Characteristics of Soil Bacterial Community in the Decomposition Process Inside and Outside Moso Bamboo Stumps

Fengna Liang (✉ fengnaliang@126.com)

Fujian Agriculture and Forestry University <https://orcid.org/0000-0003-2588-5696>

Xiao Huang

Fujian Agriculture and Forestry University

Huixin Zheng

Fujian Agriculture and Forestry University

Xiangqing Ma

Fujian Agriculture and Forestry University

Yonglai Huang

Fujian Jian'ou Forestry Bureau

Na Sun

Fujian Agriculture and Forestry University

Xuelong Qin

Fujian Agriculture and Forestry University

Cheng Jin

Fujian Agriculture and Forestry University

Le Yu

Fujian Agriculture and Forestry University

Liping Cai

Fujian Agriculture and Forestry University <https://orcid.org/0000-0002-8216-197X>

Research Article

Keywords: Moso bamboo stump, Decompose decay, Bacterial community, High throughput sequencing

Posted Date: January 3rd, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1192580/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License. [Read Full License](#)

Abstract

Purpose: Soil bacteria comprise the largest number of soil microorganisms and play an important role in moso bamboo (*Phyllostachys edulis*) stump decay; however, the characteristics of soil bacterial communities inside and outside these stumps remain unclear.

Methods: The characteristics of soil bacterial communities inside and outside *Phyllostachys edulis* bamboo stumps were analyzed under three different levels of decay using high-throughput sequencing technology.

Results: The abundance of operational taxonomic units inside and outside the bamboo stumps increased as the decay progressed; Proteobacteria, Acidobacteria, Actinobacteria, Planctomycetes, and Verrucomicrobia were the most abundant phyla in the soil inside and outside the bamboo stumps. In the outside bamboo stumps, there was a very significant positive correlation of Acidobacteria and Planctomycetes with the decaying degree of bamboo stumps. At the class level, Alphaproteobacteria, Gammaproteobacteria, and Planctomycetacia were the most abundant bacteria in the bamboo stumps. Inside the stumps, the decaying degree of bamboo stumps was significantly positively correlated with Alphaproteobacteria and significantly negatively correlated with Gammaproteobacteria and Bacilli. Principal component analysis and the heat map analysis at the genus level indicated similarities among soil bacterial communities inside the moderately and severely decayed bamboo stumps and among the communities outside the mildly and moderately decayed bamboo stumps.

Conclusion: Our results augment our understanding of the expeditious degradation process of bamboo stumps, and provide a theoretical basis and reference for microbiological research, sustainable bamboo stump operations, and degradation methods of bamboo forests.

Introduction

Moso bamboo (*Phyllostachys edulis* (Carrière) J. Houz.) is a perennial evergreen plant. Ninety percent of the world's moso bamboo resources are found in China, where they are widely distributed in the south in hilly mountainous areas below 800 m above sea level. Moso bamboo is widely used because of the fast growth, short felling period, and high yield. It is considered a bamboo with the highest economic value and the best performance. China has a long history of cultivating moso bamboo, which is the world's primary economic bamboo species in terms of the cultivation area, production, bamboo products, and export volume (Liu et al. 2019b). The management of moso bamboo forest involves cutting down sections of the mature moso bamboo forest to cultivate new bamboo shoots every year; generally, 600–750 moso bamboo stems are removed per hectare every year, while the bamboo stumps are left on the forest floor. The average area occupied by a single bamboo stump is 0.265 m², and the bamboo stumps can occupy approximately 10% of the forest area (Lin 2011). The bamboo stump is hard and naturally decays extremely slowly, taking an average of 9 years to decay completely, but it can last as long as 15 years (Zheng 2011). The bamboo stumps occupy a large amount of soil space in the bamboo forest, seriously affecting the extension of the moso bamboo flagellar system and the growth and yield of winter and spring bamboo shoots (Song 2018). Concurrently, it also causes certain obstacles to forestry operations, such as tending cutting and fertilizer application (Liu 2016). Therefore, the treatment of bamboo stumps is of great importance for the sustainable management of moso bamboo forests.

Bamboo stump treatment is an essential and important technical measure in the moso bamboo forest management process, and many scholars and researchers have explored related technologies. Currently, the main methods of cleaning bamboo stumps include mechanical removal, manual digging, chemical agents, microbial fungicides, and natural decay (Hua et al. 2000; Liu 2011; Ren et al. 2016; Zhu et al. 2005; Zhu et al. 2013). The physical measures of mechanical removal and manual digging can completely remove the bamboo stumps, but they are time-consuming and laborious, cause soil disturbance, destroy the soil structure, and easily cause soil erosion. Simultaneously, the organic matter and nutrients contained in the bamboo stumps are also removed from the forest land, resulting in loss of soil organic matter and nutrients, which affects the soil's biological environment (Zhu et al. 2013). Chemical removal is primarily done by adding chemical agents to accelerate the decay and decomposition of bamboo stumps; however, the chemical agents may remain in the soil and affect the soil environment and growth of the bamboo (Hua et al. 2000; Ren et al. 2016; Zhu et al. 2005). Microbial fungicides mainly rely on microbial decomposers to decompose bamboo stumps into organic matter and nutrients on the forest floor, which can improve the forest soil environment and promote bamboo forest growth (Li et al. 2008; Liu et al. 2015; Mieszkina et al. 2021; Zhao et al. 2018). Therefore, accelerating decomposition is an ideal ecological treatment for bamboo stumps.

The decomposition of bamboo stumps is inseparable from the composition of the microbial community. There are many types of soil microorganisms. Soil bacteria are the most abundant and widely distributed, and many can decompose lignin, hemicellulose, and cellulose. These bacteria can invade the root of moso bamboo to decompose cellulose and other macromolecules, causing their gradual decomposition (Ed-Haun et al. 2018; Fang et al. 2021; Hervé et al. 2016; Xu et al. 2013). The characteristics of the soil bacterial community affect the decay process of bamboo stumps, and it has been shown that the composition of bacterial populations changes during the decay of bamboo stumps (Li et al. 2015). However, the characteristics of the soil bacterial community during decay remain unknown. This study is based on the following questions: (1) What soil bacterial colonies exist around the roots of moso bamboo? (2) Are there any differences between soil bacteria inside and outside bamboo stumps? and (3) Which soil bacterial communities promote the decay of moso bamboo stumps? Achieving a deeper understanding of the bacterial community, its characteristics and specific functions during the decay process of moso bamboo stumps, can provide a scientific basis for accelerating the decay of bamboo stumps.

In view of this, the present study was conducted to analyze the diversity index and differences in the community structure of bacterial 16S rRNA genes in the V3+V4 region from soil collected inside and outside bamboo stumps of moso bamboo forests at different degrees of decay. A high-throughput sequencing technology was used to investigate the relationship between different decay levels and soil bacteria inside and outside moso bamboo stumps to identify the main bacterial populations that promote the decay of bamboo stumps and provide a theoretical basis and data reference for the sustainable management of moso bamboo forests and the research and degradation processes.

Materials And Methods

Study site and soil sampling

The study site is located in Fangdao Town, Jianou City, Fujian Province, with latitude 26°38–27°20N and longitude 117°58–118°57E. The area is characterized by subtropical monsoon climate with four distinct seasons, abundant rainfall, an annual average temperature of 19.3°C, and annual rainfall of 1600–1800 mm. Jianou City is the famous "Bamboo Township of China," and is the first in China by the area of moso bamboo forest and the number of standing bamboo plants. The moso bamboo forest in the study site grows intensively and covers an area of more than 70/hm². The forest is a mature forest, with an average bamboo height of 16 m and the number of standing bamboo culms of 2500/hm². The average amount of old cut-down bamboo and new bamboo was maintained between 400–600 bamboo culms/hm².

Bamboo stumps with different levels of decay were randomly selected, and soil samples were collected from inside and outside the stumps at 3 different levels of decay (Table 1). Soil outside the bamboo stumps was collected from the upper 20 cm depth, 2 cm away from the outer circumference of the bamboo stumps. Soil inside the bamboo diaphragm, the entire soil inside the bamboo diaphragm was collected. Soils collected from 8–10 bamboo stumps of the levels of decay were mixed into one sample. Three soil samples of inside and outside bamboo stumps were collected by the above method. The collected soil samples were stored at -80°C and used for determination of soil bacteria.

Table 1
Grading of the degree of decay of bamboo stumps

Decaying degree	Characteristics
Mild decay	The bamboo stumps are light gray inside and outside, the bamboo wall, bamboo flesh and bamboo yellow are hard and intact, the bamboo diaphragm is intact, moldy spots are visible, the cavity is waterlogged, and the bamboo stump is more intact.
Moderate decay	The bamboo stumps are gray to gray-brown inside and outside, the walls are slightly hard, the flesh and yellow are softened and partially hard, the bamboo diaphragm is incomplete, and some of the fine roots of the bamboo stumps are decomposed and fell off.
Heavy decay	The bamboo stumps are gray-brown to dark black inside and outside, the bamboo wall, bamboo flesh and bamboo yellow are soft and fragile, the bamboo diaphragm is decayed, a large number of vascular bundles are visible, and most of the bamboo stumps are soft and decomposed.

Determination of soil microbial diversity and composition

A DNA extraction kit (Omega Bio-tek, Norcross, GA, USA) was used to extract the total DNA genomes of soil microorganisms inside and outside moso bamboo stumps. The quality of the extracted DNA products was determined by agarose gel electrophoresis.

PCR amplification of the 16S RNA-V3+V4 region of soil bacteria inside and outside the stumps was performed using the specific primers 341F (5'-CCTACGGGNGGCWGCAG-3') and 806R (5'-GGACTACHVGGGTATCTAAT-3') with barcode. The PCR amplification system consisted of 5 µL of 10× KOD Buffer, 5 µL of 2.5 mM dNTPs, 1.5 µL of primers (5 µM), 1 µL of KOD polymerase, and 100 ng of template DNA. The amplification reaction conditions were: pre-denaturation at 95°C for 2 min, followed by denaturation at 98°C for 10 s, annealing at 62°C for 30 s, and extension at 68°C for 30 s for a total of 27 cycles, and extension at 68°C for 10 min.

PCR amplification products were recovered using a gel recovery kit (Axygen Biosciences, Union City, CA, USA) and quantified using the ABI Step One Plus real-time PCR system (Life Technologies, Foster City, USA). The purified amplification products were mixed in equal amounts, sequencing connectors were connected, sequencing libraries were constructed, and sequencing was performed using the PE250 mode of Hiseq2500 (Guangzhou Kidio Biotechnology Co., Ltd., China).

Statistical analyses

The raw sequencing data were spliced and filtered, and chimeric sequences were removed to obtain the final valid data. All valid sequences of the samples were clustered at the 97% level using Uparse software 2013 (Edgar, Independent Investigator, Tiburon, California, USA) to classify operational taxonomic units (OTUs), and the number of OTU sequences common to each treatment was calculated using R software 2021 (R Foundation for Statistical Computing, Vienna, Austri). The proportion of common and unique OTUs for each decay level was expressed in the form of a Venn diagram. The QIIME software 2010 (Caporaso et al. Department of Chemistry and Biochemistry, University of Colorado, Boulder, Colorado, USA) was used to analyze the diversity indices of bacterial communities in different samples, and the indicators of colony richness were Chao1 and Ace. The indicators of colony species diversity were the Shannon-Wiener diversity index and Simpson diversity index. Origin Pro 2019 (OriginLab,Northampton, Massachusetts, USA) was used to draw the identification results of each process at the phylum and class level into a column chart. The top 30 most abundant bacterial genus communities were subjected to heat map analysis using R sofeware 2021 (R Foundation for Statistical Computing, Vienna, Austri); the bacterial OTU and bacterial genus communities inside and outside the bamboo stumps of moso bamboo with different levels of decay were subjected to principal component analysis.

Results

OTU analysis of soil bacteria inside and outside the moso bamboo stumps with different degrees of decay

All Effective Tags sequences of soil samples from inside and outside moso bamboo stumps with different decay levels were clustered. The valid sequences of OTUs were classified by 97% sequence similarity and counted after removing rare OTUs. The results of the OTU analysis of soil bacteria inside and outside the

bamboo stumps at different decay levels identified (Table 2) that significant differences in the number of effective sequences were detected between soil samples with mild decay inside and those outside the bamboo stumps; the abundance of bacterial OTUs inside and outside the bamboo stumps increased with the degree of decay; the OTU abundance was the highest in the heavily decayed soil samples outside the bamboo stumps.

Table 2
Analysis of the differences between the sequencing results of soil bacteria inside and outside the moso bamboo stumps with different levels of decay

Samples	Effective-tag		OTU	
	Inside bamboo stump	Outside bamboo stump	Inside bamboo stump	Outside bamboo stump
Mild decay	49119 ± 990 ^{Ab}	72617 ± 6707 ^{Aa}	2486 ± 38 ^{Aa}	2418 ± 146 ^{Aa}
Moderate decay	55087 ± 576 ^{Aa}	70826 ± 5193 ^{Aa}	3113 ± 92.5 ^{Aa}	2939 ± 672 ^{Aa}
Heavy decay	50824 ± 4829 ^{Aa}	57456 ± 7375 ^{Aa}	3237 ± 0.5 ^{Aa}	3399 ± 582 ^{Aa}
Note: Data in the table are means ± standard deviations; different capital letters indicate significant differences among different decay levels at $P < 0.05$; different lowercase letters indicate significant differences between outside bamboo stumps at $P < 0.05$.				

The Venn diagram of the OTU distribution revealed that the number of shared bacterial OTUs by the three decay levels was 1351 inside and 2357 outside the bamboo stumps. The number of bacterial OTUs found both inside and outside the bamboo stumps was 1317, accounting for approximately 97.48% of the bacterial OTUs inside and 55.88% of those outside the bamboo stumps (Fig. 1). This indicates that a large number of unique bacterial populations were found outside the bamboo stumps. The highest number of specific bacterial OTUs inside and outside the bamboo stumps was detected for heavy decay. As decomposition progressed, the number of bacterial species inside and outside the moso bamboo stumps increased.

Diversity and abundance of soil bacteria community inside and outside the stumps of moso bamboo with different levels of decay

The Shannon index, Simpson index, Chao1, and ACE index of soil bacteria community inside and outside the bamboo stumps were 7.23–9.37, 0.962–0.995, 3417–4849, and 3453–4853, respectively (Table 3). The Shannon and Simpson indices of soil bacteria community inside the bamboo stumps gradually increased with the degree of decay, and the diversity of mild decay were significantly lower than that of moderate and heavy decay ($P < 0.05$). There were no significant differences in the bacterial Chao1 and ACE indices of soil bacteria community inside the bamboo stumps among the three degree of decay ($P < 0.05$). There were significant differences ($P < 0.05$) in bacterial Chao1, ACE index, and Shannon index between heavily decayed and mildly decayed outside the bamboo stumps, and the values of diversity and richness index increased gradually with decay.

Table 3
Bacterial diversity and richness index of soil inside and outside the stumps of moso bamboo at different decay levels

Samples	Shannon index		Simpson index		Chao1 index		ACE index	
	Inside bamboo stump	Outside bamboo stump	Inside bamboo stump	Outside bamboo stump	Inside bamboo stump	Outside bamboo stump	Inside bamboo stump	Outside bamboo stump
Mild decay	7.23 ± 0.07 ^{Bb}	7.87 ± 0.28 ^{Bb}	0.962 ± 0.011 ^{Ab}	0.985 ± 0.004 ^{Aa}	3683 ± 77 ^{Aa}	3417 ± 178 ^{Bb}	3697 ± 36 ^{Aa}	3453 ± 168 ^{Bb}
Moderate decay	9.23 ± 0.18 ^{Aa}	8.25 ± 0.93 ^{ABab}	0.995 ± 0.001 ^{Ba}	0.985 ± 0.008 ^{Aa}	4532 ± 116 ^{Aa}	4239 ± 889 ^{ABa}	4444 ± 116 ^{Aa}	4312 ± 864 ^{ABa}
Heavy decay	9.37 ± 0.07 ^{Aa}	9.20 ± 0.43 ^{Aa}	0.995 ± 0.001 ^{Ba}	0.994 ± 0.001 ^{Aa}	4487 ± 97 ^{Aa}	4849 ± 639 ^{Aa}	4556 ± 13 ^{Aa}	4853 ± 696 ^{Aa}
Note: Data in the table are means ± standard deviations; different capital letters indicate significant differences among different decay levels at $P < 0.05$; different lowercase letters indicate significant differences between inside and outside bamboo stumps at $P < 0.05$.								

Distribution characteristics and correlation analysis of soil bacterial communities inside and outside the stumps of moso bamboo with different levels of decay

According to the analysis of soil bacteria inside and outside the bamboo stumps at different levels of decay (Fig. 2), the dominant bacterial communities were Proteobacteria, Acidobacteria, Actinobacteria, Planctomycetes, and Verrucomicrobia. Among them, Proteobacteria accounted for the highest proportion of the bacterial community, decreasing from about 51% to approximately 29% inside the bamboo stumps and from approximately 51% to nearly 40% outside the bamboo stumps as the decay increased, although its proportion remained higher than that of other phyla. Acidobacteria and Planctomycetes accounted for the highest proportion of bacteria in samples with moderate decay within the bamboo stumps (approximately 18% and 25%, respectively), followed by samples with heavy decay (approximately 17% and 16%, respectively). The proportion of Acidobacteria and Planctomycetes gradually increased with decay outside the bamboo stumps, and the degree of decay outside the bamboo stumps was significantly positively correlated with Acidobacteria and Planctomycetes (Table 4). As the degree of decay increased, the proportion of *Actinobacteria* both inside and outside the bamboo stumps decreased and then increased, but their proportion in samples with heavy decay remained smaller than that in samples with mild decay; the degree of decay outside the bamboo stumps was significantly negatively correlated with *Actinobacteria* (Table 4). Inside the bamboo stumps, Chloroflexi accounted for 2% and 5% of bacteria in samples with mild and heavy decay, respectively, whereas outside the bamboo stumps, they accounted for 3% and 2% of the samples with heavy decay, respectively. As the degree of decay increased, the proportion of Firmicutes inside the bamboo stump first decreased and then increased, but their proportion in

samples with a heavy decay was smaller than that in samples with a mild decay. The proportion of Firmicutes outside the bamboo stump decreased gradually. Outside the bamboo stumps, the degree of decay was significantly and positively correlated with Gemmatimonadetes; however, there was no significant correlation inside the bamboo stumps. The changes in Acidobacteria in the bamboo stumps were increased by approximately 5–18% as decay increased. The phyla experiencing large changes outside the bamboo stumps were Planctomycetes, Acidobacteria, and Actinobacteria. The proportion of Planctomycetes and Acidobacteria increased from approximately 3% to about 16% and from 4% to about 14%, respectively, and the proportion of Actinobacteria decreased from about 16% to approximately 10%.

Table 4
Correlation coefficients between the degree of decay of bamboo stumps and soil bacteria at the phylum level

Related factors	Proteobacteria	Acidobacteria	Actinobacteria	Planctomycetes	Verrucomicrobia	Chloroflexi	Firmicutes	Gemmatimonadetes
Degree of decay in the bamboo stump	-0.665	0.778	0.745	0.535	0.646	0.633	-0.788	0.411
Degree of decay outside the bamboo stump	-0.63	0.851**	-0.703*	0.805**	0.473	-0.192	-0.376	0.709*
Note: * significantly correlated ($P < 0.05$); ** highly significantly correlated ($P < 0.01$).								

The distribution and relative abundance of bacterial communities at the class level (Fig. 3) showed that the dominant classes of the community were Alphaproteobacteria, Gammaproteobacteria, Planctomycetacia, Actinobacteria, and Acidobacteria. Inside the bamboo stumps, Gammaproteobacteria was the dominant class in samples with mild decay, accounting for approximately 38%. Planctomycetacia was the dominant class in samples with moderate decay, accounting for approximately 23%, and Alphaproteobacteria was the dominant class in samples with heavy decay, accounting for approximately 18%. Outside the bamboo stumps, Alphaproteobacteria were the dominant class, accounting for approximately 28%. Inside the bamboo stumps, the proportion of Alphaproteobacteria gradually increased and was significantly positively correlated with the degree of decay (Table 5). The proportions of Gammaproteobacteria and Bacilli in moderately and heavily decayed samples were significantly reduced compared with those in mildly decayed samples, and these were significantly negatively correlated (Table 5). Outside the bamboo stumps, an increase in decay resulted in a gradual increase in the proportion of Planctomycetacia, Acidobacteria, and Gemmatimonadetes from approximately 2%, 2%, and 0.3% to about 12%, 10%, and 0.8%, respectively. The degree of decay outside the bamboo stump was highly significant and positively correlated with the proportion of Planctomycetacia and Acidobacteria and significantly positively correlated with Gemmatimonadetes (Table 5).

Table 5
Correlation coefficients between the degree of decay of bamboo stumps and soil bacteria at the class level

Related factors	Alphaproteobacteria	Gammaproteobacteria	Planctomycetacia	Actinobacteria	Acidobacteria	Spartobacteria	Bacilli	Betaproteobacteria
Degree of decay in the bamboo stump	0.829*	-0.859*	0.517	-0.754	0.78	0.474	-0.816*	-0.581
Degree of decay outside the bamboo stump	-0.005	-0.405	0.818**	-0.746*	0.845**	0.511	-0.418	0.063
Note: * significantly correlated ($P < 0.05$); ** highly significantly correlated ($P < 0.01$).								

Heat map of bacteria inside and outside the stumps of moso bamboo at different decay levels

The mean values of bacterial abundance in the three decay levels inside and outside the bamboo stumps were cluster analyzed, and the top 30 soil bacteria were selected and annotated to the genus level to obtain a heat map of the dominant genera. The bacterial communities were grouped into four clusters: a cluster of communities inside the moderately and heavily decayed bamboo stumps, a cluster of communities outside the moderately and heavily decayed bamboo stumps, and a cluster of communities inside and a cluster of communities outside the mildly decayed bamboo stumps (Fig. 4). This indicates that the decay level influenced the structure of soil bacterial communities inside and outside the bamboo stumps. In terms of the change in the relative abundance of bacterial genera, *Rhodanobacter* was the dominant genus inside the mildly decayed bamboo stumps; *Others_of_DA101_soil_group* and *Others_of_Planctomycetaceae* were the dominant genera in the moderately and severely decayed stumps. *Others_of_Enterobacteriaceae* and *Exiguobacterium*

were the dominant genera for mild and moderate levels of decay outside the bamboo roots. *Singulisphaera* was the dominant genus in samples with a heavy degree of decay.

Principal component analysis of bacterial communities at OTU and genus level inside and outside the stumps of moso bamboo with different decay levels

Principal component analysis was performed with the OTU data of the bacterial communities of soil samples with different levels of decay inside and outside the bamboo roots. The results are shown in Figure 5-a. The first principal component (PCA1) represented by the horizontal axis explained approximately 30.4% of the bacterial fractions, and the second principal component (PCA2) represented by the vertical axis explained approximately 22.8% of the bacterial fractions. The samples were divided into three groups: one group for mild decay inside bamboo stumps, one for mild decay outside the bamboo stumps, and one for the rest. The number of bacterial OTUs for moderate and heavy decay inside and outside the bamboo stumps changed to some extent compared to those for mild decay, and there were some differences in the number of OTUs for mild decay inside and outside the bamboo stumps.

The PCA was performed for bacterial communities at genus level in soil samples with different levels of decay inside and outside the bamboo stumps (Fig. 5b). PC1 and PC2 explained only 49.6% and 21.8% of the bacterial genera within the community, respectively, which could be divided into four groups: one group for mild decay inside the bamboo stumps, one group for mild decay outside the bamboo stumps, moderate and heavy decay inside the bamboo stumps, and moderate and heavy decay outside the bamboo stumps. The bacterial community for mild decay inside and outside the bamboo stumps differed significantly from that for moderate and heavy decay. The bacterial communities at genus level inside and outside moderately and heavily decayed bamboo stumps were very similar.

Discussion

Effect of the decay degree inside and outside the bamboo stumps on the number, diversity, and community structure of soil bacterial OTUs

The degradation of moso bamboo stumps after felling is the result of the mutual action of several varieties of microorganisms, among which bacteria have unique degradation characteristics: small size, large specific area, fast growth and reproduction, wide distribution, diverse metabolic types, strong adaptability to variation, large number of species, strong migration ability, and many other aspects of morphological structure and physiological genetic advantages (Kuramae et al. 2019). Concurrently, collaboration and competition between bacteria are influenced by environmental and human factors, with a certain degree of relevance and complexity (Dini-Andreote et al. 2015). Soils in moso bamboo woodlands with different levels of decay have bacterial communities that are relatively rich in species. The Venn diagram of OTUs showed that the number of bacterial OTUs inside and outside the bamboo stump gradually increased with increasing decay. Bacterial species endemic to the inside and outside of bamboo stumps also gradually increased. The number of OTUs specific to the outside was higher than that limited to the inside of the bamboo stumps at different levels of decay. This phenomenon is contributed to the increased number of bacteria at the beginning of decay owing to the presence of richer nutrients. As the degree of decay increases, the material near the bamboo wall begins to decay, and bacteria use this material to grow and increase in number. The decomposition of organic matter supplies energy to soil microorganisms and they flourish (Zhang et al. 2019). A similar change in microbial community during the decomposition of fallen wood has been reported in alpine forests in western Sichuan: highly decomposed fallen wood was characterized by high levels of microbial biomass and a rich microbial community structure, with different structural components showing independent trends in microbial community structure during decomposition (Chang et al. 2014). The number of bacteria was higher outside than inside the bamboo stump because of the relatively open environment on the outside; bacteria have to break through layers of barriers as they move from the soil outside the bamboo stumps toward the root surface, inside the roots and then inside the bamboo stumps. Their advancement is similar to the bacterial invasion of plants from the roots via two invasive modes: active (microbial secretion of cell wall-degrading enzymes across the mesocolonial sheath to reach the xylem duct) and passive (passive penetration through existing channels within the tissue) (Gao et al. 2019). Alpha diversity analysis showed that the number of OTUs, Shannon index, Simpson index, and ACE index of soil bacteria inside and outside the bamboo stumps gradually increased with the increase in decay degree. This indicates that high bacterial abundance and diversity promote the decay of bamboo stumps. Similarly, the microbial diversity indices, such as Shannon, Chao1, and the number of OTUs, increased with increasing decay of lotus biomass, thus enriching the community composition of microorganisms in the sediment (Feng et al. 2018). The decomposition process of litter exhibits a similar phenomenon. The decomposition rate of litter in a mixed *Quercus acutissima* Carruth. and *Robinia pseudoacacia* L. forest and pure *Q. acutissima* forest was significantly and positively correlated with the diversity and richness indices of soil bacteria (Dong et al. 2021). A study on litter decomposition of four dominant silvicultural tree species and its effect on the soil bacterial community structure in Taishan, China, found a correlation between the litter decomposition rate and the bacterial community diversity index, suggesting that high bacterial abundance and diversity promote litter decomposition (Lu et al. 2019). As wood decay and decomposition advances, bacterial community diversity increases, as indicated by the alpha diversity indices. A more complex community structure emerges. The peak diversity occurs at the most advanced decay class (Kuramae et al. 2019).

Effect of the decay degree inside and outside the bamboo stumps on dominant soil bacterial community

The decay and degradation of moso bamboo stumps is a process of interactions between various microorganisms, in which the microbial community structure and diversity are influenced by many factors, such as climatic conditions, soil texture, geographic topography, and human activities (Liu et al. 2021; Lucas-Borja et al. 2012). During the decay and decomposition of bamboo stumps, competition for resources among microorganisms may lead to community shifts and may affect decay rates. In general, bamboo stumps with different levels of decay consist of microorganisms with specific dominant colonies. The three decay levels in this study were similar in bacterial dominant colony composition at the phylum level. The dominant phyla of bacterial communities were Proteobacteria, Acidobacteria, Actinobacteria, Planctomycetes, and Verrucomicrobia. The dominant classes of the community were Alphaproteobacteria, Gammaproteobacteria, Planctomycetacia, Actinobacteria, and Acidobacteria. Proteobacteria, Acidobacteria, and Actinobacteria have been shown to be dominant in the rhizosphere soils of different plants (Ding et al. 2018; Xie et al. 2016; Yang et al. 2015; Yuan et al. 2021). Li et al. (2020b) found that the dominance of Proteobacteria was greater than that of phylum Acidobacteria in a moso bamboo forest. The reason may be related to the original bacterial

composition. Si et al. (2020) reported that the phyla Proteobacteria, Bacteroidetes, Cyanobacteria, Acidobacteria, and Verrucomicrobia dominated in all samples during the decay of *Hydrilla verticillata* (L. f.) Royle. The Proteobacteria and Actinomycota were the main common dominant bacteria of the fallen *Larix gmelinii* (Rupr.) Kuzen. Wood at each decomposition level (Yang et al. 2021). Phyla Proteobacteria are the most abundant group of bacteria, most of which belong to the classes Alphaproteobacteria, Betaproteobacteria, and Gammaproteobacteria. Among them, in this study Alphaproteobacteria and Gammaproteobacteria belong to the main communities of the samples that were tested. It can be concluded that members of Proteobacteria are the main prokaryotic microorganisms inside and outside the bamboo stumps. Proteobacteria are mostly parthenogenic or specialized anaerobic and heterotrophic microorganisms, which are strategic bacteria (nutrient bacteria). Accelerated decomposition of soil organic matter stimulates faster growth of r-strategic bacteria, thus accelerating soil organic matter decomposition (Ember et al. 2017; Li et al. 2020a). Alphaproteobacteria are able to fix nitrogen by consuming organic matter and decomposing $\text{NH}_4\text{+N}$, CH_4 , and other constituents (Liu et al. 2019a; Xu et al. 2021). Ammonia-oxidizing bacteria of Gammaproteobacteria are generally regarded as the most important contributors to the nitrogen cycle and are able to solubilize insoluble phosphate in the soil (Wang et al. 2021b). Inside the bamboo stumps, Alphaproteobacteria were significantly and positively correlated with the degree of decay, whereas Gammaproteobacteria were significantly and negatively correlated with the degree of decay. A possible reason for such a correlation is that the bamboo stump is composed of bamboo flesh, bamboo green, and bamboo yellow (Li et al. 2021); there are more thin-walled tissues of bamboo yellow the closer they are to the inner side of bamboo stumps, the vascular bundles are larger and looser in structure, and therefore this part of bamboo stumps is easier to decompose (Li et al. 2014; Lian et al. 2020). The decay of bamboo stumps increases the content of total nitrogen, alkaline decomposition nitrogen, and fast-acting potassium in the soil, but reduces the content of effective phosphorus in the soil (Tang et al. 2013). Therefore, Alphaproteobacteria in bamboo stumps gradually increased with the increase in decay, and Gammaproteobacteria gradually decreased with the deepening of decay. At the phylum level, Acidobacteria, Planctomycetes, and Verrucomicrobia were positively correlated with the degree of decay. However, the degree of decay outside the bamboo stumps was highly significantly and positively correlated with Acidobacteria and Planctomycetes, which is similar to the results at the class level and is probably due to the fact that the pH of the soil outside the bamboo stumps is mostly acidic. Most phyla Acidobacteria are acidophilic bacteria that prefer to live in acidic soil environments (Kielak et al. 2016). This phylum contains beneficial genera of bacteria that can break down proteins and absorb acidic substances from the environment (Zhou et al. 2020). In addition, phylum Acidobacteria, such as acidophilus, degrade plant residues, participate in iron cycling, enhance photosynthesis, and participate in the metabolism of single-carbon compounds (Hu et al. 2020). Ding (2019) found that an increase in the number of moso bamboo positively affected the growth of phylum Acidobacteria and Verrucomicrobia. Phylum Planctomycetes are related to ammonia oxidation and nitrification-denitrification processes in soil nitrogen metabolism. Phylum Actinobacteria and class Actinobacteria were negatively correlated with the degree of decay, but the degree of decay outside the bamboo roots was significantly negatively correlated with both the phylum Actinobacteria and the class Actinobacteria because most actinomycetes are saprophytes. Some Actinobacteria populations can produce lignin-degrading enzymes and decompose lignin and cellulose, playing a role in decomposing organic plant residues (Xue et al. 2021). With the increase in decay, cellulose and lignin content inside and outside the bamboo stump decreased, and thereby the number of actinomycetes gradually decreased. Proteobacteria and phylum Acidobacteria may belong to oligotrophic denitrifying microorganisms, which have a high relative abundance in environments with low nutrient effectiveness, whereas Chloroflexi and phylum Actinobacteria may belong to the eutrophic denitrifying phylum, which have a higher relative abundance in environments richer in nutrients (Cao et al. 2021); these findings are consistent with the results of the present study.

According to the PCA and heat map, the bacterial communities inside the moderately and heavily decayed bamboo stumps were similar and aggregated into one group, those outside the moderately and heavily decayed bamboo stumps clustered together, and the communities inside and outside the mildly decayed bamboo stumps were each in one group. The inside of moderately decayed and heavily decayed bamboo stumps had similar bacterial community structures, and the dominant genera were *Others_of_DA101_soil_group* and *Others_of_Planctomycetaceae*, whereas *Rhodanobacter* was the dominant genus inside the mildly decayed stumps. The outside of mildly and moderately decayed bamboo stumps shared similar bacterial community structures, and their dominant genera were both *Others_of_Enterobacteriaceae* and *Exiguobacterium*, whereas *Singulisphaera* was the dominant genus in heavily decayed stumps. Cao et al. (2021) studied the structure and diversity of the nirS-denitrifying microbial community across three restoration stages in tropical forests of Xishuangbanna of Yunnan Province, China. They found that *Cupriavidus*, *Dechloromonas*, *Halomonas*, *Pseudomonas*, and *Rhodanobacter* were the dominant genera in the three sample sites. The same findings were reported in estuarine areas (Hong et al. 2015) and rice soils (Megumi et al. 2009) for *Rhodanobacter*.

Conclusion

In summary, the number, diversity, and richness of soil bacterial OTUs inside and outside the bamboo stumps gradually increased with the increase in decay. Proteobacteria, Acidobacteria, Actinobacteria, Planctomycetes, and Verrucomicrobia were the main phyla of soil bacteria inside and outside the bamboo stumps. The dominant phylum was Proteobacteria. The degree of decay outside the bamboo stumps was highly significant and positively correlated with phylum Acidobacteria and phylum Planctomycetes, but significantly negatively correlated with phylum Actinobacteria. At the class level, Alphaproteobacteria, Gammaproteobacteria, and Planctomycetacia were the most abundant bacterial class in the bamboo stumps. The degree of decay inside the bamboo stump was significantly positively correlated with Alphaproteobacteria but significantly negatively correlated with Gammaproteobacteria and Bacilli. Outside the bamboo, the degree of decay was highly significantly and positively correlated with Planctomycetacia and Acidobacteria, significantly positively correlated with Gemmatimonadetes, but significantly negatively correlated with class Actinobacteria. There are specific bacterial communities at work at different degrees of decay. Moderate and heavy decay in bamboo roots was characterized by similar soil generic structure of bacterial communities, and similar similarity in bacterial communities at the genus level was observed for mild and moderate decay outside the bamboo roots. Studying the community composition of bacteria at different decay degrees can provide new perspectives for the rapid degradation of bamboo stumps. The present study analyzed the relationship between bacterial communities during the bamboo stump decay, whereas the relationship and role of fungi and other microorganisms in bamboo stump decay will be examined in a follow-up study.

Declarations

Funding

This work was Supported by Forestry Science and Technology Extension Demonstration Project Financed by the Chinese Central Government [grant number Min (2016) TG14 to L.Cai].

Declaration of competing interest

The authors declare no competing financial interest.

Availability of data and material

Illumina MiSeq amplicon sequences of bacterial 16 S rRNA genes are available in the OMICS MART Sequence Read Archive (<http://www.omicsmart.com>).

Code availability

Not applicable.

Author contributions

The paper was written and researched by Fengna Liang and Liping Cai. Research and sample collection were completed by Xiao Huang, Huixin Zheng, Na Sun, Xuelong Qin, Cheng Jin, Le Yu and Yonglai Huang. The test plan was completed by Liping Cai and Xiangqing Ma. All authors read and approved the final manuscript.

References

- Cao Q, Wang S, Chen M, Cao R, Wang P, Zuo Q, Zhao S and Yang B (2021) The structure and diversity of nirS-denitrifying microbial community across three restoration stages of Xishuangbanna tropical forests. *Acta Ecol. Sin.* 41:626-636. (In Chinese) <https://doi.org/10.5846/stxb202004170915>
- Caporaso JG, Kuczynski J, Stombaugh J, Bittinger K, Bushman FD, Costello EK, Fierer N, Peña AG, Goodrich JK, Gordon JI, Huttley GA, Kelley ST, Knights D, Koenig JE, Ley RE, Lozupone CA, McDonald D, Muegge BD, Pirrung M, Reeder J, Sevinsky JR, Turnbaugh PJ, Walters WA, Widmann J, Yatsunenko T, Zaneveld J, Knight R (2010) QIIME allows analysis of high-throughput community sequencing data. *Nat Methods* 7:335-336. <https://doi.org/10.1038/nmeth.f.303>
- Chang C, Wu F, Yang W, Tan B, Li H, Xiao S, Gou X and He L (2014) The dynamics of microbial community structure at different stages of log decay in an alpine forest of western Sichuan. *Chin. J. Appl. Environ. Biol* 20:978-985. (In Chinese) <https://doi.org/10.3724/SP.J.1145.2014.05006>
- Ding X, Huang Y, Jing R, Ma F, An R, Tian Q and Chen B (2018) Bacterial structure and diversity of four plantations in the Yellow River Delta by high-throughput sequencing. *Acta Ecol. Sin.* 38:5857-5864. (In Chinese) <https://doi.org/10.5846/stxb201703260522>
- Ding X (2019) The effect of land management intensification on soil property and microbial community. Anhui Agricultural University, Anhui (In Chinese) <https://doi.org/10.26919/d.cnki.gannu.2019.000473>
- Dini-Andreote F, Stegen J C, van Elsland J D and Salles J F (2015) Disentangling mechanisms that mediate the balance between stochastic and deterministic processes in microbial succession. *PNAS* 112:E1326-E1332. <https://doi.org/10.1073/pnas.1414261112>
- Dong X, Gao P, Li T, Zhang J, Dong J, Xu J and Dun X (2021) Effects of soil microbial community on the litter decomposition in mixed *Quercus acutissima* Carruth. and *Robinia pseudoacacia* L. forest. *Acta Ecol. Sin.* 41:2315-2325. (In Chinese) <https://doi.org/10.5846/stxb202004120866>
- Ed-Haun C, Chiou-Pin C, Guanglong T and Chih-Yu C (2018) Replacement of natural hardwood forest with planted bamboo and cedar in a humid subtropical mountain affects soil microbial community. *APPL SOIL ECOL* 124:146-154. <https://doi.org/10.1016/j.apsoil.2017.11.006>
- Edgar, R.C (2013) UPARSE: Highly accurate OTU sequences from microbial amplicon reads, *Nature Methods*. <https://doi.org/10.1038/nmeth.2604>
- Ember M, Rebecca L M, Egbert S, Theresa A M, Paul D, Benjamin J K, Jane C M and Bruce A H (2017) Bacterial carbon use plasticity, phylogenetic diversity and the priming of soil organic matter. *ISME J.* 11:1890-1899. <https://doi.org/10.1038/ismej.2017.43>
- Fang T; Li Y; Yao Z; Li Y; Wang X; Wang Y and Yu Y (2021) Effects of planting broadleaf trees and moso bamboo on soil carbon mineralization and microbial community structure. *Chin. J. Appl. Ecol.* 32:82-92. <https://doi.org/10.13287/J.1001-9332.202101.033>
- Feng D (2018) Dynamic changes of nutrient elements and their effects on the microbial diversity of sediments during the decaying of *Nelumbo nucifera* detritus. Jiang Su University, Jiangsu (In Chinese)
- Gao J, Feng G, Yan S, Qin H, Chen J, Liang C and Xu Q (2019) Comparison on Structure and Diversity of Endophytic Bacteria between Three Species of Bamboo. *Journal of Bamboo Research* 38:39-46. (In Chinese) <https://doi.org/10.19560/j.cnki.issn1000-6567.2019.03.006>
- Hervé V, Ketter E, Pierrat J, Gelhaye E and Frey-Klett P (2016) Impact of *Phanerochaete chrysosporium* on the Functional Diversity of Bacterial Communities Associated with Decaying Wood. *PLoS One* 11:e0147100. <https://doi.org/10.1371/journal.pone.0147100>

- Hong X, Hong Y, Chen Z, Zhao C, Yang S (2015) Phylogenetic diversity of nirS-type denitrifying bacteria in Jiulong river estuary. *Microbiology* (Beijing, China) 42:1639-1650. (In Chinese) <https://doi.org/10.13344/j.microbiol.china.140953>
- Hu W, Xiang J, Xiang Y, Chen Y (2020) Effects of nitrogen-doped carbon nanoparticles on bacterial community in paddy rhizosphere soil. *Chin. J. Appl. Ecol.* 31:3842-3850. (In Chinese) <https://doi.org/10.13287/j.1001-9332.202011.033>
- Hua W and Wu L (2000) Preliminary report on the research of *Phyllostachys edulis* decay promotion technology. *Journal of Forestry Engineering* 14:38-39. (In Chinese) <https://doi.org/10.13360/j.issn.1000-8101.2000.01.015>
- Kielak A M, Barreto C, Kowalchuk G A, van Veen J A and Kuramae E (2016) The Ecology of Acidobacteria: Moving beyond Genes and Genomes. *Front. Microbiol.* 7:744. <https://doi.org/10.3389/fmicb.2016.00744>
- Kuramae E, Leite M F A, Suleiman A K A, Gough C M, Castillo B T, Faller L, Franklin R B and Syring J (2019) Wood Decay Characteristics and Interspecific Interactions Control Bacterial Community Succession in *Populus grandidentata* (Bigtooth Aspen). *Front. Microbiol.* 10:979. <https://doi.org/10.3389/fmicb.2019.00979>
- Li C, Li L, Yang K, Zhang L and Peng Z (2008) Isolating and screening of microorganisms for decomposing bamboo stump. *Forest Research* 21:253-257. (In Chinese)
- Li M, Ai W, Yang M, Meng Y, Tu J, Pu X and Liu X (2014) The changes of microorganism in the bamboo stump with different decomposition degree. *Journal of Forestry Engineering* 28:64-67. (In Chinese) <https://doi.org/10.13360/j.issn.1000-8101.2014.05.015>
- Li M; Lu J; Ai W; Yang M; Meng Y; Tu J; Pu X and Liu X (2015) Changes of microorganisms in Mao bamboo stumps at different decomposition degrees. *Agr Sci Tech* 16:1073-1077. <https://doi.org/10.16175/j.cnki.1009-4229.2015.05.049>
- Li R, He C, Peng B and Wang C (2021) Differences in fiber morphology and partial physical properties in different part of *Phyllostachys edulis*. *J. Zhejiang A F Univ.* 38:854-860. (In Chinese) <https://doi.org/10.11833/j.issn.2095-0756.20200649>
- Li S, Huang X, Lang X, Shen J, Xu F and Su J (2020a) Cumulative effects of multiple biodiversity attributes and abiotic factors on ecosystem multifunctionality in the Jinsha River valley of southwestern China. *For. Ecol. Manage.* 472. <https://doi.org/10.1016/j.foreco.2020.118281>
- Li W, Tian X, Sheng H, Ekawati D, Zhou Y and Zhang R (2020b) Response of bacterial compositions to soil biochemical properties under mulching-intensive management in a *Phyllostachys edulis* forest. *APPL SOIL ECOL* 150:103436. <https://doi.org/10.1016/j.apsoil.2019.103436>
- Lian C, Liu R, Zhang S, Yuan J, Luo J, Yang F and Fei B (2020) Ultrastructure of parenchyma cell wall in bamboo (*Phyllostachys edulis*) culms. *Cellulose* 27:7321-7329. <https://doi.org/10.1007/s10570-020-03265-9>
- Lin L (2011) A preliminary study of distribution and rotting speed of bamboo stump in *Phyllostachys heterocycla* var. *pubescens* forest. *World Bamboo and Rattan* 9:57-59. (In Chinese) <https://doi.org/10.13640/j.cnki.wbr.2011.03.020>
- Liu B, Zhang S, Zhou Y, Lin J and Sun F (2015) Mildew in bamboo flour treated with different solvents. *J. Zhejiang A F Univ.* 32:11-17. (In Chinese) <https://doi.org/10.11833/j.issn.2095-0756.2015.01.002>
- Liu C, Zhou Y, Qin H, Liang C, Shao S, Fuhrmann J J, Chen J and Xu Q (2021) Moso bamboo invasion has contrasting effects on soil bacterial and fungal abundances, co-occurrence networks and their associations with enzyme activities in three broadleaved forests across subtropical China. *For. Ecol. Manage.* 498. <https://doi.org/10.1016/J.FORECO.2021.119549>
- Liu G, Chen L, Shi X, Yuan Z, Yuan L Y, Lock T R and Kallenbach R L (2019a) Changes in rhizosphere bacterial and fungal community composition with vegetation restoration in planted forests. *LAND DEGRAD DEV* 30:1147-1157. <https://doi.org/10.1002/ldr.3275>
- Liu J (2011) Cleaning technology and equipment on bamboo roots. Chinese academy of forest, Beijing (In Chinese)
- Liu Q (2016) Absorption transformation and utilization in *Phyllostachys edulis* forests. Chinese academy of forest, Beijing (In Chinese)
- Liu X, Siemann E, Cui C, Liu Y, Guo X and Zhang L (2019b) Moso bamboo (*Phyllostachys edulis*) invasion effects on litter, soil and microbial PLFA characteristics depend on sites and invaded forests. *Plant Soil* 438:85-99. <https://doi.org/10.1007/s11104-019-04010-3>
- Lu Y, Li K, Liang Q, Li C and Zhang C (2019) Effects of leaf litter decomposition on bacterial community structure in the leaf litter of four dominant tree species in Mount Tai. *Acta Ecol. Sin.* 39:3175-3186. <https://doi.org/10.5846/stxb201806211365>
- Lucas-Borja M. E., Candel D., Jindo K., Moreno J. L., Andrés, M., and Bastida, F. (2012) Soil microbial community structure and activity in monospecific and mixed forest stands, under Mediterranean humid conditions. *Plant Soil* 354:359–370.
- Megumi Y, Satoshi I, Shigeto O and Keishi S (2009) Temporal shifts in diversity and quantity of nirS and nirK in a rice paddy field soil. *Soil Biol. Biochem.* 41:2044-2051. <https://doi.org/10.1016/j.soilbio.2009.07.012>

- Mieszkis S, Richet P, Bach C, Lambrot C, Augusto L, Buée M and Uroz S (2021) Oak decaying wood harbors taxonomically and functionally different bacterial communities in sapwood and heartwood. *Soil Biol. Biochem.* 155, 108160. <https://doi.org/10.1016/J.SOILBIO.2021.108160>
- OriginLab (2019) Version 2019b : Data analysis and graphing software. OriginLab Corporation, Northampton, MA, USA <https://www.originlab.com/>
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>.
- Ren A, Wu L, Li Y, Tan Z, Yao Z, Xu Q and Shi H (2016) Screening, lignocellulose enzyme activities and gene expression analysis of saprophytic fungi for decomposing bamboo sawdust. *J. Agric. Biotechnol.* 24:1664-1675. <https://doi.org/10.3969/j.issn.1674-7968.2016.11.004>
- Si T, Chen H, Qiu Z, Zhang L, Ohore O E and Zhang S (2020) Bacterial succession in epiphytic biofilms and deciduous layer sediments during *Hydrilla verticillata* decay: A field investigation. *J. Environ. Sci. (Beijing, China)* 93:193-201. <https://doi.org/10.1016/j.jes.2020.03.008>
- Song J (2018) 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, Hunan (In Chinese)
- Tang W (2013) Effect of bamboo stump rotting on soil physicochemical properties. *World Bamboo and Rattan* 11:31-33. (In Chinese) <https://doi.org/10.13640/j.cnki.wbr.2013.02.008>
- Wang S, Wang B, Fan S, Xiao X, Xia W and Guan F (2021b). Influence of strip cutting management on soil bacterial community structure and diversity in *Phyllostachys edulis* stands. *J. Nanjing For. Univ.* 45:60-68. (In Chinese) <https://doi.org/10.12302/j.issn.1000-2006.202004038>
- Xie X, Liu N, Yang B, Yu C, Zhang Q, Zheng X, Xu L, Li R and Liu J (2016) Comparison of microbial community in hydrolysis acidification reactor depending on different structure dyes by Illumina MiSeq sequencing. *Int. Biodeterior. Biodegrad.* 111:14-21. <https://doi.org/10.1016/j.ibiod.2016.04.004>
- Xu F, Li S and Su J (2021) Changes of soil bacterial community structure at the secondary successional stages in the pinus yunnanensis forest. *Chin. J. Appl. Ecol.* 32:887-894. <https://doi.org/10.13287/J.1001-9332.202103.039>
- Xu G, Wang L, Liu J and Wu J (2013) FTIR and XPS analysis of the changes in bamboo chemical structure decayed by white-rot and brown-rot fungi. *Appl. Surf. Sci.* 280:799-805. <https://doi.org/10.1016/j.apsusc.2013.05.065>
- Xue X, Wang L, Han X, Chen R and Wang J (2021) Effects of different tree disk mulching on soil microbial community structure and diversity in dwarfing rootstock apple orchard. *Acta Ecol. Sin.* 41:1528-1536. (In Chinese) <https://doi.org/10.5846/stxb201909191955>
- Yang L, Cui F, Huang Q, Zhu D and Xu F (2021) Analysis on bacterial diversity and composition of *Larix melinii* fallen wood with different decomposition levels. *J. Cent. South Univ. For. Technol.* 41:93-100,182. (In Chinese) <https://doi.org/10.14067/j.cnki.1673-923x.2021.04.011>
- Yang J, Zhou G, Tian Y, Liu Q, Liu C, Yang Q and Zhou J (2015) Differential analysis of soil bacteria diversity in different mixed forests of *Dalbergia odorifera*. *Acta Ecol. Sin.* 35:8117-8127. (In Chinese) <https://doi.org/10.5846/stxb201409191856>
- Yuan Z, Liu F, Liu Z, Huang Q, Zhang G and Pan H (2021) Structural variability and differentiation of niches in the rhizosphere and endosphere bacterial microbiome of moso bamboo (*Phyllostachys edulis*). *Sci. Rep.* 11:1574. <https://doi.org/10.1038/S41598-021-80971-9>
- Zhang W, Liu S, Zhang M, Li Y, Sheng K and Xu Z (2019) *Phyllostachys edulis* (moso bamboo) rhizosphere increasing soil microbial activity rather than biomass. *J. Soils Sediments* 19:2913-2926. <https://doi.org/10.1007/s11368-019-02334-2>
- Zhao J, Wang B, Li Q, Yang H and Xu K (2018) Analysis of Soil Degradation Causes in *Phyllostachys edulis* Forests with Different Mulching Years. *Forests* 9:149. <https://doi.org/10.3390/f9030149>
- Zheng R (2011) Effects of *phyllostachys pubescens* forest bamboo pockets fertilization on bamboo pockets rot and the bamboo shoot emergence. *Journal of Fujian Forestry Science and Technology* 38:72-74. (In Chinese) <https://doi.org/10.3969/j.issn.1002-7351.2011.01.18>
- Zhou L, Li J, Zhao Y, Luo Y, Bai Y, Chen J, Wu Z and Lin W (2020) Variation of bacterial communities in the rhizosphere soils of successive rotations *Casuarina equisetifolia* plantations based on high-throughput sequencing analysis. *Acta Ecol. Sin.* 40:2670-2679. <https://doi.org/10.5846/stxb201902250348>
- Zhu C (2005) Ammonium bicarbonate with salt to remove bamboo stump. *Special Economic Animals and Plants* (3): 27.
- Zhu Y, Long H, Lou C, Gu X and Yue J (2013) The technology to promote the decay of bamboo stumps. *Journal of Bamboo Research* 32:53-57.

Figures

Figure 1

Venn diagram of soil bacterial OTUs inside and outside the stumps of moso bamboo with different levels of decay. CB1, CB2, and CB3 indicate mildly decayed, moderately decayed, and heavily decayed soil samples inside the bamboo stumps, respectively; BB1, BB2, and BB3 indicate mildly decayed, moderately decayed, and heavily decayed soil samples outside the bamboo stumps, respectively.

Figure 2

Relative abundance of soil bacteria at the phylum level inside and outside the stumps of moso bamboo with different levels of decay. CB1, CB2, and CB3 indicate mildly decayed, moderately decayed, and heavily decayed soil samples inside the bamboo stumps, respectively; BB1, BB2, and BB3 indicate mildly decayed, moderately decayed, and heavily decayed soil samples outside the bamboo roots, respectively.

Figure 3

Relative abundance of soil bacteria at the class level inside and outside the stumps of moso bamboo at different decay levels. CB1, CB2, and CB3 indicate mildly decayed, moderately decayed, and heavily decayed soil samples inside the bamboo stumps, respectively; BB1, BB2, and BB3 indicate mildly decayed, moderately decayed, and heavily decayed soil samples outside the bamboo roots, respectively.

Figure 4

UPGMA clustering analysis of soil bacteria at the genus level inside and outside the bamboo stumps of moso bamboo with different levels of decay. CB1, CB2, and CB3 indicate mildly decayed, moderately decayed, and heavily decayed soil samples inside the bamboo stumps, respectively; BB1, BB2, and BB3 indicate mildly decayed, moderately decayed, and heavily decayed soil samples outside the bamboo roots, respectively.

Figure 5

Principal component analysis of soil bacterial communities at OTU (a) and genus (b) level inside and outside the stumps of moso bamboo with different levels of decay. CB1, CB2, and CB3 indicate mildly decayed, moderately decayed, and heavily decayed soil samples inside the bamboo stumps, respectively; BB1, BB2, and BB3 indicate mildly decayed, moderately decayed, and heavily decayed soil samples outside the bamboo roots, respectively.