

Article

Structural and Functional Characteristics of Soil Fungal Communities near Decomposing Moso Bamboo Stumps

Fengna Liang^{1,2,3,4}, Le Yu^{1,2,3,4}, Cheng Jin^{1,2,3,4}, Xiao Huang^{1,5}, Yonglai Huang⁶, Luhong Tang^{1,2,3,4}, Longxing Tang^{1,2,3,4}, Xiangqing Ma^{1,2,3,4} and Liping Cai^{1,2,3,4,*}

- ¹ College of Forestry, Fujian Agriculture and Forestry University, Fuzhou 350002, China; fengnaliang@126.com (F.L.); yulediyouxian@163.com (L.Y.); gssbjgcgk@163.com (C.J.); 15190664173@163.com (X.H.); tangluhong1067@163.com (L.T.); 18050263725@163.com (L.T.); lxxmxq@126.com (X.M.)
- ² Key Laboratory of State Forestry and Grassland Administration for Soil and Water Conservation in Red Soil Region of South China, Fuzhou 350002, China
- ³ Cross-Strait Collaborative Innovation Center of Soil and Water Conservation, Fuzhou 350002, China
- ⁴ National Positioning Observation and Research Station of Red Soil Hill Ecosystem in Changting, Fuzhou 350002, China
- ⁵ College of Architectural Science and Engineering, Yangzhou University, Yangzhou 225127, China
- ⁶ Fujian Jian'ou Forestry Bureau, Jian'ou 353100, China; hyl5699@163.com
- * Correspondence: fjclp@126.com

Abstract: Background and Objectives: Fungi degrade lignin and other fibers, thus playing an essential role in the decomposition of *Phyllostachys edulis* (Carrière) J.Houz. (Moso bamboo) stumps. Herein, we characterized key soil fungal communities near different levels of decomposing Moso bamboo stumps (mildly, moderately, and heavily decayed). Materials and Methods: High-throughput sequencing technology was used to analyze the soil fungal communities inside and outside of mild, moderate, and heavy decomposing Moso bamboo stumps. Results: We found nine phyla, 30 classes, 77 orders, 149 families, and 247 genera of soil fungi near the bamboo stumps. Soil fungi OTUs and diversity and richness indices were lower outside than inside the stumps, and decreased with increasing degrees of decay. Inside the bamboo stumps, Soil fungi OTUs and diversity and richness indices were the highest and lowest in moderate and heavy decay bamboo stumps, respectively. Ascomycota dominated inside (from 81% to 46%) and outside (from 69% to 49%) the stumps, and their relative abundance gradually decreased with decomposition, whereas that of Basidiomycota increased outside the stumps (from 17% to 49%). Two-way ANOVA showed that the interaction between the two factors of occurring inside and outside the bamboo stumps and the degree of decay, significantly affected Chytridiomycota and *Penicillium* ($p < 0.001$) and significantly affected Mucoromycota ($p < 0.05$). The abundance of different genera was significantly correlated with saprotrophic functional groups. Conclusion: Changes in the structure and functional groups of soil fungal communities may play an important role during different levels of decomposition of Moso bamboo stumps. This study provides a scientific basis for screening functional fungal strains that promote the decomposition of Moso bamboo stumps.

Keywords: bamboo stumps; decomposition; *Phyllostachys edulis*; soil fungal community



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1. Introduction

The bamboo forest area in China is approximately 6,410,000 ha; the country has the richest bamboo resources and is one of the earliest exploiters of bamboo in the world [1]. In China, Moso bamboo (*Phyllostachys edulis* (Carrière) J. Houz) forest has the highest yield and economic value among bamboo species, and it accounts for 73% of the bamboo forest area [2]. The growth of Moso bamboo forests follows an organic cycle of producing whip shoots, growing into bamboo, and finally producing more whip [3]. Generally,

600–750 mature bamboo per 10,000 m² is felled yearly [4]. However, a large number of hard and slowly decomposing bamboo stumps remain on the forest floor following harvest [5]. Furthermore, the stumps not only occupy great amounts of land and severely hinder the elongation of the rhizome system of Moso bamboo forests, but are also extremely unfavorable towards the growth of bamboo shoots, greatly decreasing their yield and hindering their sustainable management [6]. Bamboo stumps can provide habitats and abundant organic nutrients for decomposers, which are crucial forest carbon pool resources [7]. In addition, the decomposition products of bamboo roots and stems are essential in the soil environment of Moso bamboo woodland and the ecosystem of Moso bamboo forests in terms of material transformation and nutrient cycling [6]. Therefore, accelerating the natural decomposition of Moso bamboo stumps is conducive to maintaining good ecological activity and soil fertility.

The forest floor is rich in microbial resources [8,9], and the microbial community characteristics greatly influence the decay and decomposition of plant residues [10,11]. The natural decay of bamboo stumps mainly relies on microbial decomposition [12]. The decay of bamboo stumps is closely related to their bacteria and fungi [13]. There are differences in the bacteria, fungi, actinomycetes, and cellulose- and lignin-degrading bacteria of bamboo stumps at distinct decomposing levels [6,13]. However, previous studies mainly dealt with changes in the number of microorganisms in bamboo stumps during different decomposing processes, whereas relatively few studies have been completed on the role of soil microorganisms in the decomposing process of bamboo stumps. Previously, we analyzed the species structure characteristics of the soil bacterial community around bamboo stumps using microbial sequencing techniques, revealing the role of soil bacteria in the decomposition process [12]. Soil fungi are the pioneer species among decomposers [14], and their ability to breakdown complex organic matter is stronger than that of bacteria [15], particularly for macromolecules such as cellulose and lignin [16,17]. The wall of a bamboo stump is thick and hard, the stump distribution volume is large, and its cellulose, hemicellulose, and lignin contents are high. However, it is not clear whether there are differences in soil fungal communities outside and inside the bamboo stumps during decomposition, differences in their functional characteristics, or which fungal communities can facilitate the decomposition of bamboo stumps.

Herein, we analyzed the characteristics of soil fungal communities by collecting soil outside and inside the bamboo stumps at different levels of decomposition, and used high-throughput sequencing technology to characterize them. Our objective was to investigate the relationship between soil fungi outside and inside the bamboo stumps with different degrees of decomposition, and to identify the functional fungi that promoted the decomposition of stumps. We expect to provide a theoretical foundation for the sustainable management of Moso bamboo forests and bamboo stump decomposition.

2. Materials and Methods

2.1. Experimental Site Description and Sampling

The experimental and soil sampling sites in this study are those previously described for the study of soil bacteria communities [12]. The experimental site is in Fangdao Town, Jian'ou City, Fujian Province, China (26°38'–27°20' N, 117°58'–118°57' E) (Figure 1). The soil is ordinary mountain red soil developed by granite, and the zonal vegetation is evergreen broad-leaved forest, with the main tree species including *Phyllostachys edulis*, *Cunninghamia lanceolata*, *Phoebe bournei*, and *Schima superba*. The area has a subtropical maritime monsoon climate. The climatic conditions in this region are ideal for the growth of Moso bamboo owing to abundant rainfall, with annual rainfall of 1600–1800 mm, and annual average temperatures of 14–20 °C. Jian'ou City ranks among the top counties and cities in China in terms of Moso bamboo area regarding bamboo number, bamboo timber, and fresh bamboo shoot production [18]. The area of Moso bamboo forest in Fangdao Town is 8400 ha, accounting for more than 47% of the total forest area of the town. The area of the experimental forest is larger than 70 ha; Moso bamboo has an average density of

2500/ha and a height of 16 m, and the growth is concentrated over a large area. A range of 400–600 mature standing bamboo stands per ha are cut down annually, and a similar number of new bamboo stumps are left behind yearly.

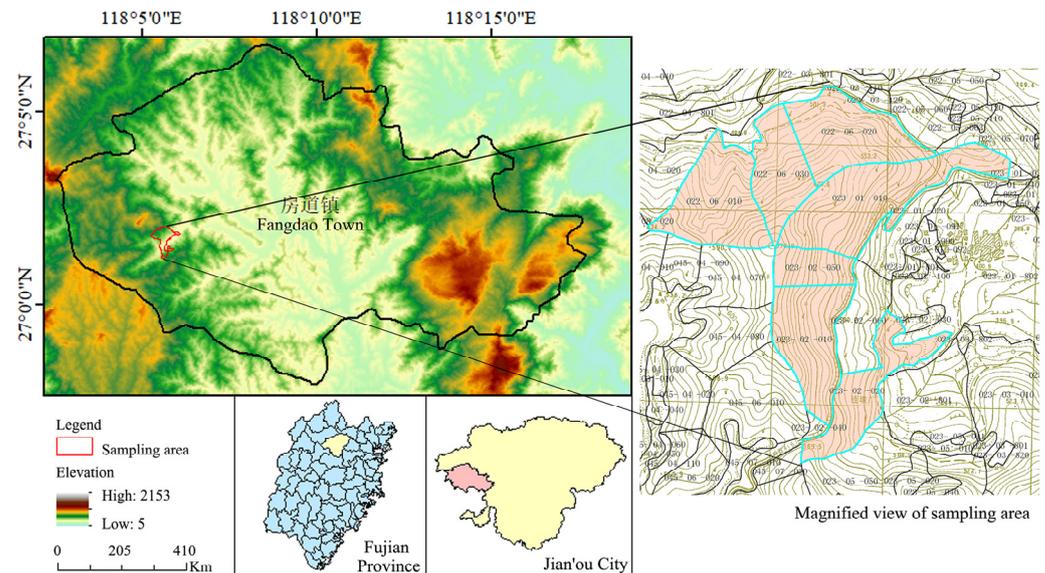


Figure 1. Study area and sampling site location distribution map.

Three decay levels (mild, moderate, and heavy) of the bamboo stumps of Moso bamboo were randomly selected in the experimental site, and the classification criteria for the decay and decomposition levels of the stumps were determined with reference to the classification criteria for the decay levels of coarse woody residues by Yan Enrong et al. [19] and those for the Moso bamboo felled stumps by Song Jing [6], as shown in Table 1. Soil samples were collected from outside and inside the bamboo stumps at three levels of decomposition. A five-point sampling method was used to collect the top 0–20 cm of soil at a distance of 0–2 cm from the bamboo stumps, and the soil collected inside the bamboo stumps was all the soil on the bamboo diaphragm. For each degree of decomposition, 8–10 soil samples were randomly selected to be mixed into one soil sample, and the collection of soil samples outside and inside the bamboo stumps were repeated three times for each degree of decomposition using the same method. The collected soil was immediately stored in an ice insulator at $-4\text{ }^{\circ}\text{C}$, after which the soil was passed through a 2 mm sieve. The sieved soil samples were stored in a refrigerator at $-80\text{ }^{\circ}\text{C}$ to determine soil fungal microorganisms.

Table 1. Classification of the degree of decomposition of bamboo stumps.

Degree of Decomposition	Characteristics			
	Color	Bamboo Green, Bamboo Flesh, Bamboo Yellow	Bamboo Diaphragm	Bamboo Stump
Mild decomposition	Light gray inside and outside of bamboo stumps	Hard and complete	Complete	More complete
Moderate decomposition	Gray to gray-brown outside and inside of bamboo stumps	Bamboo green slightly hard, Bamboo flesh and yellow become soft and partly hard	Incomplete	Some of the fine roots are decomposed and have fallen off
Heavy decomposition	Gray-brown to dark black outside and inside of bamboo stumps	Bamboo green, bamboo flesh, and bamboo yellow are soft and fragile	Decayed	A great number of vascular bundles are visible, and most of the bamboo stumps are soft and rotted

2.2. Soil Fungal Microbial Determination

Microbial DNA was extracted from soil samples using the E.Z.N.A. stool DNA Kit (Omega Bio-tek, Norcross, GA, USA) according to the manufacturer's protocols. The ITS region of the eukaryotic ribosomal RNA gene was amplified by PCR (95 °C for 2 min, followed by 27 cycles at 98 °C for 10 s, 62 °C for 30 s, 68 °C for 30 s, and a final extension at 68 °C for 10 min) using primers ITS3_KYO2F 5'-GATGAAGAACGYAGYRAA-3' and ITS4R 5'-TCCTCCGCTTATTGATATGC-3' [20], where the barcode was an eight-base sequence unique to each sample. PCR reactions were performed in triplicate as a 50 µL mixture containing 5 µL of 10 × KOD buffer, 5 µL of 2.5 mM dNTPs, 1.5 µL of each primer (5 µM), 1 µL of KOD polymerase, and 100 ng of template DNA.

Amplicons were extracted from 2% agarose gels and purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA.) according to the manufacturer's instructions, and quantified using QuantiFluor -ST (Promega, Madison, WI, USA). Purified amplicons were pooled in equimolar concentrations and paired-end sequenced (2 × 250) on an Illumina platform according to the standard protocols. The raw reads were deposited into the NCBI Sequence Read Archive (SRA) database. A flow chart of the bioinformatics analysis is shown in Figure 2. Sequencing was performed by Guangzhou Gene Denovo Biotechnology Co., Ltd. (Guangzhou, China).

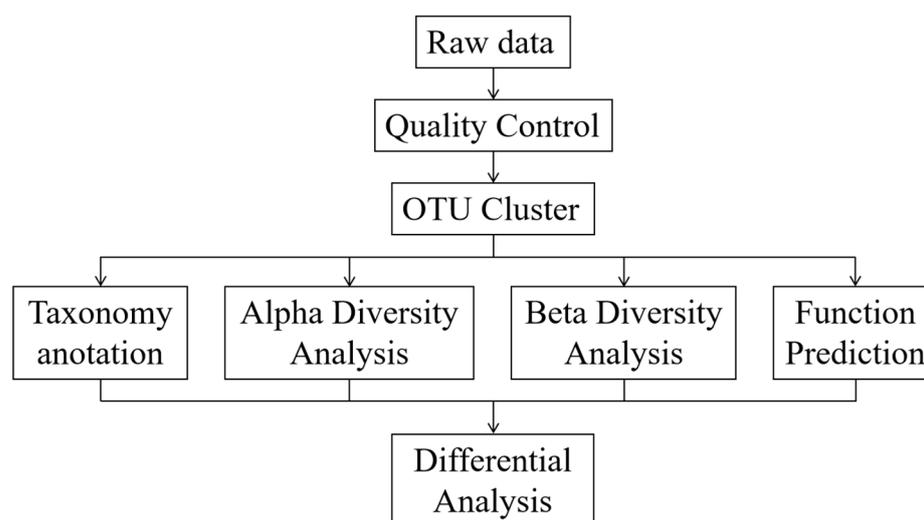


Figure 2. ITS analysis flow chart.

2.3. Statistical Analyses

The Guangzhou Gene Denovo Biotechnology Co., Ltd. data analysis platform was used for this study. The effective tags were clustered into operational taxonomic units (OTUs) of $\geq 97\%$ similarity using the UPARSE [21] pipeline. The tag sequence with the highest abundance was selected as the representative sequence within each cluster. Between groups, Venn analysis was performed in R (<https://cran.r-project.org/web/packages/VennDiagram/index.html> accessed on 2 July 2018) to identify unique and common OTUs. Based on the OTU abundance results, the alpha diversity of each sample was calculated using QIIME 2010 software (V1.9.1) [22]. Beta diversity analysis was first performed using Muscle (v3.8.31) [23] for multiple sequence comparisons based on the OTU sequences of all samples. Then, TreeBeST (v1.9.2) (<http://treesoft.sourceforge.net/treebest.shtml> accessed on 2 July 2018) was used to construct a phylogenetic tree of OTUs, and the GUniFrac (v1.0) (<https://cran.r-project.org/web/packages/GUniFrac/index.html> accessed on 2 July 2018) package in R was used to calculate the unweighted Unifrac and weighted Unifrac distances between two samples [24]. The representative sequences were classified into organisms via a naive Bayesian model using the RDP classifier [25] (Version 2.2) based on the UNITE [26] database (<https://unite.ut.ee/> accessed on 2 July 2018). The abundance

statistics of each taxonomy and phylogenetic tree were constructed in a Perl script and visualized using SVG. IBM SPSS Statistics 25 software (Statistical Package for Social Science) was used to calculate the means and standard deviations of the effective series, OTUs, and alpha diversity, and to perform a one-way ANOVA. A two-way ANOVA was performed to analyze the soil fungal communities at the level of phylum and genus outside and inside the bamboo stumps at different decomposition levels. Species annotation of fungal OTUs was conducted using the UNITE database, and histograms of species annotation information at the phylum and class levels were constructed using Origin 2019 software (Origin Lab, Northampton, MA, USA). LEfSe (v1.0) [27] was used to analyze the inter-group differences among bacteriophages, and the main bacteriophages specific to each group were identified. Symbiotic network maps were constructed based on Spearman correlations for molecular ecological networks, using random matrix theory to find the optimal correlation thresholds [28], and the interactive platform Gephi [29] was used to explore and visualize network structures. Based on OTU abundance, functional annotation of fungi was performed using FUNGuild [30], and histograms of fungal trophic types were drawn using Origin 2019 software. Pearson correlation analyses were performed between soil fungi at the genus level and functional groups, and plotted using R software 2021.

3. Results

3.1. OTUs of Soil Fungi Collected near Moso Bamboo Stumps

Our results show that the OTUs of soil fungi outside and inside the bamboo stumps differed according to the decomposition levels (Figures 3 and 4). Among the three levels of decomposition, 935 and 743 OTUs of common soil fungal were present inside and outside the stumps. There were 527 common OTUs present among all the soil samples, and the common rates of fungal OTUs outside and inside the stumps were 56.36 and 70.93%, respectively. Under moderate and heavy decomposition levels, the abundance of fungal OTUs was significantly higher ($p < 0.05$) inside than outside the stumps. The abundance of fungal OTUs gradually decreased during the decomposition process outside the stumps. There was no significant difference in OTU abundance of soil fungi among the three decomposition levels outside and inside the stumps ($p > 0.05$).

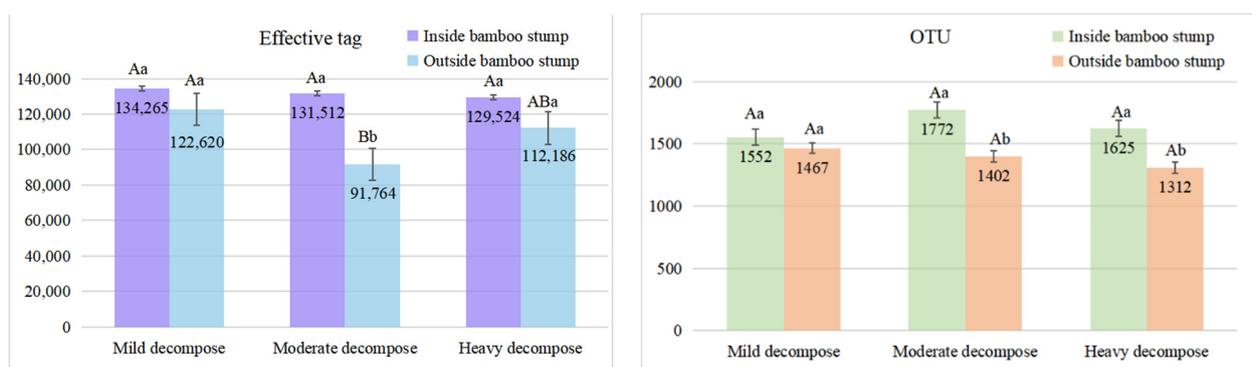


Figure 3. Differential analysis of sequencing results of soil fungi outside and inside of bamboo stumps with different levels of decomposition. Note: data in the table are the mean \pm standard deviation. Different capital letters indicate that the differences between the different levels of decomposition outside and inside the bamboo stumps are significant at the 0.05 level; different lowercase letters indicate that the differences between the same level of decomposition outside and inside the bamboo stumps are significant at the 0.05 level.

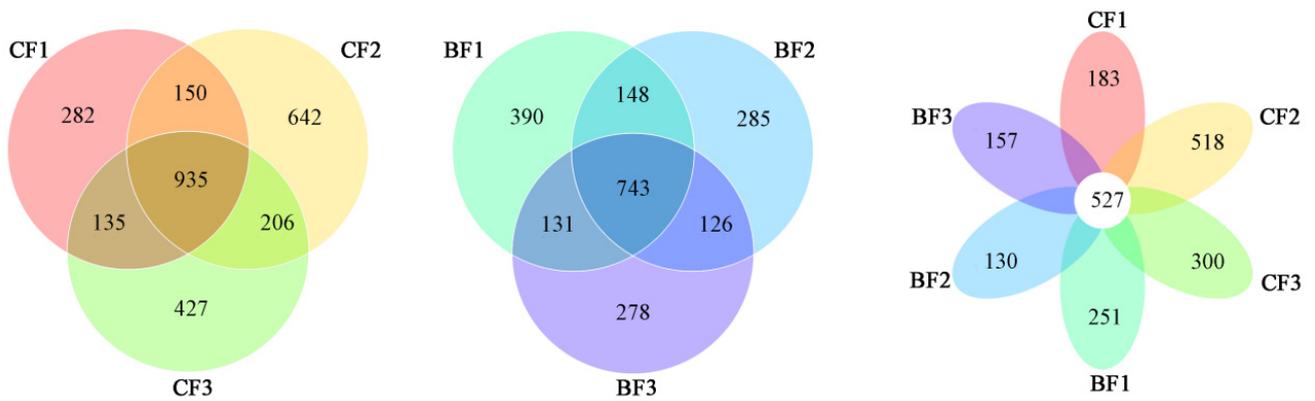


Figure 4. OTU Venn diagrams of soil fungi inside and outside of bamboo stumps with different degrees of decomposition. Note: CB1, CB2, and CB3 indicate mildly, moderately, and heavily decomposed soil samples inside the bamboo stumps, respectively; BB1, BB2, and BB3 indicate mildly, moderately, and heavily decomposed soil samples outside the bamboo stumps, respectively.

3.2. Soil Fungi Alpha Diversity and Beta Diversity near Moso Bamboo Stumps

In general, the Chao1, ACE, Shannon, and Simpson indices show that the diversity index was greater inside than outside the bamboo stumps at the same degree of decomposition. The diversity index was highest for the stumps at a moderate degree of decomposition, while the diversity index decreased with the increasing degree of decomposition outside the stumps (Figure 5a). The distance between the samples outside and inside the stump was larger than that between the samples with different degrees of decomposition (Figure 5b), which indicates that the difference in soil fungal communities outside and inside the bamboo stumps was larger than that between the different degrees of decomposition.

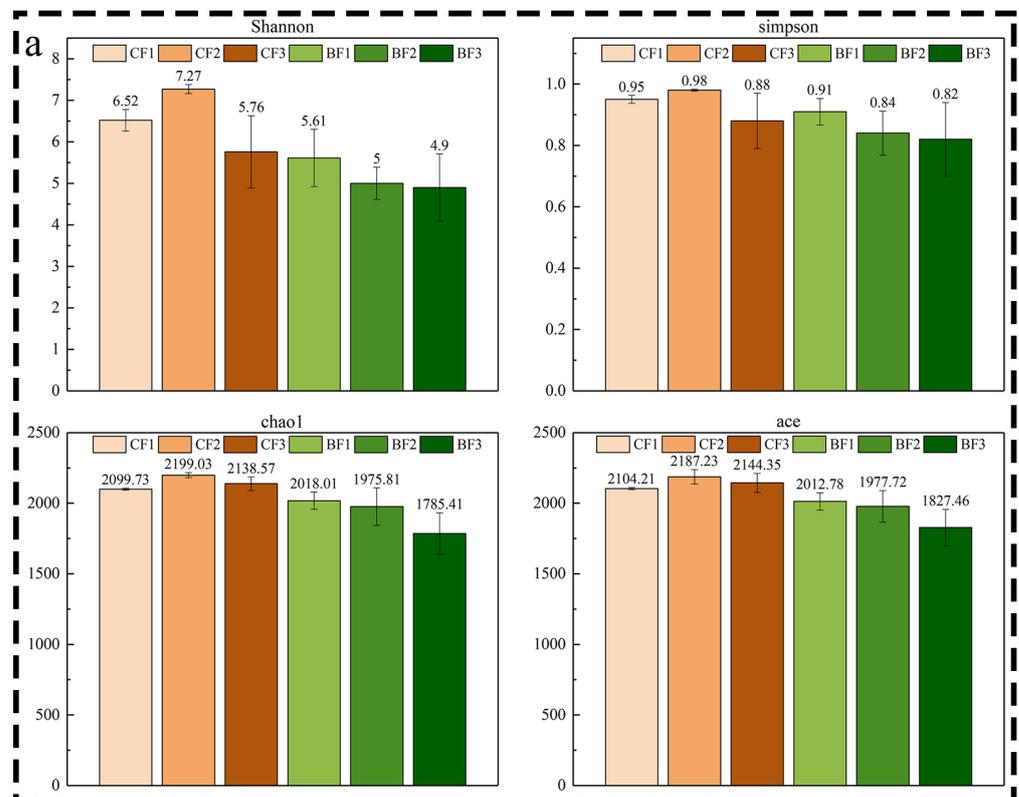


Figure 5. Cont.

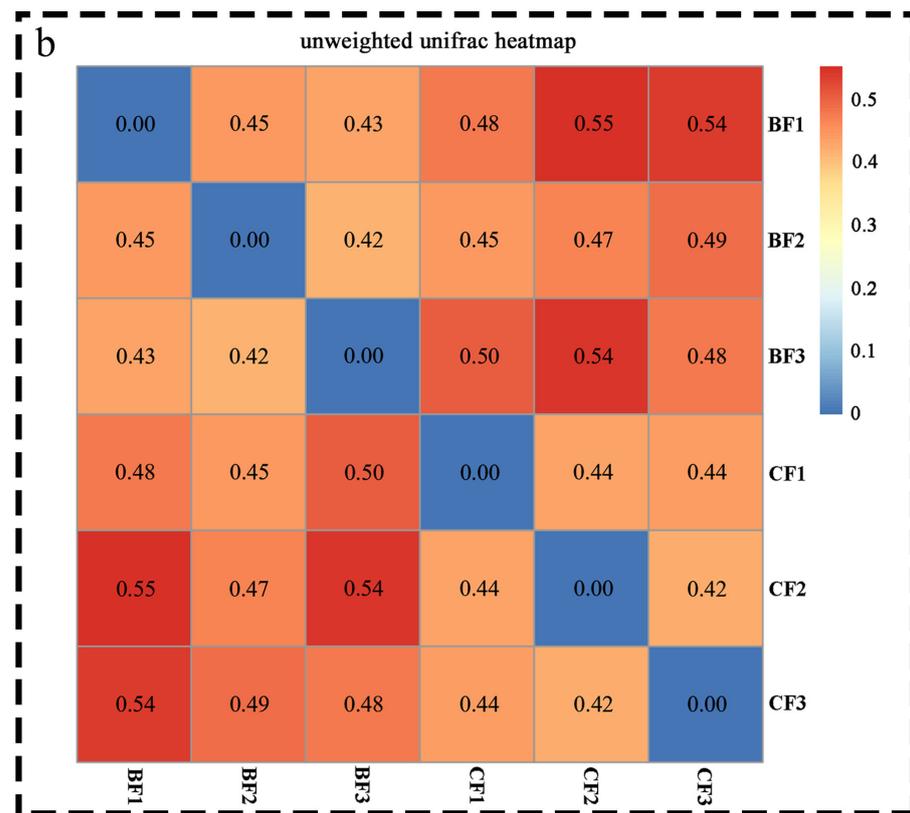


Figure 5. Diversity and richness index (a) and unweighted UniFrac distance matrix (b) of soil fungi outside and inside of bamboo stumps with different degrees of decomposition. Note: Data in the table are means, there were no significant differences. CB1, CB2, and CB3 indicate mildly, moderately, and heavily decomposed soil samples inside the bamboo stumps, respectively; BB1, BB2, and BB3 indicate mildly, moderately, and heavily decomposed soil samples outside the bamboo stumps, respectively.

3.3. Structural Composition of Soil Fungal Community near Moso Bamboo Stumps

The abundances of soil fungal communities around decaying bamboo stumps were extremely high, with nine phyla, 30 classes, 77 orders, 149 families, and 247 genera of fungi detected. The dominant phyla across the soil fungal communities were Ascomycota and Basidiomycota (Figure 6a). The proportion of Ascomycota decreased approximately from 81% to 46% inside and from 69% to 49% outside with increasing decomposition from mild to heavy. The proportion of Basidiomycota increased approximately from 17% to 49% outside with increasing decomposition levels of bamboo stumps; during heavy decomposition, the relative abundance was higher than that of Ascomycota. As the decomposition process increased from mild to heavy, the relative abundances of Mucoromycota and other phyla inside the bamboo stumps gradually increased. In all stages of decomposition, the relative abundances of Mortierellomycota, Rozellomycota, and Mucoromycota were higher inside than outside bamboo stumps, while that of Basidiomycota was the opposite.

The relative abundance of the named dominant fungal genera varied outside and inside the bamboo stumps at different levels of decomposition (Figure 6b). Inside the bamboo stumps, the dominant genera in mild decomposition were *Penicillium* (6.98%) and *Saitozyma* (2.10%); in moderate decomposition, the dominant genera were *Saitozyma* (3.72%) and *Trechispora* (3.21%); and in heavy decomposition, the dominant genera were *Saitozyma* (4.54%) and *Trichoderma* (2.70%). Outside the bamboo stumps, the dominant genera for mild decomposition were *Hymenochaete* (12.48%) and *Cyphellophora* (4.70%); in moderate decomposition, the dominant genera were *Saitozyma* (0.98%) and *Trichoderma* (0.53%); and in heavy decomposition, the dominant genera were *Hydropus* (6.85%) and *Saitozyma* (0.62%).

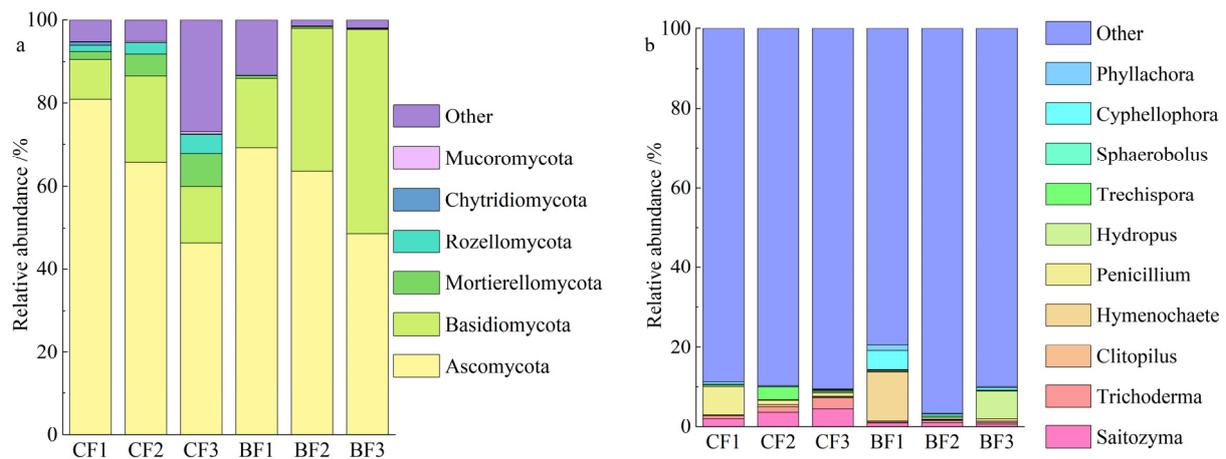


Figure 6. Relative abundance of soil fungi at the phylum level (a) and genus level (b) inside and outside of bamboo stumps with different degrees of decomposition. Note: CB1, CB2, and CB3 indicate mildly, moderately, and heavily decomposed soil samples inside the bamboo stumps, respectively; BB1, BB2, and BB3 indicate mildly, moderately, and heavily decomposed soil samples outside the bamboo stumps, respectively.

A two-way ANOVA of the fungal communities showed (Table 2) that the factor of occurring inside and outside the bamboo stumps highly significantly affected Chytridiomycota, Mucoromycota, and *Penicillium* ($p < 0.001$), and significantly affected Mortierellomycota, Rozellomycota, *Saitozyma*, and *Trichoderma* ($p < 0.05$). The factor of the degree of decomposition highly significantly affected Chytridiomycota and *Penicillium* ($p < 0.001$), and significantly affected Mucoromycota ($p < 0.05$). The interaction between the factors of occurring inside and outside the bamboo stumps and the degree of decomposition highly significantly affected Chytridiomycota and *Penicillium* ($p < 0.001$), and significantly affected Mucoromycota ($p < 0.05$).

Table 2. Two-way ANOVA for fungal community.

Fungal Communities	Inside and Outside Bamboo Stump			Degree of Decomposition			Inside and Outside Bamboo Stump \times Degree of Decomposition		
	df	F	p	df	F	p	df	F	p
Ascomycota	3	0.189	0.674	3	3.395	0.080	9	0.226	0.802
Basidiomycota	3	4.613	0.060	3	1.614	0.252	9	0.965	0.417
Mortierellomycota	3	7.671	0.022	3	0.957	0.420	9	1.29	0.322
Rozellomycota	3	6.124	0.035	3	0.590	0.574	9	0.571	0.584
Chytridiomycota	3	43.011	<0.001	3	32.342	<0.001	9	35.946	<0.001
Mucoromycota	3	57.616	<0.001	3	9.91	0.005	9	8.200	0.009
<i>Saitozyma</i>	3	10.023	0.011	3	0.636	0.552	9	0.892	0.443
<i>Trichoderma</i>	3	8.173	0.019	3	1.936	0.200	9	1.680	0.240
<i>Clitopilus</i>	3	0.197	0.668	3	0.177	0.840	9	1.285	0.323
<i>Hymenochaete</i>	3	4.667	0.059	3	4.115	0.054	9	4.144	0.053
<i>Penicillium</i>	3	591.626	<0.001	3	329.512	<0.001	9	336.624	<0.001
<i>Hydropus</i>	3	2.737	0.132	3	2.462	0.140	9	2.156	0.172
<i>Trechispora</i>	3	3.172	0.109	3	2.722	0.119	9	2.027	0.188
<i>Sphaerobolus</i>	3	0.253	0.627	3	0.914	0.435	9	0.112	0.895
<i>Cyphellophora</i>	3	1.667	0.229	3	1.047	0.390	9	0.911	0.436
<i>Phyllachora</i>	3	0.669	0.435	3	3.409	0.079	9	0.532	0.605

3.4. Composition of Specific Soil Fungi near Moso Bamboo Stumps

LEfSe analysis is used to identify important species that are significantly different between groups. The circles radiating from inside to outside in the LEfSe analysis figure refer to the taxonomic levels from phylum to species. The different colored nodes indicate the different microbial classes that play an essential role in the group: significantly different species are colored according to group, and species without significant differences

are colored uniformly in yellow (Figure 7). At the phylum level, the abundance of Mucoromycota inside heavily decomposed bamboo stumps was the highest among all the groups. At the genus level, the abundances of *Talaromyces*, *Fusicolla*, and *Volutella* inside mildly decomposed stumps were the highest among all the groups; the abundances of *Gliocladiopsis*, *Pseudophialophora*, and *Leucoagaricus* inside moderately decomposed stumps were the highest among all the groups; and the abundance of *Cercophora* in heavily decomposed stumps was the highest among all groups. The relative abundances of *Devriesia* and *Monacrosporium* outside heavily decomposed bamboo stumps were higher than those of other groups. Likewise, the relative abundance of *Hydropus* outside heavily decomposed bamboo stumps was higher than those of other groups.

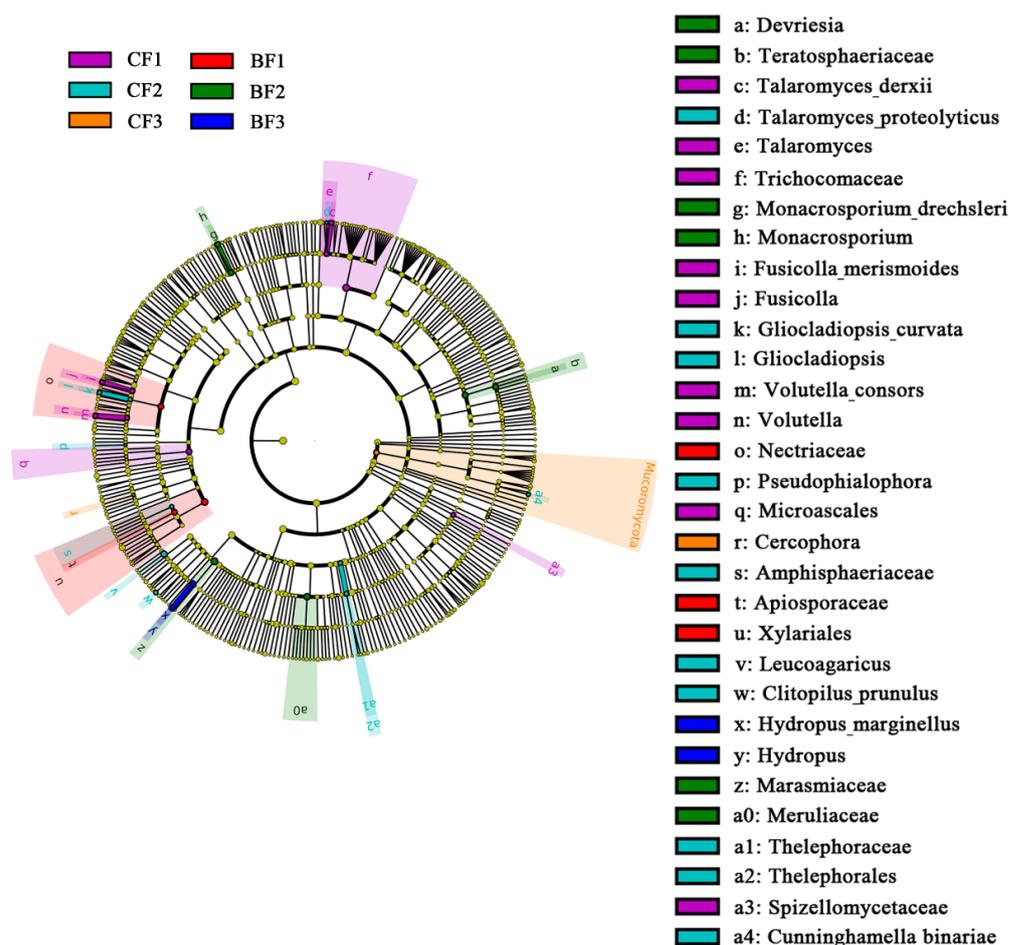


Figure 7. Distribution of different fungi in soil of Moso bamboo with different levels of decomposition. Note: CB1, CB2, and CB3 indicate mildly, moderately, and heavily decomposed soil samples inside the bamboo stumps, respectively; BB1, BB2, and BB3 indicate mildly, moderately, and heavily decomposed soil samples outside the bamboo stumps, respectively.

3.5. Soil Fungal Community Symbiotic Network and Keystone Species near Moso Bamboo Stumps

Based on the relative abundance of OTUs at the level of soil fungal genera found in samples collected from around the bamboo stumps, co-expression networks were constructed for the top 300 genera in abundance and degree of decomposition. Microbial relationship pairs were retained according to the absolute value of the Spearman correlation ($0.8, p < 0.01$), and microbial and environmental factor relationship pairs were retained according to the absolute value of the correlation coefficient ($>0.6, p < 0.05$). The results show the number of nodes (293), positive links (714), nodes associated with the degree of decomposition (37), and positive links associated with the degree of decomposition (15) for samples collected inside the bamboo stumps (Figure 8), and the number of points (296),

positive links (1234), nodes associated with the degree of decomposition (45), and positive links associated with the degree of decomposition (20) for samples collected outside the bamboo stumps. This indicates that the soil fungal communities outside the stumps exhibited more complex synergistic cooperation, whereas inside the stumps, the soil fungal communities were more competitive.

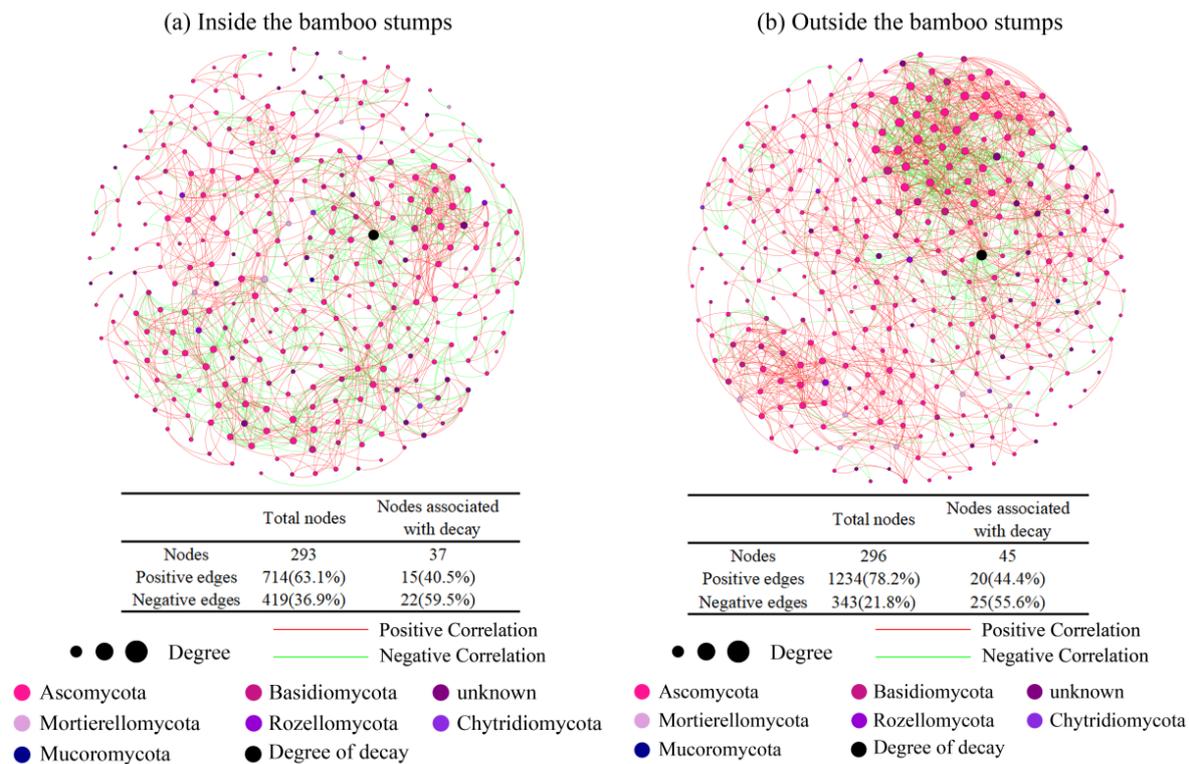


Figure 8. Symbiotic network of soil fungi OTU inside (a) and outside (b) the stumps of Moso bamboo.

3.6. Soil Fungi Trophic Types and Functional Groups near Moso Bamboo Stumps

The functional trophic modes and guilds of soil fungi around the different decomposing bamboo stumps were identified and analyzed according to FUNGuild, resulting in eight trophic modes (Figure 9) and 37 functional guilds (Figure 10). The unassigned trophic fungi represented the largest relative abundance in all soil samples (51.02%–87.38%). Among the identified trophic types, saprotroph, pathotroph, and pathotroph–saprotroph–symbiotroph were the main trophic types. The abundance of the saprotroph trophic mode (6.81%–41.61%) was the highest around the bamboo stumps. The relative abundances of saprotroph and pathotroph–saprotroph–symbiotroph trophic modes were greater inside than outside the bamboo stumps, while the opposite was true for the unassigned and pathotroph trophic modes. The relative abundances of saprotroph, pathotroph, and pathotroph–symbiotroph trophic modes inside the bamboo stumps tended to decrease with increasing decomposition, while the relative abundances of unassigned, symbiotroph, and pathotroph–saprotroph–symbiotroph trophic modes tended to increase. The number of pathotroph–symbiotroph trophic mode fungi tended to decrease outside the stumps as the decomposition level increased.

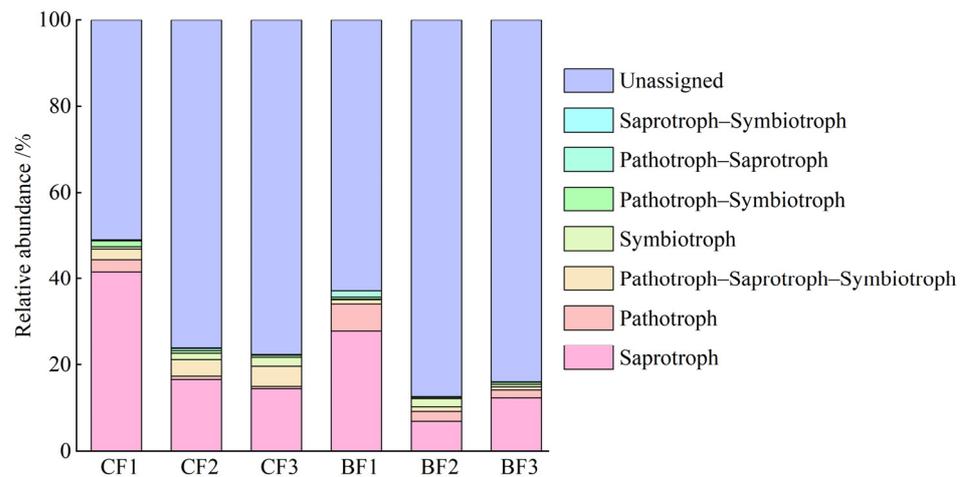
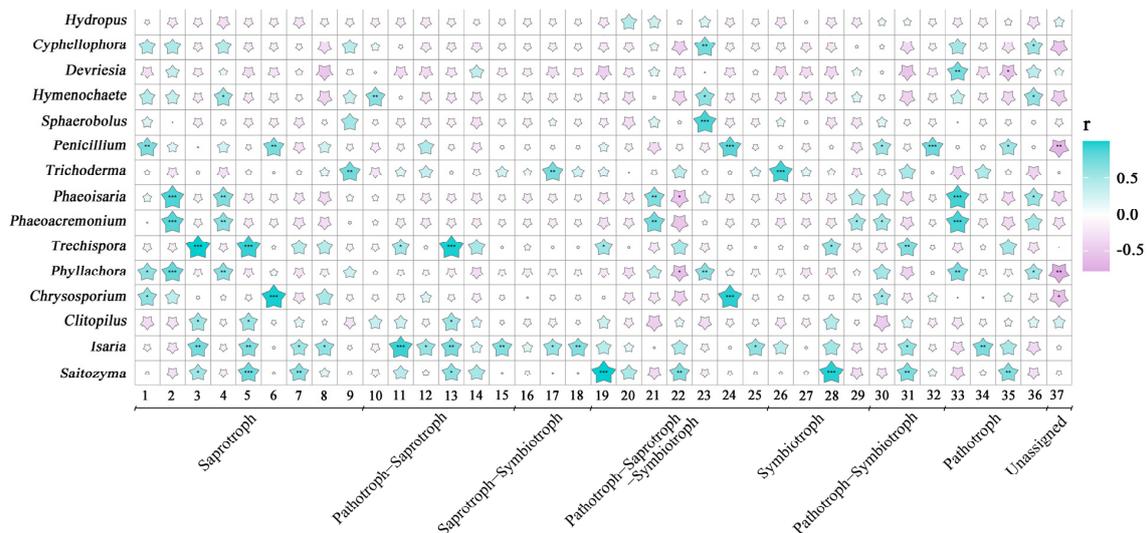


Figure 9. Relative abundance of soil fungi trophic types outside and inside of bamboo stumps with different degrees of decomposition. Note: CB1, CB2, and CB3 indicate mildly, moderately, and heavily decomposed soil samples inside the bamboo stumps, respectively; BB1, BB2, and BB3 indicate mildly, moderately, and heavily decomposed soil samples outside the bamboo stumps, respectively.



1. Undefined Saprotroph. 2. Undefined Saprotroph–Wood Saprotroph. 3. Wood Saprotroph. 4. Plant Saprotroph. 5. Soil Saprotroph. 6. Dung Saprotroph.
7. Leaf Saprotroph. 8. Dung Saprotroph–Undefined Saprotroph–Wood Saprotroph. 9. Dung Saprotroph–Soil Saprotroph–Wood Saprotroph.
10. Plant Pathogen–Soil Saprotroph–Wood Saprotroph. 11. Leaf Saprotroph–Plant Pathogen–Undefined Saprotroph–Wood Saprotroph.
12. Plant Pathogen–Wood Saprotroph. 13. Fungal Parasite–Wood Saprotroph. 14. Plant Pathogen–Undefined Saprotroph.
15. Endophyte–Plant Pathogen–Undefined Saprotroph. 16. Ectomycorrhizal–Undefined Saprotroph. 17. Undefined Saprotroph–Undefined Biotroph.
18. Endophyte–Undefined Saprotroph–Wood Saprotroph. 19. Fungal Parasite–Undefined Saprotroph.
20. Animal Pathogen–Endophyte–Plant Saprotroph–Soil Saprotroph.
21. Animal Pathogen–Dung Saprotroph–Endophyte–Plant Pathogen–Undefined Saprotroph.
22. Animal Pathogen–Endophyte–Plant Pathogen–Wood Saprotroph.
23. Animal Pathogen–Dung Saprotroph–Endophyte–Plant Saprotroph–Soil Saprotroph–Wood Saprotroph.
24. Animal Pathogen–Endophyte–Epiphyte–Plant Pathogen–Undefined Saprotroph.
25. Animal Pathogen–Endophyte–Fungal Parasite–Lichen Parasite–Plant Pathogen–Wood Saprotroph.
26. Endophyte. 27. Ectomycorrhizal. 28. Arbuscular Mycorrhizal. 29. Lichenized. 30. Endophyte–Plant Pathogen.
31. Animal Pathogen–Clavicipitaceous Endophyte–Fungal Parasite. 32. Animal Pathogen–Endophyte–Epiphyte–Plant Pathogen.
33. Plant Pathogen. 34. Animal Pathogen. 35. Fungal Parasite. 36. Fungal Parasite–Plant Pathogen. 37. Unassigned.

Figure 10. * Indicates significant correlation at the $0.01 < p < 0.05$ level, ** indicates significant correlation at the $0.001 < p \leq 0.01$ level, and *** indicates significant correlation at the $p \leq 0.001$ level.

The top 15 dominant genera with high relative abundances were selected for correlation analyses with 37 functional guilds at the genus level, identifying 12 dominant genera closely correlated with various functional fungi with saprotroph trophic modes. Among these, *Isaria* was significantly ($0.01 < p < 0.05$) or highly significantly positively correlated ($0.001 < p \leq 0.01$, $p \leq 0.001$) with 11 functional fungi with saprotroph trophic modes. The genera *Saitozyma* and *Trechispora* were significantly ($p < 0.05$) or highly significantly positively correlated ($0.001 < p \leq 0.01$, $p \leq 0.001$) with more than five functional fungi with saprotroph trophic modes. Most of the dominant fungi at the genus level were negatively correlated with undefined functional guilds, with *Penicillium* and *Phyllachora* showing highly significant negative correlations with undefined functional guilds ($0.001 < p \leq 0.01$) and *Chrysosporium* showing significant negative correlations with unassigned functional guilds ($0.01 < p < 0.05$) (Figure 10).

4. Discussion

Forest soils are rich in microorganisms [31], and the vegetation type affects soil microbial community characteristics [32–34]. The soil microbial community of Moso bamboo forests is significantly different from those of plantation forests, such as *Cunninghamia lanceolata* [35,36] and broadleaf forests [37]. It has been found that the soil outside and inside the bamboo stumps contains rich soil bacterial communities [12], and the present study also found that the soil outside and inside the bamboo stumps contains rich fungal communities. The abundance of soil fungal communities near the bamboo stumps was extremely high in this study, with nine phyla, 30 orders, 77 families, 149 families, and 247 genera of fungi detected, being more abundant than the soil fungi associated with *Ormosia hosiei* Hemsl.et Wils and *Eucalyptus robusta* Smith [38,39].

4.1. Differences in Soil Fungal Community Characteristics Inside and Outside Decomposing Bamboo Stumps

Under the action of natural and anthropogenic factors, the soil outside the bamboo stump migrates to the bamboo diaphragm inside the stump, and the soil microorganisms outside and inside the stump promote the decay and decomposition of the bamboo stump. The differences in bamboo material composition, soil, and environment around the bamboo stumps [40–42] can directly affect the soil microbial communities around the bamboo stumps. Furthermore, the differences between soil microorganisms around the bamboo stumps increase with decomposition [12]. The current study shows that the number of OTUs, and diversity and richness indices, of soil fungi inside the bamboo stumps were greater than those outside (Figures 3 and 5). This may be due to the small space and amount of soil inside the bamboo stumps, as well as the contact of the soil with the bamboo partition and inner wall, as opposed to the large space and contact of the soil outside the bamboo stumps with the outer wall of the bamboo roots. The composition and structure of bamboo stumps vary greatly from the inner to the outer wall [43]. The structure of bamboo yellow on the inner walls of bamboo stumps is looser and contains more pentosan, starch, P, and K than that of the bamboo green on the outer walls of bamboo stumps [44]. When nutrients are more abundant, more microorganisms can be recruited to reproduce and grow, and the proportion of vascular bundles, crystallinity, and tensile strength of the stumps from the inner to the outer wall gradually increase [45]. The outer wall of a bamboo stump does not decompose easily, and the nutrients produced by the decomposition of a bamboo stump that return to the soil outside are relatively sparse; thus, there were significant differences in the number of soil fungi OTUs, diversity indices, and richness indices inside and outside the bamboo stumps with the degree of decomposition. However, in this study, the number of nodes, nodes associated with the degree of decomposition, links, and positive links associated with the degree of decomposition in the fungal communities outside the bamboo stumps were greater than those inside the bamboo stumps. On the one hand, this may be because soil fungi on the periphery of bamboo stumps need to connect and interact with various soil environments on the forest floor. On the other hand, soil fungi also need

to collaborate and work together to disintegrate the densely structured outer wall of the bamboo stumps and promote decay and decomposition to obtain carbon for growth [46,47].

The dominant phyla of soil fungi identified outside and inside the bamboo stumps include Ascomycota and Basidiomycota. Members of these fungal phyla are important decomposers of organic matter, involved in material decomposition and energy flow, and are the dominant phyla of soil fungi in bamboo forests in Southern China [48–50]. In our study, the abundance of Ascomycota was higher inside than outside the bamboo stumps, while the abundance of Basidiomycota was lower inside than outside the bamboo stumps. This may be related to the material composition and structure of the inner and outer walls of the bamboo stump. The vascular bundles on the outside of the bamboo wall are small and relatively compact in structure, consisting of fiber and lignin [51]. Basidiomycota can degrade organic materials such as lignin and cellulose more effectively than other fungi in the fungal community [52–54], and therefore, promote the growth of Basidiomycota outside the bamboo stumps. *Saitozyma*, *Trechispora*, and *Hymenochaete* are fungal genera of Basidiomycota with various types of saprotrophic properties that decompose organic matter, degrade cell wall lignin, and promote mineralization of N, P, and K in the soil [55–58]. The ectomycorrhizal fungus *Hydropus* mostly grows on decaying wood, forest litter, and mosses [59]. In this study, we found that *Hydropus* was the most dominant genus and endemic to the soil outside the heavily decomposed bamboo stumps.

Two-way ANOVA showed that the factor of occurring outside and inside the bamboo stump highly significantly affected *Penicillium* ($p < 0.001$) and significantly affected *Saitozyma* and *Trichoderma* ($p < 0.05$). *Penicillium* and *Trichoderma* are the most common decomposing fungi of Ascomycota in soil; *Penicillium* can secrete laccase to degrade lignin, and *Trichoderma* can secrete phosphatase, urease, and cellulase, contributing to the release of N and P from the host organism and the degradation of structural material [60]. The outer wall of the bamboo stump is also rich in lignin and cellulose; thus, there are differences between *Penicillium* and *Trichoderma* outside and inside the bamboo stump.

4.2. Effect of Bamboo Stump Decomposition on Soil Fungal Community Characteristics

Soil fungi are involved in the decomposition of organic matter, and are essential in biogeochemical cycles. In the early stages of the decomposition of plants, fungi are more active than bacteria [61], and more inclined to utilize refractory substances in the environment (lignin and cellulose) [15]. More than 85% of the dry weight of Moso bamboo is cellulose, hemicellulose, and lignin, with small amounts of waxes, pectins, tannins, essential oils, water-soluble matter, and ash [44,45]. During the decomposition of bamboo stumps, the lignin and cellulose, which are difficult to degrade, will gradually decompose and transform into easily degradable sugars, reducing the substrate available for fungi growth, i.e., lignin and cellulose, while gradually increasing the substrate available for bacteria growth, i.e., easily degradable sugars. Therefore, soil bacteria around the bamboo stumps will gradually increase during decomposition [12]. This study also proved that the OTU abundance, diversity index, and richness index of soil fungi in samples collected outside the bamboo stumps decreased with an increase in decomposition level, but the changes were not significant. This might be because the bamboo whip in the underground part of the bamboo stumps was connected to the growing bamboo, and there were still some viable roots outside the bamboo stumps that could form symbiotic relationships with soil fungi. Whereas soil fungi and plants can form a mycorrhizal symbiosis, some fungi can specialize in breaking down decomposing organic compounds (lignin and cellulose) [62]. At the early stage of decay, bamboo stumps were rich in lignin and cellulose; however, as the degree of decomposition of bamboo stumps increased, the lignin and cellulose decomposed, the vitality of underground stumps' roots declined, and the symbiotic mycorrhizal fungi lost their host dependence. Thus, the number of soil fungi declined and was not significant.

Inside the bamboo stumps, the number of OTUs, diversity index, and richness index of soil fungi were highest in the moderately decomposed stumps and lowest in the heavily decomposed stumps (Figures 3 and 5). This may be related to the composition and structure

of the inner wall of the bamboo stumps, with the bamboo yellow decomposing more readily [44]. At a moderate level of decomposition, there is sufficient substrate for the soil fungi, leading to an increase in their relative abundance. In contrast, at a heavy level of decomposition, the substrate available for the fungi gradually decreases and competition for nutrient resources occurs among colonies, leading to a decrease in the number and diversity of fungal OTUs [13]. This is consistent with the results of wood decay [63,64] and litter decomposition [65], in which the highest fungal OTU numbers and indices of diversity and richness were found in samples taken near the moderate decomposition.

The bamboo stump is rich in cellulose and lignin, providing a suitable growth environment for both Ascomycota and Basidiomycota. Ascomycota is an important decay-causing phylum [66]. With the decomposition of the bamboo stumps, the relative abundance of Ascomycota in the soil, both outside and inside the stumps, gradually decreased, while Basidiomycota gradually occupied a dominant position outside the stumps. The Ascomycota can produce a variety of cellulases and exhibit a strong ability to decompose cellulose. Basidiomycota are the most competent microbial group for decomposing lignin [52]. When fungi decompose the same substrate, the soft rot fungi of Ascomycota can only degrade cellulose, while the white and brown rot fungi of Basidiomycota can degrade cellulose and lignin; thus, the relative abundance of Basidiomycota is higher in the later stages of decay [67]. In studies on fungi involved in the decomposition of litter and straw returning, the relative abundance of Ascomycota gradually decreased with the decomposition of organic matter, and the abundance of Basidiomycota increased, which is consistent with the present study [68,69]. In contrast, Ascomycota was found to be dominant in the decomposition of ancient trees in forest land; the proportion of Basidiomycota in the later stage of decay was significantly reduced compared with that in the early and middle stages [66]. This is inconsistent with the present study, possibly because the lignin content of wood from trees and bamboo wood differs. No significant changes in the lignin content of ancient trees were observed as the decay increased, but competition for nutrient resources occurred in the later stage of decay, resulting in a decrease in the abundance of Basidiomycota. The current study shows that the composition and structure of soil fungal communities inside and outside bamboo stumps changes during the decay process. However, the driving factors among the fungal community characteristics and their mechanisms need to be further investigated.

4.3. Functional Analysis of Soil Fungi near Decomposing Bamboo Stumps

The presence of a large number of fungi in the soil is only partially due to saprophytic fungi. In this study, the saprophytic fungi around the bamboo stumps were the main nutritional types defined, which may be related to the richness of wood fibers that can provide nutrients to the saprophytic fungi in the adjacent soil [70]. The relative abundance of saprotroph trophic modes was higher inside than outside the bamboo stumps, decreasing gradually with an increase in decomposition. The relative abundance of saprotroph trophic modes around mildly decayed bamboo stumps was significantly higher than that around moderately and heavily decayed stumps (Figure 8). This may be a result of the decay process of bamboo stumps, in which the substrate declines with decay, thus affecting the growth of saprophytic fungi and leading to their reduction [71]. The relative abundance of pathotrophic fungi was higher outside than inside the bamboo stumps, probably because pathotrophic fungi need to obtain nutrient sources from host cells. The bamboo stump felling piles are connected to the disjointed subterranean whip root system of other Moso bamboo forests, and while some of the bamboo whips are still active, they provide hosts for the growth of pathotrophic fungi, which can grow through mycelium that can successfully penetrate the pores in the soil of the forest floor [72]. In addition, most of the fungal functions (51.02%–87.38%) in this study are still not annotated, especially in fungi that are particularly abundant in the middle and late stages of bamboo stump decay. These complex fungal functions are well worth further in-depth study.

Phyllachora, *Phaeoacremonium*, and *Hymenochaete* were significantly correlated with many types of saprophytic functions, and are presumed to play important roles in the decomposition of bamboo stumps. *Phyllachora* and *Phaeoacremonium*, genera within the Sor-dariomycetes (Ascomycota), are capable of decomposing various organic matter residues and promoting the cycling of many elements, including C, N, and P [73,74], as well as decaying trees [66]. *Devriesia* belong to the pathotrophic fungi, and have been found in the soil of the windy and sandy areas of plantation forests in Northwestern Liaoning Province, among *Deyeuxia angustifolia* in the wetlands of the Sanjiang Plain, and in the tree hole soil of *Robinia pseudoacacia* [75–77]. In this study, we found that the abundance of soil fungi of the genus *Isaria* around the bamboo stump was low; however, it was significantly correlated with the function of a wider range of saprophytic types. These results suggest that *Isaria* is a genus of entomopathogenic fungi, and more than 100 species of *Isaria* fungi have been found [78]. Interestingly, the 15 genera with the highest abundances in this study were significantly correlated with 36 identified fungi in the functional correlation analysis, and almost all were positively correlated, while all were negatively correlated with unassigned functional guilds. In this paper, we found that more than half of the fungi still belonged to undefined trophic fungi. Future research on this group should further clarify their fungal functions, improving the prediction of soil fungal functions and providing a scientific basis for the screening of fungal strains with decay functions.

5. Conclusions

In this study, we preliminarily analyzed the structural and functional characteristics of soil fungal communities outside and inside bamboo stumps at different levels of decomposition, and the specific conclusions are as follows:

1. The soil fungi OTUs and diversity and richness indices were higher inside than outside the stumps. The soil fungi OTUs and diversity and richness indices outside the bamboo stumps decreased with increasing degrees of decomposition. The soil fungi OTUs and diversity and richness indices inside the bamboo stumps were highest in moderate decomposition and lowest in heavy decomposition.
2. Ascomycota and Basidiomycota were the dominant soil fungi outside and inside the bamboo stumps; the relative abundance of Ascomycota decreased with the increase in decomposition, while the relative abundance of Basidiomycota increased with the increase in decomposition. The genera *Penicillium*, *Trechispora*, and *Saitozyma* were the dominant genera inside the bamboo stumps. *Hymenochaete*, *Hydropus*, *Devriesia*, and *Cyphellophora* were the dominant genera of soil fungi outside the bamboo stumps. The interaction between the factors of occurring outside and inside bamboo stumps and the degree of decomposition significantly affected Chytridiomycota, *Penicillium* ($p < 0.001$), and Mucoromycota ($p < 0.05$).
3. Around bamboo stumps, the relative abundance of soil fungi with undefined functions was highest (51.02%–87.38%), followed by that of saprophytic soil fungi (6.81%–41.61%). The relative abundance of saprophytic functional fungi was significantly higher in mild vs. moderate and heavy decomposing bamboo stumps. Symbiotic trophic fungi and other undefined functional fungi increased progressively with increasing degrees of decomposition.

Changes in the structure and functional groups of soil fungal communities may play an important role during different levels of decomposition of Moso bamboo stumps, providing a scientific basis for screening for functional fungal strains that promote the decomposition of Moso bamboo stumps. However, there are some limitations to this study, and in future research, the present techniques should be combined with macro-genomics, functional gene chip technology, and gene prediction analysis to strengthen the linkage between microbial species diversity, structure, and function, and to further understand the specific roles of microorganisms in bamboo stump decay.

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References

1. Yuan, Z.; Liu, F.; Liu, Z.; Huang, Q.; Zhang, G.; Pan, H. Structural variability and differentiation of niches in the rhizosphere and endosphere bacterial microbiome of moso bamboo (*Phyllostachys edulis*). *Sci. Rep.* **2021**, *11*, 1574. [[CrossRef](#)] [[PubMed](#)]
2. Administration, S.F. *Report for Chinese Forest Resource—The 8th National Forest Inventory*; China Forestry Publishing House: Beijing, China, 2014. (In Chinese)
3. Zhang, M.; Chen, S.; Jiang, H.; Cao, Q. The water transport profile of *Phyllostachys edulis* during the explosive growth phase of bamboo shoots. *Glob. Ecol. Conserv.* **2020**, *24*, e01251. [[CrossRef](#)]
4. Huang, M.; Wang, W.; Zhou, Z.; Tang, C. High-yield rhizome shoot cultivation technology for moso bamboo in Suichang county, Zhejiang province. *World Bamboo Ratt.* **2021**, *19*, 65–67, 71. (In Chinese)
5. Zheng, R. Effects of *phyllostachys pubescens* forest bamboo pockets fertilization on bamboo pockets rot and the bamboo shoot emergence. *J. Fujian For. Sci. Technol.* **2011**, *38*, 72–74. (In Chinese) [[CrossRef](#)]
6. Song, J. *Study on the Change of Components of Bamboo Stumps in Bamboo Forest of Phyllostachys Edulis and Artificially Promoting Decomposition Technology*; Central South University of Forestry and Technology: Changsha, China, 2018. (In Chinese)
7. Li, Q.; Ma, Q.; Gao, J.; Zhang, J.; Li, Y.; Shi, M.; Peng, C.; Song, X. Stumps increased soil respiration in a subtropical Moso bamboo (*Phyllostachys edulis*) plantation under nitrogen addition. *Agric. For. Meteorol.* **2022**, *323*, 109047. [[CrossRef](#)]
8. Xu, Q.; Jiang, P.; Wu, J.; Zhou, G.; Shen, R.; Fuhrmann, J. Bamboo invasion of native broadleaf forest modified soil microbial communities and diversity. *Biol. Invasions* **2015**, *17*, 433–444. [[CrossRef](#)]
9. Xu, H.; Yu, M.; Cheng, X. Abundant fungal and rare bacterial taxa jointly reveal soil nutrient cycling and multifunctionality in uneven-aged mixed plantations. *Ecol. Indic.* **2021**, *129*, 107932. [[CrossRef](#)]
10. Gillespie, L.; Hättenschwiler, S.; Milcu, A.; Wambsganss, J.; Shihan, A.; Fromin, N. Tree species mixing affects soil microbial functioning indirectly via root and litter traits and soil parameters in European forests. *Funct. Ecol.* **2021**, *35*, 2190–2204. [[CrossRef](#)]
11. Yang, X.; Wang, X.; Xiao, S.; Liu, Z.; Zhou, X.; Du, G.; Liu, K.; Wang, Y.; Chen, S.; Nielsen, U. Dominant plants affect litter decomposition mainly through modifications of the soil microbial community. *Soil Biol. Biochem.* **2021**, *161*, 108399. [[CrossRef](#)]
12. Liang, F.; Huang, X.; Zheng, H.; Ma, X.; Huang, Y.; Sun, N.; Qin, X.; Jin, C.; Yu, L.; Cai, L. Characteristics of the soil bacterial community in the decomposition process inside and outside moso bamboo stumps. *Plant Soil* **2022**, *478*, 635–650. [[CrossRef](#)]
13. Li, M.; Ai, W.; Yang, M.; Meng, Y.; Tu, J.; Pu, X.; Liu, X. The changes of microorganism in the bamboo stump with different decomposition degree. *J. For. Eng.* **2014**, *28*, 64–67. (In Chinese)
14. Richter, A.; Schöning, I.; Kahl, T.; Bauhus, J.; Ruess, L. Regional environmental conditions shape microbial community structure stronger than local forest management intensity. *For. Ecol. Manag.* **2018**, *409*, 250–259. [[CrossRef](#)]
15. Ding, X. *The Effect of Land Management Intensification on Soil Property and Microbial Community*; Anhui Agricultural University: Hefei, China, 2019. (In Chinese) [[CrossRef](#)]
16. Van, D.; Bardgett, R.; Bever, J.; Bezemer, T.; Casper, B.; Fukami, T.; Kardol, P.; Klironomos, J.; Kulmatiski, A.; Schweitzer, J.; et al. Plant-soil feedbacks: The past, the present and future challenges. *J. Ecol.* **2013**, *101*, 265–276. [[CrossRef](#)]
17. Galetto, L.; Torres, C.; Martínez Pastur, G. Variable retention harvesting: Conceptual analysis according to different environmental ethics and forest valuation. *Ecol. Process.* **2019**, *8*, 40. [[CrossRef](#)]
18. Zhuang, S.; Ji, H.; Zhang, H.; Sun, B.; Gui, R. Carbon storage of *Phyllostachy edulis* ecosystems in Jian'ou city. *Ecol. Environ. Sci.* **2012**, *21*, 1200–1204. (In Chinese) [[CrossRef](#)]
19. Yan, E.; Wang, X.; Huang, J. Concept and classification of coarse woody debris in forest ecosystems. *Acta Ecol. Sin.* **2005**, *1*, 158–167. (In Chinese) [[CrossRef](#)]

20. Toju, H.; Tanabe, A.; Yamamoto, S.; Sato, H. High-Coverage ITS Primers for the DNA-Based Identification of Ascomycetes and Basidiomycetes in Environmental Samples. *PLoS ONE* **2012**, *7*, e40863. [CrossRef]
21. Edgar, R. UPARSE: Highly accurate OTU sequences from microbial amplicon reads. *Nat. Methods* **2013**, *10*, 996–998. [CrossRef]
22. Kemp, P.; Aller, J. Bacterial diversity in aquatic and other environments: What 16S rDNA libraries can tell us. *FEMS Microbiol. Ecol.* **2004**, *47*, 161–177. [CrossRef]
23. Edgar, R. MUSCLE: Multiple Sequence Alignment with High Accuracy and High Throughput. *Nucleic Acids Res.* **2004**, *32*, 1792–1797. Available online: <http://www.drive5.com/muscle/> (accessed on 2 July 2018). [CrossRef]
24. Lozupone, C.; Knight, R. Unifrac: A new phylogenetic method for comparing microbial communities. *Appl. Environ. Microbiol.* **2005**, *71*, 8228–8235. [CrossRef]
25. Wang, Q.; Garrity, G.; Tiedje, J.; Cole, J. Naive Bayesian Classifier for Rapid Assignment of rRNA Sequences into the New Bacterial Taxonomy. *Appl. Environ. Microbiol.* **2007**, *73*, 5261–5267. [CrossRef]
26. Kõljalg, U.; Larsson, K.; Abarenkov, K.; Nilsson, R.; Alexander, I.; Eberhardt, U.; Erland, S.; Høiland, K.; Kjølner, R.; Larsson, E.; et al. UNITE: A database providing web-based methods for the molecular identification of ectomycorrhizal fungi. *New Phytol.* **2005**, *166*, 1063–1068. [CrossRef] [PubMed]
27. Segata, N.; Izard, J.; Waldron, L.; Gevers, D.; Miropolsky, L.; Garrett, W.S.; Huttenhower, C. Metagenomic biomarker discovery and explanation. *Genome Biol.* **2011**, *12*, R60. [CrossRef] [PubMed]
28. Deng, Y.; Jiang, Y.; Yang, Y.; He, Z.; Luo, F.; Zhou, J. Molecular ecological network analyses. *BMC Bioinf.* **2012**, *13*, 113. [CrossRef] [PubMed]
29. Bastian, M.; Heymann, S.; Jacomy, M. Gephi: An Open Source Software for Exploring and Manipulating Networks. In Proceedings of the International AAAI Conference on Web and Social Media, San Jose, CA, USA, 17–20 May 2009.
30. Nguyen, N.; Song, Z.; Bates, S.; Branco, S.; Tedersoo, L.; Menke, J.; Schilling, J.; Kennedy, P. FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecol.* **2016**, *20*, 241–248. [CrossRef]
31. Lladó, S.; López-Mondéjar, R.; Baldrian, P. Drivers of microbial community structure in forest soils. *Appl. Microbiol. Biotechnol.* **2018**, *102*, 4331–4338. [CrossRef] [PubMed]
32. Burton, J.; Chen, C.; Xu, Z.; Ghadiri, H. Soil microbial biomass, activity and community composition in adjacent native and plantation forests of subtropical Australia. *J. Soils Sediments* **2010**, *10*, 1267–1277. [CrossRef]
33. Chodak, M.; Klimek, B.; Niklińska, M. Composition and activity of soil microbial communities in different types of temperate forests. *Biol. Fertil. Soils* **2016**, *52*, 1093–1104. [CrossRef]
34. Wang, X.; Sasaki, A.; Toda, M.; Nakatsubo, T. Changes in soil microbial community and activity in warm temperate forests invaded by moso bamboo (*Phyllostachys pubescens*). *J. Res.* **2016**, *21*, 235–243. [CrossRef]
35. Wang, C.; Xue, L.; Dong, Y.; Jiao, R. Effects of stand density on soil microbial community composition and enzyme activities in subtropical *Cunninghamia lanceolata* (Lamb.) Hook plantations. *For. Ecol. Manag.* **2021**, *479*, 118559. [CrossRef]
36. Fang, H.; Liu, Y.; Bai, J.; Li, A.; Deng, W.; Bai, T.; Liu, X.; Lai, M.; Feng, Y.; Zhang, J.; et al. Impact of Moso Bamboo (*Phyllostachys edulis*) Expansion into Japanese Cedar Plantations on Soil Fungal and Bacterial Community Compositions. *Forests* **2022**, *13*, 1190. [CrossRef]
37. Li, Y.; Li, Y.; Chang, S.; Xu, Q.; Guo, Z.; Gao, Q.; Qin, Z.; Yang, Y.; Chen, J.; Liang, X. Bamboo invasion of broadleaf forests altered soil fungal community closely linked to changes in soil organic C chemical composition and mineral N production. *Plant Soil* **2017**, *418*, 507–521. [CrossRef]
38. Liu, B. *The Effects of Different Eucalyptus Stand on Soil Fungal Community Structures and Functions*; Nanjing Forestry University: Nanjing, China, 2020. (In Chinese)
39. Peng, H.; Zhou, H.; Zhang, G.; Wang, H. Composition structure and diversity of soil fungi community in *Ormosia hosiei* plantations at different ages. *J. Cent. South Univ. For. Technol.* **2021**, *41*, 129–135. (In Chinese)
40. Zheng, Y.; Hong, W. *Moso Bamboo Management*; Xiamen University Press: Xiamen, China, 1998.
41. Fang, K.; Yang, Q.; Shi, J.; Wu, L.; Guo, Q.; Li, J.; Yang, G. A primary study on chemical characteristics' variation of moso bamboo wood from subtropical zone. *Acta Agric. Univ. Jiangxiensis* **2009**, *31*, 679–684. (In Chinese)
42. Tang, W. Effect of bamboo stump rotting on soil physicochemical properties. *World Bamboo Ratt.* **2013**, *11*, 31–33. (In Chinese) [CrossRef]
43. He, L.; Chen, L.; Shai, H.; Qi, J.; Jiang, Y.; Xiao, H.; Chen, Y.; Huang, X.; Xie, J. Microstructure and physicochemical properties of the anisotropic moso bamboo (*Phyllostachys pubescens*) surface. *Eur. J. Wood Prod.* **2022**, *80*, 277–288. [CrossRef]
44. Fan, F. *Seasonal Variation of Starch Content in Dendrocalamus giganteus and Phyllostachys edulis and Its relationship to Insect Damages*; Southwest Forestry University: Kunming, China, 2010. (In Chinese)
45. Yang, X.; Pang, X.; Liu, X.; Yang, S.; Li, X. Determining the pore structure and radial variability of moso bamboo (*Phyllostachys edulis*). *Wood Sci. Technol.* **2023**, *57*, 345–357. [CrossRef]
46. Wen, T. *The Research on Bamboo Lignin Degradation and Efficiency Composite Construction of Strains in the Fermentation Process*; Central South University of Forestry and Technology: Changsha, China, 2016. (In Chinese)
47. Wei, X.; Wang, G.; Smith, L.; Chen, X.; Jiang, H. Effects of gradient distribution and aggregate structure of fibers on the flexibility and flexural toughness of natural moso bamboo (*Phyllostachys edulis*). *J. Mater. Res. Technol.* **2022**, *16*, 853–863. [CrossRef]

48. Wu, C. *Early Response of Soil Microbial Community Structure after Strip Cutting in Moso Bamboo Forest in Central Fujian*; Chinese Academy of Forest: Beijing, China, 2020. (In Chinese)
49. Yan, S. *The Different Soil Microbial Characteristics of Moso Bamboo and Chinese Fir as well as Its Affecting Mechanism*; Zhejiang A&F University: Hangzhou, China, 2021. (In Chinese)
50. Yan, S.; Liu, M.; Liu, C.; Zhao, M.; Qiu, W.; Gu, J.; Feng, G.; Gao, J.; Cai, L.; Xu, Q. Soil Microbial Diversity is Higher in Pure Stands of Moso Bamboo than in Pure Stands of Chinese Fir. *Acta Pedol. Sin.* **2022**, *59*, 1704–1717. (In Chinese) [[CrossRef](#)]
51. Wei, X.; Yuan, J.; Wang, G.; Chen, F.; Chen, X.; Jiang, H.; Smith, L.; Deng, J. Effect of chemical composition and cell structure on water vapor sorption behavior of parenchyma cells and fiber cells in moso bamboo (*Phyllostachys edulis*). *Ind. Crop. Prod.* **2022**, *178*, 114652. [[CrossRef](#)]
52. Hellequin, E.; Monard, C.; Quaiser, A.; Henriot, M.; Klarzynski, O.; Binet, F. Specific recruitment of soil bacteria and fungi decomposers following a biostimulant application increased crop residues mineralization. *PLoS ONE* **2018**, *13*, e0209089. [[CrossRef](#)]
53. Dong, X. *Changing Characteristics and Influencing Factors of the Soil Microbial Community during Litter Decomposition in the Mixed Quercus acutissima Carruth. and Robinia pseudoacacia L. Forest*; Shandong Agricultural University: Tai'an, China, 2021. (In Chinese)
54. Fuke, P.T.M.; Kumar, M.; Sawarkar, A.; Pandey, A.; Singh, L. Role of microbial diversity to influence the growth and environmental remediation capacity of bamboo: A review. *Ind. Crop. Prod.* **2021**, *167*, 113567. [[CrossRef](#)]
55. Cairney, J. Basidiomycete mycelia in forest soils: Dimensions, dynamics and roles in nutrient distribution. *Mycol. Res.* **2005**, *109*, 7–20. [[CrossRef](#)] [[PubMed](#)]
56. Lundell, T.; Mäkelä, M.; Hildén, K. Lignin-modifying enzymes in filamentous basidiomycetes-ecological, functional and phylogenetic review. *J. Basic Microbiol.* **2010**, *50*, 5–20. [[CrossRef](#)]
57. Yang, J. *Taxonomy and Phylogeny of Hymenochaete in China*; Beijing Forestry University: Beijing, China, 2016. (In Chinese)
58. Aliyu, H.; Gorte, O.; Neumann, A.; Ochsenreither, K. Draft genome sequence of the oleaginous yeast *Saitozyma podzolica* (syn. *Cryptococcus podzolicus*) DSM 27192. *Microbiol. Resour. Announc.* **2019**, *8*, e01676-18. [[CrossRef](#)]
59. Cai, L. *Relationship between Ecological Stoichiometric Characteristics and Fungal Diversity of Fallen Logs and Soil*; South China Agricultural University: Guangzhou, China, 2018. (In Chinese)
60. Wang, L. *Influence Mechanism of the Increasing Stand Age on Litter Decomposition of the Robinia Pseudoacacia Plantations in the Loess Hilly Region*; Yan'an University: Yan'an, China, 2022. (In Chinese)
61. Wang, Q.; Gao, M.; Liu, M.; Wang, H.; Dong, Y.; Wang, Y. Illumina Miseq sequencing-based fungal community of rhizosphere soils along root orders of poplar plantation. *Chin. J. Appl. Ecol.* **2017**, *28*, 1177–1183. [[CrossRef](#)]
62. Janowski, D.; Leski, T. Landscape-scale mapping of soil fungal distribution: Proposing a new NGS-based approach. *Sci. Rep.* **2023**, *13*, 10280. [[CrossRef](#)] [[PubMed](#)]
63. Wang, X.; Wei, Y. Population difference of polypores in northwest and southeast of China. *Chin. J. Appl. Ecol.* **2015**, *26*, 3160–3166. (In Chinese) [[CrossRef](#)]
64. Zhang, L.; Wei, Y. Species diversity and distribution characters of wood-decaying fungi in Fenglin Nature Reserve. *Chin. J. Ecol.* **2016**, *35*, 2745–2751. (In Chinese) [[CrossRef](#)]
65. Long, J.; Zhao, C.; Zhang, M.; Wu, J.; Wu, Q.; Huang, B.; Zhang, J. Effect of litter decomposition on soil microbes on different slopes. *Chin. J. Ecol.* **2019**, *39*, 2696–2704. (In Chinese) [[CrossRef](#)]
66. Lin, Y. *State of Disease During the Decay of Cryptomeria fortunei from Tianmu Mountain and Preliminary Control Measures for C. fortunei Decay*; Shanghai Normal University: Shanghai, China, 2020. (In Chinese)
67. Wang, S. *Study on the Humic Substance Formed by Fungi Utilizing Cellulose and Lignin and Its Structural Characteristics*; Jilin Agricultural University: Changchun, China, 2013. (In Chinese)
68. Dong, H. *Effects of Bamboo Litter Input on Soil Enzyme Activity, Microbial Community and Soil Organic Carbon Mineralization in a Broad-Leaved Forest*; Zhejiang A&F University: Hangzhou, China, 2021. (In Chinese)
69. Kong, D. *Effect on Nitrogen and Carbon Content and Microbial Community Structure of Wheat-Soybean Rotation Soil under Straw Return and Fertilizer Application Treatments*; Northwest A&F University: Xianyang, China, 2020. (In Chinese)
70. Feng, B.; Yang, Z. Ectomycorrhizal symbioses: Diversity of mycobionts and molecular mechanisms that entail the development of ectomycorrhizae. *Sci. Sin. Vitae* **2019**, *49*, 436–444. (In Chinese) [[CrossRef](#)]
71. Nan, Z.; Liu, Z.; Meng, W.; Dai, H.; Xu, J.; Wang, N.; Liu, L.; Wang, X.; Liu, K. Structure and Function of Soil Fungal Community in Rotation Fallow Farmland in Alluvial Plain of Lower Yellow River. *Chin. J. Environ. Sci.* **2022**, *44*, 482–493. [[CrossRef](#)]
72. Sun, P.; Luo, Z.; Li, L.; Niu, Y.; Cai, L.; Liu, J.; Wang, X. Influences of continuous monoculture of alfalfa and rotation of annual crops on soil fungal communities in the semi-arid Loess Plateau. *Chin. J. Eco-Agric.* **2022**, *30*, 965–975. (In Chinese) [[CrossRef](#)]
73. Luo, Q. New advances in research of the genus *Penicillium*. *Chin. J. Pharm. Biotechnol.* **2016**, *23*, 452–456. (In Chinese) [[CrossRef](#)]
74. Liu, S.; Wu, H.; Wu, H.; Zhang, H.; Fan, Z. Diversity of Cellulose-decomposing Fungi and the Characteristic of Decomposition Under Planting Corn of Black Soil in Jilin Province. *J. Maize Sci.* **2008**, *16*, 112–116. (In Chinese) [[CrossRef](#)]
75. Sui, X.; Zhang, R.; Xu, N.; Liu, Y.; Chai, C.; Wang, J.; Fu, X.; Zhong, H.; Ni, H. Fungal Community Structure of Different Degeneration *Deyeuxia angustifolia* Wetlands in Sanjiang Plain. *Chin. J. Environ. Sci.* **2016**, *37*, 3598–3605. (In Chinese) [[CrossRef](#)]
76. Shao, Q.; Dong, C.; Zhang, Z.; Zheng, H.; Zou, X.; Han, Y.; Liang, Z. A preliminary investigation on fungal community in tree hole soil of *Robinia pseudoacacia* grown with different plants. *Mycosystema* **2019**, *38*, 822–830. (In Chinese) [[CrossRef](#)]

77. Deng, J.; Zhu, W.; Zhang, Y.; Yin, Y.; Zhou, Y. Studies on soil fungal community composition and function characteristics of different plantations of sandy area, northwest Liaoning province. *For. Res.* **2020**, *33*, 44–54. (In Chinese) [[CrossRef](#)]
78. Chen, W.; Yuan, W.; Guan, X.; Hu, Q. Biodiversity of *Isaria* in soil and its activity against *Phyllotreta striolata*. *J. South China Agric. Univ.* **2021**, *42*, 75–82. (In Chinese)

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