

Diversity and function of rhizosphere microorganisms in medicinal plant *Polygonatum cyrtoneura* Hua

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Abstract

In China, *Polygonatum cyrtoneura* Hua (Huangjing) is known for its medicinal and edible properties. Multiple environmental factors can shape plant-microbiome interactions. The cultivated sample sites were enriched characteristic fungi by *Clonostachys divergens* and *Archaeorhizomyces* spp. whereas wild sample sites were enriched particular by *Geminibasidium* spp. and *Bifiguratus* spp. The number of observed species was lower in cultivated soil samples compared with wild ones by alpha diversity analysis. Functional annotation showed that the xylanolysis metabolism pathway was more abundant in rhizosphere microorganisms of cultivated *P. cyrtoneura* Hua. The co-occurrence network showed positively interacted between *Mucoromycota* and *Rozellomycota* in the cultivated rhizosphere soil. Moreover, this result indicated that biomass of cultivated plant was significantly greater than that of the wild samples, and the polysaccharide content of the cultivated rhizomes was higher. In this study, we may predict basic and potential microbes that beneficial for the *P. cyrtoneura* Hua rhizosphere improve the productivity and quality.

Introduction

Polygonatum cyrtoneura Hua is a well-known traditional Chinese medicine for the treatment of upset stomachs, lung diseases, and diabetes that widely distributed in south China (Zhao et al., 2018; Xie et al., 2023). *Polygonatum* rhizomes are commonly cultivated for reproduction and are often widely used as functional foods and ornamental plants (Zhao et al., 2018). With the increasing demand for rhizomes, wild *P. cyrtoneura* Hua medicinal plants have been over-collected, causing an acute shortage (Zhang et al., 2021). Currently, the annual demand for *Polygonatum* is up to 4000 tons in China. Thus, cultivation techniques have been used to meet the increasing market demand for *Polygonatum* rhizomes (Zhang et al., 2021; Tian et al., 2021). Most *Polygonatum* plants grow in moist and shady areas, typically forests or bushes with thick and fertile soils (Zhao et al., 2018).

In agricultural and natural environments, various fungi and bacteria are closely associated with plant (Gams et al., 2007; Tian et al., 2020), which positively regulate plant productivity and growth (Meesters et al., 2023). Microorganisms living in the soil (FAO 2003) provide various health benefits to the host plant (Srivastava et al., 2020). Evidence has shown that many beneficial soil-borne microorganisms have been found to boost the growth capacity of the aboveground parts of plants (Srivastava et al., 2020; Zhao et al., 2021). The reproductive growth stages of soybean plants are influenced by rhizosphere microbial communities (Xu et al., 2009). The roots of *Arabidopsis* colonized by the plant-control soil bacterium *Bacillus subtilis* FB17 greatly improves aboveground plant tissue growth (Berendsen et al., 2012). *Bacillus* spp. (Kim et al., 1997) and *Trichoderma* spp. (Duffy et al., 1996) can suppress the growth of *Gaeumannomyces graminis* var. *tritici* in wheat rhizosphere (Weller et al., 2015). Specific microorganisms directly or indirectly promote plant growth, which is efficacy influenced by the rest of the root or soil microbial community on plant health (Weller et al., 2019). Bacteria and fungi in the soil can impact and promote plant growth, increasing crop productivity.

By taking advantage of the abundant forests in Lishui City, the development of a medicinal economy in the forests has improved land utilization. Interplanting *P. cyrtanema* Hua in *Cunninghamia lanceolata* forest to study rhizomes in different growing soil environments can further identify special beneficial microbes, which is important for conducting multi-omics studies on plant growth associated with microbes in the forest. To ensure that microbes and plant roots are more effective in the field, an understanding of the interactions between the soil microbiota communities is required. Moreover, few researches have systematically investigated the effects of soil microbiota on functional metabolites of *P. cyrtanema* in the wild and artificially cultivated fields in *C. lanceolata* forests. Therefore, it is necessary to study the different relationships between microorganisms in *Polygonatum* rhizomes cultivated in the wild and artificially planted soils without fertilizers in a *C. lanceolata* forest.

Materials and methods

Field treatments

Wild and cultivated samples of *P. cyrtanema* were collected from plantations in Suichang Baima Mountain (28°37'28"N, 119°8'12"E; altitude 1,225.2 m), Zhejiang Province (Southeast, China), in April 2023. The *P. cyrtanema* rhizomes were grown for three years and randomly arranged in two *C. lanceolata* forests. In each habitat, wild and cultivated *P. cyrtanema* were selected randomly; all samples were more than 20 m apart at the time of collection to ensure the independence of each sample.

Growth and biomass assay

The wild and cultivated *P. cyrtanema* Hua rhizomes were age-controlled and of the same species and were both grown in a *C. lanceolata* forest for 3 years with temperatures ranging 15–24°C and at an altitude of 1,225.2 m. Plant growth was assessed by measuring stem length ($n = 12$). Cultivated and wild rhizomes were washed twice with sterilized deionized water. Then, absorbent paper was used to absorb water and weigh the fresh rhizomes. Rhizome roots were removed, dried, and crushed into a powder. Polysaccharides in *P. cyrtanema* Hua powder was detected using the method described by Laulloo et al. (2003).

P. cyrtanema soil sample collection

The samples were collected on April 15, 2023. From each of these sites, we selected five *P. cyrtanema* Hua. We collected five soil cores (diameter = 4.0 cm, depth = 10 cm), and mixed them into a single composite soil sample after removing litter from the soil (Yang et al., 2021). The climate humidity was 95% and the mean temperature was 15–24°C. Approximately 5 g of fresh rhizosphere soil was collected, the soil was carried in dry ice and stored ultra-low temperature freezer (– 80°C) until these soil samples were used to test the fungi and bacteria abundance based on high throughput sequencing (Tian et al., 2021). We randomly collected five replicates of wild and cultivated root plants soils from *C. lanceolata* forests. Five soil samples from *P. cyrtanema* Hua were grown for three years in a wild field (wild), and

another five soil samples from *P. cyrtoneuma* Hua were grown for three years in an artificial cultivation field (cultivated). The soil samples were used for microbial sequencing analysis.

DNA extraction and amplification

Soil DNA kit (Omega, USA) was used to extract wild and artificially cultivated plant rhizome soil DNA, through the manufacturer's protocol. The 1.0% agarose gel electrophoresis was used to determine the quality of the DNA, and a NanoDrop2000 spectrophotometer (Thermo Scientific, United States) was used to detect the concentration of the DNA. The ITS region of fungi (ITS1F/ITS2R) (Liu et al., 2016) and 16S rRNA gene of bacteria (338F/806R) (Huse et al., 2008) were amplified. According to the manufacturer's instructions and quantified using Qubit 4.0 (Thermo Fisher Scientific, USA), the product of PCR was purified by the PCR Clean-Up Kit (Shanghai, China). The amplicon libraries were sequenced on an Illumina MiSeq PE300 platform by Majorbio Medical Technology Co., Ltd. (Shanghai, China) (Pang et al., 2022).

Isolation and identification of fungi

Isolation of potential fungi from the soil were incubated in potato dextrose agar (PDA) for 7 d at 28°C. ITS was amplified using the fungal primers ITS1F/ITS4R to isolate the strains (Liu et al., 2016). Nucleotide BLAST (<https://blast.ncbi.nlm.nih.gov/>) was aligned with the ITS (fungi) database to determine approximate phylogenetic affiliation.

Statistical Analysis

The microbiota of soil analysis was performed applying the Majorbio Cloud platform (<https://cloud.majorbio.com>). Data analysis was performed applying one-way analysis of variance followed by Tukey's honest significant difference, and expressed as the mean $\pm$ SD. Statistical analyses the data was used by Prism 8 (GraphPad), and statistical significance was set at $P < 0.05$.

Results

The change in biomass of *P. cyrtoneuma*

The cultivated *P. cyrtoneuma* plants displayed longer stems (108.6 ± 12.89 mm) than wild *P. cyrtoneuma* plants (63.4 ± 10.74 mm), suggesting that the cultivated soil microbial community may promote *P. cyrtoneuma* growth (Fig. 1A and C). Additionally, the size of the fresh rhizome was significantly heavier in the cultivated plants compared to the wild plants (Fig. S1). The cultivated *P. cyrtoneuma* plants displayed a three-year-old rhizome that was larger than that of the wild rhizome, compared with that of the wild plants ($n = 5$; average, 32.12 g; $P < 0.05$), the fresh weight of the cultivated plants was significantly heavier ($n = 5$; average, 80.39g) (Fig. 1B and Fig. S1). The polysaccharide content of the cultivated plants was higher (25.61 ± 5.13 mg/g) compared with those in the wild plants (18.43 ± 1.74 mg/g) (Fig. 1D). This result suggests that artificial cultivated soil microorganisms had a positive effect on the biomass of *P. cyrtoneuma* Hua.

Microbial community and diversity of *P. cyrtoneuma* soil

Notably, the alpha diversity of both the fungal and bacterial communities was not significantly altered in the wild and cultivated soils (Shannon index and other alpha diversity indices, Tables S3 and S4). Principal component analysis (PCA) at the genus level revealed the fungal and bacterial community compositions were clear and well clustering in the soils from both the wild and cultivated samples via to the analysis of similarities (ANOSIM) test (Fig. 2A and B). The first principal coordinates of the conditions explained 29.89% (bacteria) and 19.64% (fungi) of the total variance (Fig. 2A and B). Wild and cultivated soils did not overlap, indicating that two soil compartments about the fungal communities were generally different. Analyses of community abundance also showed an increased abundance of the fungal genera *Geminibasidium* (10.22%), *Basidiomycota* (12.25%), *Bifiguratus* (7.09%), and *Fusidium* (1.90%) compared with cultivated soils (0.01%, 3.10%, 0%, and 0%, respectively). However, cultivated soil was an increased abundance of the fungal genera *Saitozyma* (14.06%), *Archaeorhizomycetes* (11.05%), and *Metarhizium* (2.6%) compared to wild soils (4.76%, 0.40%, and 1.30%, respectively). In addition, the bacterial genera *Gemmataceae* (5.05%) and *Rokubacterales* (1.57%) were more abundant in the wild soils than in the cultivated soils (1.06% and 0.22%, respectively) (Fig. 2C and D). These results revealed that the microbiota *Saitozyma* and *Archaeorhizomycetes* in cultivated soils may had the impact on the development of *P. cyrtonema* plants.

Potential and beneficial fungi and bacteria

As a result of the detecting microbiome sequencing, concerning the differences in the microbiota between wild and cultivated rhizosphere soils, beneficial fungi were isolated from the soil of the plants. Additionally, some potentially biocontrol bacteria and fungi were isolated from the cultivated *P. cyrtonema* root soil (Fig. 3A). The proportions of *Clonostachys divergens* and *Archaeorhizomycetes* spp. were significantly higher in cultivated plant soil ($P < 0.05$; Fig. 3B and D), but these fungi were significantly reduced in wild plants. Interestingly, some species of the fungal genus *Clonostachys* are used as a plant growth-promoting fungus in solanaceous fruit vegetables, tomatoes, peppers, and eggplants (Han et al., 2020). In addition, the proportions of *Geminibasidium* spp. and *Bifiguratus* spp. were clearly higher in the wild plant soil than in the cultivated plant soil. Wild soil microbiomes were associated with *Geminibasidium* and *Bifiguratus* fungi. *Bifiguratus adalaidae* may have a symbiotic function in the roots and has been detected in orchid and chestnut roots (Timothy et al., 2017). There are interesting similarities between *B. adalaidae* and *Archaeorhizomyces* (Rosling et al., 2011; 2013). Moreover, several bacteria of the genus *Bacillus* were significantly enriched in the cultivated soils ($P < 0.05$; Fig. 3C). However, *Geminibasidium* and *Rokubacterales* were detected in wild plant soil (Fig. 3A and C). Based on these results, the fungi *Clonostachys divergens* and *Archaeorhizomycetes* sp., and bacteria *Bacillus* were significantly enriched in the cultivated soil.

Tracking changes in function

To identify the beneficial fungi that affect the growth increased for *P. cyrtonema*, we isolated beneficial fungi and investigated their functions. The differences were evaluated by two-tailed Wilcoxon rank-sum test in the relative abundances of fungi and bacteria at the genus level between the wild and cultivated

soils (Fig. 4A and Fig. S2). *Basidiomycota*, *Archaeorhizomycetes*, *Geminibasidium*, *Bifiguratus*, and *Rozellomycota* were the significantly different fungal genera (Fig. 4A). A co-occurrence network was used to analyze the complexity of the connections within the rhizosphere soil microbiomes of *P. cyrtanema*. The cultivated plants showed a high level of complexity with negative and positive interactions, whereas the wild plants presented a less complex diversity of fungi (Fig. 4C). In addition, we isolated three fungi genera with the ITS sequence and performed BLAST in NCBI. *Trichoderma* spp., *Aspergillaceae* spp., and *Mucor* spp. (Fig. 4B) as candidate biocontrol strains were identified to the *Trichoderma*, *Aspergillaceae*, and *Mucor* genera. The plate confrontation tests have shown their potential antifungal ability (Fig. 4B).

In wild soil, the results showed that potentially pathogenic bacteria were largely enriched compared with cultivated plant soil (Fig. 5C). In the FAPROTAX method, cultivated soil was more enriched by xylanolysis, aromatic compound degradation, nitrogen fixation and chemoheterotrophy, etc. The function heatmap showed that xylanolysis was remarkably upregulated in cultivated-type plants (Fig. 5A).

Discussion

Recently, the important role of plant microbiota has been described. *Beauveria*, *Metarhizium*, *Cladosporium*, *Clonostachys*, and *Isaria* species can act as endophytes, providing many benefits to the plant, such as increased plant growth (Beneduzi et al., 2012; Bamisile et al., 2023). Although, the results of Alpha diversity analysis showed that the observed species number was lower in cultivated rhizosphere soil when compared with wild rhizosphere soil, which might be the result of artificial operation. In addition, the soil microbiota *Clonostachys divergens* and *Archaeorhizomycetes* spp. were significantly enriched in cultivated rhizosphere. *Clonostachys rosea* ST1140 is a plant growth-promoting fungus used in solanaceous fruit vegetables, tomatoes, peppers, and eggplants (Türkölmez et al., 2023). An increased abundance of the fungal genera *Saitozyma* (14.06%), *Archaeorhizomycetes* (11.05%) and *Metarhizium* (2.6%) in cultivated soil. *Metarhizium brunneum* promotes the growth of tomatoes following its endophytic establishment within plants after treatment with seeds, which primarily includes the enhancement of plant growth (Krell et al., 2018). *M. robertsii* endophytically colonizes tomato plants, resulting in their improved growth (Oliveira-Siqueira et al., 2020). The fungus *Saitozyma* spp. is more closely related to cultivated soils and is associated with coffee production (Veloso et al., 2023). Moreover, the proportion of sequences of *Bacillus* species was significantly enriched in cultivated rhizomes soils. *Bacillus* T8 and *Bacillus* OSU-142 (Arikan et al., 2016) have great potential to enhance the plant and wild growth of sour cherry; therefore, they have been recommended for promoting the sour cherry cultivation growth (Arikan et al., 2016). However, *Geminibasidiales* and *Bifiguratus* species were enriched in wild rhizomes soil of *P. cyrtanema* Hua. *Geminibasidiales* and *Bifiguratus* have unclear plant-associated functions. In addition, our results showed that the fresh weight and polysaccharide content of cultivated rhizomes were higher than those of wild rhizomes. The cultivated soil specific microbes may play a key role for promoting the growth and activity of medicinal *P. cyrtanema* Hua, such as plant height, shoot length, and root weight.

The co-occurrence of networks showed the dominance of positive correlations among potential interactions in the rhizosphere microbial community (Yu et al., 2022). The result showed that *Mucoromycota* positively interacted with *Rozellomycota* and negatively interacted with *Ascomycota*. Hyphal growth of *Trichoderma* sp. and *Mucor* sp. was inhibited by *Aspergillus* sp. Plant-beneficial fungi constitute a diverse group of fungi belonging to diverse genera (Meesters et al., 2023), such as *Aspergillus*, *Penicillium*, *Fusarium*, *Trichoderma* and *Glomus* (Hyakumachi et al., 1994; Singh et al., 2017), Entomopathogenic fungi, such as *Metarhizium* and *Beauveria*, have need to adopted an endophytic lifestyle that one of a diverse array of benefits were convenient for providing an nutrient for host plants (Gange et al., 2019; Vidal et al., 2015; Vega, 2018). In our result, the co-occurrence network showed a high level of complexity with negative and positive interactions in the cultivated rhizosphere soil. Some key microbes in the rhizosphere soil may have synergistic effects in increase growth of plant, and this potential cooperative relationship may be reinforced in the rhizosphere for broader biomass of *P. cyrtonema* Hua.

In conclusion, our results have important implications for cultivating and managing the quality and productivity of *P. cyrtonema* Hua compared with wild plants. This may result in artificial management have an increase in one of the potentially medicinal active ingredients (e.g., polysaccharide content) of *P. cyrtonema* Hua. Beneficial microbes recruited to the plant rhizosphere and stably associated with *C. lanceolata* roots can potentially reduce biotic stress or increase the biomass according to management. Moreover, both wild and cultivated rhizosphere soil collected in *C. lanceolata* forests, *C. lanceolata* forest ecosystems may play an important role in the function of the interaction between rhizosphere microorganisms and *P. cyrtonema* Hua. In the future, research on microbial interactions involved in coping with pathogen attack are understood under *C. lanceolata* forest.

Declarations

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Conflict of interest statement

All authors declared no conflicts of interest to this work.

Data availability statement

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and materials

All data generated or analysed during this study are included in this published article.

Competing interests

All authors declared no conflicts of interest to this work.

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Authors' contributions

Duanxu Zhou and Haiyan Liu wrote the main manuscript text and support the data, Jing Hou and Yingying Sun prepared figures1-5. All authors reviewed the manuscript.

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Not applicable

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Daunxu Zhou work in Lishui University, Yingying Sun work in Wenzhou medical University, Jing Hou and Haiyan Liu both work in Lishui University.

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Figures

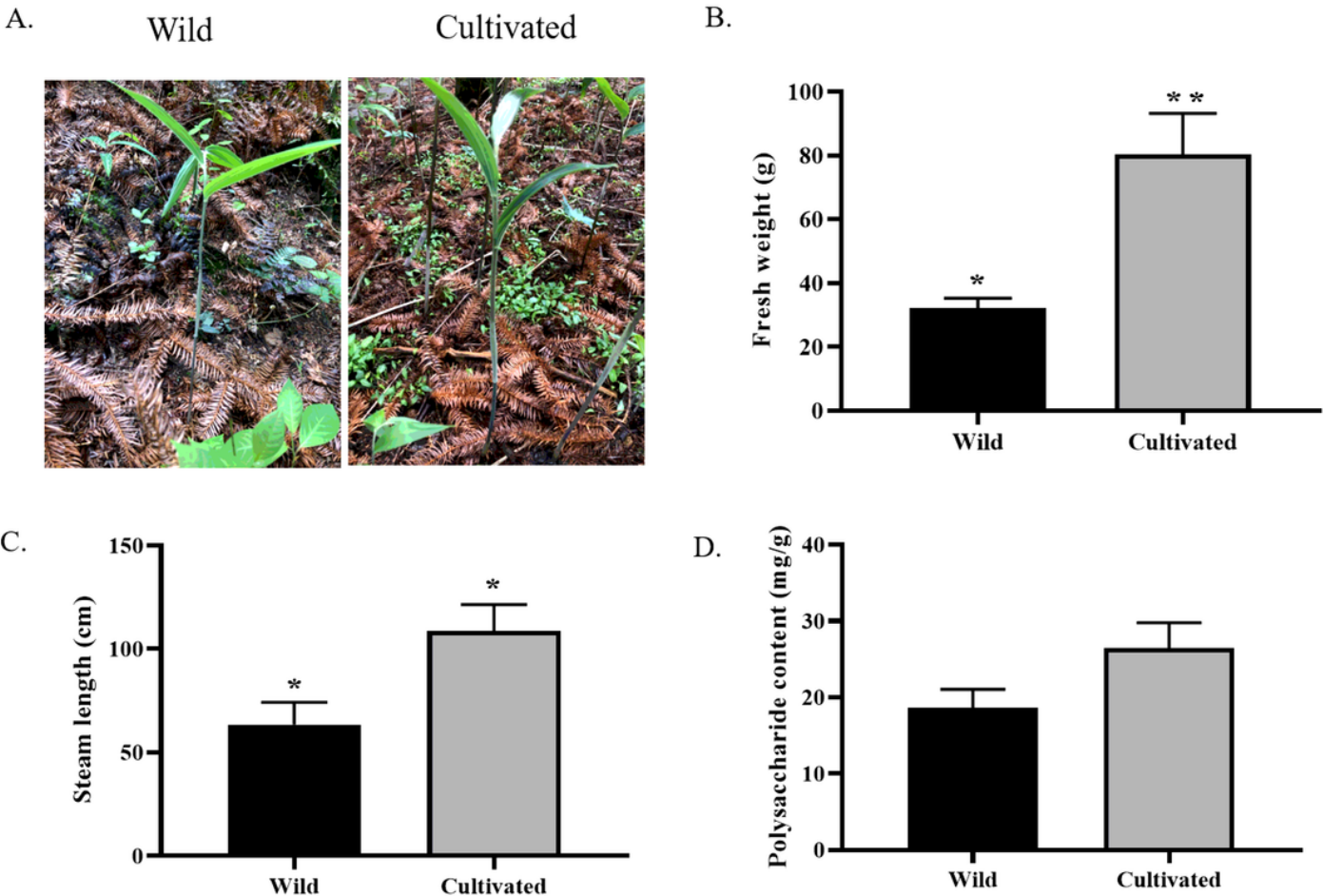


Figure 1

Rhizome growth analysis of wild and cultivated plants. A. The height of the plant stem in wild and cultivated plants; B. Fresh weight of two samples; C. Stem length of two samples; D. Polysaccharide content of two samples; t-test, $P<0.05$.

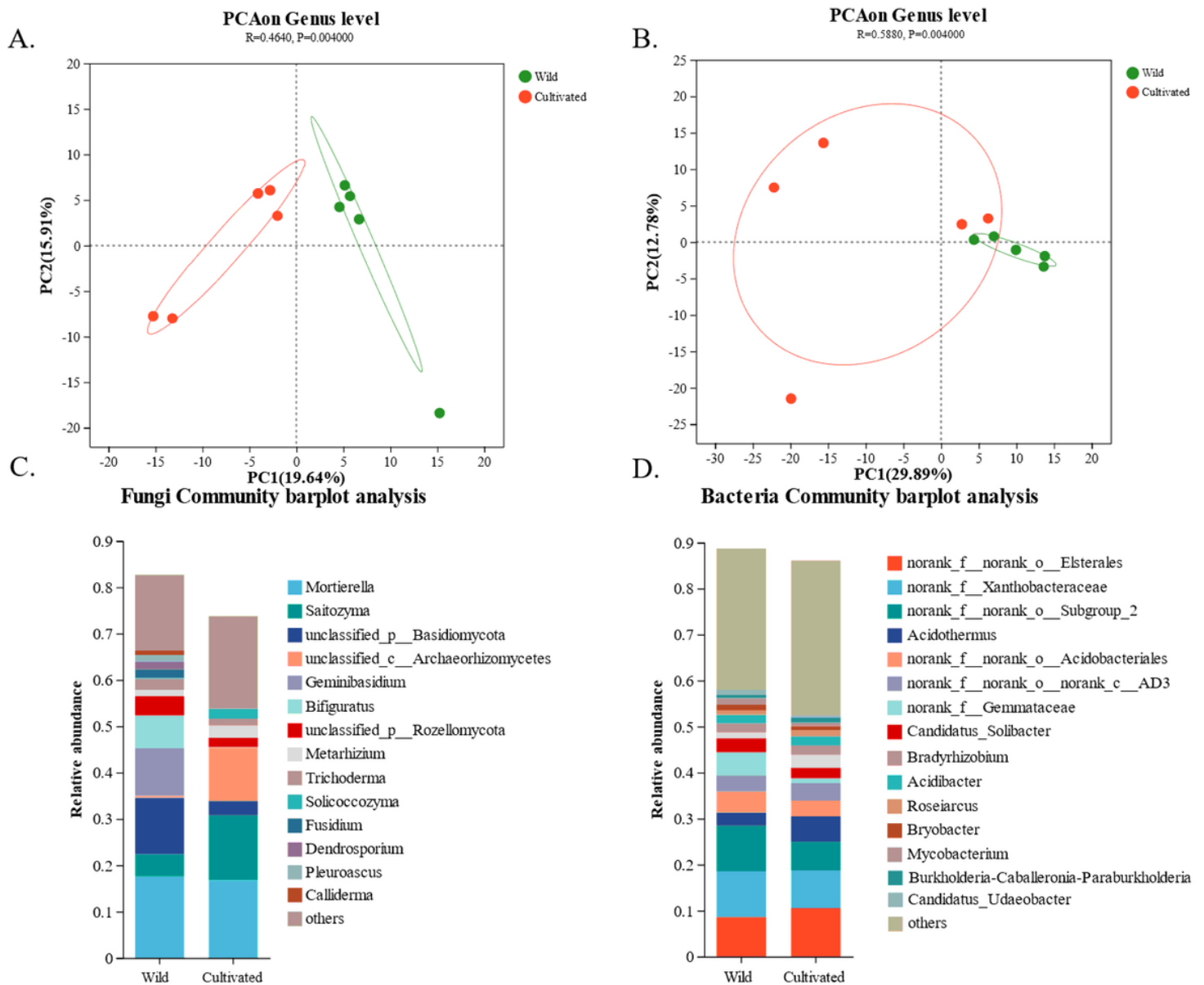
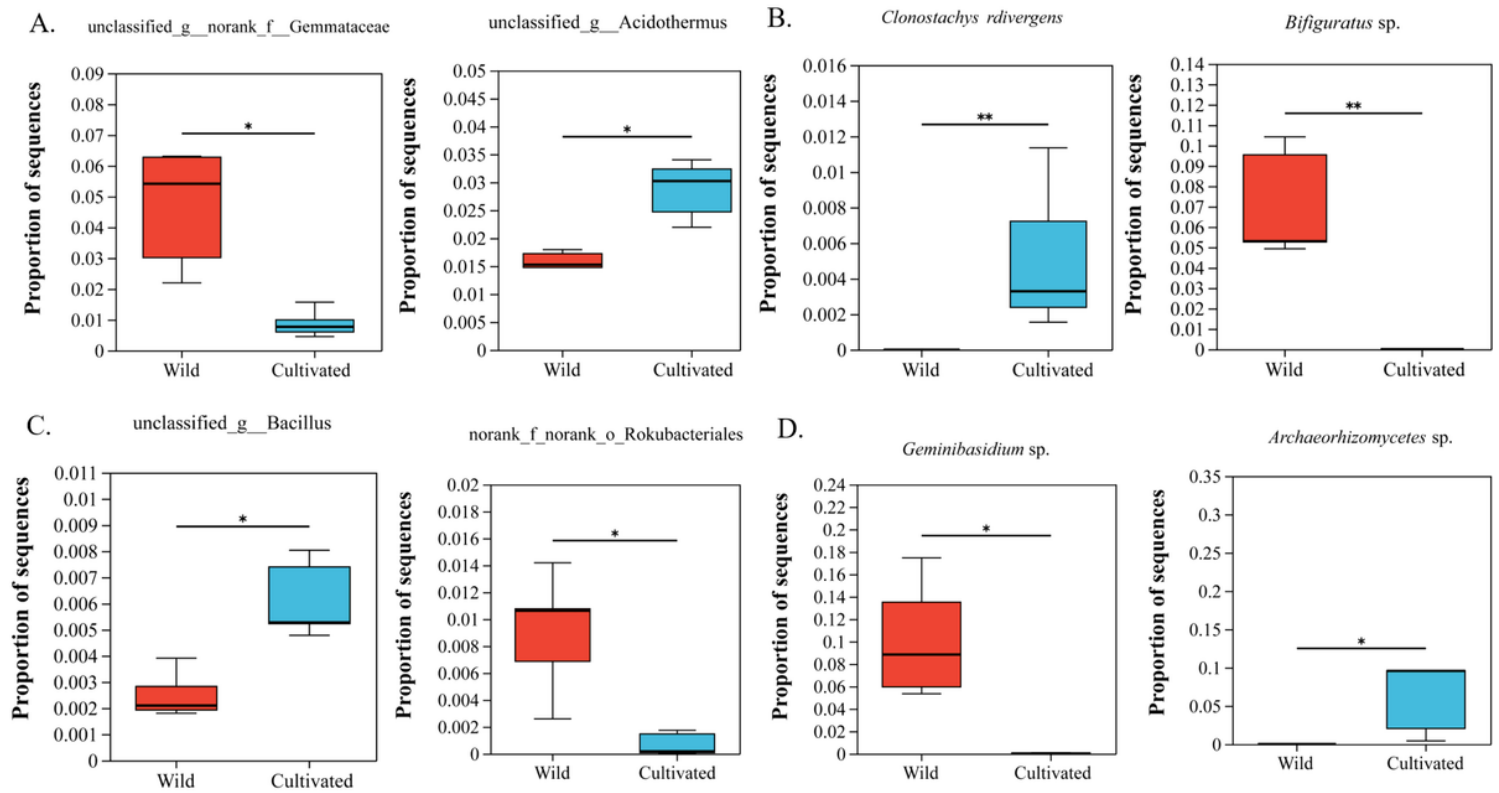


Figure 2

Student's t-test. (A and B) PCA of bacterial and fungal community beta diversity of two samples (ANOSIM; bacterial: $R = 0.5880$, $P = 0.004$; fungal: $R = 0.4640$, $P = 0.004$). (C and D) Relative abundance of the most abundant ($\geq 15\%$) bacterial and fungal taxa in wild and cultivated plants.



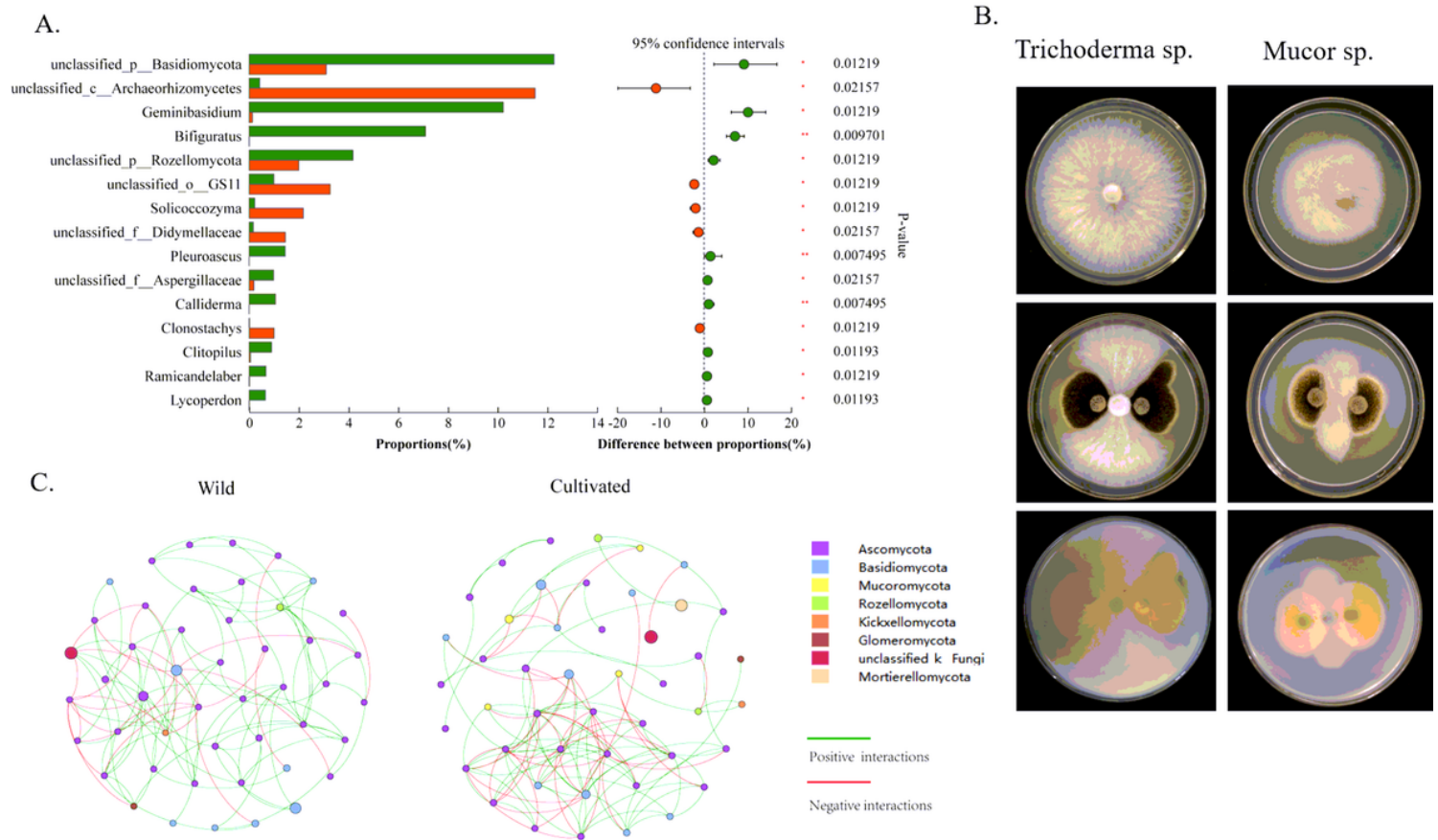


Figure 4

A. Significance test between wild and cultivated rhizosphere soil fungal community groups, conducted via Wilcoxon rank sum test. B. Inhibitory effects of *Aspergillus* spp. on *Trichoderma* spp. and *Mucor* spp. C. Co-occurrence networks of initial microbiomes that later became associated with wild (left) and cultivated (right) plants.

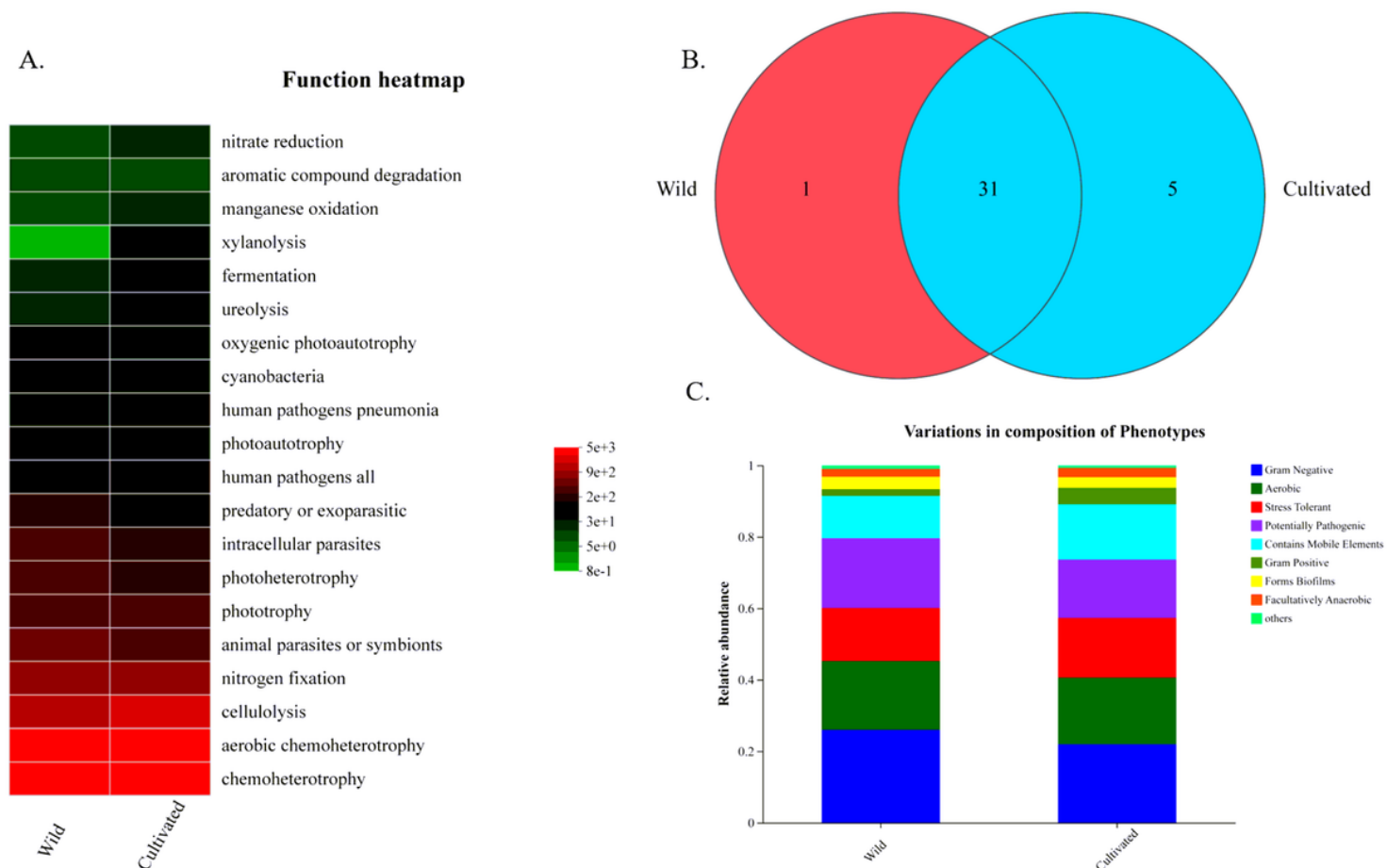


Figure 5

A. Function heatmap; B. Venn diagram of bacteria; C. Variations in phenotype composition in bacteria.

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