



ORIGINAL ARTICLE

Open Access



Impact of planting *Phallus rubrovolvatus* on physicochemical and microbial properties and functional groups of soil

Xu Gao^{1†}, Mengjiao Ding^{2,3†}, Tao Wu⁴, Xiaohua Deng^{1*} and Qiang Li^{1*}

Abstract

Purpose Soil microbial communities are critically important to agricultural ecosystems. The present study aimed to evaluate the changes in soil microbial community composition and functional groups after planting *Phallus rubrovolvatus*.

Methods Illumina platform were adopted to characterize the bacterial and fungal diversity in the soil cropped with *P. rubrovolvatus* for 0 and 1 year.

Results The results showed that planting *P. rubrovolvatus* reduced the bacterial and fungal diversity in the soil, and the dynamics of the soil bacterial diversity changed more drastically. This study also indicated that, as keystone taxa, the dominant bacteria (*Actinobacteria*, *Sphingomonas*, *Xanthobacteraceae*, and *Gemmatimonadaceae*) and dominant fungi (*Mortierellales* and *Eurotiales*) served as a key component in the network of soil microbial communities. Moreover, the bacterial and fungal communities in the soil planted with *P. rubrovolvatus* formed more similar and weak networks.

Conclusion Planting *P. rubrovolvatus* significantly influenced the structure and composition of microbial communities. In the future, we will focus on ways to improve the soil environment after planting *P. rubrovolvatus*.

Keywords *Phallus rubrovolvatus*, Continuous-cropping obstacle, Environmental factors, Microbial community

Core ideas

1. Planting *P. rubrovolvatus* altered the ecological balance of the soil microbial communities.
2. Bacterial composition was more sensitive than fungal composition to changes after planting *P. rubrovolvatus*.
3. Planting *Phallus rubrovolvatus* could result in risk for soil quality in terms of soil microbial community structure and stability.

Introduction

Phallus rubrovolvatus (*P. rubrovolvatus*) is widely grown in Southwest China due to its rich nutritional value and the good taste of its fruiting bodies (Yuan et al. 2021).

[†]Xu Gao and Mengjiao Ding contributed equally to this work.

*Correspondence:

Xiaohua Deng

yzdxh@163.com

Qiang Li

zqiangli@163.com

¹ College of Agronomy of Hunan Agricultural University, Changsha 410128, China

² College of Tobacco Science of Guizhou University, Guiyang 550025, China

³ Guizhou Provincial Key Laboratory for Tobacco Quality, College of Tobacco Science, Guizhou University, Guiyang 550025, China

⁴ College of Agronomy of Sichuan Agricultural University, Chengdu 411830, China



It is known as the “Queen of mushrooms” with a white net-like veil (Sun et al. 2017). *P. rubrovolvatus* contains various biologically active substances, such as polysaccharides, polyphenols and flavonoids (Lv et al. 2022; Wang et al. 2022). Therefore, regular consumption of bamboo fungi contributes to improving human immunity (Chen et al. 2021). Many studies on biological compounds with antioxidant properties isolated from *P. rubrovolvatus* have been reported (Lu et al. 2014; Pan et al. 2015). Recently, the cultivation of *P. rubrovolvatus* has developed rapidly and become an important economic source and characteristic industry in Guizhou Province. However, the sustainable production of *P. rubrovolvatus* has been affected by some problems, especially the aggravation of diseases and pests in a continuous cropping system.

So far, it is common for farmers mono-cropping in the same field due to the limited cultivated land in Guizhou Province (Yu et al. 2021), causing continuous cropping obstacles (Zheng et al. 2016). Crop growth may deteriorate with reduced crop yields and increased pests and diseases, although normal management is performed in continuous cropping systems (Yang et al. 2018). An increasing number of scientists have started to study continuous cropping obstacles. However, the objects are mainly fruit, vegetables, Chinese herbs, and crops, whereas few studies on edible mushrooms (Hu et al. 2017; Liu et al. 2007; Liu et al. 2021a, b, c; Lou et al. 2017; Wang et al. 2014). *Auricularia auricula* in the soil where it has been continuously cropped for more than 2 years has a higher probability of rotting and a 20% lower yield than that grown in new soil (Li and Gao 2004). Long-term continuous cultivation of *Pleurotus geesteranus* is an important factor resulting in the high incidence of diseases (Xing et al. 2012). Similar to the interrelationship and dynamic change processes between the growth of other edible mushrooms and soil microorganisms, those between the growth of *P. rubrovolvatus* and soil microorganisms are still studied at the exploratory stage, and practical ways to solve continuous cropping obstacles are lacking (Gong et al. 2018; Benucci et al. 2019).

In general, a contributing factor is that mono-cropping eliminates crop and biological diversity (Liu et al. 2021a, b, c). Numerous works indicated that soil microorganisms can be indicators of soil quality (Cardinale et al. 2019; Fan et al. 2019; Liu et al. 2021a, b, c). Relatively high levels of species richness in soil are associated with nutrient cycling, and the species often regulate soil fertility (Zhang et al. 2022b). The content of soil organic carbon, total phosphorus and alkaline decomposition nitrogen were significantly increased after planting *Phallus echinvolvatus* (Liang et al. 2019). Interplanting *Dictyophora echinvolvata* significantly increased the organic matter contents of soil and

the pH value raised by 4.97% in soil of *Phyllostachys heterocyclus* cv. *Pubescens* (Wang et al. 2016). The contents of the organic matter, total nitrogen, total phosphorus, total potassium, available nitrogen, available potassium, and pH increased significantly under the *Stropharia rugosoannulata* and strawberry rotation system (Mao et al. 2020). The abundance and diversity of fungal community were significantly reduced in the soil after planting *Morchella* spp., and the Ascomycetes was increased over the years (Han et al. 2023). Additionally, Ascomycetes were positively correlated with available potassium, available phosphorus, ammonium nitrogen, and water content. After 3 years of continuous-cropping *Phallus echinvolvatus*, the population and diversity of soil bacteria were decreased, and the relative abundance of *Bradyrhizobium* and *Chthoniobacter* were increased (Liang et al. 2019). After planting *Phallus echinvolvatus*, the abundance of functional genes changed significantly, especially the abundance of enzyme genes involved in signal transduction, methanogenic metabolism, nitrogen metabolism and other processes increased, indicating that the planting *Phallus echinvolvatus* could change soil function (Wang et al. 2016). The relative abundance of saprophytic fungi increased by 15.2% after planting *Morchella* in the same plot for many years (Li et al. 2022). Saprophytic fungi often carry pathogens, indicating that the hidden dangers of soil pests and diseases are increasing.

The imbalance of soil microbial diversity can lead to the enrichment of pathogenic microorganisms, causing various soil-borne diseases (Tian et al. 2018). Reduced microbial species and incomplete availability of nutrients required for microbial metabolic activity leads to low microbial diversity (Huang et al. 2021). However, many scholars have focused on community composition without considering the key factors changed by the cropping obstacle of *P. rubrovolvatus*. In this study, we aimed to (i) understand the effects of *P. rubrovolvatus* on the functions of soil microorganisms; (ii) characterize the complex interactions among different microbial species; (iii) evaluate the key factors in yield reduction of *P. rubrovolvatus*.

Materials and methods

Sample description

The study area is located in Nayong City in the north of Guizhou Province, China (26°46′39″ N, 105°22′57″ E). *P. rubrovolvatus* has been cultivated for a long time here and is highly affected by the continuous-cropping obstacle, requiring renewing soil every year. The greenhouse with an air humidity of 70% and room temperature of 26 °C is suitable for the large-scale cultivation of *P. rubrovolvatus*. The test soil was collected from a farmland which located in Nayong City. The soil type of local

area was yellow loam soil and the farmland was originally planted with corn. The experimental plots (20×20 m) were set in a greenhouse. The distance between each plot was 5 m. Total 200 mushroom sticks of *P. rubrovolvatus* were buried into soil with 3 cm thickness of soil on the top of sticks in 20 April, 2022. For each experimental plot 5 equally spaced repetitions were performed in 21 July, 2022. The soil samples were immediately transported to the laboratory with dry ice. Visible residues were removed, and part of samples was dried naturally to measure soil physical and chemical indices. Another part was stored at −80 °C for measuring microbial indicators.

Determination of physical and chemical properties of soil

Soil chemical properties were determined following standard methods, and each sample was analyzed in triplicate. Soil organic matter (SOM) was measured using the dichromate redox colorimetric method. Alkali-hydrolyzable nitrogen (Nah) was analyzed using the alkaline hydrolysis diffusion method (Roberts et al. 2011). Available phosphorus (AP) was measured using the molybdenum blue colorimetric method. Available potassium (AK) was measured via flame photometry with neutral ammonium acetate extraction. Soil pH was determined in suspensions with a soil–water (w/w) ratio of 1:2.5.

DNA library construction and sequencing

According to the manufacturer's protocols, DNA was extracted from 0.25 g soil samples using a EZNA Soil DNA Kit (Tiangen DP812, Beijing, China) and quantified spectrophotometrically (Nanodrop ND-1000, NanoDrop Technologies Inc., USA). The bacterial primers 338F and 806R were used to amplify the V3–V4 hypervariable regions of the 16S rRNA gene (Huang et al. 2020). The primers ITS1F and ITS2R were used to amplify the ITS region of the fungal rRNA gene (Wang et al. 2017). The PCR products were purified by DNA Extraction Kit (T1020L, MA, USA). Equal amounts of the PCR products of each sample were quantified by QuantiFluor™-ST (Promega, USA). Then, the purified amplicons employed for library construction using an Illumina Novaseq 6000 platform (Illumina, CA, USA). The SEED 2.1.2 pipeline was used for processing of the amplicon sequencing data (Vetrovský et al. 2018). Sequence alignment, denoising, chimera check, and clustering were carried out by using a

set of Seed 2 external programs (USEARCH/ v 7.0.1090, MAFFT v 7.215, MOTHUR v1.34.4). For each OTU, a representative sequence was selected and used to assign taxonomic composition by using the Mothur method (Schloss, et al. 2009) and SILVA132r (Edgar 2013).

Bioinformatics and Statistical analyses

One-way analysis of variation (ANOVA) was used to assess the significance of the effects of bacterial and fungal composition and diversity (Xing et al. 2014). We estimated microbial community richness using Chao1 and ACE indexes; larger values of both indexes indicated higher community richness. The functional potentials of bacteria and fungi were investigated with PICRUST2 and FUN Guild, respectively. All analyses were performed on the BMK Cloud platform (Biomarker Technology Co., Ltd., Beijing, China). Finally, to confirm difference in the abundances of individual taxonomy between the two groups, results were evaluated using SPSS 20.0. The data was expressed as mean ± SD of replicated values where indicated.

Results

Soil physicochemical properties

Changes in the chemical properties of soils in response to planting *P. rubrovolvatus* are shown in Table 1. After planting *P. rubrovolvatus*, the fluctuation of soil pH was small, and all samples showed weak acidity. In contrast, SOM, Nah, AP, and AK values changed significantly that exhibited a similar increasing trend. The SOM, Nah, AP, and AK values of soil were significantly affected by planting *P. rubrovolvatus*.

Diversity of microbial communities in the cultivated soil of *P. rubrovolvatus*

All sequence data have been deposited in the NCBI (accession number: PRJNA878607). We obtained 480,134 clean reads for bacteria and 518,037 clean reads for fungi. The clean bacterial reads included 239,924 for CK (cropping of *P. rubrovolvatus* for 0 year) and 240,210 for T1 (cropping of *P. rubrovolvatus* for 1 year). The clean fungal reads included 292,666 for CK and 225,371 for T1. The alpha diversity of the bacteria indicated that the bacterial diversity tended to decrease after planting *P. rubrovolvatus* (Fig. 1A, B). The observed bacterial

Table 1 Physicochemical properties of fallow farmland soil and planting *P. rubrovolvatus* soil samples

Samples	SOM (g/kg)	Nah (mg/kg)	AP (mg/kg)	AK (mg/kg)	pH
CK	7.61 ± 0.01	39.13 ± 0.05	4.23 ± 0.01	107.52 ± 0.85	5.93 ± 0.01
T1	21.52 ± 0.30	97.05 ± 0.30	8.00 ± 0.03	488.46 ± 0.71	5.72 ± 0.01

CK soil from fallow farmland, T1 soil from planting *P. rubrovolvatus* for 1 year. Data are presented as the mean ± standard error (n = 3)

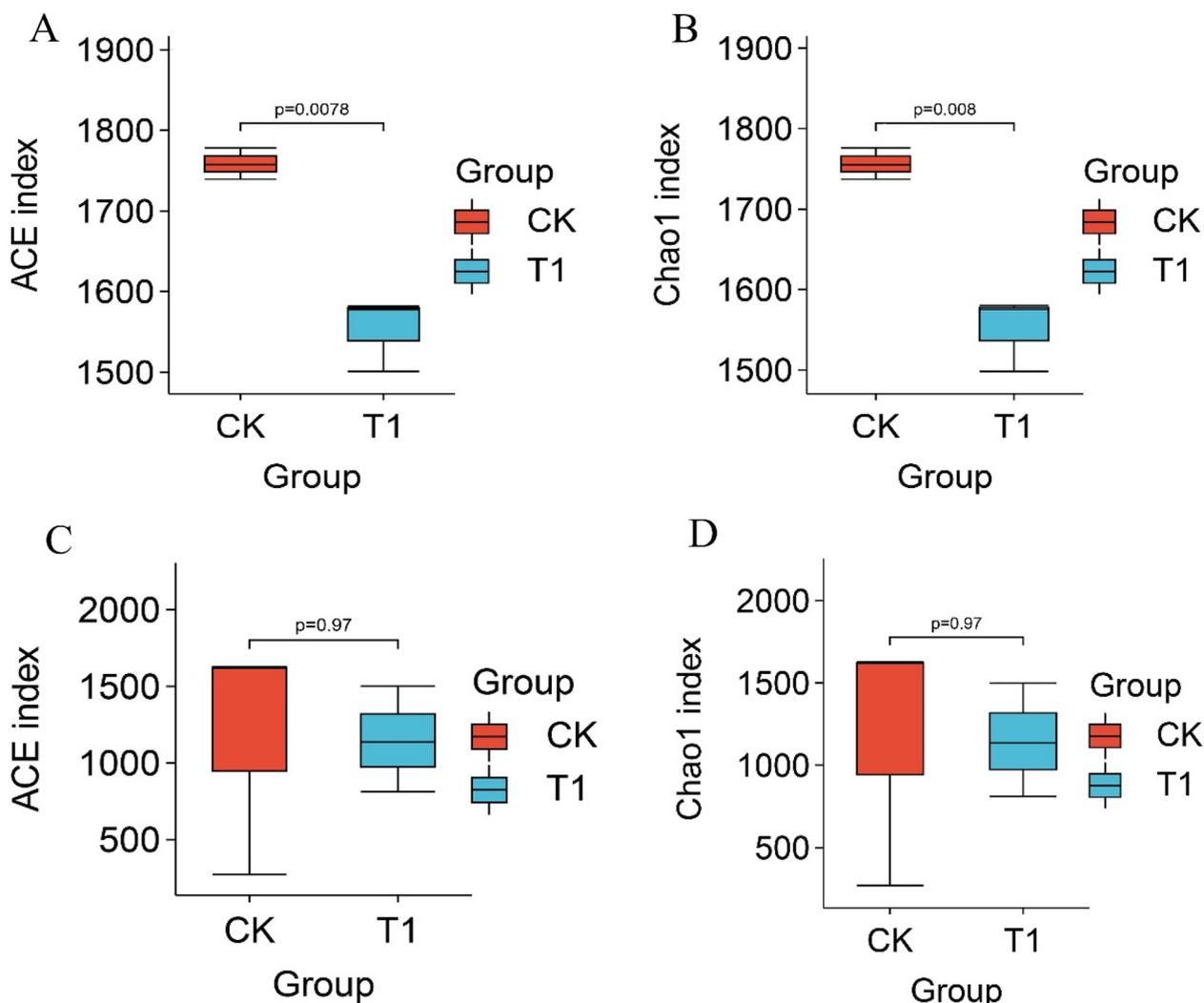


Fig. 1 Alpha diversity indices of bacterial and fungal communities of soil samples. **A, B** The bacterial abundance is reflected in the ACE and Chao1 index; the ACE and Chao1 index was significantly different between the two groups ($p < 0.05$). **C, D** The fungal abundance is reflected in the ACE and Chao1 index. CK: soil from fallow farmland. T1: soil from planting *P. rubrovolvatus* for 1 year

species changed significantly from 1737 to 1776 in CK and from 1498 to 1580 in T1. However, the fungal diversity and richness both tended to increase following the cultivation of *P. rubrovolvatus*, and no significant difference was found (Fig. 1C, D).

Composition and differences of microbial communities in the cultivated soil of *P. rubrovolvatus*

According to OTUs, the cultivated soil of *P. rubrovolvatus* contained 35 phyla, 92 classes, 257 orders, 461 families, and 798 genera of bacteria. The top six abundant bacterial phyla were Proteobacteria (15.15–36.37%), Acidobacteriota (14.39–17.06%), Actinobacteriota (5.77–22.54%), Chloroflexi (3.23–12.1%), Methylo-

mirabilota (2.21–11.25%), and Myxococcota (2.59–8.03%), accounting for more than 85% of sequences among both treatments. Proteobacteria and Actinobacteriota dominated the T1 group occupying 58.9% of all sequences (Fig. 2A). Their relative abundance in the cultivated soil of *P. rubrovolvatus* was significantly higher than that in CK. In addition, significant decreases were found in the relative abundances of Acidobacteriota, Chloroflexi, Methylo-

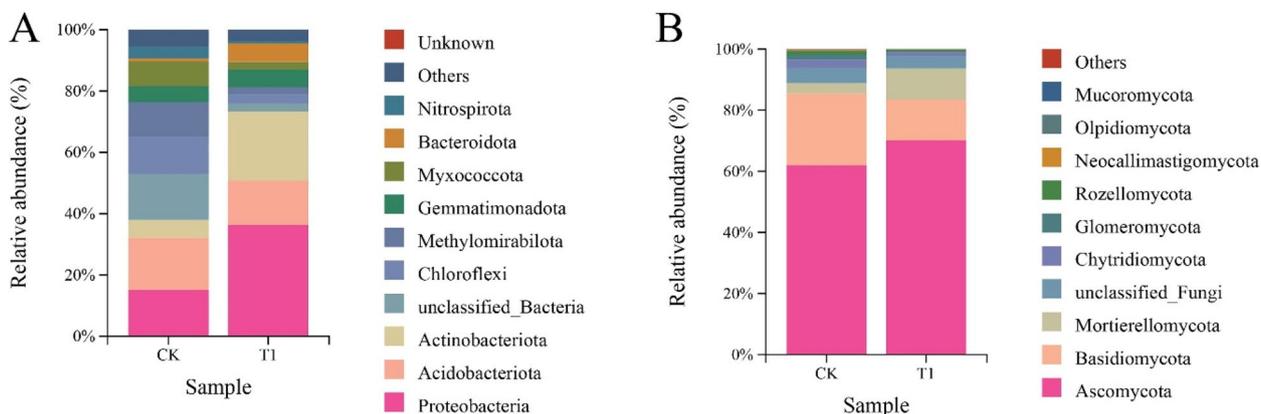


Fig. 2 Relative abundance of bacterial and fungal communities of soil samples at phylum level. **A** Bacterial phyla. **B** Fungal phyla. Phyla representing less than 1% of the total reads are grouped as “Others.” CK: soil from fallow farmland. T1: soil from planting *P. rubrovolvatus* for 1 year

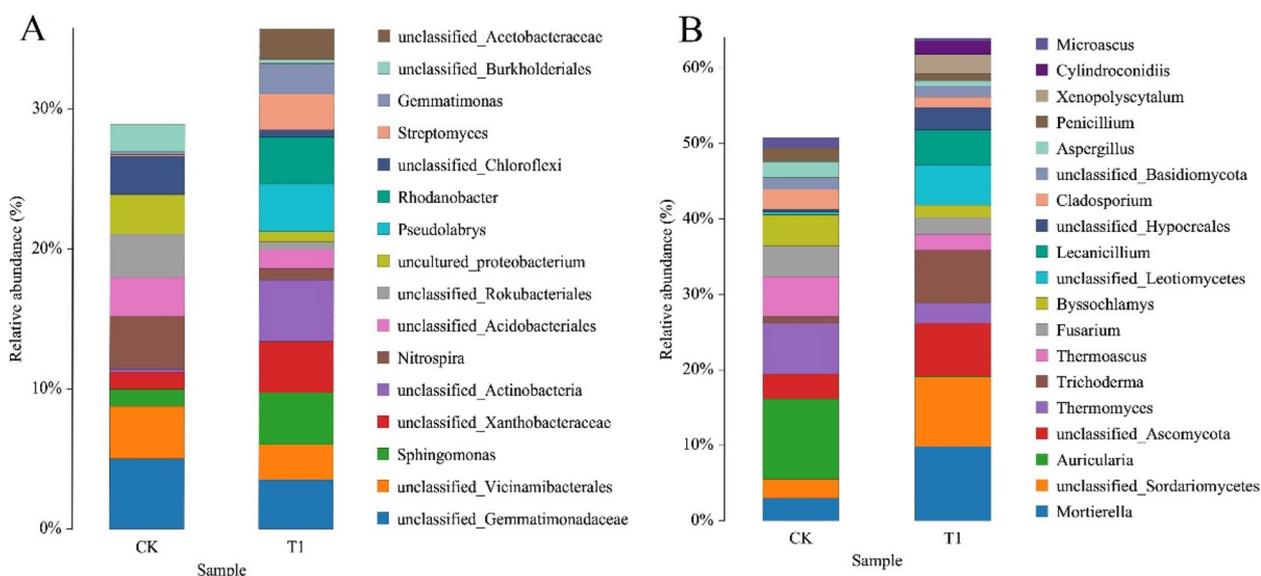


Fig. 3 Relative abundance of bacterial and fungal communities of soil samples at genus level. **A** Bacterial genera. **B** Fungal genera. CK: soil from fallow farmland. T1: soil from planting *P. rubrovolvatus* for 1 year

the relative abundances of seven genera (*Sphingomonas*, *Xanthobacteraceae*, *Actinobacteria*, *Gemmatimonas*, *Streptomyces*, *Pseudolabrys*, and *Acetobacteraceae*) in T1 were significantly higher than those in CK. In each sample, Gemmatimonadaceae was the most important bacterial genus, and its proportion in CK (5.04%) was significantly higher than in T1 (3.51%). Nitrospira was the second most important bacterial genus, with its proportion in CK (3.80%) being significantly higher than in T1 (0.79%).

Similarly, 18 phyla, 60 classes, 142 orders, 317 families, and 733 genera of fungi were contained in the cultivated soil of *P. rubrovolvatus*. The top three abundant fungal phyla were Ascomycota (62.04–70.14%), Basidiomycota

(13.45–23.43%), and Mortierellomycota (3.37–10.05%), accounting for more than 90% of sequences among both treatments (Fig. 2B). Ascomycota dominated in T1, occupying 70.14% of all sequences. In addition, its relative abundance in the T1 was significantly higher than that in CK. The relative abundance of Basidiomycota in T1 was lower than that in CK. The relative abundances of nine genera (*Auricularia*, *Thermomyces*, *Thermoascus*, *Byssoschlamys*, *Fusarium*, *Cladosporium*, *Aspergillus*, *Penicillium*, and *Microascus*) in CK were significantly higher than those in T1 (Fig. 3B). However, the relative abundances of five genera (*Mortierella*, *Trichoderma*, *Leotiomyces*, *Hypocreales*, and *Lecanicillium*) in T1 were significantly higher than those in CK. It is noteworthy

that the relative abundance of *Thermomyces* in CK was 6.78%, while that in T1 was 2.59%. Interestingly, the relative abundances of *Mortierella* had upward trends, being higher in T1 (9.82%) than in CK (3.01%).

Co-occurrence networks in the bacterial and fungal communities in the cultivated soil of *P. rubrovolvatus*

The co-occurrence networks at the OTU level were further explored the interactions of bacterial and fungal co-occurrence patterns (Supplemental Figure S1–4). For the bacterial community, the T1 and CK networks consisted of 50 and 74 nodes, respectively, indicating that the CK network had a larger size with more nodes than the T1 network. The T1 network had far more simple interactions in terms of connectivity than the CK network. The OTUs with the highest betweenness centrality scores were regarded as keystone taxa (Fan et al. 2019). We also found that *Actinobacteria*, *Sphingomonas*, *Xanthobacteraceae*, and *Gemmatimonadaceae* were keystone taxa in the cultivated soil of *P. rubrovolvatus*. In addition, *Gemmatimonadaceae*, *Nitrospira* and *Vicinamibacterales* were categorized as keystone taxa in CK.

The network structures of the fungal community were significantly simpler than those of the bacterial community. The T1 and CK networks consisted of 53 and 61 nodes, respectively. The proportion of the nodes having positive interactions with others in the CK network (51%) was higher than that in the T1 network (34%), indicating the high stability and complexity of the CK network. We

also identified many differences in keystone taxa between all samples. *Mortierellales* and *Eurotiales* were categorized as keystone taxa in the cultivated soil of *P. rubrovolvatus*. *Eurotiales*, *Auriculariales*, and *Sordariales* were regarded as keystone taxa in the CK group. The results of the correlation heatmap showed that AK and pH had the greatest influence in shaping the bacterial and fungal keystone taxa (Fig. 4). AK exerted a positive effect on *Actinobacteria* and *Gemmatimonadaceae*. pH exerted a strong negative influence on *Sphingomonas*, *Xanthobacteraceae*, and *Mortierellales*.

Prediction of bacterial and fungal community functions in the cultivated soil of *P. rubrovolvatus*

We used functional annotation of prokaryotic taxa to predict the abundances of different metabolic pathways (Fig. 5). The results showed that chemoheterotrophy, aerobic chemoheterotrophy, predatory or exoparasitic and aromatic compound degradation dominate the metabolic pathways. Additionally, the abundance of genes related to chemoheterotrophy, aerobic chemoheterotrophy, and aromatic compound degradation were significantly higher in T1 than in CK.

The FUNGuild database was introduced to annotate fungi and found different microbial functional communities in the cultivated soil of *P. rubrovolvatus*. The results showed that pathoproth increased rapidly after planting *P. rubrovolvatus*, and the relative abundance increased from 13.33 to 26.73% (Fig. 6A). The relative abundances

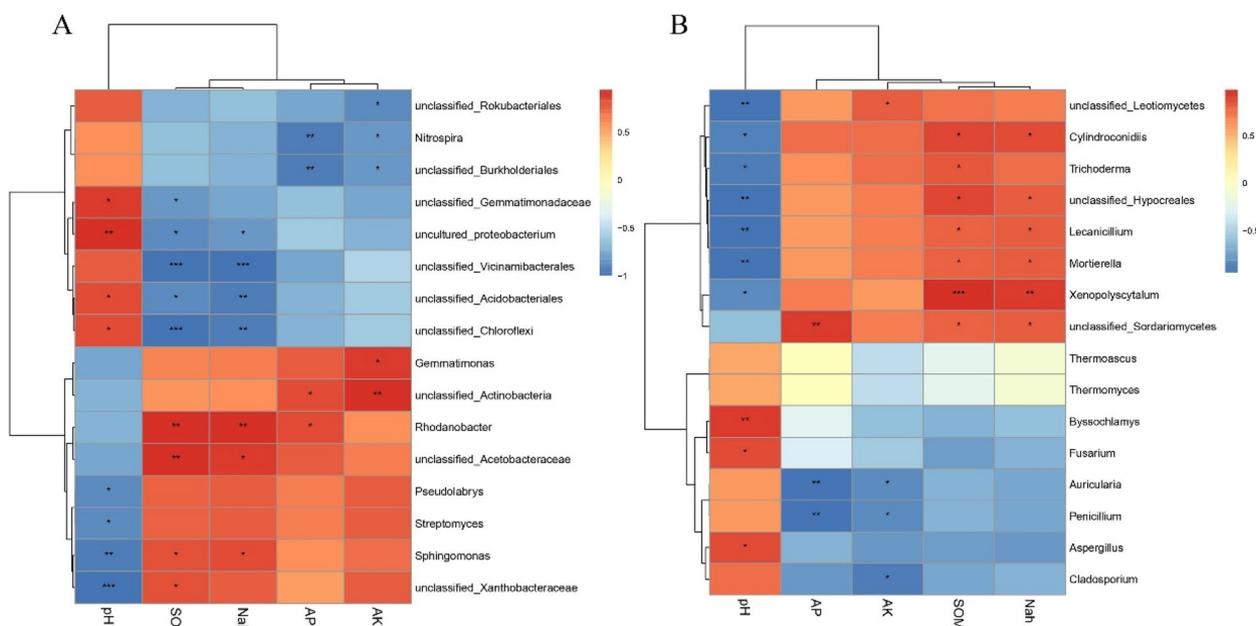


Fig. 4 A correlation heatmap between environmental factors and bacterial (A) and fungal (B) communities at the genus level. Correlations between environmental factors and genera were indicated by different colors and “**”

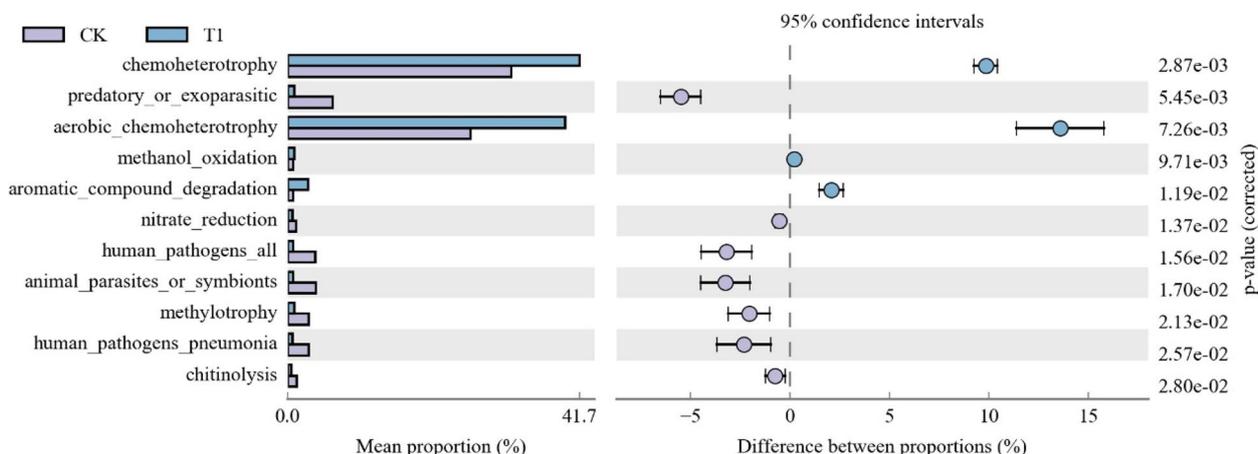


Fig. 5 Changes of in functional groups on bacterial OUT data in soil samples. CK: soil from fallow farmland. T1: soil from planting *P. rubrovolvatus* for 1 year

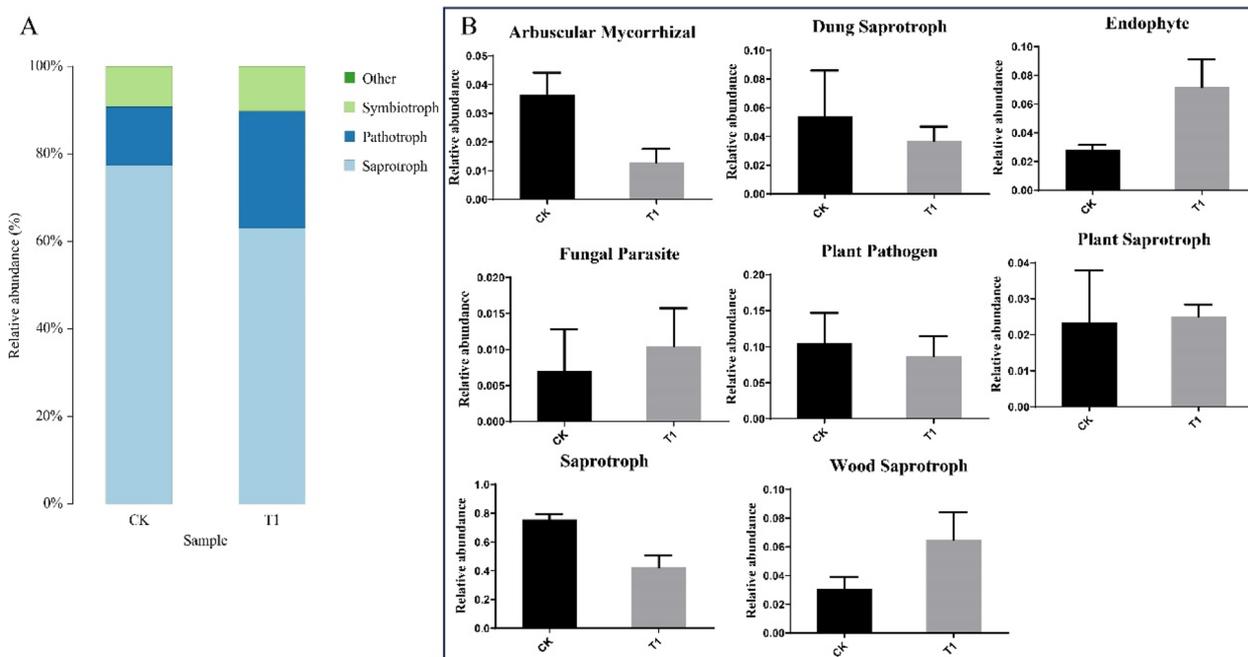


Fig. 6 Changes of in functional groups on fungal OUT data in soil samples. **A** Functional prediction of Fungi. **B** Changes of selected fungal functional groups in soil samples. CK: soil from fallow farmland. T1: soil from planting *P. rubrovolvatus* for 1 year

of endophytes, fungal parasites, and wood saprotrophs in T1 were significantly higher than those in CK. In contrast, the abundances of arbuscular mycorrhizal, dung saprotrophs and saprotrophs decreased significantly (Fig. 6B). However, the abundances of plant pathogens and plant saprotrophs had no significant changes.

Discussions

The growth of *P. rubrovolvatus* is essentially the interaction between mycelium and below-ground microorganisms (Huang et al. 2018). In the present study, we found significant changes in the characteristics of soil microbial communities after planting *P. rubrovolvatus*. The alpha analysis indicated that the bacterial and fungal diversity was reduced after planting *P. rubrovolvatus*. It is noteworthy that the dynamics of soil

bacterial diversity changed more drastically. Previous findings indicated that, after planting *Dictyophora echinovolvata*, the soil bacterial diversity first increased in the first year and then decreased in the following year (Liang et al. 2019). In this work, the level of bacterial diversity in the soil tended to decrease, the levels of soil fungal diversity and richness both tended to increase, and no significant difference existed after planting *P. rubrovolvatus*. This result is contrary to that of Liang et al. (2019). In this study, we found that Proteobacteria and Actinobacteriota were the dominant phyla, and the relative abundances of Acidobacteriota, Chloroflexi, and Myxococcota decreased at different levels. Previous findings indicated that Proteobacteria and Actinobacteriota were fast-growing copiotrophic bacteria. Acidobacteria, Chloroflexi, and Myxococcota were considered as oligotrophic bacteria and they usually dominant in harsh environments (Teixeira et al. 2010; Xu et al. 2022). The abundances of Proteobacteria and Actinobacteriota were relatively high in the cultivated soil of *P. rubrovolvatus*, probably due to nutrients released from mushroom sticks and mycelium secretions. The increase in soil nutrients might inhibit the growth of Acidobacteria, Chloroflexi, and Myxococcota.

Numbers of reports have pointed that Ascomycota and Basidiomycota were considered as the dominant fungal phyla in many soil types (Huang et al. 2020; Sun et al. 2022). In the present study, we found that Ascomycota, Basidiomycota and Mortierellomycota were the dominant phyla. In addition, Ascomycota was the most abundant in all samples. Basidiomycota degraded more complex lignocellulose components in soil. This finding confirms our assumption that planting *P. rubrovolvatus* can provide simple nutrients in the soil which can be easily accessed by microorganisms. With an increase in continuous cropping years, the relative abundances of *Hypocreales*, *Mortierella*, *Sordariales*, and *Trichoderma* decreased (Bai et al. 2015; Schlatter et al. 2015). Previous studies displayed that many fungi belonging to *Hypocreales* (e.g., *Fusarium*) were potential pathogens of *P. rubrovolvatus* (Hubbard et al. 2011). The increased relative abundance of *Hypocreales* may increase the risk of crop diseases. For instance, an increase in the contents of *Mortierella* and *Trichoderma* in the fungi of the soil may be an important reason for the high incidence of “mildew disease” in planting *P. rubrovolvatus*.

Our results indicated that the difference in the abundances of main soil microbial communities in the cultivated soil of *P. rubrovolvatus* might be caused by different soil nutrient conditions. Bacterial composition was more sensitive than fungal composition to changes after planting *P. rubrovolvatus*. In this work, we also observed that the keystone taxa were considered ubiquitous species in

the soil of each sample. *Actinobacteria*, *Sphingomonas*, *Xanthobacteraceae*, and *Gemmatimonadaceae* as bacterial keystone taxa in the cultivated soil of *P. rubrovolvatus*, meanwhile *Mortierellales* and *Eurotiales* were categorized as fungal keystone taxa. In contrast, *Actinobacteria* tend to dominate in acidic environment where pH is low (Ho et al. 2017). The release of acids during the growth of *P. rubrovolvatus* may have also reduced the pH, thus favoring the growth of *Acidobacteria*. *Xanthobacteraceae* were known to have hydrolytic ability and are recognized as slow acting decomposers of plant-derived organic matter (Ivanova et al. 2017). *Sphingomonas* and *Gemmatimonadaceae* were identified as aerobic heterotrophs and also involved in organic matter degradation (Zhou et al. 2015). Changes in the abundance of these three genera may affect soil reactive N and organic matter decomposition strongly. *Mortierellales* and *Eurotiales* as Saprophytic fungal contributed to the acquisition of soil nutrients and decomposition of organic matter (Nguyen et al. 2016). The keystone taxa drove the structure and functioning of microbial communities (Liu et al. 2016). The weakened interactions after planting *P. rubrovolvatus* were mainly due to reduced links between bacterial and fungal taxa. Taxa with high relative abundances may have critical role in the network of soil microbial communities. Thus, an in-depth analysis on the key functional taxa of these types may contribute to reducing the harm caused by soil pathogens (Cipollini et al. 2012).

We adopted the principal component analysis to analyze the bacterial and fungal community structures in the cultivated soil of *P. rubrovolvatus* (Fig. 7). An obvious separation between the CK and T1 indicated that planting *P. rubrovolvatus* contributed to changing the microbial communities of the soil and forming different taxonomic units. Compared to the bacterial and fungal communities in the soil in CK, those in the cultivated soil of *P. rubrovolvatus* formed more similar and weak networks. The bacterial and fungal networks of CK had a larger size with more nodes, indicating its higher stability and complexity. According to this finding, the previous study also found similar results. A previous study reported that soil microbial diversity was reduced due to the cultivation of *Morchella sextelata* (Zhang et al. 2022a). The continuous cropping of *Phallus echinovolvatus* caused an imbalance in microbial populations by converting soil microorganisms from bacterial to fungal types (Liang et al. 2019).

Microorganisms depend on nutrients to support growth and reproduction under the nutrient competition hypothesis (Orwin et al. 2011). The prediction result of bacterial community functions showed that chemoheterotrophy, aerobic chemoheterotrophy, predatory or exoparasitic, and aromatic compound degradation were dominant. As

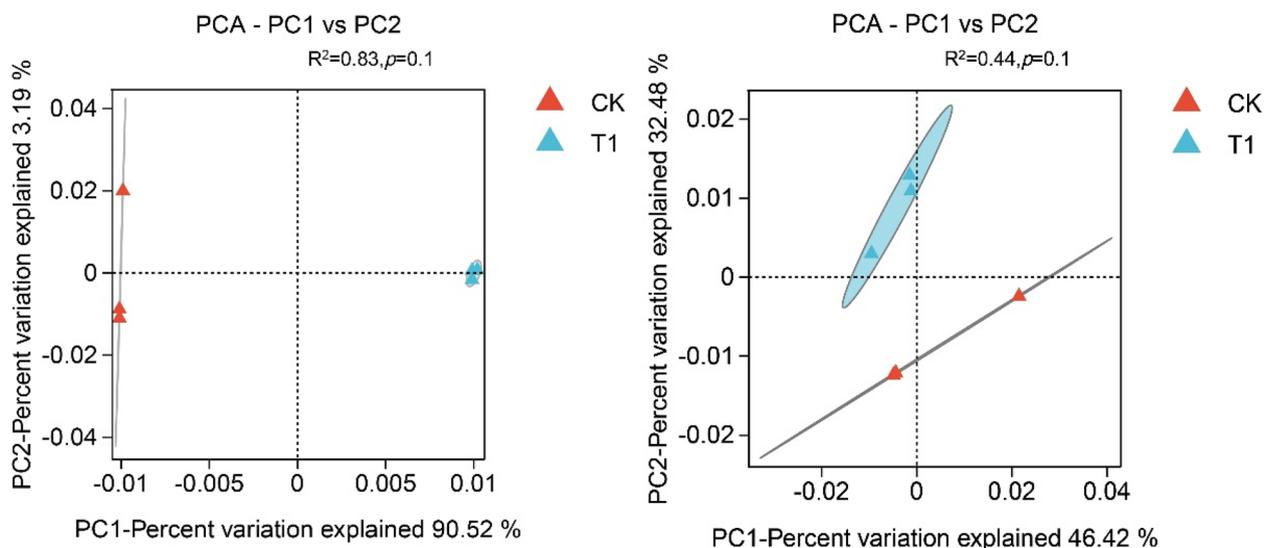


Fig. 7 Major variations in the bacterial (A) and fungal (B) communities in soil samples detected by the PCA of the OTUs. CK: soil from fallow farmland. T1: soil from planting *P. rubrovolvatus* for 1 year

for the fungal community functions, pathoproth increased rapidly after planting *P. rubrovolvatus*, and the relative abundance increased from 13.33 to 26.73%. We suspected that there were two main reasons for those results. As macro-fungi, *P. rubrovolvatus* fungi were artificially cultivated into the soil and might crowd out the ecological niches of soil microorganisms, breaking the balance of the soil microbial communities (Xing et al. 2012). High humidity and the bio-thermal energy produced by mushroom sticks could alter the microbial environment and species diversity of the soil (Chen et al. 2021). This study showed that planting *P. rubrovolvatus* altered the ecological balance of the soil microbial communities. The duration of this change and the method of restoring the soil microbiology to levels similar to the previous ones require to be further studied.

Conclusions

Soil microbial communities changed significantly after planting *P. rubrovolvatus*. According to our results, the bacterial and fungal diversity was reduced due to the cultivation of *P. rubrovolvatus*, probably leading to changes in corresponding functions. We also observed that the keystone taxa, such as bacteria including *Actinobacteria*, *Sphingomonas*, *Xanthobacteraceae*, and *Gemmatimonadaceae* and fungi including *Mortierellales* and *Eurotiales*, with high relative abundances, and play an important part in the network of soil microbial communities. In the future, an in-depth analysis should focus on the way to improve the soil environment after planting *P. rubrovolvatus*.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13213-023-01727-6>.

Additional file 1: Supplemental Figure S1–4. The co-occurrence network of soil bacteria and fungi in soil samples. The node of each network is colored according to the phylum and sized according to the degree. The edges connecting the nodes are represented by red lines to indicate co-occurrence and green lines for mutualistic exclusion. **Supplemental Figures S1 and S2.** The co-occurrence network of soil bacteria and fungi from fallow farmland. **Supplemental Figures S3 and S4.** The co-occurrence network of soil bacteria and fungi from planting *P. rubrovolvatus* for 1 year.

Acknowledgements

We would like to thank the anonymous reviewers for their valuable comments on this study. The work was supported by the Science and Technology Project of Guizhou Tobacco Company (Grant No. 2021XM21, 2022XM06), and the Research Foundation of Education Bureau of Hunan Province, China (Grant No. CX20190515; SCX1840).

Authors' contributions

Xu Gao: guide the completion of this experiment and revise their papers. Mengjiao Ding: do experiments, data analysis completed the first draft paper. Tao Wu: experiment, record data. Xiaohua Deng and Qiang Li: participating in the experiment, finished draft paper together with the second author. The authors read and approved the final manuscript.

Funding

This study was funded by the Science and Technology Project of Guizhou Tobacco Company (Grant Nos. 2021XM21 and 2022XM06), and the Research Foundation of Education Bureau of Hunan Province, China (Grant Nos. CX20190515 and SCX1840).

Availability of data and materials

All data generated and analyzed during this study are included in this article.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Received: 20 January 2023 Accepted: 21 June 2023

Published online: 19 September 2023

References

- Bai L, Cui J, Jie W, Cai B (2015) Analysis of the community compositions of rhizosphere fungi in soybeans continuous cropping fields. *Microbiol Res* 180:49–56
- Benucci GMN, Longley R, Zhang P, Zhao P, Bonito G, Yu FQ (2019) Microbial communities associated with the black morel *Morchella sextelata* cultivated in greenhouses. *Peer J* 7:e7744
- Cardinale M, Suarez C, Steffens D, Ratering S, Schnell S (2019) Effect of different soil phosphate sources on the active bacterial microbiota is greater in the rhizosphere than in the endorhiza of barley (*Hordeum vulgare* L.). *Microb Ecol* 77:689–700
- Chen X, Zhou X, Zhao J, Tang X, Pasquali M, Migheli Q et al (2021) Occurrence of green mold disease on *Dictyophora rubrovolvata* caused by *Trichoderma koningiopsis*. *J Plant Pathol* 103:981–984
- Cipollini D, Rigby CM, Barto EK (2012) Microbes as targets and mediators of allelopathy in plants. *J Chem Ecol* 38:714–727
- Edgar RC (2013) UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nat Methods* 10:996
- Fan Z, Lu S, Liu S, Guo H, Peng X (2019) Changes in plant Rhizosphere microbial communities under different vegetation restoration patterns in karst and non-karst ecosystems. *Sci Rep* 9:8761
- Gong S, Chen C, Zhu J, Qi G, Jiang S (2018) Effects of wine-cap *Stropharia* cultivation on soil nutrients and bacterial communities in forestlands of northern China. *Peer J* 6:e5741
- Han YT, Yue ZL, Zhang GY, Gao J, Li P, Wang LA, Li SM, Zhao ZC, Liu XW, Wang L (2023) Fungal diversity and metabolic pathways in the rhizosphere soil of *Morchella esculenta* with different planting years. *Jiangsu Agric Sci* 51:212–218
- Ho A, Di Lonardo DP, Bodelier PLE (2017) Revisiting life strategy concepts in environmental microbial ecology. *FEMS Microbiol Ecol* 93:fix006
- Hu W, Zhang Y, Huang B, Teng Y (2017) Soil environmental quality in greenhouse vegetable production systems in eastern China: Current status and management strategies. *Chemosphere* 170:183–195
- Huang Y, Li XQ, Wang XH, Dai F, Chen X, Ding MJ et al (2021) The effect of compound biofertilizers on nitrogen metabolism and microbial diversity of soil rhizosphere in tobacco fields. *Agron J* 114:2002–2010
- Huang Y, Xiao X, Huang HY, Jing JQ, Zhao HJ, Wang L et al (2018) Contrasting beneficial and pathogenic microbial communities across consecutive cropping fields of greenhouse strawberry. *Appl Microbiol Biotechnol* 102:5717–5729. <https://doi.org/10.1007/s00253-018-9013-6>
- Huang C, Yang W, Chen Y, Han X, Khan S, Gao Z, Yang Z (2020) Ridge-furrow and film-mulching sowing practices enhance enzyme activity and alter fungi communities. *Agron J* 112:4775–4787
- Hubbard JP, Harman GE, Eckenrode C (2011) Interaction of a biological control agent, *Chaetomium globosum*, with seed coat microflora. *Can J Microbiol* 28:431–437
- Ivanova AA, Naumoff DG, Miroshnikov KK, Liesack W, Dedysh SN (2017) Comparative genomics of four *Isosphaera* planctomycetes: a common pool of plasmids and glycoside hydrolase genes shared by *Paludisphaera borealis* PX4T, *Isosphaera pallida* IS1BT, *Singulisphaera acidiphila* DSM 18658T, and strain SH-PL62. *Front Microbiol* 8:412
- Li JY, Hua R, Sun DF, Wen XQ, Li XS, Ma M, Gao ZH, He Y, Liu SX (2022) Research on White Mold Disease on *Morchella* spp. and Fungal Community Structure of Soil Samples. *Edible Fungi of China* 41:50–54
- Li XT, Gao MB (2004) Effects of *Auricularia auricula* polysaccharide on scavenging reactive oxygen species and protecting mitochondria. *J Food Sci* 1:171–173
- Liang JF, Yu F, Shi J (2019) Effects of continuous cropping of *Phallus echinovolvatus* on Rhizosphere soil bacteria. *J Hunan Ecol Sci* 6:1–10
- Liu B, Gumpertz ML, Hu S, Ristaino JB (2007) Long-term effects of organic and synthetic soil fertility amendments on soil microbial communities and the development of southern blight. *Soil Biol Biochem* 39:2302–2316
- Liu ZX, Liu JJ, Yu ZH, Yao Q, Li YS, Liang AZ, Zhang W, Mi G, Jin J, Liu XB, Wang GH (2020) Long-term continuous cropping of soybean is comparable to crop rotation in mediating microbial abundance, diversity and community composition - ScienceDirect. *Soil Tillage Res* 197:104503
- Liu JL, Li SQ, Yue SC, Tian JQ, Chen H, Jiang HB, Siddique KHM, Zhan A, Fang QX, Yu Q (2021a) Soil microbial community and network changes after long-term use of plastic mulch and nitrogen fertilization on semiarid farmland. *Geoderma* 396:115086
- Liu QW, Wang SW, Li K, Qiao J, Guo YS, Liu ZD, Guo XW (2021b) Responses of soil bacterial and fungal communities to the long-term monoculture of grapevine. *Appl Microbiol Biotechnol* 105:7035–7050
- Liu S, Wang ZY, Niu JF, Dang KK, Zhang SK, Wang SQ (2021c) Changes in physicochemical properties, enzymatic activities, and the microbial community of soil significantly influence the continuous cropping of *Panax quinquefolius* L. (*American ginseng*). *Plant Soil* 463:427–446
- Lou Z, Sun Y, Zhou X, Baig SA, Hu B, Xu X (2017) Composition variability of spent mushroom substrates during continuous cultivation, composting process and their effects on mineral nitrogen transformation in soil. *Geoderma* 307:30–37
- Lu YY, Gui Y, Gong GL, Wei SY, Zhu GS (2014) Genetic diversity of 18 *Dictyophora rubrovolvata* germplasm resources from Guizhou. *Guizhou Agric Sci* 42:17–20
- Lv J, Yao L, Li S, Dong J, Ye M, Fan D, Li C, Tian F, Li Y (2022) New aniline derivatives from the volva of *Phallus rubrovolvatus* and their anti-inflammatory activity. *Bioorg Chem* 119:105577
- Mao N, Jia HY, Wang JC, Zhou TL, Yang JX (2020) Effects of rotation of *Stropharia rugosoannulata*, *Lentinus edodes* and strawberry on soil and strawberry growth. *Edible Fungi China* 39:61–64
- Nguyen NH, Song Z, Bates ST, Branco S, Tedersoo L, Menke J, Schilling JS, Kennedy PG (2016) FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecol* 20:241–248
- Orwin KH, Kirschbaum MUF, John MGS, Dickie IA (2011) Organic nutrient uptake by mycorrhizal fungi enhances ecosystem carbon storage: a model-based assessment. *Ecol Lett* 14:493–502
- Pan GC, Long HW, Di WU, Chen X, Dai LH, Sun Y, Zhou FL (2015) Occurrence of bark-rot disease on *Dictyophora rubrovolvata* and Its Prevention in Guizhou Province. *Edible Fungi China* 34:72–75
- Roberts TL, Ross WJ, Norman RJ, Slaton NA, Wilson CE (2011) Predicting nitrogen fertilizer needs for rice in Arkansas using alkaline hydrolyzable-nitrogen. *Soil Sci Soc Am J* 75:1161–1171
- Schlatter DC, Bakker MG, Bradeen JM, Kinkel LL (2015) Plant community richness and microbial interactions structure bacterial communities in soil. *Ecol* 96:134–142
- Schloss PD, Westcott SL, Ryabin T, Hall JR, Hartmann M, Hollister EB (2009) Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Appl Environ Microbiol* 75:7537–7541
- Sun L, Bao C, Chang W, Zhuang Y (2017) Preparation, characterisation, antioxidant and antiglycation activities of the novel polysaccharides from the pileus of *Dictyophora rubrovolvata*. *Int J Food Sci Technol* 52:161–170
- Sun Y, Wang Y, Qu Z, Mu W, Mi W, Ma Y, Su L, Si L, Li J, You Q (2022) Microbial communities in paddy soil as influenced by nitrogen fertilization and water regimes. *Agron J* 114:379–394
- Teixeira LC, Peixoto RS, Cury JC, Sul WJ, Pellizari VH, Tiedje J, Rosado AS (2010) Bacterial diversity in rhizosphere soil from Antarctic vascular plants of Admiralty Bay, maritime Antarctica. *The Isme J* 4:989–1001
- Tian X, Fan H, Zhang F, Wang K, Ippolito J, Li J, Jiao Z, Li Y, Li Y, Su J, Li W, An M (2018) Soil carbon and nitrogen transformations under soybean as influenced by organic farming. *Agron J* 110:1883–1892

- Větrovský T, Baldrian P, Morais D (2018) SEED 2: a user-friendly platform for amplicon high-throughput sequencing data analyses. *Bioinf* 34:2292–2294
- Wang M, Wu C, Cheng Z, Meng H, Zhang M, Zhang H (2014) Soil chemical property changes in eggplant/garlic relay intercropping systems under continuous cropping. *PLoS ONE* 9:e111040
- Wang B, Shen Q, Zhu W, Shen X, Li Q (2016) Effects of interplanting dictyophora echinovolvata on physicochemical properties, phospholipid fatty acids characters and enzyme activities in soil of *Phyllostachys heterocyclus* cv. *Pubescens*. *For Environ Sci* 32:28–32
- Wang R, Zhang H, Sun L, Qi G, Chen S, Zhao X (2017) Microbial community composition is related to soil biological and chemical properties and bacterial wilt outbreak. *Sci Rep* 7:343
- Wang DM, Liu GY, Yang NL, Fan CW, Qin S (2022) Analysis of the quality characteristics of *Phallus rubrovolvatus* in Weijin City. *South China Agric* 16:88–91
- Xing XM, Feng GJ, Jin Z (2012) Integrated control of diseases and pests of *Pleurotus geesterani* in Southern Anhui Province. *Edible Fungi* 34:54–56
- Xing L, Zhang J, Gu T, Zhang W, Shen Q, Yin S, Qiu H (2014) Microbial community diversities and taxa abundances in soils along a seven-year gradient of potato monoculture using high throughput pyrosequencing approach. *PLoS One* 9:e86610
- Xu Y, Li C, Zhu W, Wang Z, Wu L, Du A (2022) Effects of enrichment planting with native tree species on bacterial community structure and potential impact on *Eucalyptus* plantations in southern China. *J for Res* 33:1349–1363
- Yang L, Tan L, Zhang F, Gale WJ, Cheng Z, Sang W (2018) Duration of continuous cropping with straw return affects the composition and structure of soil bacterial communities in cotton fields. *Can J Microbiol* 64:167–181
- Yu Y, Song Y, Zhong X, Li Y, Ying B (2021) Growth decline mechanism of *Zanthoxylum planispinum* var. *dintanensis* in the canyon area of Guizhou Karst Plateau. *Agron J* 113:852–862
- Yuan X, Peng K, Li C, Zhao Z, Zeng X, Tian F, Li Y (2021) Complete genomic characterization and identification of *Saccharomycopsis phalluae* sp. nov., a novel pathogen causes yellow rot disease on *Phallus rubrovolvatus*. *J Fungi* 7:707
- Zhang S, Li X, Chen K, Shi JM, Wang Y, Luo PY, Yang JF (2022a) Long-term fertilization altered microbial community structure in an aeolian sandy soil in northeast China. *Front Microbiol* 13:979759
- Zhang YZ, Bo GD, Shen MC, Shen GM, Yang JM, Dong SY, Shu ZH, Wang ZB (2022b) Differences in microbial diversity and environmental factors in ploughing-treated tobacco soil. *Front Microbiol* 13:924137
- Zheng W, Sui C, Liu Z, Geng J, Tian X, Yang X, Li C, Zhang M (2016) Long-term effects of controlled-release urea on crop yields and soil fertility under wheat–corn double cropping systems. *Agron J* 108:1703–1716
- Zhou J, Guan D, Zhou B, Zhao B, Ma M, Qin J, Jiang X, Chen S, Cao F, Shen D, Li J (2015) Influence of 34-years of fertilization on bacterial communities in an intensively cultivated black soil in northeast China. *Soil Biol Biochem* 90:42–51

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Ready to submit your research? Choose BMC and benefit from:

- fast, convenient online submission
- thorough peer review by experienced researchers in your field
- rapid publication on acceptance
- support for research data, including large and complex data types
- gold Open Access which fosters wider collaboration and increased citations
- maximum visibility for your research: over 100M website views per year

At BMC, research is always in progress.

Learn more biomedcentral.com/submissions

