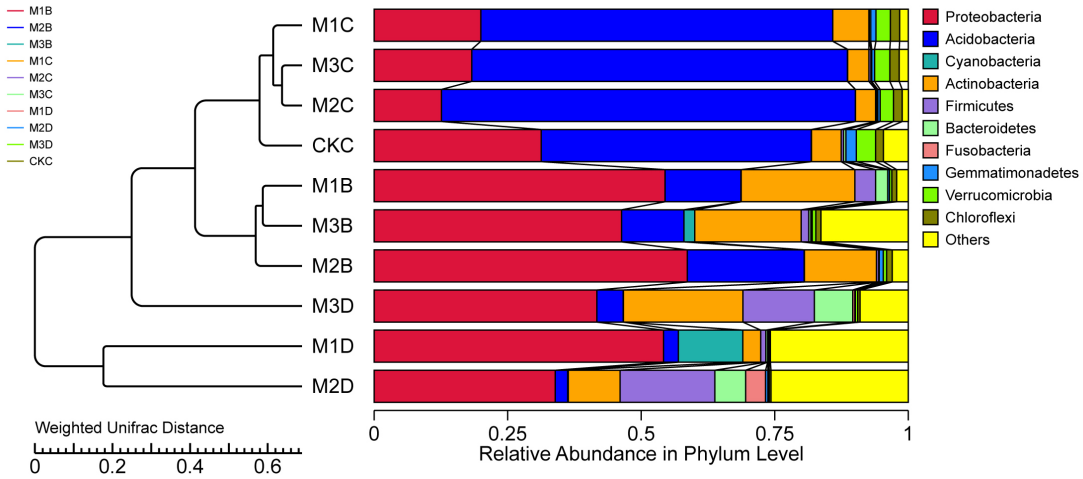

Fig. 6. UPGMA clustering tree based on unweighted UniFrac distances. UPGMA, unweighted pair group method with arithmetic mean.

unique OTUs during the period of formation of winter shoots among all the rhizospheric soil samples. Studies have shown that the there are the fewest levels of nutrients in the rhizospheric soil during the entire growth cycle of bamboo shoots [10]. It is possible that the roots are preparing for the bamboo shoots to break through the soil at this stage, which deprives them of a large amount of soil nutrients, such as organic N, inorganic N and water among others [36]. This resulted in a decrease in the activity of the bacterial population during this period. However, as shown by the alpha-diversity index, the diversity and richness of rhizospheric soil bacteria were not greatly affected by the growth of bamboo shoots. In addition, there were fewer OTUs in the rhizospheric soil samples during the entire process of growth and development of bamboo shoots than that of the forest soil samples, indicating that the bacterial population gradually decreased from the forest soil to the inner root circle during this period. The explanation for this phenomenon was that the metabolism of the rhizosphere of moso bamboo was vigorous during the growth of bamboo shoots and produced a large amount of exudates to change the chemical properties of the rhizospheric soil [37]. Thereby, it has a certain selectivity for bacteria and can inhibit some bacteria from entering the root inner circle [38]. Thus, only a fraction of the bacterial population can be maintained in the rhizosphere. After experiencing the growth and development of bamboo shoots, the rhizospheric soil bacteria gradually retained a unique, highly abundant, and less diverse but stable microbial population [39]. As a result, the alpha-diversity of the rhizospheric soil samples was relatively stable, but the number of OTUs was lower than that of the forest soil samples, which is consistent with the previous results of research on rhizosphere microorganisms in the Poaceae [40].

For bamboo tissues, the number of unique OTUs in the rhizome root samples (M2B) was the highest during the formation of winter bamboo shoots. During the same period, the number of unique OTUs in the winter bamboo shoots (M2D) was much greater than that in the spring bamboo shoots and shoot buds, and the number of bacterial OTUs

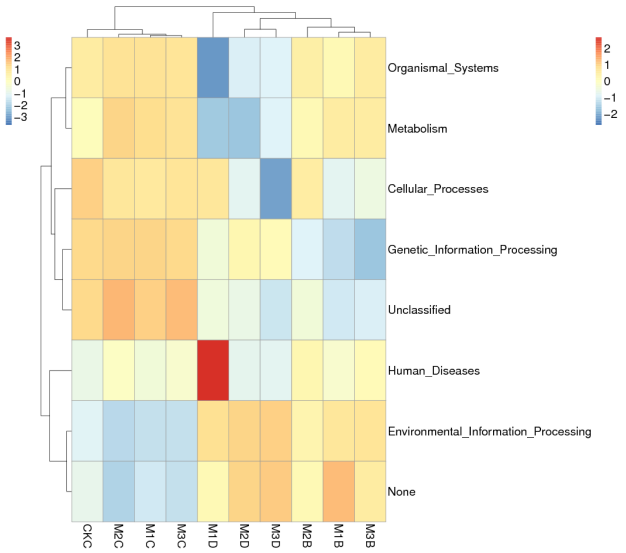

Fig. 7. PICRUSt heatmap of feature annotation and clustering.

in this sample was the largest among all the samples. This shows that during the formation of winter shoots, there were the highest numbers of species of endophytic bacteria in the winter shoots and root zone tissues. It also shows that during this period, moso bamboo has more opportunities to come encounter pathogenic bacteria and is prone to succumbing to disease [41]. Thus, corresponding protective measures should be taken during this period [31]. There were the fewest numbers of OTUs and unique OTUs in the rhizome roots (M3B) during the formation of spring bamboo shoots among all the rhizome root samples, the number of OTUs in shoot buds (M1D) was also lower than those of the winter bamboo shoots and spring bamboo shoots. This is because the shoot buds (M1D) and rhizome roots (M3B) that form during the developmental period of spring bamboo shoots are all new tissues, and the endophytic bacteria had just begun to colonize and had not yet stably colonized at this time [42].

4.2 Effects of the Bacterial Communities Composition and Changes on the Growth of Bamboo Shoots

4.2.1 Rhizome Roots and Rhizospheric Soil

During the growth of bamboo shoots, the rhizome root samples showed overall stability in the composition and relative abundance of their bacterial communities. Proteobacteria represented by *Rhizobium* has always been the dominant population in the rhizome root samples. Bamboo may produce compounds that are attractive to rhizobia, which encourages their growth and colonization. *Rhizobium* may be able to compete more effectively with other microorganisms for resources in bamboo. Proteobacteria are beneficial because they increase the contents of available P, available potassium, and total P (TP) in the soil [15]. Among them, there are a large number of bacteria involved in C and N cycling, and some probiotics that can inhibit plant pathogenic bacteria in the α-proteobacteria group [43]. *Pseudomonas* in the γ-proteobacteria can assist in dissolving insoluble phosphate in the soil [17]. They all had some proportion of Proteobacteria in the root tissue samples of moso bamboo. Actinomycetes and Acidobacteria were the subdominant populations of rhizome root samples, and they helped to increase the content of TP and alkaline N in the soil nutrients [44]. These all play an important role in the acquisition of nutrients during the growth of moso bamboo.

In addition, during the growth of bamboo shoots, the composition and relative abundance of the bacterial communities in the rhizospheric soil samples and forest soil samples were also stable. Among them, Acidobacteria was always the dominant community in the rhizospheric soil, and the Acidobacteria populations tend to colonize soils with a low content of soluble organic C [45]. They can adapt to and utilize the C source environment in the rhizosphere, seize ecological niches, and rapidly increase their numbers [41,44]. In addition, the soil where the samples were collected is acidic red soil, which is more suitable for the reproduction of acidophilic Acidobacteria. Thus, it predominates in the soil samples. However, some populations of Acidobacteria play an important role in the N cycle in soil [44,46].

The relative abundance of bacterial communities in the rhizome root and soil samples was relatively stable during the growth of bamboo shoots, indicating that under long-term growth succession and environmental influence, the bacterial community components in the roots and rhizospheric soil are closely related to the growth of bamboo shoots. Thus, a balance was reached [47].

4.2.2 Tissue Samples of Bamboo Shoots

The endophytic bacterial community composition of bamboo shoot tissue samples was quite different. Overall, with the growth of bamboo shoots, the proportion of Actinomycetes and Bacteroidetes continued to increase. Bacteroides are responsible for the degradation of complex organic matter, particularly polysaccharides and proteins [46], and play beneficial roles in the degradation of organic matter [48]. However, the proportion of Proteobacteria first decreased and then increased. It has been reported that the abundance of Proteobacteria was directly proportional to the nutritional conditions of plants [11]. It is possible that they all play key roles in the construction of bacterial communities during the growth of bamboo shoots [49]. Although the winter bamboo shoot sample (M2D) had the largest number of OTUs, the largest difference was found in the spring bamboo shoot sample (M3D). Compared with the shoot bud sample (M1D) and the winter bamboo shoot sample (M2D), the composition of the endophytic bacterial community of M3D belonged to different groups on the UPGMA clustering tree. For example, the proportion of cyanobacteria in the shoot buds reached 12.07%, mak-

ing it the second most prevalent phylum. However, the proportion of Firmicutes was only 0.96%, which was far lower than that of the winter bamboo shoots and spring bamboo shoots. It was hypothesized that bacterial colonization presents dynamic changes owing to the vigorous metabolism of new tissues during the formation of bamboo shoots, and suitable bacteria are constantly selected to colonize the appropriate niche of plant tissues during the whole process [50]. However, the reasons for the large differences in the flora merit further study.

According to the detailed analysis of the genus level, the bacterial community composition of shoot buds also differed from those of the winter and spring bamboo shoots. The changes in abundance of these bacterial genera may also affect the nutrient and energy intake of bamboo shoots in different periods, particularly the intake of soil nutrients [51]. The bacterial community composition of shoot buds plays a crucial role in the growth of moso bamboo shoots [19]. The dominance of *Brevundimonas* and *Paleobacter* in the shoot buds may facilitate the absorption of nutrients from the soil and contribute to the overall health and growth of the bamboo plant. Conversely, a decrease in their abundance could negatively impact the uptake and growth of nutrients. During the winter season, when the bamboo shoots are dormant, *Brevundimonas* and *Cetella* are the dominant bacterial genera in the winter bamboo shoots. These genera may aid in the accumulation of nutrients and storage of energy during the winter season. In contrast, *Streptococcus* is the dominant genus in the spring bamboo shoots during the spring, and it may play a role in the mobilization and utilization of these stored nutrients and energy for the growth of new shoots.

5. Conclusions

Through an in-depth understanding of the composition and changes of bacterial communities during the formation of bamboo shoots, it was known that during the formation of bamboo shoots, the species of bacteria in rhizosphere soil samples were less than those in forest soil samples. Among them, the rhizospheric soil (M2C) had the least species of bacteria among all the rhizosphere soil samples. The types and numbers of endophytic bacteria in winter bamboo shoots (M2D) tissue were the most among all tissue samples. Proteobacteria represented by *Rhizobium* have always been the dominant flora in rhizome roots. Acidobacteria were always the dominant community in the rhizospheric soil. The relative abundance of bacterial communities in the rhizome root and soil samples was relatively stable during the growth of bamboo shoots. In the future, researchers and growers can combine this knowledge with the dynamics of soil nutrients and choose different fertilization and farming methods to better manage the soil bacterial community, which could help to develop better strategies for the cultivation and management of bamboo forests [52].

Availability of Data and Materials

The original sequences obtained by sequencing have been uploaded to the NCBI SRA database under accession number were from SRR19212974 to SRR19213003 (https://www.ncbi.nlm.nih.gov/bioproject/836717).

Author Contributions

ZSY and HP designed the research study. FL performed the research. ZHZ analyzed the data. ZSY, 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 and agreed to be accountable for all aspects of the work.

Ethics Approval and Consent to Participate

Not applicable.

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Conflict of Interest

The authors declare no conflict of interest.

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